ICES COOPERATIVE RESEARCH REPORT

RAPPORT DES RECHERCHES COLLECTIVES

NO. 300

FEBRUARY 2010

Proceedings of the "Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic (WKZEM)"

Editors

Astthor Gislason and Gabriel Gorsky

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer
H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

Recommended format for purposes of citation:

Gislason, A., and Gorsky, G. (Eds). 2010. Proceedings of the "Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic (WKZEM)". ICES Cooperative Research Report No. 300. 91 pp.

Series Editor: Emory D. Anderson

ISBN 978-87-7482-070-3

ISSN 1017-6195

Contents

Foreword

Astthor Gislason and Gabriel Gorsky

In October 2008, scientists from the ICES Working Group of Zooplankton Ecology (WGZE) and the Mediterranean Science Commission (CIESM) held a workshop in Crete, Greece, to compare the zooplankton ecology of the Mediterranean with that of the North Atlantic. The idea to hold such a workshop – the Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic (WKZEM) – was originally proposed at the 2005 meeting of WGZE in Lisbon. It was felt that such a workshop was important in addressing and discussing issues of common interest and, for comparative purposes, to explore similarities and differences between the two ecosystems. Thus, the objectives of the workshop were to provide a forum in which scientists would present and discuss the results of ongoing research projects in the North Atlantic and Mediterranean, focusing on the structure and functioning of the regional ecosystems, emphasizing the comparative aspects.

The Workshop was divided into four theme sessions, with 34 presentations, 5 posters, and 2 informal theme discussion sessions. From the papers and posters submitted, 16 were evaluated and accepted for publication. It is our hope that the interaction between the ICES and CIESM scientific communities during the workshop as well as the present proceedings will mutually enrich the research activity on zooplankton and the lower trophic levels of marine systems in general.

We take this opportunity to thank the members of the WKZEM Scientific Advisory Committee, Mohamed Nejib Daly Yahia, Roger Harris, Steve Hay, Ioanna Siokou-Frangou, Kremena Stefanova, and Luis Valdés, for their collaboration and advice, as well as Emory D. Anderson, Editor of the *ICES Cooperative Research Report* series, Bill Anthony, ICES Executive Editor, and Søren Lund, ICES Technical Editor, for much appreciated help with the editorial work.

The Workshop received financial support from EUR-OCEANS (European Network of Excellence for Ocean Ecosystems Analysis) and CIESM (Mediterranean Science Commission). In addition, the Hellenic Centre for Marine Research provided logistical support. The support of these bodies is greatly appreciated.

1. Spatial distribution of zooplankton communities in the Algarve coastal zone (Northeast Atlantic Ocean)

Radhouan Ben-Hamadou, Maria Alexandra Chícharo, Joana Cruz, Cristina Madeira, Pedro Morais, and Luis Chícharo

Introduction

The Gulf of Cadiz is strategically located, connecting the open Atlantic Ocean with the Mediterranean Sea. The nutrient enrichment of local coastal waters is assumed a consequence of discharge from the Guadalquivir River (Huertas *et al.*, 2006) and the Guadiana River (Chícharo *et al.*, 2006; Cravo *et al.*, 2006). Moreover, sea surface temperature remote sensing and *in situ* temperature observations demonstrate the occurrence of upwelling off the Algarve coast (Fiúza, 1983; Folkard *et al.*, 1997), thus contributing to the enrichment of the coastal water and providing a well-diversified plankton community within the Gulf of Cadiz. This local productivity in the coastal areas of the Gulf of Cadiz is exported to other regions, namely the western basin of the Mediterranean, assisted by Atlantic surface water entering through the Strait of Gibraltar.

This continuous inflow of surface Atlantic water into the Mediterranean Sea has an important influence on the ecology and hydrology of the western and eastern basins. Andersen *et al.* (2001) suggested that relatively high zooplankton diversities in the study zone of the western Mediterranean might be the result of exchange with the Atlantic Ocean. This environment in general, and the Algarve coastal zone in particular, has been scarcely studied from the physical–planktonic coupling perspective (García *et al.*, 2002; Ruiz and García-Lafuente, 2006), which contrasts with the extensive oceanographic literature on the Strait of Gibraltar and the other adjacent basin, the Alboran Sea (e.g. Gómez *et al.*, 2001; Echevarría *et al.*, 2002). This work is a first attempt to characterize the mesozooplankton community in the Algarve coastal zone and to help understand the dynamics of the Gulf of Cadiz planktonic assemblages.

Material and methods

Samples were collected during an oceanographic cruise of the RV "D. Carlos I", organized by the Environmental Marine Investigation Centre (CIMA) of the University of Algarve (Portugal). The cruise took place from 1 to 6 October 2006, and samples were taken at 27 sampling stations distributed along nine transects off the Algarve coast (Portugal; Figure 1.1). Zooplankton sampling consisted of 30 m vertical tows using conical plankton nets (200 μm mesh; 37 cm mouth diameter); in shallower water, the entire water column was sampled. Station bottom depths ranged from 15 to 40 m nearshore, 40 to 80 m midshore, and 84 to 283 m offshore. The volume of water filtered was calculated by multiplying the mouth area of the net by the length of the sampled water column. Zooplankton organisms were preserved in 4% buffered formaldehyde solution. In the laboratory, zooplankton organisms were counted and identified to the lowest taxonomic level possible using a binocular microscope. Taxa abundance was expressed as the number of individuals m^{-3}. Vertical profiles of temperature, conductivity, fluorescence, and dissolved oxygen were obtained at all stations using an SBE-911 CTD (Sea-Bird Electronics 911 Current, Temperature, Depth) system. Results are also presented for relative frequency (number of stations where species were encountered vs. the total number of stations) and relative abundance (total abundance of the species vs. total abundance of zooplankton).

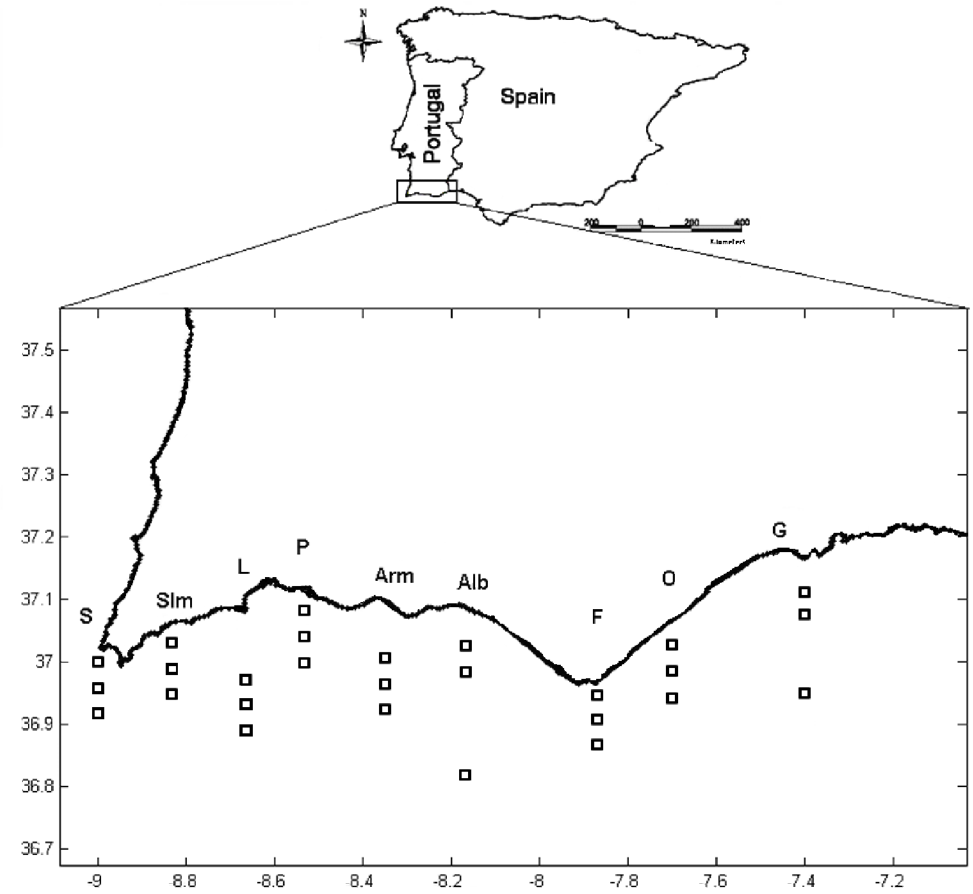

Figure 1.1. Map of the Algarve coast showing the nine transects, each consisting of three stations: Guadiana (G), Olhão (O), Faro (F), Albufeira (Alb), Armação (Arm), Portimão (P), Lagos (L), Salema (Slm), and Sagres (S).

Results and discussion

Total zooplankton abundance during the investigation varied from ~700 to 6000 individuals m^{-3}, with an average of ~1300 individuals m^{-3}. Table 1.1 summarizes features of zooplankton taxa abundance and frequency during the sampling period. There were no clear differences between total zooplankton abundance at nearshore and offshore stations, although the highest values occurred off the Albufeira–Lagos area (Figure 1.2). Remote sensing imaging and *in situ* temperature records (not shown here) suggest that an upwelling event was occurring during the sampling period, particularly off the Lagos area, which might explain the higher zooplankton abundance found in this region. Chícharo (1998) demonstrated high zooplankton density off the Algarve coast during upwelling events on the west coast and under the influence of cold, upwelled waters turning around Sagres and flowing east. This hydrodynamic factor, combined with the predominantly westward Algarve coastal circulation (Fiúza, 1983), would have contributed to an aggregation of the planktonic organisms near the Lagos and Albufeira transects.

Table 1.1. Abundance and frequency of zooplankton taxa sampled off the Algarve coast, 1–6 October 2006. Minimum (Min), maximum (Max), and mean (MA) abundance; standard deviation (s.d., individuals m^{-3}); relative frequency (RF); and relative abundance (RA). Calculations were made using abundances found over all sampled stations.

Taxon	Min	Max	MA	s.d.	RF	RA
Copepoda	494.5	4053.8	1404.7	707.5	100.0	55.67
Nauplii	1.9	7.5	2.9	2.9	59.3	0.12
Paracalanus/Clausocalanus spp.	162.3	1607.9	716.9	290.4	100.0	28.41
Calanus helgolandicus	3.8	15.1	1.4	3.3	22.2	0.06
Calocalanus spp.	3.8	3.8	0.7	1.5	18.5	0.03
Eucalanus spp.	1.9	3.8	0.2	0.8	7.4	0.01
Temora longicornis	1.9	7.5	1.0	2.0	25.9	0.04
Temora styilifera	3.8	75.5	16.9	17.1	77.8	0.67
Temora spp.	3.8	64.2	14.0	15.5	63.0	0.55
Centropages spp.	7.5	75.5	33.3	20.5	96.3	1.32
Acartia clausi	11.3	162.3	57.5	37.2	96.3	2.28
Oithona spp.	7.5	445.4	128.1	99.4	100.0	5.08
Oncaea spp.	11.3	2827.1	393.2	552.0	100.0	15.58
Corycaeus spp.	3.8	45.3	15.3	12.0	92.6	0.61
Euterpina acutifrons	1.9	105.7	15.4	23.0	92.6	0.61
Microstella spp.	1.9	7.5	1.3	2.3	29.6	0.05
Clytemnestra spp.	3.8	3.8	0.3	1.0	7.4	0.01
Harpacticoida (unidentified)	1.9	45.3	6.0	9.7	55.6	0.24
Caligoida (unidentified)	7.5	7.5	0.3	1.5	3.7	0.01
Cladocera	60.4	2879.9	802.0	672.4	100.0	31.79
Podon spp.	3.8	64.2	26.8	17.7	100.0	1.06
Penilia avirostris	15.1	2815.8	753.5	659.0	100.0	29.86
Evadne spp.	3.8	79.3	21.7	20.1	81.5	0.86
Foraminifera	11.3	192.5	68.2	42.0	100.0	2.70
Globigerina spp.	11.3	192.5	66.1	41.8	100.0	2.62
Discorbis spp.	3.8	3.8	0.3	1.0	7.4	0.01
Sarcodina	3.8	15.1	1.9	3.8	25.9	0.07
Siphonophora	3.8	196.3	67.2	53.4	100.0	2.66
Diphyies spp.	3.8	173.6	52.9	43.7	100.0	2.10
Muggiaea spp.	3.8	37.7	10.0	10.3	66.7	0.40
Lensia spp.	3.8	26.4	4.3	6.2	48.1	0.17
Hydromedusae	3.8	86.8	10.8	18.1	70.4	0.43
Chaetognatha						
Sagitta frederici	1.9	49.1	15.3	13.6	92.6	0.61
Ophiuroidea	3.8	86.8	25.3	22.7	85.2	1.03
Ophiopluteus	3.8	86.8	21.3	20.8	85.2	1.00
Juvenile	3.8	26.4	4.0	6.9	33.3	0.84
Echinoidea larvae	3.8	30.2	7.4	9.5	51.9	0.16
Ichthyoplankton	3.8	124.6	33.9	38.7	81.5	1.34
Eggs	3.8	124.6	33.2	39.1	74.1	1.32
Larvae	3.8	3.8	0.7	1.5	18.5	0.03
Appendicularia	3.8	264.2	44.0	70.8	70.4	1.75
Oikopleura spp.	3.8	256.7	43.1	69.6	70.4	1.71
Fritillaria spp.	3.8	7.5	1.0	2.2	18.5	0.04
Decapoda larvae	3.8	49.1	8.7	11.3	70.4	0.35
Cirripedia	3.8	81.2	12.4	17.0	70.4	0.49
Nauplii	3.8	81.2	11.3	16.8	66.7	0.45

Cyprids	3.8	7.5	1.2	2.4	22.2	0.05
Thallacea						
Doliolidea	3.8	56.6	11.1	15.5	55.6	0.44
Polychaeta						
Spionidae larvae	1.9	18.9	2.9	4.5	44.4	0.11
Gastropoda	1.9	22.6	3.7	6.0	44.4	0.15
Veligera	1.9	15.1	2.8	4.1	44.4	0.11
Echinospiral veligera	3.8	7.5	0.9	2.3	14.8	0.04
Isopoda	1.9	7.5	1.6	2.8	29.6	0.06
Mysidacea	3.8	7.5	1.0	2.2	18.5	0.04
Ostracoda						
Halocyprida	3.8	7.5	0.8	1.9	18.5	0.03
Euphausiacea	3.8	7.5	1.0	2.2	22.2	0.04
Caliptopis	3.8	7.5	0.8	2.2	14.8	0.03
Furcilia	3.8	3.8	0.1	0.7	3.7	0.01
Amphipoda	3.8	7.5	0.6	1.7	11.1	0.02
Nudibranchia larvae	3.8	3.8	0.1	0.7	3.7	0.01
Actinotropha larvae	3.8	5.7	0.3	1.3	3.7	0.01
Total zooplankton	762.4	5695.7	2523.2	1226.0	100.0	100.0

Copepods numerically dominated zooplankton along all transects, accounting for 55.7% of the total abundance, followed by cladocerans (31.8%), foraminiferans (2.7%), and siphonophorans (2.7%). Copepods and siphonophorans had spatial distributional patterns similar to those of the total zooplankton, although cladocerans demonstrated greater abundance in the frontal Albufeira area (Figure 1.2). Other groups generally accounted for less than 2% of the total abundance. Among copepods, *Paracalanus* spp. and *Clausocalanus* spp. (grouped together), *Oncaea* spp., *Oithona* spp., and *Acartia clausi* were the best represented and together contributed up to 92% of the total abundance of copepods. Concerning the cladocerans, *Penilia avirostris* was the most dominant species, representing 29.9%, although the genera *Podon* and *Evadne* were much less abundant (1.1% and 0.9%, respectively). Fish eggs and larvae were also found during this study at almost all sampling stations (relative frequency: 81.5%), but demonstrated much greater abundance off the Guadiana River and the Ria Formosa lagoon system (Figure 1.2). This result emphasizes the importance of these ecosystems as spawning and nursery areas, where ichthyoplankton encounter suitable conditions for enhanced development (Faria *et al.*, 2009).

In general, zooplankton assemblages seemed very similar to those observed in several previous studies conducted in the Alboran Sea (Andersen *et al.*, 2001; Calbet *et al.*, 2001). Prior to our study, Koppelmann *et al.* (2004) highlighted similarities in zooplanktonic species between the Mediterranean and Atlantic populations, suggesting the possible influence of the Atlantic inflow within the Mediterranean.

Although zooplankton taxa richness appears homogeneous throughout the sampled regions and presents potential similarities to zooplankton communities in the western Mediterranean, zooplankton abundance demonstrated distinct spatial patterns between transects. This differential abundance probably results from local to mesoscale variability of environmental conditions, mainly forced by upwelling events, from mesoscale eddy circulation resulting from the crossover of cold, south-flowing water and a westward circulation, and finally, from continental nutrient enrichment from the Guadiana and Arade rivers and Ria Formosa coastal lagoon.

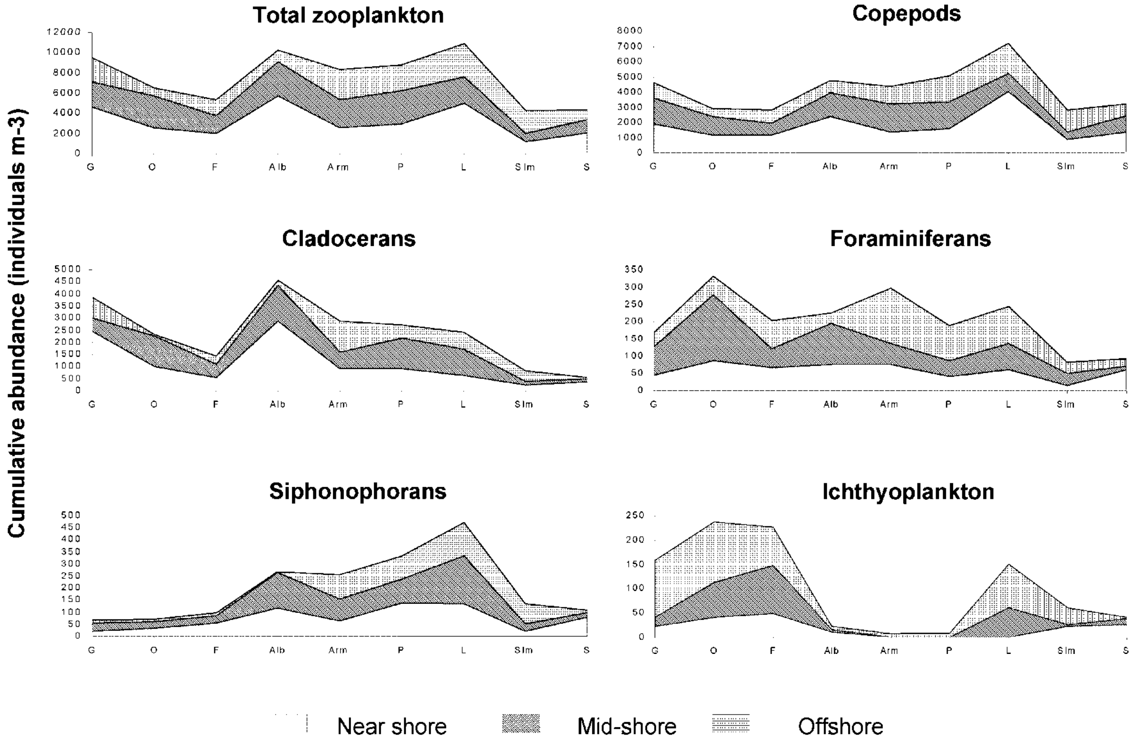

Figure 1.2. Cumulative abundance (near-, mid-, and offshore) of total zooplankton and major groups off the Algarve coast. Stations were sampled at three depth ranges off Guadiana (G), Olhão (O), Faro (F), Albufeira (Alb), Armação (Arm), Portimão (P), Lagos (L), Salema (Slm), and Sagres (S). For locations of the transects, see Figure 1.1.

Acknowledgements

This study was supported by the GUADIRIA project "Nutritional condition of fish larvae in two marine protected areas of the South of Portugal (Ria Formosa and Guadiana estuary"; POCI/BIA-BDE/59200/2004). The work of J. Cruz (SFRH/BD/28198/2006) and P. Morais (SFRH/BPD/40832/2007) was supported by fellowships granted by Fundação para a Ciência e a Tecnologia (Portugal). The authors are grateful to Tomasz Boski for the opportunity to participate to the CIMA cruise.

References

Andersen, V., Nival, P., Capparoy, P., and Gubanova, A. 2001. Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 1. Abundance and specific composition. Journal of Plankton Research, 23: 227–242.

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., and Duarte, C. M. 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. Journal of Plankton Research, 23: 319–331.

Chícharo, M. A. 1998. Nutritional condition and starvation in field caught *Sardina pilchardus* (L.) larvae from southern Portugal compared with some environmental factors. Journal of Experimental Marine Biology and Ecology, 225: 123–137.

Chícharo, L., Chícharo, M. A., and Ben-Hamadou, R. 2006. Use of a hydrotechnical infrastructure (Alqueva Dam) to regulate planktonic assemblages in the Guadiana estuary: basis for sustainable water and ecosystem services management. Estuarine, Coastal and Shelf Science, 70: 3–18.

Cravo, A., Madureira, M., Felícia, H., Rita, F., Bebianno, M. J. 2006. Impact of outflow from the Guadiana River on the distribution of suspended particulate matter and nutrients in the adjacent coastal zone. Estuarine, Coastal and Shelf Science, 70: 63–75.

Echevarría, F., García-Lafuente, J., Bruno, M., Gorsky, G., Goutx, M., González, N., García, C. M., *et al.* 2002. Physical–biological coupling in the Strait of Gibraltar. Deep Sea Research Part II, 49: 4115–4130.

Faria, A., Morais, P., and Chícharo, M. A. 2006. Ichthyoplankton dynamics in the Guadiana and adjacent coastal area (SE-Portugal/SW-Spain). Estuarine, Coastal and Shelf Science, 70: 85–97.

Fiúza, A. F. G. 1983. Upwelling patterns off Portugal. *In* Coastal Upwelling: Its Sediment Record, pp. 85–98. Ed. by E. Suess and J. Thiede. NATO Conference Series IV, Marine Science (10a), Plenum Publishing Corporation, New York.

Folkard, A. M., Davies, P. A., Fiúza, A., and Ambar, I. 1997. Remotely sensed sea surface thermal patterns in the Gulf of Cadiz and the Strait of Gibraltar: variability, correlations, and relationships with the surface wind field. Journal of Geophysical Research, 102: 5669–5683.

García, C. M., Prieto, L., Vargas, M., Echevarría, F., García-Lafuente, J., Ruiz, J., and Rubín, J. P. 2002. Hydrodynamics and the spatial distribution of plankton and TEP in the Gulf of Cádiz (SW Iberian Peninsula). Journal of Plankton Research, 24: 817–833.

Gómez, F., Gorsky, G., Striby, L., Vargas, J. M., Gonzalez, N., Picheral, M., García-Lafuente, J., *et al.* 2001. Small-scale temporal variations in biogeochemical features in the Strait of Gibraltar, Mediterranean side – the role of NACW and the interface oscillation. Journal of Marine Systems, 30: 207–220.

Huertas, I. E., Navarro, G., Rodríguez-Gálvez, S., and Lubián, L. M. 2006. Temporal patterns of carbon dioxide in relation to hydrological conditions and primary production in the northeastern shelf of the Gulf of Cadiz (SW Spain). Deep Sea Research Part II, 53: 1344–1362.

Koppelmann, R., Weikert, H., Halsband-Lenk, C., and Jennerjahn, T. 2004. Mesozooplankton community respiration and its relation to particle flux in the oligotrophic eastern Mediterranean. Global Biogeochemical Cycles, 18: GB1039, doi:10.1029/2003GB002121.

Ruiz, J., and García-Lafuente, J. 2006. The Gulf of Cádiz oceanography: a multidisciplinary view. Deep Sea Research Part II, 53: 1141–1143.

2. Are the outbreaks of *Pelagia noctiluca* (Forsskål, 1775) more frequent in the Mediterranean basin?

Mohamed Nejib Daly Yahia, Mirna Batistic, Davor Lucic, Maria Luz Fernández de Puelles, Priscilla Licandro, Alenka Malej, Juan-Carlos Molinero, Ioanna Siokou-Frangou, Soultana Zervoudaki, Laura Prieto, Jacqueline Goy, and Ons Daly Yahia-Kéfi

Introduction

In pelagic ecosystems, medusae are considered key predators, affecting zooplankton abundance and fish recruitment by preying on their larvae or competing for food (Purcell, 1997, 2003; Lynam *et al.*, 2005). Thus, these gelatinous carnivores may be considered top predators as well as fish competitors (Purcell and Arai, 2001; Purcell, 2003). Several studies have demonstrated a significant increase in jellyfish abundance in different areas of the northern hemisphere, probably related to climate change and foodweb modifications (Brodeur *et al.*, 1999; Mills, 2001; Lynam *et al.*, 2004). *Pelagia noctiluca* is a holoplanktonic and oceanic, non-selective, top predator that exercises top–down control in marine foodwebs and whose importance in the Mediterranean Sea became evident in the early 1980s during the so-called "*Pelagia* years" (CIESM, 2001).

Pelagic ecosystems in the Mediterranean Sea, and specifically in the western basin, are extremely sensitive to the influence of North Atlantic climate (Molinero *et al.*, 2005a). In this region, northern hemisphere climate patterns related to the North Atlantic drive the interannual variability of sea surface temperature (SST) and shape the prevailing northern hemisphere winter conditions.

To date, most relevant climate-related changes in marine ecosystems have been identified at high latitudes and in productive temperate seas, where the underlying mechanisms linking climate and oceanographic patterns have been recognized (Hare and Mantua, 2000; Beaugrand *et al.*, 2002; Edwards *et al.*, 2002). In northern European marine ecosystems, changes appear to be related to significant modifications in the North Atlantic ocean–atmosphere circulation, and were noticed particularly in the mid-1980s (Alheit *et al.*, 2005). As the North Atlantic climate strongly affects atmospheric conditions in the western Mediterranean, similar forcing is expected to act on its hydrological structure and marine foodweb. Accordingly, coupling between the North Atlantic climate and the marine ecosystem of the Mediterranean is possible by using appropriate chronological records and statistical techniques (Molinero, 2008). In fact, downscaling methods of climate–ocean interactions have revealed close relationships between some copepods and jellyfish species in the western Mediterranean and climate variability in the North Atlantic (Molinero *et al.*, 2005a, 2005b).

In this paper, we present an overview of the recent outbreaks of *P. noctiluca* in the Mediterranean basin, with the aim of assessing the potential link between climate oscillations and long-term changes in the abundance of *P. noctiluca.*

Material and methods

Information was taken from long-term records of *P. noctiluca* in four selected regions of the Mediterranean Sea (Figure 2.1):

1) The Balearic Sea, located in the western Mediterranean (WM), is characterized by a thermohaline circulation that is governed by meridional

exchanges between the relatively saline, cold, and nutrient-rich waters of the northern basin and the less saline, warmer, and more oligotrophic waters of the Algerian basin. This region is of interest because interannual changes in hydrographic patterns are indicative of basin-scale dynamics of the water masses.

2) The Gulf of Tunis is located in the southwestern Mediterranean. The region is under the influence of Modified Atlantic Waters (MAWs). Interannual variations in hydrographic features in the Gulf of Tunis may therefore be related to changes in the variability of the Algerian Current.

3) The Adriatic Sea is linked to the eastern Mediterranean by the Otranto Strait and is shallow in its northern part, with an average depth of 35 m. It is strongly influenced by the northern Italian rivers, particularly the Po River. The southern Adriatic is considerably deeper, with an average depth of 900 m. In the Adriatic, there are two different water mass formations:

    3.1) Northern Adriatic Dense Water, occurring in the northern half of the basin and formed during winter in the Gulf of Trieste;

    3.2) Adriatic Bottom Water (ABW), formed by mixing between the Ionian surface waters and the relatively warmer and more saline Modified Levantine Intermediate Water (MLIW) entering the southern Adriatic.

4) The Aegean Sea is a distinct subsystem of the eastern Mediterranean, with a very complex morphology characterized by an alternation of shallow and deep basins and a large number of islands, gulfs, and bays. The general circulation within the Aegean Sea is cyclonic; the highly saline (>38.8 psu) and very oligotrophic water of Levantine origin, dominant in the southern Aegean, travels northwards along the west coast of Turkey (Theocharis *et al.*, 1999). A surface layer of brackish (~30 psu) water is formed in the northeastern Aegean by the inflow of modified Black Sea Water through the Dardanelles Strait.

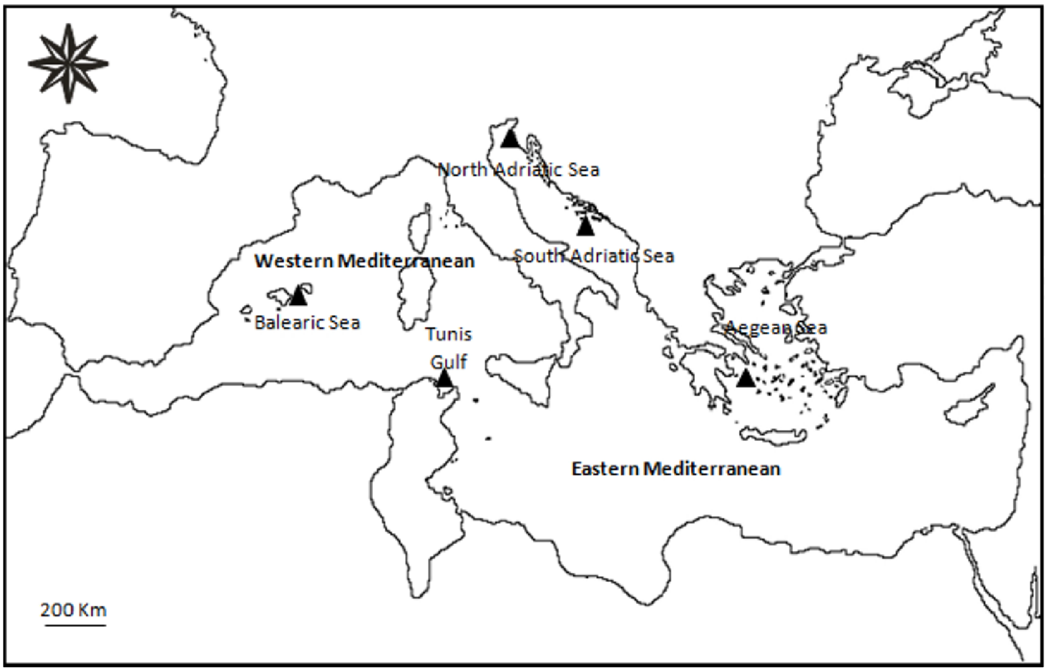

Figure 2.1. Map of the eastern and western Mediterranean basins showing the stations where *Pelagia noctiluca* was monitored and collected.

Biological data and sampling strategy

Pelagia noctiluca outbreaks were recorded semi-quantitatively in the Balearic Sea (1994–2008), the Adriatic Sea (1978–2006), and the Aegean Sea (1983–2008). The frequency of the observations varied between seasonal and monthly. In coastal waters of the Gulf of Tunis, quantitative records of *P. noctiluca* were collected between 1993 and 2008 by vertical tows (20 m to the surface) using a WP-2 net (200 μm mesh) and a handnet (estimated filtered volume 1000–5000 m^3 in surface and subsurface). The sampling frequency was monthly to weekly during *P. noctiluca* outbreaks.

Data analysis

The abundance of *P. noctiluca* was estimated semi-quantitatively. The species was classed as absent, rare (1–10 individuals 1000 m^{-3}), abundant (10–100 individuals 1000 m^{-3}), or very abundant (>100 individuals 1000 m^{-3}).

Various climatic and hydrological indices were used to test a possible relationship between *P. noctiluca* outbreaks and hydroclimatic variability:

i) the North Atlantic Oscillation (NAO), which drives climate variability over the North Atlantic, North Sea, Europe (Beaugrand *et al.*, 2002; Lynam *et al.*, 2004), and western Mediterranean Sea, affecting marine ecosystems;

ii) the northern hemisphere temperature (NHT), a proxy of temperature anomalies in the northern hemisphere;

iii) SST in the Mediterranean Sea;

iv) the regional atmospheric index (RAI), calculated by means of principal component analysis on a climatological matrix comprising 500 hPa geopotential height, precipitation, sea level pressure, and SST (a detailed description of the methods is given in Molinero *et al.*, 2005a);

v) at a local scale, climatological variables, i.e. atmospheric average annual temperature (AAT), calculated from the monthly average air temperature at Tunis–Carthage meteorological station; annual temperature deviation (ATD), which represents the annual difference between minimum winter temperature and maximum summer temperature; and total annual precipitation (TAP).

Results and discussion

The model developed by Goy *et al.* (1989) suggested a 2- to 3-year cycle for the western Mediterranean, characterized by *Pelagia* outbreaks and followed by a period of very low abundance of the species. A period of 11–12 years has also been observed between two sets of *Pelagia* years when analysing qualitative data collected over two centuries in the northwestern Mediterranean.

The analysis of semi-quantitative records of *P. noctiluca* indicates a different seasonal cycle in the five areas (Figure 2.2). According to the decadal model of Goy *et al.* (1989), the peaks of *P. noctiluca* observed in the Balearic Sea and the Gulf of Tunis in 1993–1995 and 2004–2006 may be considered normal or predictable outbreak events. However, the outbreaks observed in these two regions in 1998 and 1999 did not match the expected periodicity. In addition, a further anomalous change was the increasing occurrence and persistence of *Pelagia* outbreaks from 1998 in both ecosystems.

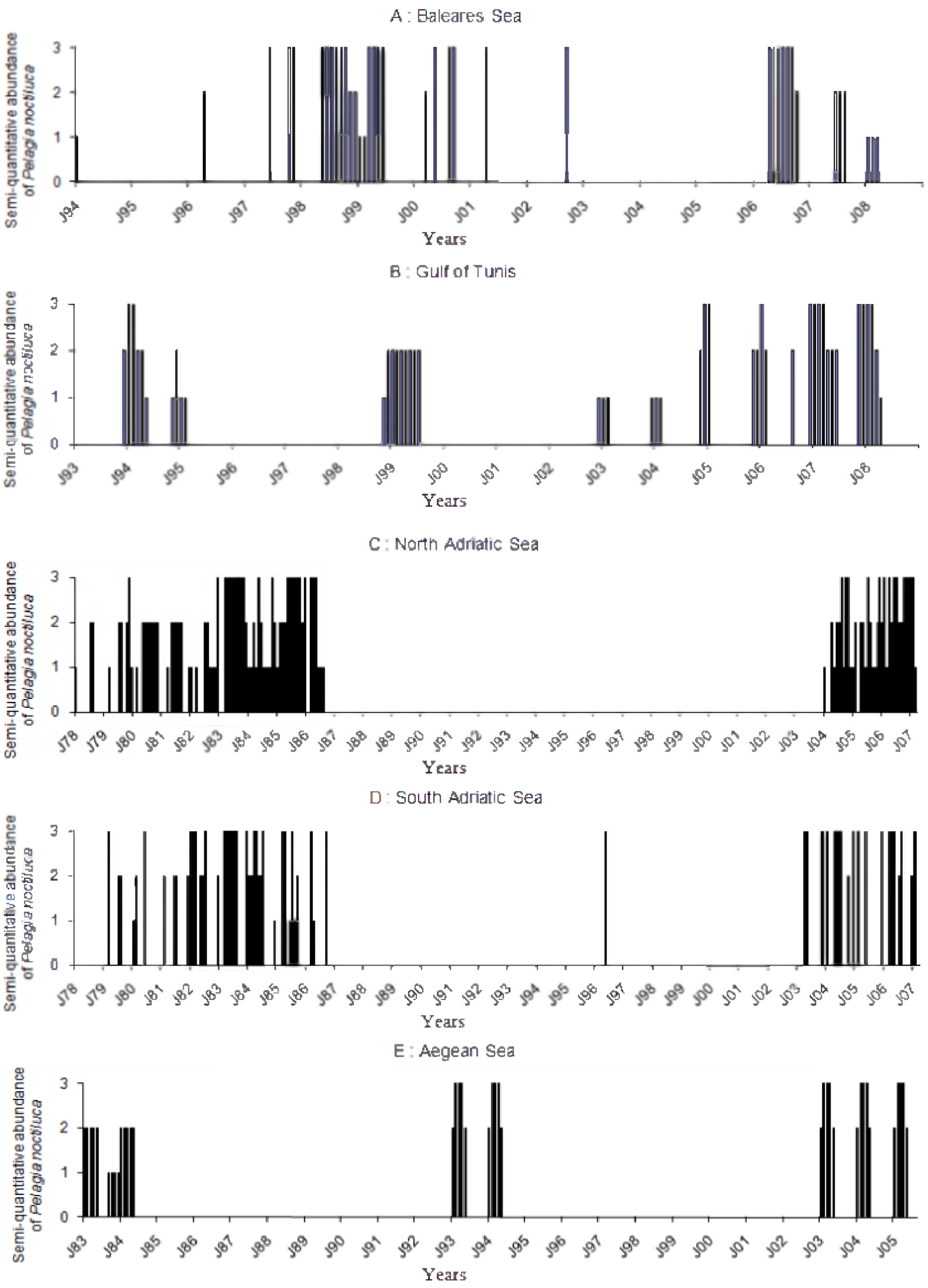

Figure 2.2. Abundance of *Pelagia noctiluca* in different ecosystems in the Mediterranean basin: A = Balearic Sea; B = Gulf of Tunis; C = north Adriatic Sea; D = south Adriatic Sea; E = Aegean Sea. Estimates are semi-quantitative: 1 = rare (1–10 individuals 1000 m^{-3}); 2 = abundant (10–100 individuals 1000 m^{-3}); 3 = very abundant (>100 individuals 1000 m^{-3}).

In the Adriatic Sea, *Pelagia* years seem to follow a different variability, with a 20-year cycle and with outbreaks persisting during the 8–10 years when hydrological and trophic conditions are favourable. In the Aegean Sea, we observed decadal outbreaks over 2–3 years, in agreement with the model of Goy *et al.* (1989).

To assess possible relationships between regional modifications in the abundance and timing of *P. noctiluca* and interannual changes in large-scale and/or local hydro-climatic processes, we performed a principal components analysis on hydroclimatic variables and quantitative abundance of *P. noctiluca* recorded in the Gulf of Tunis from 1999 to 2007 (Figure 2.3).

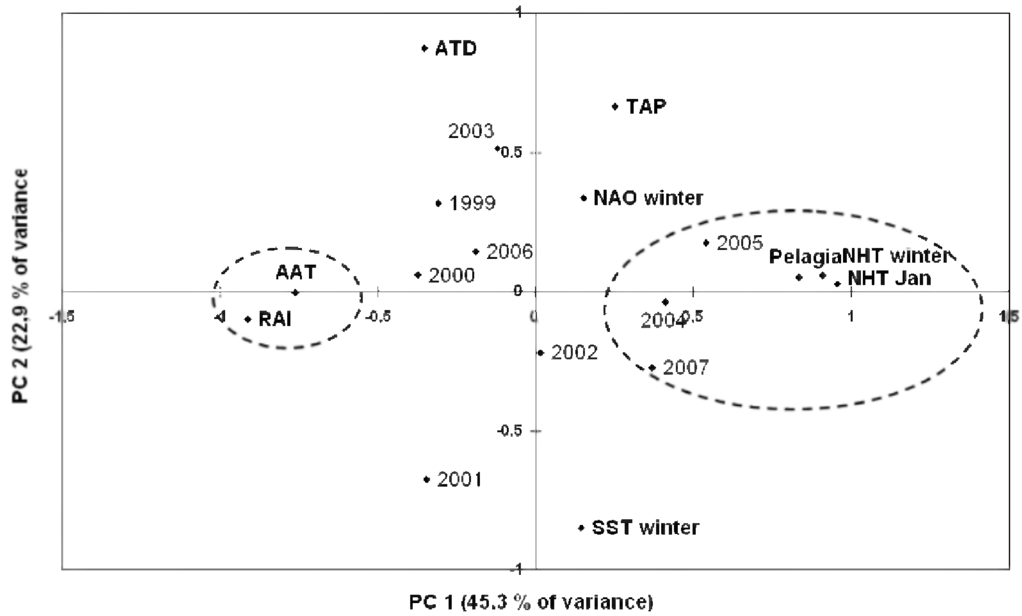

Figure 2.3. Principal Component Analysis between hydroclimatic variables and abundance of *Pelagia noctiluca* in the Gulf of Tunis for the period 1999–2007. AAT = average annual temperature; ATD = annual temperature deviation; NAO winter = North Atlantic Oscillation index from December to March; NHT winter = northern hemisphere temperature index from December to March; NHT Jan = NHT January; Pelagia = *Pelagia* average abundance; RAI = regional atmospheric index for north Tunisia; SST winter = sea surface temperature in winter; TAP = total annual precipitation.

In Figure 2.3, the results (PC1, 45.3% of total variance) indicate that, during 2004, 2005, and 2007, *P. noctiluca* abundance was associated with variations of the NHT index from December to March (NHT winter) and with the NHT index in January (NHT January), and negatively associated with the RAI and the atmospheric AAT. In contrast, the NAO index seems not to be related to the *P. noctiluca* abundance. In the southwestern Mediterranean (Gulf of Tunis), the positive anomalies of the NHT winter index are associated with negative phases of RAI and a decrease in atmospheric AAT. These climatic conditions correspond to mild winters, which seem to favour *P. noctiluca* reproduction and probably determine optimal conditions for the success of *P. noctiluca* outbreaks and their maintenance for several months and even years.

Pelagia noctiluca can be considered an indicator of climate variability in the Mediterranean. The recent climatic and hydrological conditions of the Mediterranean seem to promote higher frequency of *P. noctiluca* peaks.

The preliminary results of this work raise new questions.

1) Why have *P. noctiluca* outbreaks in the western Mediterranean not followed the periodicity described by Goy *et al.* (1989) after 1998? Is this attributable to global warming, which affects hydrological and trophic winter conditions in the western Mediterranean, thus creating a new environmental niche more favourable for *P. noctiluca* reproduction and development success?

2) What alterations are likely to occur in the structure of the western Mediterranean pelagic foodweb because of the persistent presence of *P. noctiluca*?

References

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science, 62: 1205–1215.

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692–1694.

Brodeur, R. D., Mills, C. E., Overland, J. E., Walters, G. E., and Schumacher, J. D. 1999. Substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fisheries Oceanography, 8: 296–306.

CIESM (Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée). 2001. Gelatinous Zooplankton Outbreaks: Theory and Practice, 29 August–1 September 2001, Naples, Italy. CIESM Workshop Series No. 14. 112 pp. Available online at www.ciesm.org/publications/Naples01.pdf.

Edwards, M., Beaugrand, G., Reid, C., Rowden, A., and Jones, M. 2002. Ocean climate anomalies and the ecology of the North Sea. Marine Ecology Progress Series, 239: 1–10.

Goy, J., Morand, P., and Etienne, M. 1989. Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusae) in the western Mediterranean Sea: prediction by climatic variables. Deep Sea Research Part I, 36: 269–279.

Hare, S. R., and Mantua, N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography, 47: 103–145.

Lynam, C. P., Hay, S. J., and Brierley, A. S. 2004. Inter-annual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnology and Oceanography, 49: 637–643.

Lynam, C. P., Heath, M. R., Hay, S. J., and Brierley, A. S. 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. Marine Ecology Progress Series, 298: 157–167.

Mills, C. E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia, 451: 55–68.

Molinero, J. C. 2008. Large contribution of the North Atlantic Ocean climate on the variability of plankton communities in the northwestern Mediterranean. Globec International Newsletter, 14(1): 76–77.

Molinero, J. C., Ibanez, F., Nival, P., Buecher, E., and Souissi, S. 2005a. The North Atlantic climate and northwestern Mediterranean plankton variability. Limnology and Oceanography, 50: 1213–1220.

Molinero, J. C., Ibanez, F., Souissi, S., Chifflet, M., and Nival, P. 2005b. Phenological changes in the northwestern Mediterranean copepods *Centropages typicus* and *Temora stylifera* linked to climate forcing. Oecologia, 145: 640–649.

Purcell, J. E. 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. Annales de l'Institut Océanographique, 73: 125–137.

Purcell, J. E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata*, and *Aequorea aequorea*, in Prince William Sound, Alaska. Marine Ecology Progress Series, 246: 137–152.

Purcell, J. E., and Arai, M. N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia, 451: 27–44.

Theocharis, A., Nittis, K., Kontoyiannis, H., Papageorgiou, E., and Balopoulos, E. 1999. Climatic changes in the Aegean Sea influence the thermohaline circulation of the eastern Mediterranean (1986–1997). Geophysical Research Letters, 26: 1617–1620.

3. Zooplankton variability in the western Mediterranean: comparative study of two neritic time-series during 1995–2004

Maria Luz Fernández de Puelles and Maria Grazia Mazzocchi

Introduction

The Mediterranean Sea plays a critical role in the global climate system and is considered one of the most sensitive areas in the world with respect to effects of climate variability (Lionello *et al*., 2006). It is located at the border of two different climate cells and regimes, and is therefore exposed to both mid-temperate latitudinal and tropical variability. It is a semi-enclosed sea area which, via the Strait of Gibraltar, is in contact with the Atlantic Ocean, where similar processes take place. Although smaller than the North Atlantic, the Mediterranean Sea has a varied morphology, with many distinct orographic features and a complex seabed topography. Its tormented geological history and present-day variety of climatic and hydrological conditions contributes to different hydrographic and ecological regions. Apart from the Adriatic Sea, two main sub-basins can be clearly distinguished: the western and the eastern Mediterranean. Both exhibit differences in temperature and salinity characteristics, and in plankton productivity. Overall, temperature and salinity values are lower, and productivity higher, in the western part than in the eastern part.

It is important to analyse long time-series of data in order to detect changes relative to global climate change in the marine ecosystem. However, the abiotic changes and the biological responses of the pelagic ecosystem can be very complex because of the synergistic links that exist between climate and human activities (Harley *et al*., 2006). Therefore, it is important to investigate how the marine communities are changing in their abundance and structure and the causes of their variability in different regions. In the North Atlantic, there are already several programmes and international initiatives focused on this goal (e.g. GLOBEC (Global Ocean Ecosystem Dynamics), IOC (Intergovernmental Oceanographic Commission), IGBP (International Geosphere–Biosphere Programme), OSPAR (Oslo/Paris) Commission) that realize the complexity of time-series studies and the importance of maintaining them. During the last decade, the ICES Working Group on Zooplankton Ecology (WGZE) has collected information on the main characteristics of zooplankton in more than 37 monitoring sites; in their last report, six Mediterranean sites were also included (O'Brien *et al*., 2008).

The aim of this contribution is to compare two of the time-series of the western Mediterranean and to identify overall indications, at basin scale, of how climatic variability affects zooplankton abundance and the composition of main groups and species. The areas chosen are located in two neighbouring, but hydrographically different, western Mediterranean regions, where sampling was undertaken during the same period (1995–2004).

Material and methods

The sampling sites, Stn PA in the Balearic Sea southwest of Mallorca (39°28.59′N 2°25.63′E) and Stn MC in the inner Gulf of Naples (40°48.50′N 14°15.00′E), are both located at mid-Mediterranean latitudes, close to the coast and at similar depths (~75 m; Figure 3.1). Stn PA (Baleares) is in a boundary area between the northern and southern regions of the western Mediterranean and is exposed to the influence of offshore waters. Stn MC (Naples) is at the boundary between the offshore Tyrrhenian waters and the coastal area facing a densely populated region and is heavily influenced by land run-off. The two stations are long-term monitoring sites for zooplankton, where comparable sampling methods, both in the field and in the laboratory, have been used (Mazzocchi and Ribera d'Alcalà, 1995; Fernández de Puelles *et al.*, 2007) for the period 1995–2004.

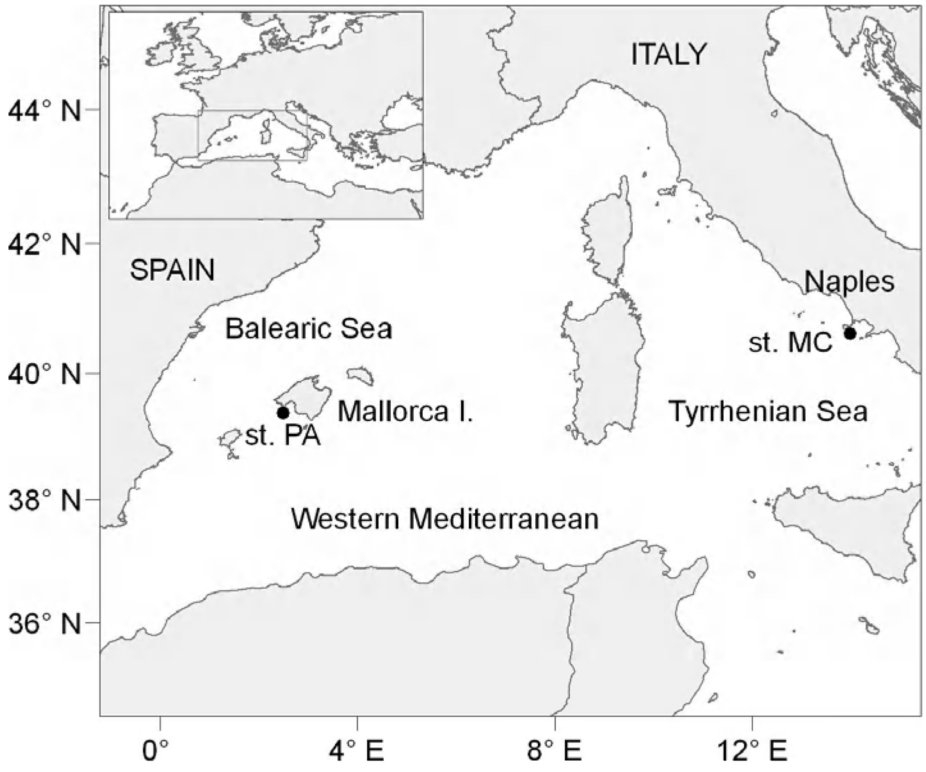

Figure 3.1. Map of the western Mediterranean showing the two sites: Stn PA in the Balearic Sea and Stn MC in the Gulf of Naples.

Results and discussion

Seasonal variability

The seasonal pattern of surface temperature was very similar at both sites, ranging from 13°C in late winter to almost 29°C in late summer. The water column was entirely mixed during winter and highly stratified for more than seven months.

Salinity, even at the surface, was higher than in the Atlantic waters and differed in range and seasonal pattern between the Baleares (37.6–37.8 psu) and Naples (37.9–38.1 psu) sites. The seasonal pattern demonstrated lower values in spring at Naples, and in summer and autumn at Baleares, indicating that the two sites are influenced by different water masses throughout the year.

Chlorophyll *a* (Chl *a*) concentrations were lower at Baleares than at Naples and had a higher winter peak, demonstrating the oceanic characteristics of this area (Fernández de Puelles *et al.*, 2007); the higher concentrations at Naples, with three annual peaks, are characteristic of a more coastal area (Ribera d'Alcalà, 2004).

Mean annual cycles of total zooplankton abundance at the two sites were very similar in December–March, but differed markedly during the rest of the year (Figure 3.2). At Baleares, the pattern was smooth, with a period of greatest abundance (around 1000 ind. m^{-3}) in March–July, whereas at Naples, the pattern was characterized by a sharp peak in August of up to >3000 ind. m^{-3}, comprised mainly of cladocerans.

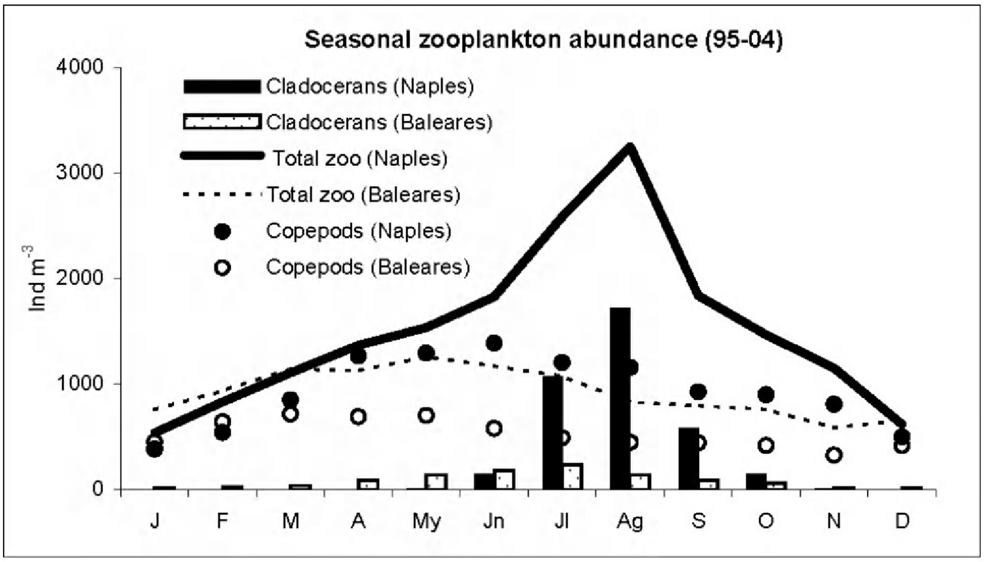

Figure 3.2. Average seasonal abundance between 1995 and 2004 of total zooplankton, copepods, and cladocerans at Stn MC (Naples) and Stn PA (Baleares). For location of stations, see Figure 3.1.

Communities at both sites were dominated by copepods, which contributed slightly less at Baleares (57%) than at Naples (62%). The main difference between the two sites in terms of community structure was the percentages of cladocerans (9% at Baleares, 21% at Naples) and meroplankton (3% at Baleares, 4% at Naples). Appendicularians ranked second and contributed year-round, more so at Baleares (17%) than at Naples (10%). This was also observed for siphonophores (3% and <1%, at Baleares and Naples, respectively) and ostracods (1% and <1%, respectively), which were almost nonexistent at Naples. Doliolids and chaetognaths were abundant year-round and contributed more at Baleares (4% and 2%, respectively) than at Naples (2% and 1%, respectively), where they occurred mainly in autumn.

A common feature at both sites was the high diversity of copepods, with the occurrence of more than 130 species and a predominance of small individuals. The most important contributors at both sites were the genera *Clausocalanus* and *Oithona*. Both demonstrated peaks in spring and autumn, but *Clausocalanus* was more important in spring and *Oithona* in autumn at Baleares. *Acartia clausi*, *Centropages typicus*, *Paracalanus parvus*, and *Temora stylifera* were important in the whole copepod assemblages during May–October, but were more abundant at Naples than at Baleares, with differences in their seasonal timing. The top species of copepod were defined at the two sites. In addition, *Ctenocalanus vanus*, *Calocalanus* spp., and *Oncaea* spp. were also important at both sites.

Interannual variability

Surface temperatures differed markedly between the Baleares and Naples sites. In the former, the pattern was very stable during the whole period, with the exception of relatively high annual means in 1997 and 1998, whereas in the latter, an increasing trend appeared, superimposed on marked interannual fluctuations. During the decade, salinity increased at Baleares but not at Naples, whereas the opposite was observed for Chl *a*. Particularly interesting were the years 2001 and 2002, when the highest concentrations were recorded at Baleares (cold winters) and the lowest at Naples (warm winters and changes in the wind regime).

On the interannual scale, zooplankton demonstrated greater abundance and variability at Naples than at Baleares (Figure 3.3). In the Naples series, copepods demonstrated a regular increasing trend until 2000, which was followed by an abrupt decrease but was resumed after 2002. The interannual variability was even greater in the Baleares series, with recurrent patterns of abundance for both copepods and total zooplankton, although the highest values were observed in 1996 and 2000 in relation to cool years in the Baleares area.

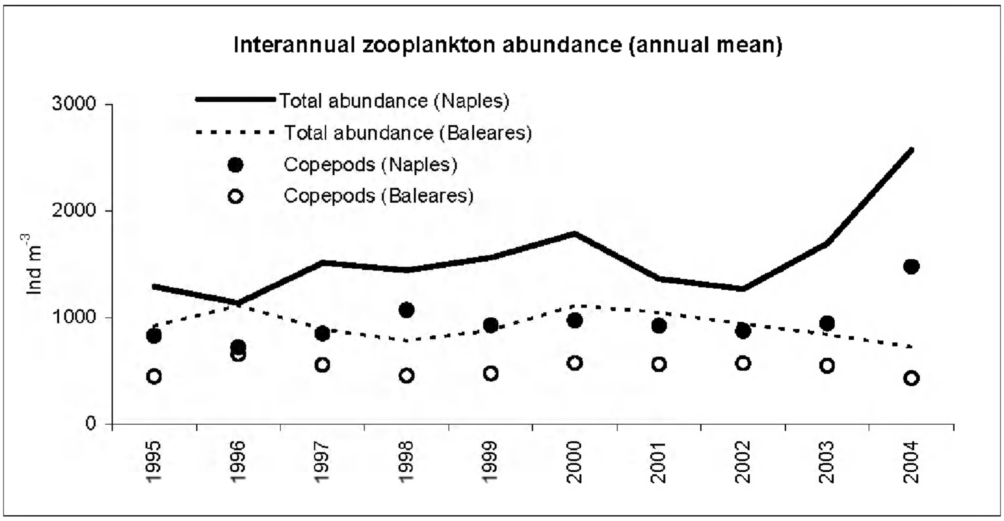

Figure 3.3. Interannual abundance of total zooplankton and copepods (annual means) at Stn MC (Naples) and Stn PA (Baleares). For location of stations, see Figure 3.1.

Cladocerans demonstrated marked interannual variability, particularly at Naples. Lesser abundance was observed at Baleares, with the highest values observed during the highest concentrations of Chl *a* in 2001 and 2002. Appendicularians did not show any clear interannual pattern, whereas other, less abundant groups, such as doliolids and chaetognaths, demonstrated opposite trends at the two sites, decreasing at Baleares and increasing at Naples. This was related to the conditions of the water masses in both areas, namely the increasing and decreasing trends in salinity at Baleares and Naples, respectively. In the Baleares area, both groups were negatively correlated with salinity and temperature (Fernández de Puelles *et al.*, 2007). Siphonophores and ostracods, which were more abundant in winter than summer, increased in the Baleares area, although they had no apparent interannual pattern at Naples. The low abundance of siphonophores and ostracods in the Naples area may be an indication of the offshore characteristic of these groups, as is their relatively great abundance in the open waters of the Baleares area.

The four most abundant copepod species exhibited a remarkable interannual variability, with different patterns at the two sampling sites. No major trends were observed at Baleares, whereas at Naples, the regular increasing trend observed for *A. clausi* until year 2000 was followed by an abrupt decrease in 2001 and a recovery starting from 2003. *C. typicus* exhibited irregular and opposite fluctuations, with greater abundance during the last years at Baleares. *Paracalanus parvus* and *Temora stylifera* were more abundant at Naples than at Baleares, and they increased during the last period, particularly at Naples. The genus *Clausocalanus* increased in abundance from 1995 to 2004 in both areas, but especially at Baleares, whereas *Oithona* demonstrated an opposite pattern, with abundance increasing at Naples and decreasing at Baleares.

Very complex interactions appear between the zooplankton community and regional conditions of the hydrography of both areas that, in turn, may be affected by climatic effects. Almost all groups and many species can be considered hydrographic fingerprints; however, the responses varied according to their life histories. Further studies have to be conducted in which the zooplankton community can be used as a valuable indicator of basin-scale environmental variability and global warming.

Conclusions

Although somewhat preliminary, the present contribution provides an important comparative analysis of two zooplankton time-series in the western Mediterranean, aimed at investigating how regional hydrology and the zooplankton community were affected by climate effects at the basin scale during a ten-year period. The decade considered here was very irregular in terms of environmental conditions and too short to highlight any temporal trend. However, a rapid community response appears to emerge from the strong environmental forcing that occurs in this area of the western Mediterranean. The areas studied here reflect the main western Mediterranean characteristics, but further and more detailed studies are needed in order to reach firm conclusions. However, some clear observations can be highlighted from this study.

- Zooplankton communities strongly reflect the offshore (Stn PA in the Balearic Sea off Mallorca) vs. coastal (Stn MC in the inner Gulf of Naples) characteristics of the two sites, both at seasonal and interannual scales.
- Differences in the distribution of water masses at local scales, as indicated by temperature and salinity characteristics, seemed to act as main drivers of zooplankton variability. The increase in temperature observed at the Naples site (Stn MC) was not as clear at the Baleares site (Stn PA), and the salinity increase at the Baleares site, particularly after 2000, was not observed in the Gulf of Naples.
- Copepods, the most abundant group at both sites, were highly diversified and dominated by small genera/species. In addition to *Clausocalanus* and *Oithona*, four key species (*A. clausi, C. typicus, P. parvus, and T. stylifera*) were considered to be of interest for further studies of climate change in the western Mediterranean.
- Abundance and temporal patterns of other main zooplankton components differed at the two sites according to offshore or coastal influences, and were related both to their life history and to changes in the hydrographic regime.
- Although the period considered is too short to investigate indications of climate effects at larger temporal scales, the synchronies observed in zooplankton patterns at both sites suggest common responses to indications at the basin scale.

References

Fernández de Puelles, M. L., Alemany, F., and Jansa, J. 2007. Zooplankton time series in the Balearic Sea (western Mediterranean): variability during the decade 1994–2003. *In* Ecological Functioning of the Iberian Seas: A Synthesis of GLOBEC Research in Spain and Portugal, pp. 329–354. Ed. by F. Echevarría, J. L. Acuña, S. H. León, E. Saiz, A. M. P. Santos, and M. Barange. Progress in Oceanography, 74: 95–422.

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. J., Sorte, C. J. B., Thorner, C. S., Rodriguez, L. F., *et al.* 2006. The impact of climate change in coastal marine systems. Ecology Letters, 9: 228–241.

Lionello, P., Malanotte-Rizzoli, P., and Boscolo, R. (Eds). 2006. Mediterranean Climate Variability. Developments in Earth and Environmental Sciences, 4, Elsevier, Amsterdam. 421 pp.

Mazzocchi, M. G., and Ribera d'Alcalà, M. 1995. Recurrent patterns in zooplankton structure and succession in a variable coastal environment. ICES Journal of Marine Science, 52: 679–691.

O'Brien, T. D., López-Urrutia, A., Wiebe, P. H., and Hay, S. (Eds). 2008. ICES Zooplankton Status Report 2006/2007. ICES Cooperative Research Report No. 292. 168 pp.

Ribera d'Alcalà, M. 2004. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. Scientia Marina, 68(Suppl. 1): 65–83.

4. Comparison of mesozooplankton faecal pellet characteristics from the southern North Sea and the Mediterranean Sea during spring bloom conditions

Constantin Frangoulis and Jean-Henri Hecq

Introduction

Mesozooplankton faecal pellets participate in the carbon and nutrient cycles, in the nutrition of marine organisms, and in the transport of toxins, pollutants, and sediments. The importance of this role depends on their nature and production, which are highly variable parameters that, in turn, depend on many factors. For example, a phytoplankton bloom may significantly change the nature of mesozooplankton faecal pellets because it affects their shape, content, density, and volume (Frangoulis *et al.*, 2005).

The aim of the present study is to compare the eutrophic southern North Sea and the oligotrophic Bay of Calvi in the Mediterranean Sea with respect to the seasonal variability of faecal pellet characteristics (shape, size, sinking speed, density) during bloom conditions.

Material and methods

Samples were taken in the Mediterranean Sea, close to oceanographic station STARESO in the Bay of Calvi, Corsica, in spring 1999, and in the southern North Sea during eight cruises on board RV "Belgica" in spring 1995, 1996, and 1997. In both areas, 0.25–1.5 l of subsurface water (2 or 3 m) was filtered for phytopigment analysis by HPLC (high-performance liquid chromatography). Details of HPLC methodology can be found in Frangoulis *et al.* (2001) and Goffart *et al.* (2002).

Collection of faecal pellets was started within 5 min of a mesozooplankton collection with a subsurface haul (~5 m) using a 200 µm mesh WP-2 net. Organisms were placed in a bucket containing a hollow cylinder, the bottom of which was covered with a net (200 µm mesh in the southern North Sea and 100 µm mesh in the Bay of Calvi) that retained the copepods but not their faecal pellets. Organisms were allowed to defecate for 3–5 h in the dark at ambient temperatures. The pellets were then concentrated using "reverse filtration": a smaller cylinder with a 20 µm mesh net at the bottom was used to ladle water from within the cylinder. After reducing the initial volume of water to ~100 ml, pellets were collected using a screen of 25 µm mesh. After collection, the faecal pellets were either immediately fixed with 4% formalin or preserved at 4°C for no more than 24 h and then fixed with formalin.

The sinking speed of faecal pellets was measured using the method described by Frangoulis *et al.* (2001). A large glass burette (85 cm high, 6.5 cm inside diameter) was filled with seawater filtered through GF/F glassfibre filters and left to stabilize for a minimum of 1 h. Several faecal pellets at a time were gently released under the water's surface using a Pasteur pipette. A 200 µm mesh net was placed 5 cm below the water's surface to retain aggregates of faecal pellets. After the pellets had passed through the netting, the net was slowly removed and a stopwatch was started once the pellets had sunk 5 cm. After a delay of 2 or 3 min, the tap of the burette was opened and 1.5 ml samples were taken every 20 sec. This procedure was continued for approximately 30 min. The sinking speed was calculated from the time taken to collect each sample and the distance covered (taking into account the decrease in height of the water column caused by the sampling). Intact pellets in each sample were counted and measured (length and width) under a stereomicroscope. Estimates of faecal pellet density were obtained from the values for faecal pellet length, width, and sinking speed, based on the relationship of Komar *et al.* (1981).

Results and discussion

The dominant shape of faecal pellets in both areas was cylindrical (<1% being elliptical). As copepods were dominant in both areas, it is likely that almost all cylindrical pellets were released by copepods. In the Bay of Calvi, faecal pellet volume values varied from $0.4 \times 10^4\ \mu m^3$ to $149 \times 10^4\ \mu m^3$, with a mean of $11 \times 10^4\ \mu m^3$, whereas in the southern North Sea, the values were higher, varying from $1.8 \times 10^4\ \mu m^3$ to $183 \times 10^4\ \mu m^3$, with a mean of $38 \times 10^4\ \mu m^3$ (Figure 4.1a). Pellet size is known to be influenced by body size/weight, food concentration, and food quality (Frangoulis *et al.*, 2005). In the Bay of Calvi, pellet volume was positively related to the subsurface mean dry weight of mesozooplankton individuals ($r^2 = 0.61$, $p < 0.001$; Figure 4.1d), as already reported in other studies (Paffenhöfer and Knowles, 1979; Uye and Kaname, 1994). However, there appeared to be no relationship with Chlorophyll *a* (Chl *a*), probably because variations in food concentration (Chl *a* <0.5 $\mu g\ l^{-1}$) were small when pellet volume was measured; this was indicated by Dagg and Walser (1986), who obtained a positive relationship between pellet volume and Chl *a* only above 0.5 μg Chl *a* l^{-1}. In the southern North Sea, a negative, but not significant, correlation ($r^2 = 0.40$, $p = 0.18$) with Chl *a* appeared (Figure 4.1c). This lack of relationship between faecal pellet volume and Chl *a* in the southern North Sea can be explained by changes in phytoplankton quality during its bloom (presence of *Phaeocystis* colonies, which are commonly considered unpalatable to mesozooplankton), resulting in less food being available (Frangoulis *et al.*, 2001).

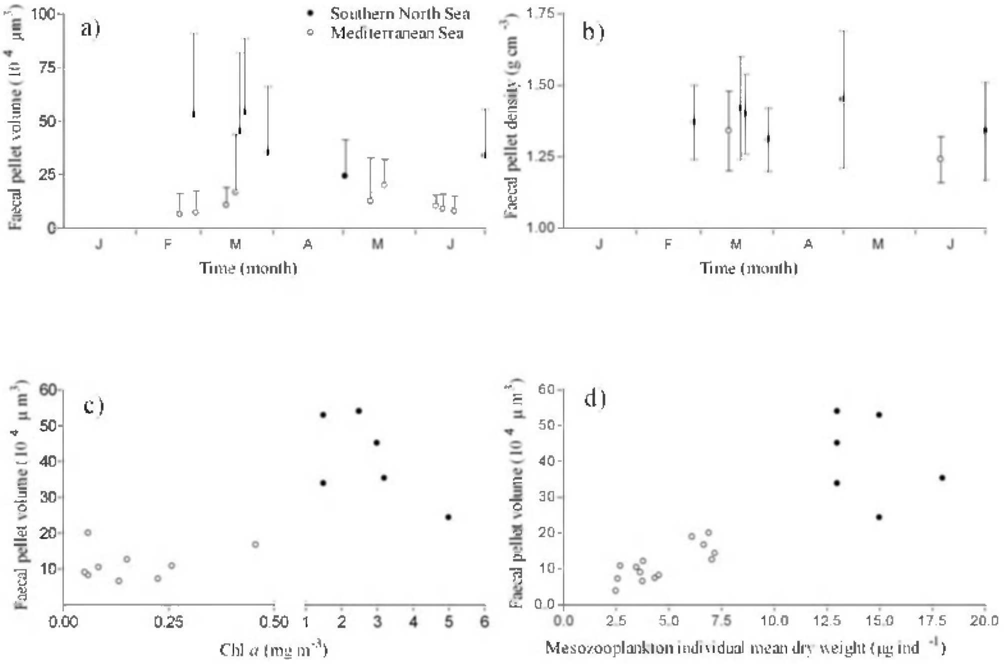

Figure 4.1. Seasonal variations of subsurface mesozooplankton faecal pellets in the southern North Sea and in the western Mediterranean Sea (Bay of Calvi): (a) volume; (b) density. Values are means, and vertical bars show standard deviations. (c) Relationship between mean faecal pellet volume and Chl *a*. (d) Relationship between mean faecal pellet volume and subsurface mesozooplankton individual mean dry weight. Data from southern North Sea are taken from Frangoulis *et al.* (2001).

In both areas, the sinking speed of mesozooplankton faecal pellets was positively related to faecal pellet volume ($r^2 > 0.5$, all $p < 0.05$). Values varied from 14 to 57 m d^{-1} in the Bay of Calvi and from 37 to 251 m d^{-1} in the southern North Sea. Estimated faecal pellet density varied seasonally in both the Bay of Calvi and the southern North Sea (Figure 4.1b). As faecal pellet density depends on the concentration and packing of ingested material into pellets and the type of material ingested (see e.g. Fowler and Small, 1972; Urban *et al.*, 1993; Hansen *et al.*, 1996), the higher density values during the phytoplankton bloom period could be attributable to a change in diet during and after the phytoplankton bloom period. In the case of the Mediterranean, this is probably caused partly by the transition from a more herbivorous diet of phytoplankton, dominated by small flagellates, to a more carnivorous diet of mesozooplankton after the bloom, whereas, in the case of the North Sea, it is probably caused by the transition from a diatom-dominated bloom to a *Phaeocystis* sp.-dominated bloom.

References

Dagg, M. J., and Walser, W. E. J. 1986. The effect of food concentration on faecal pellet size in marine copepods. Limnology and Oceanography, 31: 1066–1071.

Fowler, S. W., and Small, L. F. 1972. Sinking rates of euphausiid faecal pellets. Limnology and Oceanography, 17: 293–296.

Frangoulis, C., Belkhiria, S., Goffart, A., and Hecq, J. H. 2001. Dynamics of copepod faecal pellets in relation to a *Phaeocystis* dominated phytoplankton bloom: characteristics, production, and flux. Journal of Plankton Research, 23: 75–88.

Frangoulis, C., Christou, E. D., and Hecq, J. H. 2005. Comparison of marine copepod outfluxes: nature, rate, fate, and role in the carbon and nitrogen cycles. Advances in Marine Biology, 47: 251–307.

Goffart, A., Hecq, J. H., and Legendre, L. 2002. Changes in the development of the winter-spring phytoplankton bloom in the Bay of Calvi (northwestern Mediterranean) over the last two decades: a response to the changing climate? Marine Ecology Progress Series, 236: 45–60.

Hansen, B., Fotel, F. L., Jensen, N. J., and Mansen, S. D. 1996. Bacteria associated with a marine planktonic copepod in culture. II. Degradation of fecal pellets produced on a diatom, a nanoflagellate, or a dinoflagellate diet. Journal of Plankton Research, 18: 275–288.

Komar, P. D., Morse, A. P., Small, L. F., and Fowler, S. W. 1981. An analysis of sinking rates of natural copepod and euphausiid fecal pellets. Limnology and Oceanography, 26: 172–180.

Paffenhöfer, G. A., and Knowles, S. C. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. Journal of Marine Research, 37: 36–47.

Urban, J. L., Deibel, D., and Schwinghamer, P. 1993. Seasonal variations in the densities of fecal pellets produced by *Oikopleura vanhoeffeni* (C. Larvacea) and *Calanus finmarchicus* (C. Copepoda). Marine Biology, 117: 607–613.

Uye, S., and Kaname, K. 1994. Relations between fecal pellet volume and body size for major zooplankters of the Inland Sea of Japan. Journal of Oceanography, 14: 343–358.

5. Zooplankton abundance and community structure off the Algerian coast and affinities with Atlantic fauna

Aziz Hafferssas and Rabia Seridji

Introduction

The circulation of water masses along the Algerian coast is characterized by intensive, mesoscale dynamics (García-Olivares *et al.*, 2007). The Atlantic inflow into the Mediterranean creates a sharp boundary in both physical and biological properties (Raimbault *et al.*, 1993). Across the current, there are large horizontal gradients, both in salinity and in the biomass and species composition of phytoplankton and zooplankton communities (Seridji and Hafferssas, 2000). The offshore band of the Atlantic Current is a region of high biological productivity; resulting from the mixing of coastal Modified Atlantic Water (MAW) and offshore Surface Mediterranean Water (SMW), it is surrounded by areas of low productivity (Anxelu *et al.*, 2001). The phytoplankton, chlorophyll concentration, and species abundance along the offshore band of the Atlantic Current is strongly linked to the interactions between Atlantic and Mediterranean waters (Raimbault *et al.*, 1993).

The present study focuses on the impacts of the Atlantic Current on the abundance and community structure of copepods off the Algerian coast.

Material and methods

Four surveys aimed at locating and characterizing copepod communities off the Algerian coast were carried out along transects during 1990, 1998, 2000, and 2004 in the area bordered by 8°14′E, 1°10′E, 35°29′N, and 37°06′N. All transects extended from nearshore to offshore waters (Figure 5.1). Zooplankton sampling was conducted using WP-2 nets (200 µm mesh). A flowmeter was used to estimate the volume of seawater filtered (UNESCO, 1968).

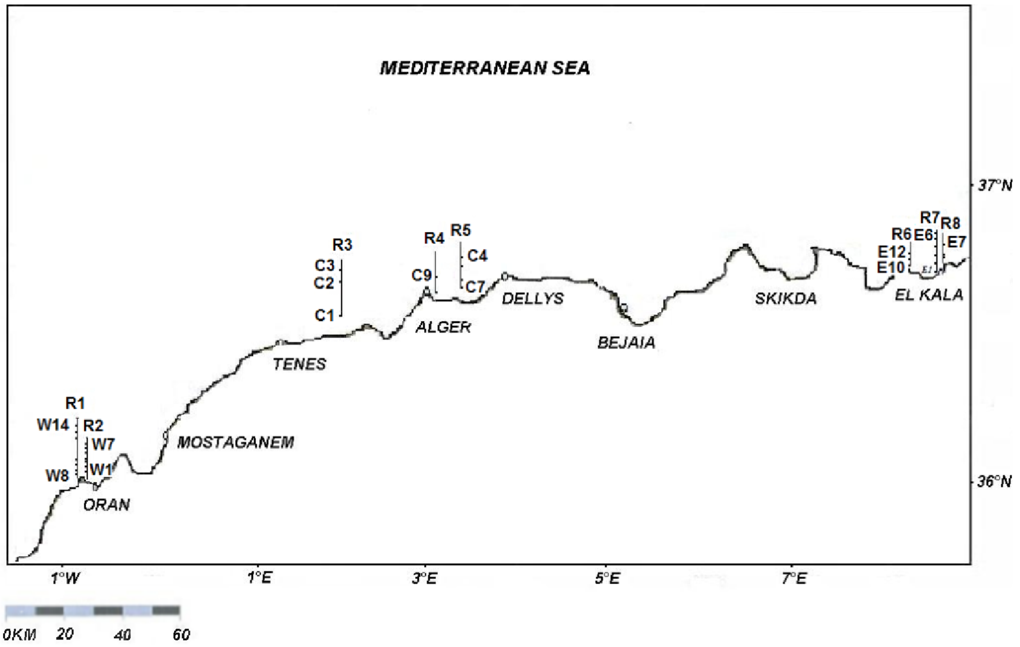

Figure 5.1. Map of the Algerian coast showing the sampling stations.

All tows were made by vertical hauls between 200 m and the surface. Samples were preserved in 4% buffered formaldehyde solution. In the laboratory, only copepod species were counted. Population characteristics were described following traditional taxonomic determination using a dissecting microscope. Five subsamples were counted per sample (Bourdillon, 1964). Abundance values were converted into individuals m^{-3}. Principal component analysis (PCA) was carried out in order to identify objectively the spatial changes in structure of the zooplankton community (composition, abundance). The software SYSTAT for Macintosh was used for the statistical treatments. In all cases, data were log-transformed $\log_{10} (x + 1)$ to avoid the strong influences of the most abundant copepods and to meet the assumptions for parametric multivariate analysis (Frontier and Pichod-Viale, 1991). Further mathematical details of the technique and treatments are given in Legendre and Legendre (1998).

Results

Copepod biodiversity

Copepod biodiversity was characterized by an east–west gradient, with lower diversity in the east (24 species) than in the west (145 species). There were 24 copepod species recorded beyond 8°E, of which one was Atlantic, eight neritic, and seven bathypelagic. In contrast, of the 145 copepod species recorded off the western part of the coast, 10 were Atlantic, 9 neritic, and 13 bathypelagic. Between 2°15′E and 3°09′E, an area of intermediate biodiversity, 85 species were recorded, of which 10 were Atlantic, 11 neritic, and 13 bathypelagic.

Distribution of Atlantic species along the Algerian coast

A large number of Atlantic species *(Mesocalanus tenuicornis, Temora longicornis, Centropages chierchiae, C. violaceus, Acartia danae, Calocalanus pavo, Calanoïdes carinatus, Pleuromamma abdominalis,* and *Farranula carinata)* was recorded. Their numbers in the upper 200 m of the column generally remained small off the eastern part of the coast (< 1 individual m^{-3}) but increased sharply between the central and western parts of the coast (1–4.35 individuals m^{-3}). Their distributions appeared to be linked to Atlantic inflow.

Copepod abundance and community structure

We found that the species off the Algerian coast could be grouped into three communities, corresponding to the dynamic structure of the area (Figure 5.2). The quantitative compositions of the coastal MAW and the offshore SMW communities were significantly different. Group 1, the frontal community, included five species (*Paracalanus parvus, Clausocalanus furcatus, C. arcuicornis, Mesocalanus tenuicornis,* and *Eucalanus elongates)* that reach their maximum abundance in the frontal region. These species were located in the boundary zone between the MAW and the SMW, where the salinity gradient was between 36.6 and 36.8 and the deep chlorophyll maximum layer (DCM) contained more than 1.5 mg m^{-3} Chlorophyll a (Chl *a*).

Group 2, the coastal MAW community, included species that were relatively abundant at the inshore station in the MAW. This area was strongly influenced by the Atlantic inflow (surface salinity <36.6) and the weak water resurgence (DCM ca. 1 mg m^{-3}). The copepods in this group were neritic species, such as *Acartia clausi, Euterpina acutifrons, Oithona nana,* and *Temora stylifera.*

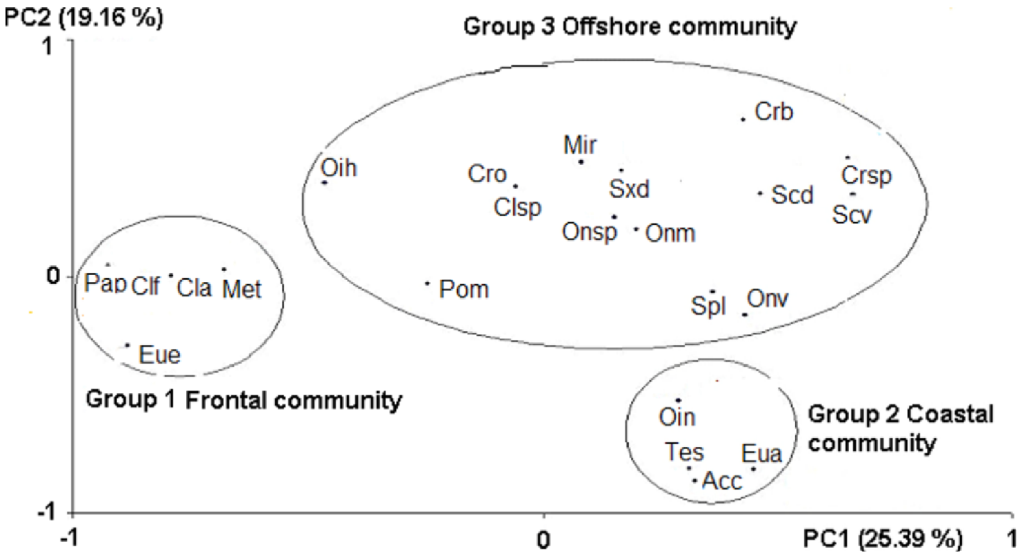

Figure 5.2. Ordination of selected species in space configured by the first and second axes of PCA. Species labels are: Onm = *Oncaea media*; Scd = *Scolecithricella dentate*; Oin = *Oithona nana*; Cla = *Clausocalanus arcuicornis*; Acc = *Acartia clause*; Onsp = *Oncaea* sp.; Onv = *Oncaea venusta*; Eue = *Eucalanus elongates*; Pap = *Paracalanus parvus*; Clf = *Clausocalanus furcatus*; Met = *Mesocalanus tenuicornis*; Crb = *Corycaeus brehmi*; Cro = *Corycaeus ovalis*; Oih = *Oithona helgolandica*; Tes = *Temora stylifera*; Spl = *Spinocalanus longicornis*; Pom = *Pontella mediterranea*; Clsp = *Clausocalanus* sp.; Mir = *Microsetella rosea*; Eua = *Euterpina acutifrons*; Scv = *Scolecithricella vitata*; Sxd = *Scolecithrix danae*; Crsp = *Corycaeus* sp.

Group 3, the offshore SMW community, consisted mainly of 13 species with a broad distribution. These species (*Scolecithricella dentata, S. vittata, Oncaea venusta, O. media, Oncaea* spp., *Microsetella rosea, Oithona helgolandica, Corycaeus ovalis, C. brehmi, Corycaeus* spp., *Spinocalanus longicornis, Scolecithrix danae,* and *Clausocalanus* spp.) were also recorded in relatively small numbers in the upper 200 m in frontal and coastal waters.

Discussion

In the world ocean, 2443 species of pelagic copepods have been catalogued (Razouls *et al.*, 2005–2008). The Mediterranean Sea contains 530 species (21% of the total), most of which (75%) originate in the Atlantic (Razouls *et al.*, 2005–2008). The copepod fauna of the Algerian coast was represented by 145 species (ca. 25% of Mediterranean copepod populations). In the south of the western Mediterranean basin, from the Algerian coast to the Balearic Islands, the copepod fauna is composed of more than 200 taxa. For comparison, Razouls *et al.* (2005–2008) found 370 taxa in the eastern Atlantic.

We found that the species composition of copepod communities off the Algerian coast reflected the dynamic structure of the area, and we recognised three zones: a frontal zone and two other zones that supported oligotrophic communities of different origins.

In the frontal zone, the quantitative composition of the community (Group 1) was significantly different from that of the coastal MAW and offshore SMW communities (Groups 2 and 3, respectively). Frontal systems have a wide range of effects on pelagic organisms (Sournia *et al.*, 1990). In this case, the frontal zone in the Algerian basin supports a distinct community, as evidenced by its physical and biological characteristics (Seridji and Hafferssas, 2000). Legendre and Legendre (1984) suggested that very high biological activity in an unstable and disturbed environment, with the copepod community in a stressed condition, may lead to a predominance (concentrations as high as 800 individuals m^{-3}) of opportunistic populations of *P. parvus*, *C. arcuicornis*, *C. furcatus*, and *M. tenuicornis*.

In the coastal zone, hydrodynamic processes, such as cyclonic and anticyclonic eddies, may generate small upwellings, which may in turn lead to high concentrations of chlorophyll in the epipelagic layer (Millot *et al.*, 1997. Here, the coastal MAW community (Group 2; *A. clausi*, *E. acutifrons*, *O. nana*, and *T. stylifera*), grazing heavily on diatoms, was in a period of active reproduction (Thibault *et al.*, 1994). These populations demonstrated a substantial increase in abundance.

Off the Algerian coast, Groups 1 and 2 contained copepod species that were originally advected from the Atlantic Ocean into the Algerian Current.

Compared with other regions of the same biogeographical province – the Alboran Sea (Youssara and Gaudy, 2001), Catalan Sea (Calbert *et al.*, 1996), Liguro-Provencal Sea (Boucher *et al.*, 1987), and North Atlantic (Clark *et al.*, 2001) – the zooplankton distribution off the Algerian coast, as evidenced by the present study, has a well-defined spatial structure that closely corresponds to the major hydrographical features in the region. The peaks of abundance were closely associated with productive systems.

References

Anxelu, X. G., Taupier-Letage, I., Vázquez-Domínguez, E., Ruiz, S., Arin, L., Raimbault, P., and Estrada, M. 2001. Physical-biological coupling in the Algerian Basin (SW Mediterranean): influence of mesoscale instabilities on the biomass and production of phytoplankton and bacterioplankton. Deep Sea Research Part I, 48: 405–437.

Boucher, J., Ibanez, F., and Prieur, L. 1987. Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to physical structure in the Ligurian sea front. Journal of Marine Research, 45: 133–174.

Bourdillon, A. 1964. Quelques aspects du problème de l'échantillonage du plancton marin. La Terre et la Vie, 1: 77–93.

Calbert, A., Alcaraz, M., Saiz, E., Estrada, M., and Trepat, I. 1996. Planktonic herbivorous food webs in the Catalan Sea (NW Mediterranean): temporal variability and comparison of indices of phyto-zooplankton coupling based on state variables and rate processes. Journal of Plankton Research, 18: 2379–2347.

Clark, D. R., Aazeem, K. V., and Hays, G. C. 2001. Zooplankton abundance and community structure over 4000 km transect in the north-east Atlantic. Journal of Plankton Research, 23: 365–372.

Frontier, S., and Pichod-Viale, D. 1991. Ecosystèmes, Structure, Fonctionnement, Evolution. Masson, Paris.

García-Olivares, A., Isern-Fontane, J., and García-Ladona, E. 2007. Dispersion of passive tracers and finite-scale Lyapunov exponents in the western Mediterranean Sea. Deep Sea Research Part I, 54: 253–268.

Legendre, L., and Legendre, P. 1984. Ecologie numérique. 2. La structure des données écologique. Masson, Pariset Presse de l'Université de Québec. 260 pp.

Legendre, L., and Legendre, P. (Eds). 1998. Numerical Ecology. Elsevier Science BV, Amsterdam. 853 pp.

Millot, C., Benzohra, M., and Taupier-Letage, I. 1997. Circulation off Algeria inferred from the Mediprod-5 current meters. Deep Sea Research Part I, 44: 1467–1495.

Raimbault, P., Coste, B., Boulahdid, M., and Boudjellal, B. 1993. Origin of high phytoplankton concentration in deep chlorophyll maximum (DCM) in a frontal region of the southwestern Mediterranean Sea (Algerian Current). Deep Sea Research Part I, 40: 791–804.

Razouls, C., de Bovée, F., Kouwenberg, J., and Desreumaux, N. 2005–2008. Diversité et répartition géographique chez les Copépodes planctoniques marins. Available online at http://copepodes.obs-banyuls.fr.

Seridji, R., and Hafferssas, A. 2000. Copepod diversity and community structure in the Algerian basin. Crustaceana, 73: 1–23.

Sournia, A., Brylinski, J. M., Dallot, S., Le Corre, P., Leveau, M., Prieur, L., and Froget, C. 1990. Fronts hydrologiques au large des côtes françaises. Les sites ateliers du programme Frontal. Oceanologica Acta, 13: 413–438.

Thibault, D., Gaudy, R., and Le Fèvre, J. 1994. Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria-Oran Front, western Mediterranean Sea). Significance of pelagic food webs. Journal of Marine Systems, 5: 297–313.

UNESCO. 1968. Zooplankton Sampling. Ed. by D. J. Tranter. Monographs on Oceanic Methodology No. 2, UNESCO, Paris. 174 pp.

Youssara, F., and Gaudy, R. 2001. Variations of zooplankton in the frontal area of the Alboran Sea (Mediterranean Sea). Oceanologica Acta, 24: 361–376.

6. Zooplankton time-series analyses in the English Channel: potential for regional multimetric foodweb indices

Claudia Halsband-Lenk and Elvire Antajan

Introduction

We compare long-term plankton time-series from two coastal stations in the western and eastern English Channel and explore their potential to reveal regional differences in biodiversity patterns and ecosystem function. Through collaborations along the British and French coasts, within the framework of a regional, multidisciplinary ecosystem-based approach (CHannel integrated Approach for marine Resource Management = CHARM), these analyses will provide a resource for the development of a comprehensive plankton inventory of the English Channel (Figure 6.1).

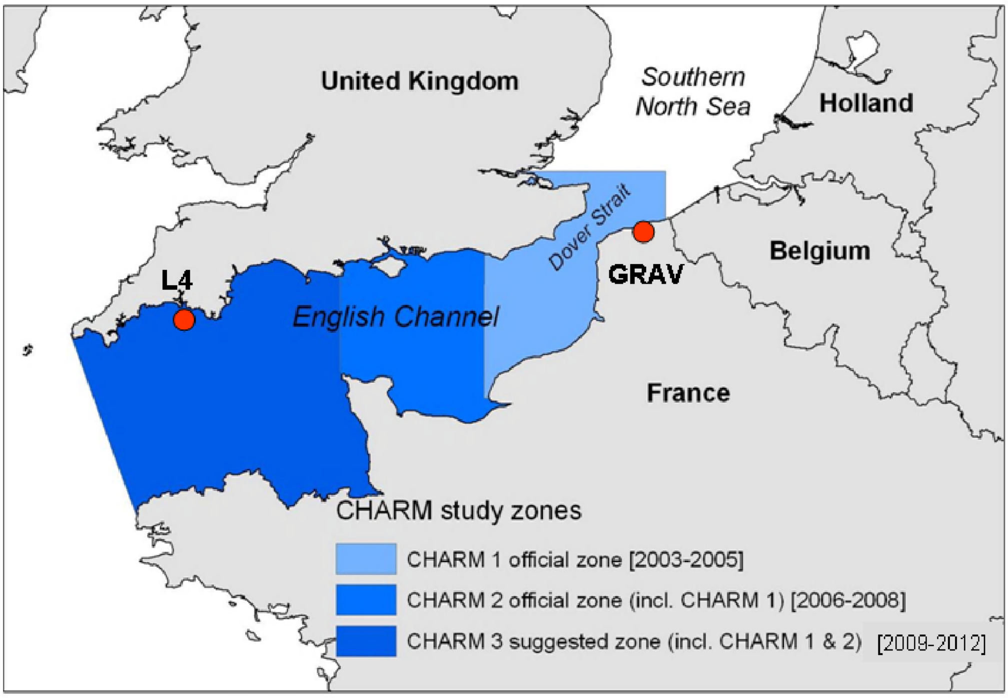

Figure 6.1. Map of the English Channel showing the western (L4) and eastern (Gravelines) sampling stations of the plankton time-series.

At Plymouth Marine Laboratory, a range of physical, chemical, and biological parameters has recently been placed in the context of an integrated Western Channel Observatory[1] (WCO). The WCO, which has a history of more than 100 years of *in situ* sampling and represents both oceanic and coastal environments, will feed data into ecosystem models (e.g. the European Regional Seas Ecosystem Model, ERSEM) to enable the assessment of changes in the marine environment (Southward *et al.*, 2005). One of the stations contributing to this database is L4.

Similarly, the French Research Institute for Exploitation of the Sea (Ifremer) has instituted a monthly time-series of zooplankton species, which has been in operation since 1975, at Gravelines, a coastal station on the French coast of Dover Strait. This survey comes within the framework of a research programme designed to monitor

---

[1] http://www.westernchannelobservatory.org

the effects of nuclear power plants on the environment and living resources, and includes the following parameters, measured on a weekly basis: temperature and salinity, ammonium, nitrate, Chlorophyll *a* (Chl *a*) and phaeopigment concentrations, as well as phytoplankton abundance. Ifremer archives these measurements in the database Quadrige[2], to which zooplankton species abundance will soon be added.

Combining and comparing the datasets from these two stations will allow the development of multimetric foodweb indices at the gateway between the North Sea and the open North Atlantic.

Material and methods

We selected a range of physico-chemical and biological parameters, which had been measured at both study sites (stations L4 and Gravelines), for a preliminary comparison. These parameters include sea surface temperature (SST), surface Chl *a* concentration, diatom abundance, dinoflagellate abundance, and abundance of the small calanoid copepod *Temora longicornis*, a common zooplankton species in both locations. The selected period is 1988–2007, for which temperature and zooplankton data are available from both sites. Chlorophyll and phytoplankton measurements were added in 1992 at L4, whereas the Gravelines series includes chlorophyll data for the entire period, but phytoplankton abundance only since 1997.

SST was measured in a bucket of surface water with a mercury thermometer at L4 and with a digital thermometer at Gravelines. Surface chlorophyll was measured using a Turner fluorometer. Diatom and dinoflagellate abundance was estimated following the Utermölh method (Hasle, 1978) from cell counts under an inverted microscope of samples taken at 10 m depth at L4 and from the surface at Gravelines and preserved in Lugol's solution. *T. longicornis* abundance was quantified from formalin-preserved samples taken at 55 m depth with vertical net tows at L4 and at 7 m depth with oblique net tows at Gravelines. A WP-2 net with a mesh size of 200 µm and an opening area of 0.25 m^2 (UNESCO, 1968) was used in both cases.

Results

The SST cycles were very similar at L4 and Gravelines, with no major differences in the average anomalies (not shown). However, Gravelines temperatures had much greater amplitudes, with more extreme values for both maximal and minimal temperatures than L4. Temperatures there often exceeded 20 °C in summer and usually fell to 5 °C in winter. Summer SSTs at L4 remained well below 20 °C (except in 1997) and winter temperatures were more variable, ranging between 7 and 10 °C (Figure 6.2a).

---

[2] http://www.ifremer.fr/delao/francais/valorisation/quadrige/

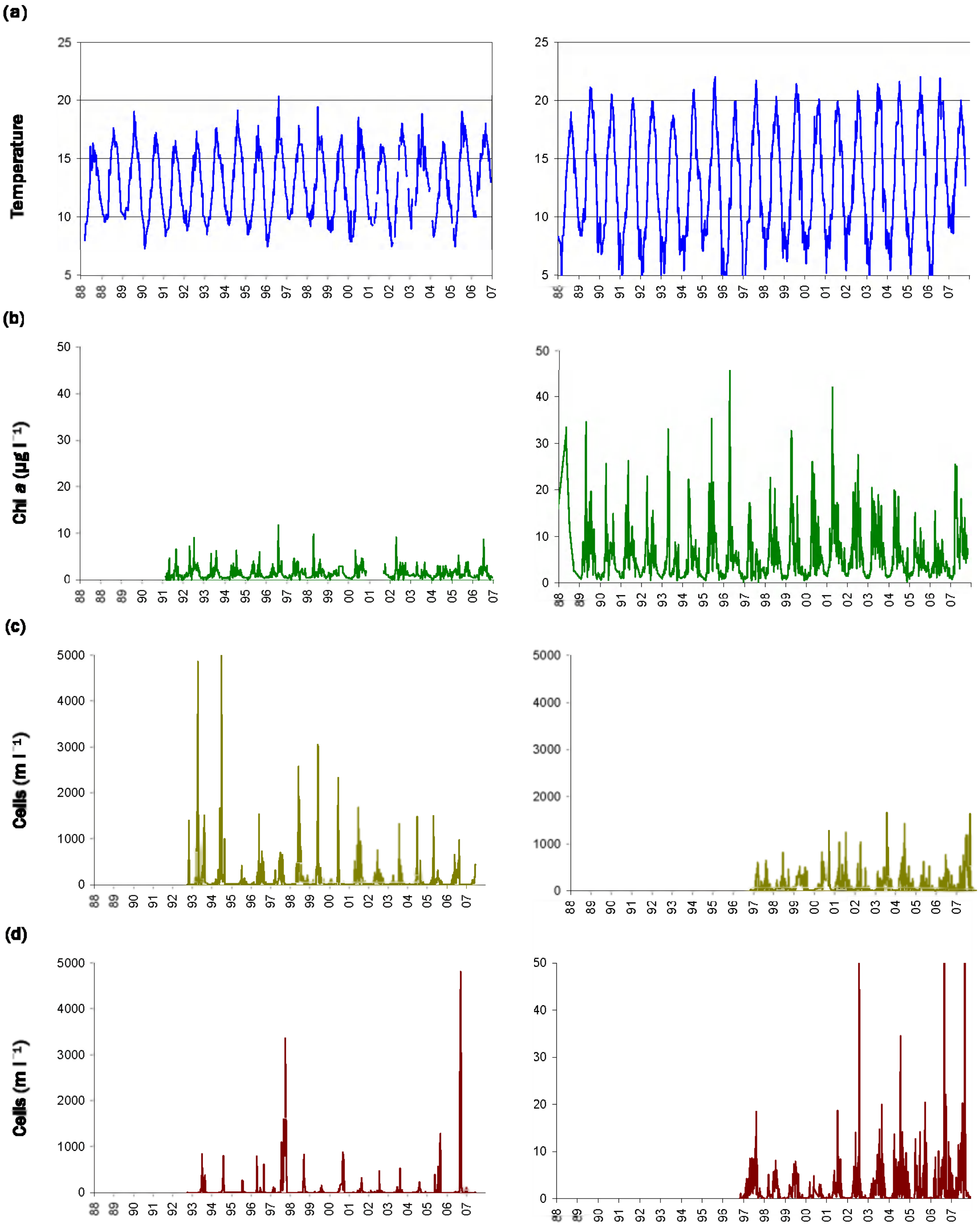

Figure 6.2. Physico-chemical and biological parameters for the period 1988–2007 at stations L4 and Gravelines: (a) temperature, (b) integrated chlorophyll *a*, (c) diatom abundance, and (d) dinoflagellate abundance. Note the difference in ordinate scale in (d).

Chlorophyll concentrations were significantly different at both sites (Figure 6.2b). Although both locations showed a peak in spring, Chl *a* levels at L4 were generally much lower, rarely exceeding 10 µg l^{-1}, whereas maxima at Gravelines ranged from 18 to 47 µg l^{-1}. This result is in striking contrast to the diatom and dinoflagellate abundance (Figure 6.2c and 6.2d). Both phytoplankton groups were more numerous at L4, with dinoflagellate numbers exceeding those at Gravelines by an order of magnitude. In addition, the highest diatom peaks at L4 occurred in spring, whereas some of the major diatom blooms at Gravelines occurred in autumn. Dinoflagellate abundance patterns seemed to follow a more regular seasonal cycle at Gravelines compared with the sudden and singular outbreaks at L4.

Abundance of *T. longicornis* was, on average, similar at both stations, but peaks were more extreme at Gravelines (Figure 6.3). When considering the entire data series at Gravelines, starting in 1978, a shift from higher to lower maximal *Temora* abundance becomes apparent in the mid-1980s. This trend is also reflected in the yearly average anomalies (Figure 6.4), where negative values dominate. Although this general pattern applies to both datasets, there are also some very dissimilar years, e.g. 1989, 1993–1995, and 2000–2002.

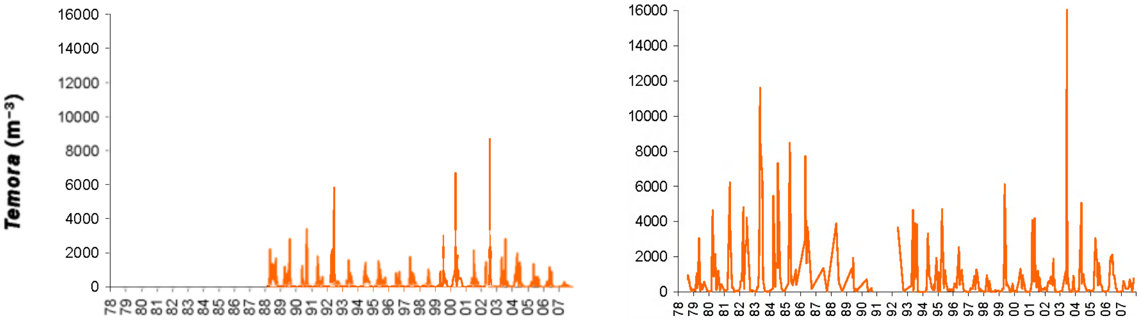

Figure 6.3. Abundance of the calanoid copepod *Temora longicornis* at stations L4 (left) and Gravelines (right) for the period 1978–2007.

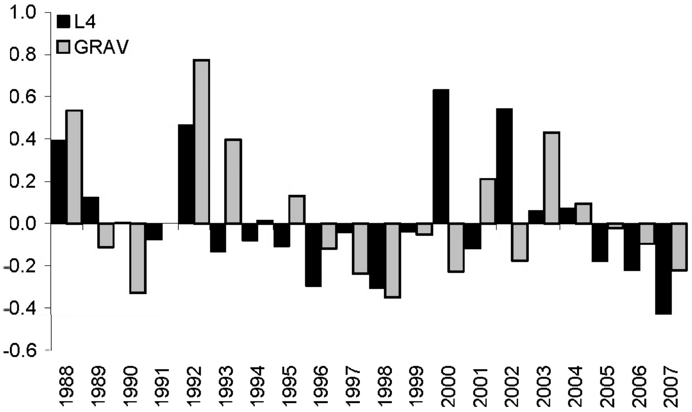

Figure 6.4. Abundance anomalies *of Temora longicornis* at stations L4 and Gravelines for the period 1988–2007.

Discussion

A first comparative analysis of the long-term datasets in the western Channel at L4 and in the eastern Channel at Gravelines reveals both similarities and site-specific differences. The difference in SST patterns clearly confirms that Gravelines is a much more coastal and shallow location that responds readily to fluctuations in atmospheric temperature (Woehrling *et al.*, 2005). This is also reflected in the higher levels of Chl *a*, associated with weak or absent summer stratification.

The striking differences and apparently contradictory results, in terms of phytoplankton concentrations, require further analysis. Although Chl *a* concentrations were generally lower at L4, the concentrations of diatoms, particularly dinoflagellates, were much higher at L4 than at Gravelines. These data need to be validated in order to exclude differences owing to methodology. If the differences are true, smaller flagellates and other pico- and nanophytoplankton may contribute to the high Chl *a* values in the more turbulent waters at Gravelines, rather than large diatoms and dinoflagellates. These latter taxa may have an advantage at L4, where waters are stratified in late spring and summer (Southward *et al.*, 2005). In contrast, the prymnesiophyte *Phaeocystis globosa* can reach very great abundance at Gravelines, to an order of magnitude higher than at L4, reflecting important differences in nutrient supply (not shown).

Nitrate and phosphate levels are significantly elevated at Gravelines and thus represent more eutrophic conditions than at L4. These dissimilarities provide the opportunity to study the impact of environmental factors on phytoplankton composition and community structure along a longitudinal gradient and the respective responses of the next trophic levels. Changes in phytoplankton dominance in diatom–*Phaeocystis* ecosystems are known to affect copepod diet and reproduction (Nejstgaard *et al.*, 2007; Daro *et al.*, 2008) and may explain some site-specific variability of zooplankton abundance.

The important grazer *T. longicornis* exhibited an overall decreasing trend in abundance over the last 20 years in both datasets. Although the patterns at the two stations were generally very similar, they showed signs of being opposite in some years, e.g. in the first half of the 1990s and in 2000 and 2002, indicating different environmental impacts in the eastern and western parts of the Channel. It would be interesting to explore further the differences in environmental pressures that lead to this site-specific variability. The negative trend of *T. longicornis,* a common cold–temperate species with thermal optima between 10 °C and 15 °C (Halsband-Lenk *et al.*, 2002, 2004), supports the hypothesis that the North Sea and the Channel are in a transition towards a warmer system with significant community changes, including impacts on commercially important fish (Beaugrand *et al.*, 2003; Beaugrand, 2009). Integrated trophodynamic models on both sides of the Channel that encompass the microbial and planktonic systems are needed in order to develop regional multimetric foodweb indices (Rodriguez *et al.*, 2000). A comparison of the variability of key species phenologies in both locations and resulting trophic interactions will help to assess how the plankton system in the Channel will respond to environmental change.

Acknowledgements

We acknowledge all contributors to the various datasets made available within the framework of the Western Channel Observatory, as well as the crews of RV "Quest" and RV "Sepia". The Gravelines data were collected within the framework of the research programme IGA (Impact des Grands Amenagements), conducted by Ifremer, and with financial support from the EDF (Electricité de France). Additional temperature records were supplied directly by the Institut Pasteur de Lille, which provided weekly measurements from 1986 onwards.

This work was funded in part by the EU under the INTERREG 4a scheme and ERDF (CHARM phase III project).

References

Beaugrand, G. 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. Deep Sea Research Part II, 56: 656–673.

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. Nature, 426: 661–664.

Daro, M-H., Breton, E., Antajan, E., Gasparini, S., and Rousseau, V. 2008. Do *Phaeocystis* colony blooms affect zooplankton in the Belgian Coastal Zone? *In* Current Status of Eutrophication in the Belgian Coastal Zone, pp. 61–72. Ed. by V. Rousseau, C. Lancelot, and D. Cox. University of Brussels Press, Belgium. 122 pp.

Halsband-Lenk, C., Hirche, H-J., and Carlotti, F. 2002. Temperature effects on reproduction and development of congener copepod populations in the North Sea and the Mediterranean. Journal of Experimental Marine Biology and Ecology, 271: 121–153.

Halsband-Lenk, C., Carlotti, F., and Greve, W. 2004. Life-history strategies of calanoid congeners under two different climate regimes: a comparison. ICES Journal of Marine Science, 61: 709–720.

Hasle, G. R. 1978. The inverted microscope method. *In* Phytoplankton Manual, pp. 88–96. Ed. by A. Sournia. Monographs on Oceanographic Methodology No. 6, UNESCO, Paris. 337 pp.

Nejstgaard, J. C., Tang, K. W., Steinke, M., Dutz, J., Koski, M., Antajan, E., and Long, J. D. 2007. Zooplankton grazing on *Phaeocystis*: a quantitative review and future challenges. Biogeochemistry, 83: 147–172.

Rodriguez, F., Fernández, E., Head, R. N., Harbour, D. S., Bratbak, G., Heldal, M., and Harris, R. P. 2000. Temporal variability of virus, bacteria, phytoplankton and zooplankton in the western English Channel off Plymouth. Journal of the Marine Biological Association of the UK, 80: 575–586.

Southward, A. J., Langmead, O., Hardman-Mountford, N. J., Aiken, J., Boalch, G. T., Dando, P. R., Genner, M. J., *et al.* 2005. Long-term oceanographic and ecological research in the western English Channel. Advances in Marine Biology, 47: 1–105.

UNESCO. 1968. Zooplankton Sampling. Ed. by D. J. Tranter. Monographs on Oceanic Methodology No. 2, UNESCO, Paris. 174 pp.

Woehrling, D., Lefebvre, A., Le Fèvre-Lehoërff, G., and Delesmont, R. 2005. Seasonal and longer term trends in sea temperature along the French North Sea coast, 1975 to 2002. Journal of the Marine Biological Association of the UK, 85: 39–48.

7. Understanding climate-driven change in zooplankton communities: a case study from the North Pacific Subtropical Gyre

Cecelia Hannides (née Sheridan), Michael Landry, and Brian Popp

Introduction

Over the past decade, numerous studies have demonstrated links between large-scale changes in marine zooplankton communities and climate variations. For example, reversals in climate oscillations, such as the Pacific Decadal Oscillation (PDO) and North Atlantic Oscillation (NAO), have coincided with fluctuations in zooplankton biomass and abundance (Fromentin and Planque, 1996; Peterson and Schwing, 2003). Climate-driven warming in northern latitudes has led to the poleward movement of warm-water copepod species (Beaugrand *et al.*, 2002). Earlier warming in temperate marine environments has also driven changes in plankton phenology, with spring plankton blooms occurring earlier than documented in past decades (Edwards and Richardson, 2004).

Although variability in plankton biomass, community structure, and phenology has important implications for marine biogeochemical cycles and the maintenance of fish stocks, it remains difficult to prove the link between climate and marine ecosystem changes. In this paper, we demonstrate a new method, compound-specific isotope analysis (CSIA), which may be used to understand climate impacts on marine zooplankton communities. Specifically, we show that the nitrogen isotope composition ($\delta^{15}N$) of individual amino acids (AAs) from zooplankton species (determined by CSIA) can be used to assess the nitrogen source at the base of the zooplankton foodweb. Thus, by using CSIA and whole-animal stable isotope analyses, we unequivocally demonstrate the impact of climate-driven changes on nutrient delivery in zooplankton. Although we focus on plankton populations in the North Pacific Subtropical Gyre (NPSG), the techniques we describe may be broadly applicable to understanding climate impacts on plankton populations throughout the world's oceans.

Material and methods

Data and samples used in this study were collected at Stn ALOHA (22°26′59″N 158°W) in conjunction with the Hawaii Ocean Time-series (HOT) programme. Zooplankton were sampled from the euphotic zone (0–160 m) with a 200 µm mesh net on monthly cruises from 1994 to 2005 and analysed for biomass, as in Sheridan and Landry (2004). Zooplankton species composition was further analysed in subsamples from each cruise.

Target zooplankton species (*Euchaeta rimana* and *Neocalanus robustior*) were subjected to CSIA, as in Hannides *et al.* (2009a). This resulted in $\delta^{15}N$ values for AAs from each target species, with a standard deviation for triplicate injections of 0.5‰. Whole-animal ("bulk") stable nitrogen isotope compositions were also determined for *E. rimana* and *N. robustior* from each cruise. The bulk analyses were described by Hannides *et al.* (2009a), and standard deviations for animals analysed in duplicate were ≤0.2‰.

Results and discussion

NPSG zooplankton at the HOT Stn ALOHA is dominated by copepods, higher Crustacea (e.g. euphausiids, amphipods, shrimp), and Larvacea. The copepod community is very diverse, comprising at least 179 species. However, as also found in the Mediterranean and many subtropical systems (Siokou-Frangou *et al.*, 1997; Paffenhöfer and Mazzocchi, 2003), the population is consistently dominated in abundance by small calanoid and cyclopoid copepods, i.e. *Clausocalanus paululus, C. furcatus, Oithona plumifera, O. setigera,* and *Mecynocera clausi.*

Over the past decade, the biomass of NPSG zooplankton has increased. This trend was found in small zooplankton that reside in the euphotic zone throughout the day (Sheridan and Landry, 2004), as well as in zooplankton that migrate into the euphotic zone at night (Hannides *et al.*, 2009b). Application of the regime-shift detection method of Rodionov (2006) indicates that the increase may be described as a step function, with higher zooplankton biomass observed in 2000–2005 than in 1994–2000 (Figure 7.1). At the same time, several other ecosystem parameters also increased in a step-like manner at Stn ALOHA. For example, primary production, microalgae pigments, and particle flux increased during 1998–1999 (Figure 1 in Bidigare *et al.*, 2009).

It is difficult, at this moment, to ascribe the observed ecosystem changes to a "regime shift" (abrupt switch between two stable ecosystem states), owing to the short length of the time-series. However, CSIA and whole-animal isotope measurements of the copepods *E. rimana* and *N. robustior* aid our interpretation of the time-series and indicate that enhanced delivery of deep-water nitrate is the most likely driver of the observed increase in ecosystem productivity. First, the trophic position of *E. rimana* and *N. robustior*, calculated using CSIA, or AA $\delta^{15}N$ values (Equation 1 in Hannides *et al.*, 2009a), did not change over a decade at Stn ALOHA (in 1995, 2000, and 2005). Thus, any change in whole-animal $\delta^{15}N$ values over the time-series is solely the result of changes in nitrogen source, not in the animal's trophic position (Hannides *et al.*, 2009a). Second, this bulk $\delta^{15}N$ record demonstrated particularly strong interannual variability during winter at Stn ALOHA (Figure 7.2). In 1998–2001, an enhanced contribution of a high $\delta^{15}N$-value nitrogen source, i.e. deep-water nitrate (Casciotti *et al.*, 2006), was observed, when compared with 1994–1997 or 2002–2005. Thus, our CSIA and bulk isotope analyses indicate that changes in plankton biomass and productivity at Stn ALOHA were driven by change in the nitrogen source at the base of the plankton foodweb.

The foodweb structure and nitrogen source of NPSG plankton changed during 1998–2001, a period of instability in the upper water column (Corno *et al.*, 2007). During this period, cold, salty water overlaid relatively warmer and fresher water within the euphotic zone. Based on our stable isotope analyses, it appears that this destabilization of the upper water mass led to enhanced delivery of nitrate from the main thermocline during winter, the season of deepest mixed-layer depths and most reduced water-column stability at Stn ALOHA. As the change in water-column stability, and therefore foodweb nitrogen source, was probably instigated by the significant changes in Pacific climate observed in 1997–1998 (Corno *et al.*, 2007), our analyses support the hypothesis of strong links between climate forcing, density stratification, nutrient availability, and plankton production in the NPSG. These analyses should be expanded to investigate climate forcing in other regions of the world's oceans where fluctuations in nitrogen source may be linked to change in plankton community structure and function.

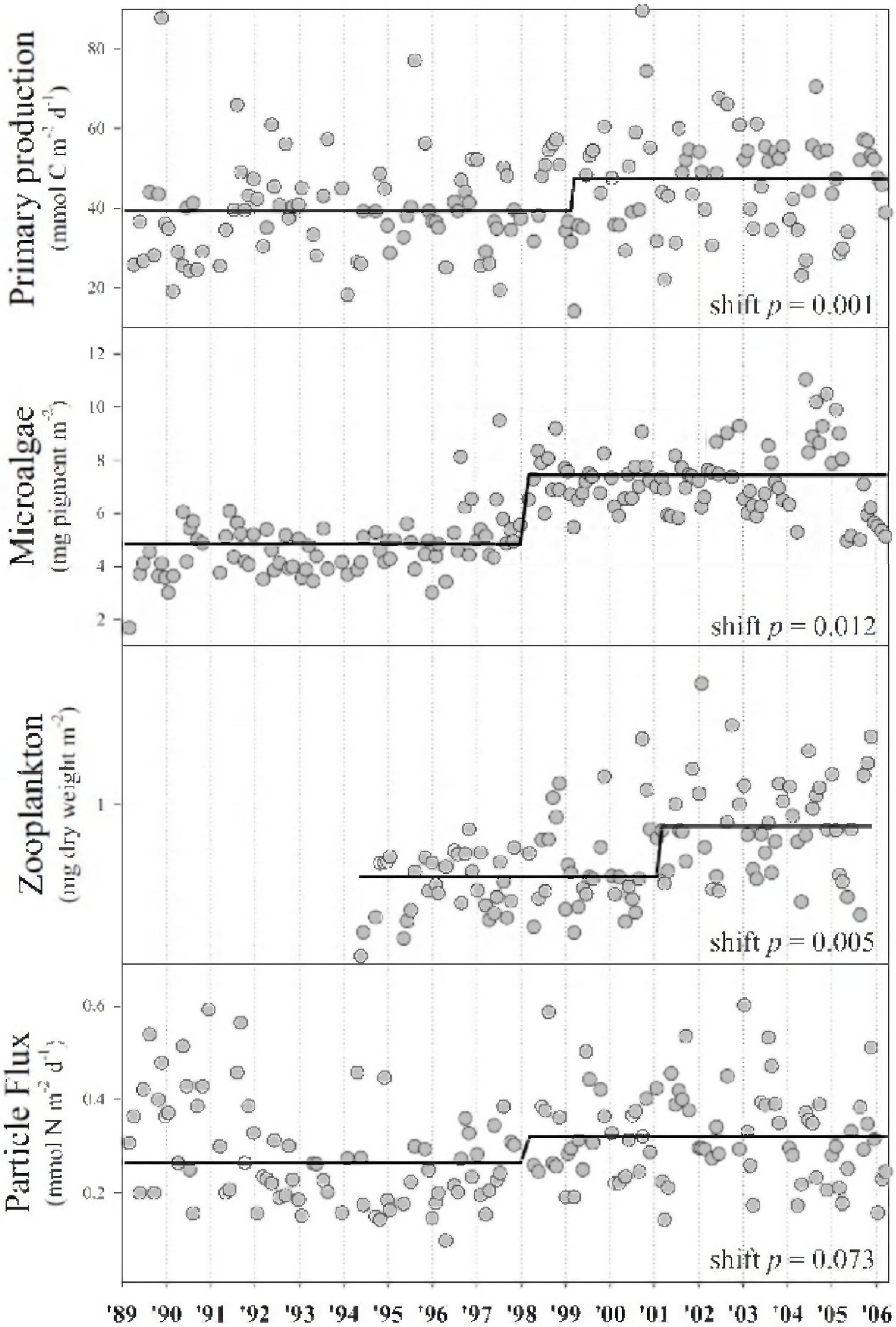

Figure 7.1. Change in the NPSG ecosystem 1989–2006. Ecosystem parameters include 0–200 m net primary production, 0–200 m microalgae pigments (19′-hexanoloxyfucoxanthin), 0–165 m zooplankton (daytime collections), and particulate N flux at 150 m (sediment trap-collected). A significant ecosystem shift with time is denoted by the line for each panel and was performed using $p = 0.2$, $l = 10$, and $h = 1$ or 2, using an IP4 red-noise estimation algorithm to remove red-noise components (Rodionov, 2006). Data on primary production, microalgae, and particle flux from (Bidigare *et al.*, 2009).

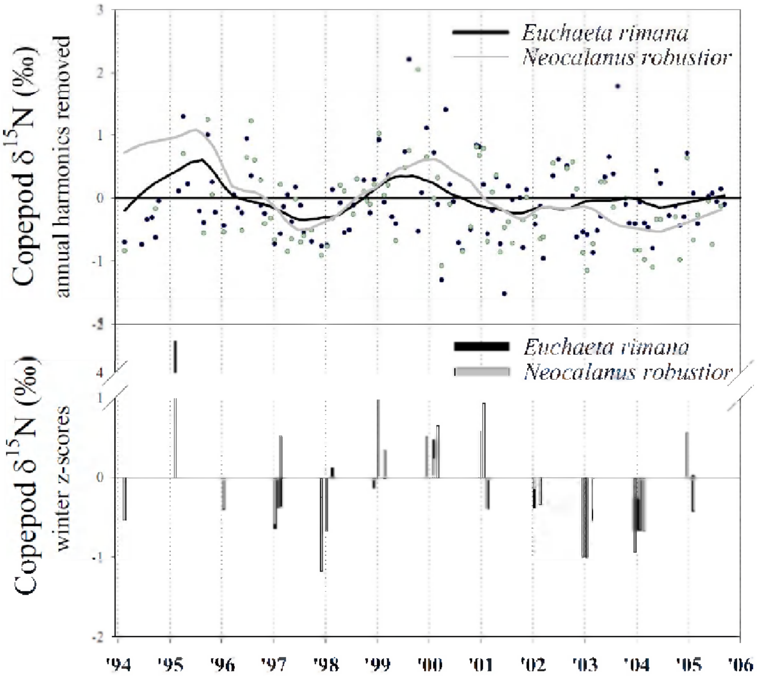

Figure 7.2. (Top panel) Copepod $\delta^{15}N$ values smoothed using LOWESS ($p = 0.25$). The $\delta^{15}N$ values are the residuals following removal of the annual harmonic signal. (Bottom panel) Winter copepod $\delta^{15}N$ normalized to the mean and standard deviation of all winter values (winter z-scores).

References

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692–1694.

Bidigare, R. R., Chai, F., Landry, M. R., Lukas, R., Hannides, C. C. S., Christensen, S., Karl, D. M., *et al.* 2009. Subtropical ocean ecosystem structure changes forced by North Pacific climate variations. Journal of Plankton Research, 31: 1131–1139.

Casciotti, K. L., Dehairs, F., and Trull, T. 2006. Nitrogen and oxygen isotopes in nitrate from contrasting sites in the Pacific. 13th Ocean Sciences Meeting, 20–24 February 2006, Honolulu, Hawaii. Eos, Transactions of the American Geophysical Union, 87, Ocean Sciences Meeting Suppl.: Abstract OS26A-08.

Corno, G., Karl, D. M., Church, M. J., Letelier, R. M., Lukas, R., Bidigare, R. R., and Abbott, M. R. 2007. Impact of climate forcing on ecosystem processes in the North Pacific Subtropical Gyre. Journal of Geophysical Research, 112: C04021, doi: 04010.01029/02006JC003730.

Edwards, M., and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881–884.

Fromentin, J. M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. 2. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 111–118.

Hannides, C. C. S., Popp, B. N., Landry, M. R., and Graham, B. S. 2009a. Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. Limnology and Oceanography, 54: 50–61.

Hannides, C. C. S., Landry, M. R., Benitez-Nelson, C. R., Styles, R. M., Montoya, J. P., and Karl, D. M. 2009b. Export stoichiometry and migrant-mediated flux of phosphorus in the North Pacific Subtropical Gyre. Deep Sea Research Part I, 56: 73–88.

Paffenhöfer, G. A., and Mazzocchi, M. G. 2003. Vertical distribution of subtropical epiplanktonic copepods. Journal of Plankton Research, 25: 1139–1156.

Peterson, W. T., and Schwing, F. B. 2003. A new climate regime in northeast pacific ecosystems. Geophysical Research Letters, 30, doi:10.1029/2003GL017528.

Rodionov, S. 2006. Use of prewhitening in climate regime shift detection. Geophysical Research Letters, 33: L12707, doi:12710.11029/12006GL025904.

Sheridan, C. C., and Landry, M. R. 2004. A 9-year increasing trend in mesozooplankton biomass at the Hawaii Ocean Time-series Station ALOHA. ICES Journal of Marine Science, 61: 457–463.

Siokou-Frangou, I., Christou, E. D., Fragopoulou, N., and Mazzocchi, M. G. 1997. Mesozooplankton distribution from Sicily to Cyprus (eastern Mediterranean). II. Copepod assemblages. Oceanologica Acta, 20: 537–548.

8. Terrestrial run-off and hydrographic influences on trophic relationships and pelagic foodweb structure in the central and southern North Sea

Benjamin Kürten, Suzanne J. Painting, and Ulrich Struck

Introduction

Stable isotope analysis (SIA) of C and N allows the description of foodwebs and organic matter transfer within animal communities (Michener and Schell, 1994) and the tracing of terrestrial organic matter (TOM) in estuarine environments (Darnaude, 2005). The combined evaluation of phytoplankton pigments and $\delta^{13}C$ of phospholipid-derived fatty acid (PLFA) profiles has only recently been established to characterize the sources, composition, and fate of organic matter from primary producers to consumers (Boschker and Middelburg, 2002; Boschker *et al.*, 2005). The underlying principle is that the proportional abundance of some pigments (Jeffrey *et al.*, 1997) and PLFA (Dalsgaard *et al.*, 2003) parallels taxonomic traits.

Large amounts of nutrients enter the southern North Sea via the rivers Thames, Humber, and Wash, with pronounced influx of TOM in winter as a result of high riverine run-off and low biological uptake (Nedwell *et al.*, 2002; Weston *et al.*, 2008). The aim of this contribution is to present current work about the effects of terrestrial run-off on seston composition and on the key species of coastal and offshore plankton communities of the southern and central North Sea, such as *Calanus* and *Sagitta*.

Material and methods

Seven research cruises were conducted with RV "Cefas Endeavour", visiting three hydrodynamically distinct locations in the southern and central North Sea: the Sean Gas field (SB, 53°9′N 2°48′E), the Oyster Ground (OG, 54°24′N 4°2′E), and a station on the northern slope of the Dogger Bank (DB, 55°41′N 2°17′E). Cruise dates were 20–27 February, 17–25 April, 16–23 May, 13–20 September, 26 October–3 November in 2007, and 16–22 January and 21–30 April in 2008.

Seawater was collected from the surface mixed layer (SML) at night, screened over 60 µm sieves, and immediately filtered over precombusted, preweighed GF/F glassfibre filters. Zooplankton sampling was carried out at night with vertical tows of ringnets (1 m diameter, 200 µm mesh), and double-oblique net tows (10–20 min, 1 knot, 2 m diameter, 1000 µm mesh). Extraction and measurement of phytoplankton pigments via high-performance liquid chromatography (HPLC) followed the protocol of Dijkman and Kromkamp (2006). Adult female calanoid copepods or specimens of *Sagitta* (Chaetognatha), regardless of gender, were prepared for bulk SIA and PLFA analysis. Particulate organic matter (POM) and zooplankton were analysed for bulk C and N isotope abundance (ThermoElectron Delta V, Museum of Natural History Berlin). Lipid extraction and measurement by gas-chromatograph, combustion-interface, isotope-ratio, mass spectrometry (GC-c-IRMS) followed the method of Boschker *et al.* (1999). Isotope ratios are expressed in conventional δ notation (del) as a measure of heavy to light isotope following

$$\delta X\ (‰) = [(R_{sample}/R_{standard})-1]\ 10^3,$$

where δX is ^{13}C or ^{15}N, and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio.

Results

All stations, with variable magnitude, displayed a pronounced spring maximum, as indicated by Chl *a* measurements via HPLC (data not shown). A strong correlation between the carotenoid fucoxanthin and Chl *a* (Pearson, 0.978, $p < .001$, $n = 95$), supported the notion that Bacillariophyceae were responsible for most of the primary production (proxy Chl *a*). At the year-round well-mixed SB site, the PLFA content of seston was evenly distributed among the PLFA categories throughout the year, indicating a constantly lower nutritious quality. Elevated polyunsaturated fatty acid (PUFA) concentrations of POM were recorded during the spring bloom in April and May at the DB and OG sites, respectively, and in the zooplankter *Sagitta* (data not shown).

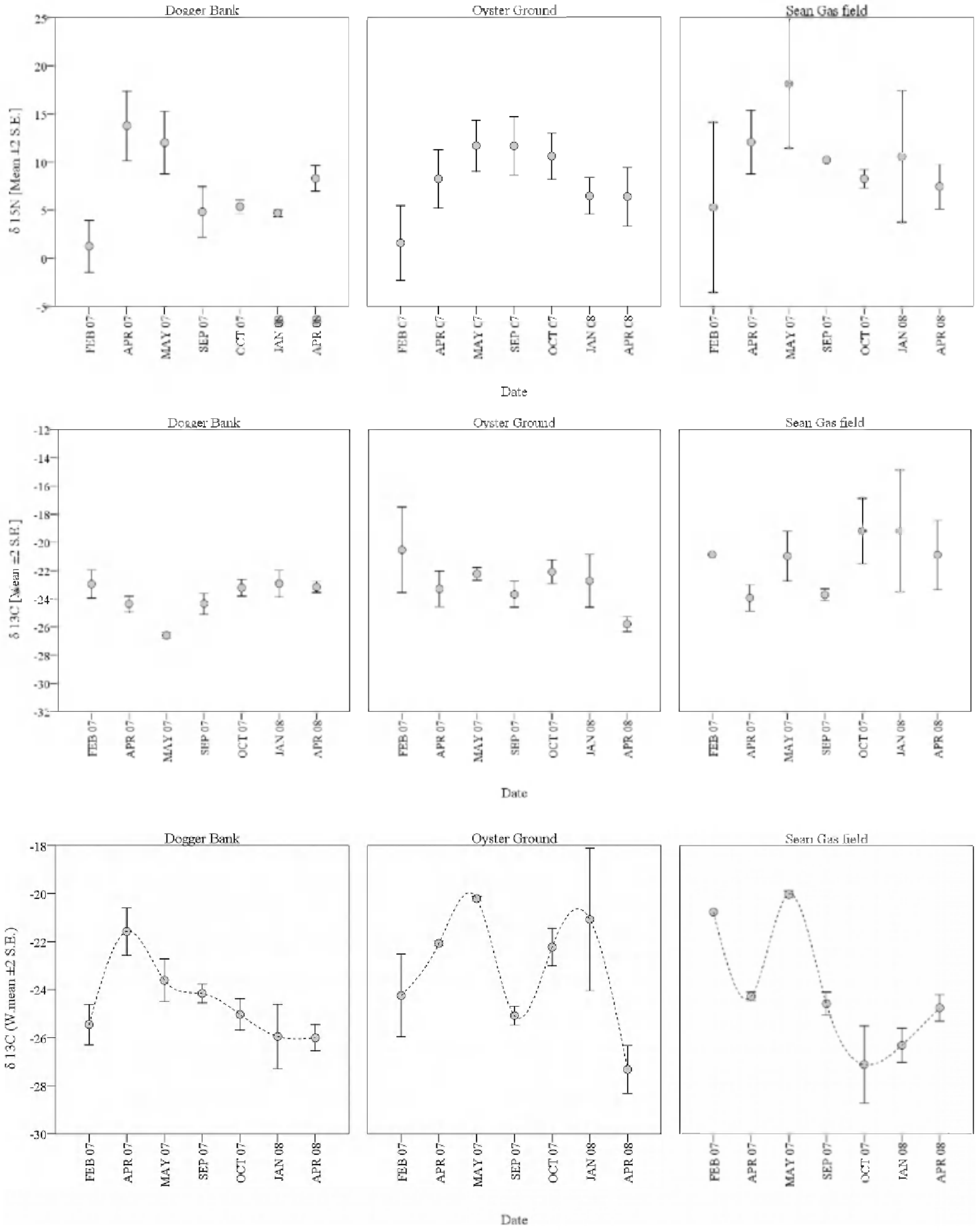

Figure 8.1. Seasonal and spatial variation of bulk $\delta^{15}N$ (top panel) and $\delta^{13}C$ (middle panel), and concentration-weighted mean PLFA $\delta^{13}C$ values in 0.7–60 µm particulate organic matter (POM; most n = 3; bottom panel) collected in the North Sea from February 2007 to April 2008 at the site north of the Dogger Bank, at the Oyster Ground, and at the Sean Gas field in the southern Bight. The sample subset for bulk $\delta^{13}C$ stable isotope analysis (SIA) was fumed with HCl (24 h) under light vacuum to remove inorganic carbonates prior to SIA.

The abundance of bulk $\delta^{13}C$ and $\delta^{15}N$, and $\delta^{13}C$ of PLFA (concentration-weighted mean of PLFA $\delta^{13}C$) varied in the 0.7–60 µm seston fraction across locations and with season (Figure 8.1). POM $\delta^{13}C$ and $\delta^{13}C$ PLFA ratios appear to be decoupled, despite their high variability at the SB site. At the SB and DB sites, increased $\delta^{15}N$ values were recorded in spring, whereas at the OG site, maximal $\delta^{15}N$ values were measured during stratified conditions. Maximal $\delta^{15}N$ values of mesozooplankton were mainly recorded in late autumn and in winter and did not coincide with maximal $\delta^{15}N$ POM values in spring (Figure 8.2). The chaetognath *Sagitta* has been commonly recognized as a predator of mesozooplankton, but the offset of the trophic level indicator $\delta^{15}N$ of *Calanus* sp. relative to POM and to *Sagitta* indicates different food sources. However, the high PUFA content of *Sagitta* was remarkable.

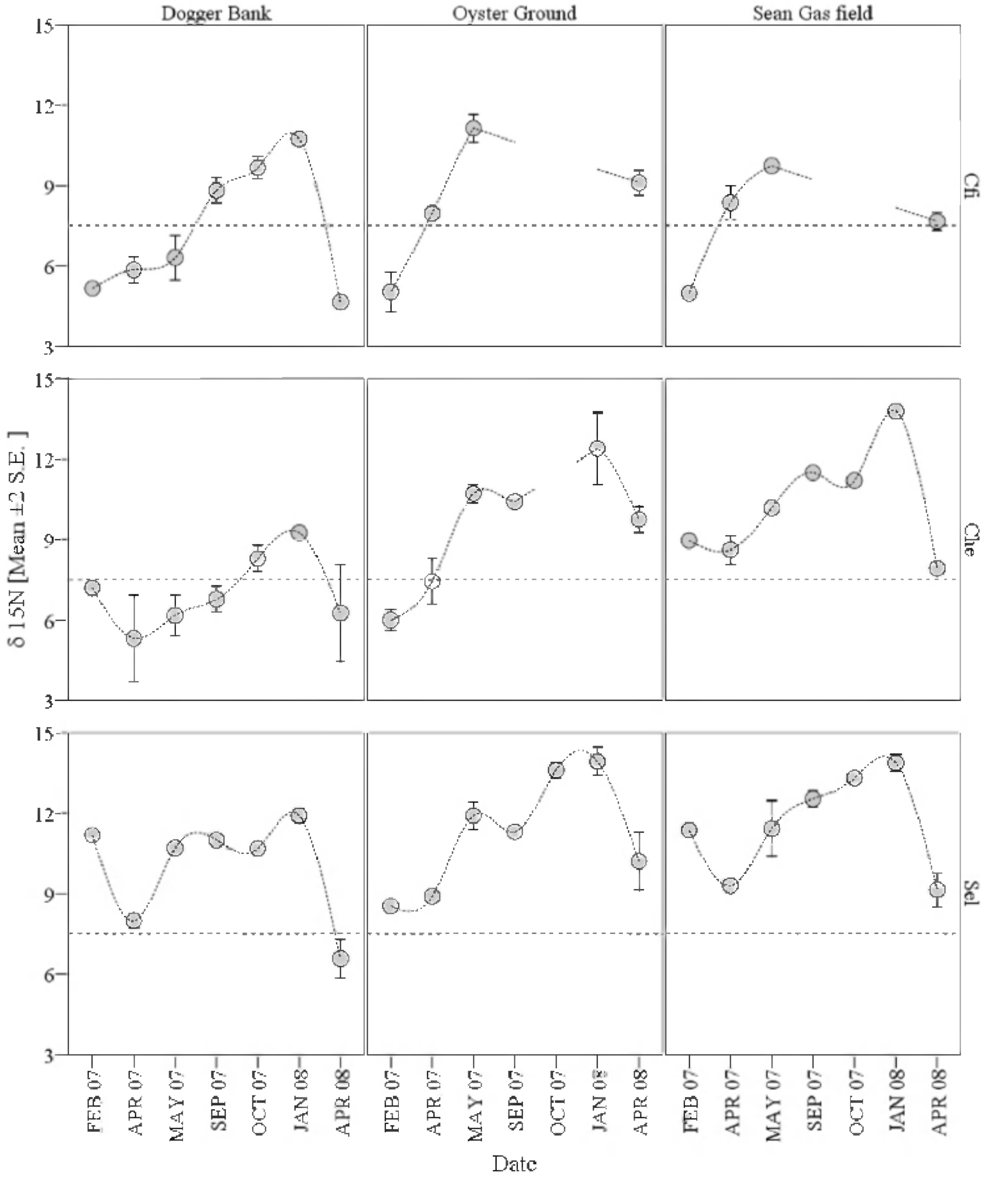

Figure 8.2. Seasonal and spatial variation of $\delta^{15}N$ values of zooplankton collected from February 2007 to April 2008 in the North Sea at the site north of the Dogger Bank, at the Oyster Ground, and at the Sean Gas field in the southern Bight. Between 5 and 30 specimens per species and sample were picked, briefly rinsed in Ultra pure water, packed in acetone-rinsed Sn capsules, oven-dried (60°C, 24 h), and stored in desiccating cabinets prior to bulk stable isotope analysis (Cfi = *Calanus finmarchicus*; Che = *C. helgolandicus*; Sel = *Sagitta elegans*; most n = 3; dashed line at 7.5‰ = visual reference point; dotted lines = putative interpolations between data points).

Discussion

Particulate organic matter (POM) is commonly used to represent seston, which consists of all particles suspended in the water column and is composed of a complex mixture of organic and inorganic material, including bacterio-, phyto-, and microzooplankton, detritus of marine or terrestrial origin, faecal pellets, or resuspended sediment. Differences in isotopic signatures between microphytoplankton and other components affect the concept that SML seston isotope ratios obtained in coastal regions can be integrated as a baseline in foodweb reconstructions without difficulty, as recently demonstrated for the Gulf of Lions (Harmelin-Vivien *et al.*, 2008). The decoupling of zooplankton isotopic composition from POM isotope abundance in the shallow southern North Sea (this study) corroborates these results. Furthermore, the results from the central North Sea (sampling station DB) point towards similar conclusions for offshore environments.

Chaetognatha and *Calanus helgolandicus* are known to feed on eggs, nauplii, and copepodites (Feigenbaum and Maris, 1984; Bonnet *et al.*, 2004); thus, comparable $\delta^{15}N$ values may indicate similar food sources. At the SB and OG sites, elevated $\delta^{15}N$ of seston in general, and elevated $\delta^{15}N$ in *C. helgolandicus* in particular, suggested a higher degree of heterotrophism utilizing (indirectly) TOM, transported mainly via the East Anglia plume as particulates across the southern North Sea (Weston *et al.*, 2004).

Although phytoplankton PLFA are usually depleted, compared with total biomass (Schouten *et al.*, 1998), the opposite trend of bulk $\delta^{13}C$, compared with the weighted mean of $\delta^{13}C$ PLFA ratios, suggests that only parts of the seston fraction are accessed by calanoid copepods, such as *Calanus* spp.

Bacillariophyceae typically contain C, with $\delta^{13}C$ values between −15‰ and −19‰ (Fry and Wainwright, 1991). As PLFA abundance of PUFA increased during spring, parallel with increasing Chl *a* and accessory pigment fucoxanthin concentrations, we consider the increase in PLFA $\delta^{13}C$ to be a result of Bacillariophyceae-derived primary production. After prolonged periods of stratified conditions, usually dominated by flagellate-based foodwebs (St John and Lund, 1996), the accumulation of Dinophyceae and bacterial PLFA in *C. helgolandicus* (data not shown), together with elevated $\delta^{15}N$, may provide further evidence of multivorous foodwebs at the OG and SB sites, including the microbial foodweb (Painting *et al.*, pers. comm.).

Acknowledgements

This is a contribution to the EURopean network of excellence for OCean Ecosystems ANalysiS (EUR-OCEANS, project WP6-SYSNS-1098). The fieldwork was co-funded by Defra, contract ME3205, Marine Ecosystem Connections. The authors thank the master and crew of RV "Cefas Endeavour", and several cruise participants for their support. We also thank M. Houtekamer and P. van Rijswijk for analytical assistance, and J. Middelburg, C. Heip, and N. Polunin for guidance and supervision.

References

Bonnet, D., Titelman, J., and Harris, R. P. 2004. *Calanus* the cannibal. Journal of Plankton Research, 26: 937–948.

Boschker, H. T. S., and Middelburg, J. J. 2002. Stable isotopes and biomarkers in microbial ecology. FEMS Microbiology Ecology, 40: 85–95.

Boschker, H. T. S., de Brouwer, J. F. C., and Cappenberg, T. E. 1999. The contribution of macrophyte-derived organic matter to microbial biomass in salt-marsh sediments: stable isotope analysis of microbial biomarkers. Limnology and Oceanography, 44: 309–319.

Boschker, H. T. S., Kromkamp, J. C., and Middelburg, J. J. 2005. Biomarker and carbon isotopic constraints on bacterial and algal community structure and functioning in a turbid, tidal estuary. Limnology and Oceanography, 50: 70–80.

Dalsgaard, J., St John, M., Kattner, G., Müller-Navarra, D. C., and Hagen, W. 2003. Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, 46: 225–340.

Darnaude, A. M. 2005. Fish ecology and terrestrial carbon use in coastal areas: implications for marine fish production. Journal of Animal Ecology, 74: 864–876.

Dijkman, N. A., and Kromkamp, J. C. 2006. Phospholipid-derived fatty acids as chemotaxonomic markers for phytoplankton: application for inferring phytoplankton composition. Marine Ecology Progress Series, 324: 113–125.

Feigenbaum, D. L., and Maris, R. C. 1984. Feeding in Chaetognatha. Oceanography and Marine Biology Annual Review, 22: 343–392.

Fry, B., and Wainwright, S. C. 1991. Diatom sources of ^{13}C-rich carbon in marine foodwebs. Marine Ecology Progress Series, 76: 149–157.

Harmelin-Vivien, M. L., Loizeau, V., Mellon, C., Beker, B., Arlhac, D., Bodigel, X., Ferraton, F., *et al.* 2008. Comparison of C and N stable isotope ratios between surface particulate organic matter and microphytobenthos in the Gulf of Lions (NW Mediterranean). Continental Shelf Research, 28: 1911–1919.

Jeffrey, S. W., Mantoura, R. F. C., and Wright, S. W. (Eds). 1997. Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. Monographs on Oceanographic Methodology No. 10, UNESCO, Paris. 688 pp.

Michener, R. H., and Schell, D. M. 1994. Stable isotope ratios as tracers in marine aquatic food webs. *In* Stable Isotopes in Ecology and Environmental Science, pp. 138–157. Ed. by K. Lajtha and R. H. Michener. Blackwell Scientific Publications, London.

Nedwell, D. B., Dong, L. F., Sage, A., and Underwood, G. J. C. 2002. Variations of the nutrient loads to the mainland UK estuaries: correlation with catchment areas, urbanization and coastal eutrophication. Estuarine, Coastal and Shelf Science, 54: 951–970.

Schouten, S., Klein Breteler, W. C. M., Blokker, P., Schogt, N., Rijpstra, W. I. C., Grice, K., Baas, M., *et al.* 1998. Biosynthetic effects on the stable carbon isotopic composition of algal lipids: Implications for deciphering the carbon isotopic biomarker record. Geochimica et Cosmochimica Acta, 62: 1397–1406.

St John, M., and Lund, T. 1996. Lipid biomarkers: linking the utilization of frontal plankton biomass to enhanced conditions of juvenile North Sea cod. Marine Ecology Progress Series, 131: 75–85.

Weston, K., Jackals, T. D., Fernand, L., and Parker, E. R. 2004. Nitrogen cycling in the southern North Sea: consequences for total nitrogen transport. Estuarine, Coastal and Shelf Science, 59: 559–573.

Weston, K., Greenwood, N., Fernand, L., Pearce, D. J., and Sivyer, D. B. 2008. Environmental controls on phytoplankton community composition in the Thames plume. UK Journal of Sea Research, 60: 246–254.

9. Recovery of Black Sea ecosystem as indicated by the distribution of gelatinous organisms in the southern region[3]

Erhan Mutlu

Introduction

The Black Sea has been chronically exposed to a succession of stressors, thereby characterizing it as a changing but quickly responding ecosystem. The stressors include an increase in nutrient inputs and eutrophication (Weilguni and Humpesch, 1999; Kroiss *et al.*, 2006), invasive gelatinous zooplankton (*Mnemiopsis leidyi* and *Beroe ovata*), overfishing (Daskalov, 2002; Gucu, 2002; Knowler, 2007), and a reduction of nutrient inputs.

In a preliminary study in 1991–1993, Mutlu *et al.* (1994) found that the average biomasses of *Aurelia aurita, M. leidyi,* and *Pleurobrachia pileus* in the Black Sea were approximately the same (200 g m^{-2}). Mutlu (1999, 2001) and Mutlu and Bingel (1999) also studied the abundance, morphometry, and size distribution of these species and their respective zooplankton food sources in the southern Black Sea during 1991–1995, and Kideys and Romanova (2001) studied their spatial and temporal distributions from seven cruises during 1996 to 1999.

Although the northern Black Sea has been well studied (Weisse and Gomoiu, 2000; Weisse *et al.*, 2002; Finenko *et al.*, 2003; Lebedeva *et al.*, 2003; Shiganova *et al.*, 2003), no extensive study on the distribution and size structure of populations of gelatinous organisms in the southern Black Sea has been carried out since the introduction of *B. ovata* in 1997.

The aim of the present investigation was to determine the densities and size structure of populations of *A. aurita, M. leidyi, P. pileus,* and *B. ovata* in the southern Black Sea during June and October 2006, and May 2007, following the introduction of *B. ovata,* and to compare the results with data from the northern Black Sea. In addition, we aimed to highlight the interactions between the zooplankton biomasses and catches of dominant pelagic fish in the Black Sea since 1987 and to compare different methods of biomass measurements of gelatinous organisms.

Material and methods

The spatial distribution, abundance, and biomass of gelatinous zooplankton (*A. aurita, M. leidyi, P. pileus,* and *B. ovata*) in the southern Black Sea were determined during three 18- to 21-day cruises aboard the RV "Bilim" of the Institute of Marine Sciences-METU, Turkey. Ctenophores and jellyfish were collected with a Hansen net (0.7 m diameter, 300 μm mesh) during three cruises in June and October 2006 and May 2007, respectively, from the anoxic zone to the surface off the shelf and from 2 m above the seabed to the surface on the shelf (Figure 9.1).

---

[3] This extended abstract is based on a paper published in Marine Biology (Mutlu, 2009).

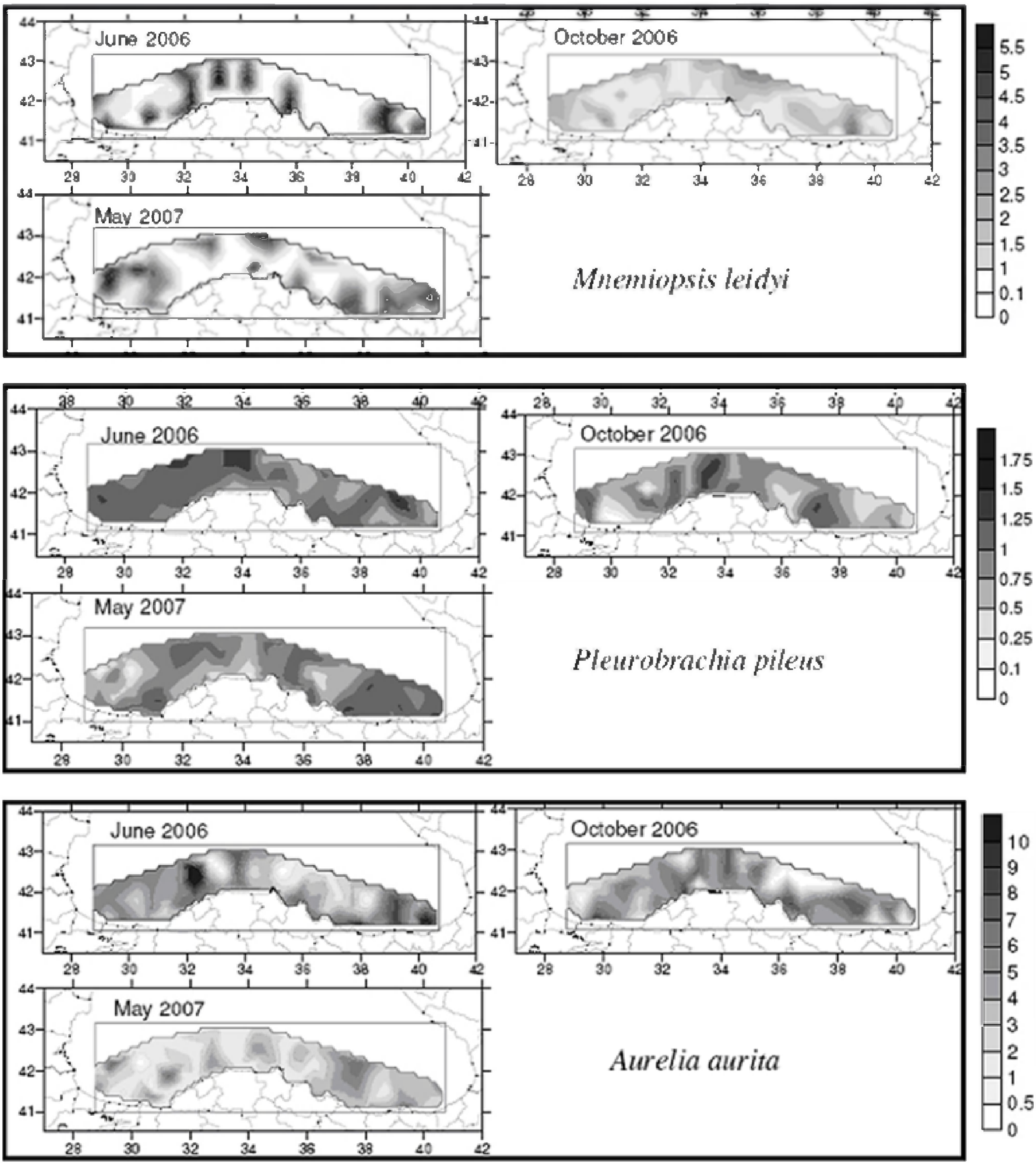

Figure 9.1. Study area and averaged body size (cm) distribution of the gelatinous organisms in the southern Black Sea.

On board, the gelatinous organisms were separated from the other mesozooplankton using a 2 mm mesh sieve. In June 2006, at each station, individuals of each species were frozen in a nylon bag for comparison of *in situ* weights, measured on board using a mechanical hand balance (h-balance), and *ex situ* weights, measured in the laboratory using an electronic balance (e-balance, for comparison). Length–weight (LW) relationships for each species were also tested in order to determine any significant differences among different regions in the Black Sea.

On all cruises, specimens of each ctenophore species were grouped into three size classes, according to their aboral length (AL). These classes corresponded to the larval, transitional, and lobate stages, although the respective sizes differed for each species. *A. aurita* was grouped into four size classes according to disc diameter. The size classes were as follows: *M. leidyi:* <10 mm, 10–30 mm, and >30 mm (Mutlu, 1999); *P. pileus:* <10 mm, 10–20 mm, and >20 mm (Mutlu and Bingel, 1999); *B. ovata:* <10 mm, 10–50 mm, and >50 mm (Finenko *et al.*, 2003); *A. aurita*: <10 mm, 10–50 mm, 50–100 mm, and >100 mm (Mutlu, 2001).

In order to test the differences between the intercept and slopes of the LW relationships, the series of $\log_{10}$-transformed lengths and $\log_{10}$-transformed weights were subjected to multicomparison analyses of covariance (ANOCOVA; version 7.0, The MathWorks, Inc.). The biomass estimates were also tested for the dependence of the LW relationships on size structure using a "paired *t*-test".

In addition, annual catches of the four dominant pelagic fish species (anchovy, *Engraulis encrasicolus*; horse mackerel, *Trachurus mediterraneus*; Atlantic bonito, *Sarda sarda*; and bluefish, *Pomatomus saltatrix*) were re-evaluated in relation to monthly zooplankton biomass in the Black Sea (Mutlu, 2009).

Results

In June 2006, three different methods (h-balance, e-balance, and LW relationships) were used to cross calibrate the biomass estimations for *M. leidyi*, *P. pileus*, and *A. aurita* and to standardize our estimates to date. No significant differences were found between the biomass estimates from the h- and e-balances for each species at $p < 0.05$ (paired *t*-test). Differences between the estimates based on the LW relationships were significantly variable, depending on the length distribution of each species during October 2006 and May 2007 (paired *t*-test, $p < 0.05$). Multicomparison analyses demonstrated that, overall, both the slopes and intercepts of the LW relationships were significantly different (at $p < 0.05$) for each species, both among the different seas and within the Black Sea. Therefore, biomass estimates by LWs were highly variable and dependent upon the size composition of the species in space and time.

Mnemiopsis leidyi and *B. ovata* were the least numerous (1.7–7 individuals m^{-2} and 1.4 individuals m^{-2}, respectively), whereas *P. pileus* was the most numerous (139–274 individuals m^{-2}). Numbers of *A. aurita* ranged from 6 to 24 individuals m^{-2}. Despite the differences in abundance, the average biomass exhibited a similar range for all ctenophores (~8.9 g m^{-2} for *B. ovata*; 26–52 g m^{-2} for *M. leidyi*; 35–88 g m^{-2} for *P. pileus*) and 80–400 g m^{-2} for *A. aurita*. The total average biomass of all four species in the southern Black Sea amounted to 537 g m^{-2} in June 2006, 150 g m^{-2} in October 2006, and 417 g m^{-2} in May 2007. Abundance and biomass were calculated in units of individuals m^{-2} and g m^{-2}, respectively.

The lengths of *B. ovata* ranged from 23 to 65 mm, with an average length of 35 mm in October 2006. Mean length was significantly greater in the southwest (40 mm ± 11.3) than in the southeast (29 mm ± 5.3), at $p < 0.05$ (*U*-test). Specimens with lengths of 10–50 mm formed 85% of the population, while larger individuals (>50 mm) accounted for ca. 15%; no smaller individuals (<10 mm) were found.

The mean AL of *M. leidyi* was 48 mm in June 2006, 210 mm in October 2006, and 390 mm in May 2007 (Figure 9.1). Specimens with an AL >30 mm dominated the population in June 2006 (90%) and May 2007 (70%). Transitional stage individuals (10–30 mm) composed 50% of the population in October 2006.

Pleurobrachia pileus with lengths >20 mm accounted for between 40% and 60% of the population in 2006–2007. Larval stage individuals (<10 mm) contributed greatly in October 2006, when small specimens were widely distributed in the western Black Sea (Figure 9.1).

The largest individual specimens of *A. aurita* had disc diameters of 230 mm (in June 2006 and May 2007) and 160 mm (in October 2006). Individuals with a disc diameter of 10–50 mm dominated the population in May 2007. Larger specimens accounted for more than 70% of the population in both June and October 2006 (Figure 9.1).

The anchovy seems to be affected mainly by the presence of a large biomass of *M. leidyi* over a long period, e.g. 1989–1991 and 1995–1996. Catches of medium-sized pelagic fish (Atlantic bonito) fluctuated inversely with catches of anchovy during 1988–2006 and were more marked in 2005, when the Atlantic bonito was abundantly present for the first time in three or four decades.

Discussion

The correlations between the biomasses obtained using the h-balance and the e-balance were lower for *P. pileus* than for both *A. aurita* and *M. leidyi,* and the slopes were far from the ideal of 1. Biomass measurements of gelatinous organisms from the nets and methods have been discussed extensively by other authors (Niermann *et al.*, 1995; Weisse and Gomoiu, 2000; Kideys and Romanova, 2001; Weisse *et al.*, 2002). Spatio-temporal variations in relation to the length and wet weight of the gelatinous organisms could introduce a bias in the increased estimates of biomass of the catch-at-length, owing to a discrepancy in the slopes and intercepts. Katsanevakis *et al.* (2007) emphasized that the simple linear models assume a continuous change in allometry, and discontinuity at breakpoints should be considered in allometric growth studies.

The spatio-temporal horizontal distribution of the gelatinous organisms was found to be related to the general circulation of currents (rim currents and anticyclonic eddies) and sea surface temperature and salinity, as stated in 1991–1995 (Mutlu *et al.*, 1994; Mutlu, 1999, 2001; Mutlu and Bingel, 1999). In the southern Black Sea, the densities of the ctenophores were considerably less in 2006–2007 than those in 1991–1995 (Mutlu *et al.*, 1994; Mutlu, 1999, 2001; Mutlu and Bingel, 1999) and 1996–1999 (Kideys and Romanova, 2001). Individual mean biomass of *M. leidyi* did not exceed 5 g m^{-2} during 1991–1995 (Mutlu, 1999), except in June 1991 (16 g m^{-2}). The average abundance of *M. leidyi* was 7 individuals m^{-2}, with an average biomass of 27 g m^{-2} composed of smaller specimens (individual mean biomass 3.5 g m^{-2}), in October 2006.

The size structure of the *B. ovata* population in October 2006 was very similar to the findings of Finenko *et al.* (2003). These authors also demonstrated that juvenile *B. ovata* (<10 mm) was the only size class in September 2000 and comprised 90% of the population in August 2001. Overall, mean ALs of *M. leidyi* were greater in 2006–2007 than in 1992–1995 (Mutlu, 1999). In contrast to the earlier results (Mutlu, 1999), specimens >30 mm dominated (>70% cf. <13%) the spring and summer populations.

Pleurobrachia pileus with lengths <10 mm formed <40% of the population in the period, prior to the introduction of *B. ovata* (Mutlu and Bingel, 1999), but varied between 40% and 60% after the introduction of *B. ovata,* which feeds on other ctenophores.

The mean disc diameter of *A. aurita* ranged from 80 to 105 mm during 1992–1995 (Mutlu, 2001), but decreased to <80 mm in 2006–2007. The diameters of the largest individuals ranged from 177 to 280 mm in winter, 305 to 430 mm in spring, and 214 to 230 mm in summer in the earlier period (Mutlu, 2001), but varied between 160 mm (autumn) and 230 mm (spring/summer) in the later period.

Anchovy catches were reduced by a factor of 3.5 in 1989 and 2005, and by a factor of 1.5 in 1996. The reductions in 1989 and 1996 were correlated with the high, long-term standing biomass of *M. leidyi*, while the 2005 reduction coincided with increased catches of Atlantic bonito. Previously, these reductions have also been attributed to eutrophication, pollution, alien species introductions, and climatic variations (Vinogradov *et al*., 1989; Humborg *et al*., 1997; Weilguni and Humpesch, 1999; Kideys, 2002; Shiganova *et al*., 2003; Oguz *et al*., 2006), as well as overfishing (Daskalov, 2002; Gucu, 2002; Oguz and Gilbert, 2007). The present work demonstrates that the introduction of *B. ovata* into the southern Black Sea has considerably reduced the numbers and biomass of *M. leidyi*.

In turn, it was the long-term high biomass of *M. leidyi* and predation on anchovy by bonito, as seen in 2005, that led to the collapse of the anchovy fisheries, irrespective of climate effects and the different fishing seasons of these two species in the Black Sea.

Acknowledgements

This work was funded by the Scientific and Technical Research Council of Turkey (TUBITAK) and carried out within the framework of the TUBITAK CAYDAG-104Y289 project on "Assessment of the present state of the Black Sea ecosystem and forecasting its future behavior".

References

Daskalov, G. M. 2002. Overfishing drives atrophic cascade in the Black Sea. Marine Ecology Progress Series, 225: 53–63.

Finenko, G. A., Romanova, Z. A., Abolmasova, G. I., Anninsky, B. E., Svetlichny, L. S., Hubareva, E. S., Bat, L., *et al*. 2003. Population dynamics, ingestion, growth and reproduction rates of the invader *Beroe ovata* and its impact on plankton community in Sevastopol Bay, the Black Sea. Journal of Plankton Research, 25: 539–549.

Gucu, A. C. 2002. Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? Estuarine, Coastal, and Shelf Science, 58: 439–451.

Humborg, C., Ittekkot, V., Cociasu, A., and Bodungen, B. V. 1997. Effect of Danube River dam on Black Sea biogeochemistry and ecosystem structure. Nature, 386: 385–388.

Katsanevakis, S., Thessalou-Legaki, M., Karlou-Riga, C., Lefkaditou, E., Dimitriou, E., and Verriopoulos, G. 2007. Information-theory approach to allometric growth of marine organisms. Marine Biology, 151: 949–959.

Kideys, A. E. 2002. Fall and rise of the Black Sea ecosystem. Science, 297: 1482–1484.

Kideys, A. E., and Romanova, Z. 2001. Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996–1999. Marine Biology, 139: 535–547.

Knowler, D. 2007. Estimation of a stock–recruitment relationship for Black Sea anchovy (*Engraulis encrasicolus*) under the influence of nutrient enrichment and the invasive comb-jelly, *Mnemiopsis leidyi*. Fisheries Research, 84: 275–281.

Kroiss, H., Zessner, M., and Lampert, C. 2006. daNUbs: lessons learned for nutrient management in the Danube Basin and its relation to Black Sea eutrophication. Chemist and Ecology, 22: 347–357.

Lebedeva, L. P., Shushkina, E. A., Vinogradov, M. E., Lukasheva, T. A., and Anokhina, L. L. 2003. Long-term transformation of the mesoplankton structure from the coastal waters of the northeastern Black Sea under the impact of the ctenophores-invaders. Oceanology, 43: 670–675.

Mutlu, E. 1999. Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. Marine Biology, 135: 603–613.

Mutlu, E. 2001. Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. Marine Biology, 138: 329–339.

Mutlu, E. 2009. Recent distribution and size structure of gelatinous organisms in the southern Black Sea and their interactions with fish catches. Marine Biology, 156: 935–957.

Mutlu, E., and Bingel, F. 1999. Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. I. *Pleurobrachia pileus*. Marine Biology, 135: 589–601.

Mutlu, E., Bingel, F., Gucu, A. C., Melnikov, V. V., Niermann, U., Ostr, N. A., and Zaika, V. E. 1994. Distribution of the new invader *Mnemiopsis* sp. and the resident *Aurelia aurita* and *Pleurobrachia pileus* populations in the Black Sea in the years 1991–1993. ICES Journal of Marine Science, 51: 407–421.

Niermann, U., Kideys, A. E., Besiktepe, S., Nicolae, B., Goubanova, A., Khoroshilov, V., Mikaelyan, A., *et al*. 1995. An assessment of recent phyto- and zooplankton investigations in the Black Sea and planning for future. Report on the Meeting of Marine Biologists in Erdemli, Turkey, 20 February–3 March 1995. TU-Black Sea Project, NATO Science for Stability Program. Institute of Marine Sciences, Middle East Technical University, Erdemli, Turkey. 100 pp.

Oguz, T., and Gilbert, D. 2007. Abrupt transitions of the top–down controlled Black Sea pelagic ecosystem during 1960–2000: Evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. Deep Sea Research Part I, 54: 220–242.

Oguz, T., Dippner, J. W., and Kaymaz, Z. 2006. Climatic regulation of the Black Sea hydrometeorological and ecological properties at interannual-to-decadal time scales. Journal of Marine Systems, 60: 235–254.

Shiganova, T. A., Musaeva, E. I., Bulgakova, Yu V., Mirzoyan, Z. A., and Martynyuk, M. L. 2003. Invaders ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* (Mayer 1912), and their influence on the pelagic ecosystem of northeastern Black Sea. Biology Bulletin, 30: 180–190.

Vinogradov, M. E., Shushkina, E. A., Musayeva, E. I., and Sorokin, P. Yu. 1989. A newly acclimated species in the Black Sea: the ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). Oceanology, 29: 220–224.

Weilguni, H., and Humpesch, U. H. 1999. Long-term trends of physical, chemical and biological variables in the River Danube 1957–1995: a statistical approach. Aquatic Science, 61: 234–259.

Weisse, T., and Gomoiu, M. T. 2000. Biomass and size structure of the scyphomedusa *Aurelia aurita* in the northwestern Black Sea during spring and summer. Journal of Plankton Research, 22: 223–239.

Weisse, T., Gomoiu, M. T., Scheffel, U., and Brodrecht, F. 2002. Biomass and size composition of the comb jelly *Mnemiopsis* sp. in the north-western Black Sea during spring 1997 and summer 1995. Estuarine, Coastal, and Shelf Science, 54: 423–437.

10. Niche separation of *Clausocalanus* spp. in the Mediterranean Sea and the Atlantic Ocean

Àurea Peralba, Maria Grazia Mazzocchi, and Roger P. Harris

Introduction

The epipelagic copepod genus *Clausocalanus* is numerically important in the world's oceans over a wide range of latitudinal and trophic conditions (Frost and Fleminger, 1968; Peralba, 2008). It is a major component of the small-size (≤1 mm) fraction of mesozooplankton that is now attracting attention because of its abundance and the role it plays in the oceans. This genus presents unique features among small copepods, such as two different spawning modes (some species carry their eggs, whereas others are broadcast spawners; Saiz and Calbet, 1999; Peralba, 2008) and a very fast and convoluted swimming behaviour (Mazzocchi and Paffenhöfer, 1998, 1999; Uttieri *et al.*, 2008). However, difficulties in taxonomic identification and problems in rearing these copepods in the laboratory have limited the number of studies on the ecology and biology of this genus at the species level.

In the present study, which is part of a PhD thesis (Peralba, 2008), we investigated the distribution of eight species (*Clausocalanus paululus*, *C. pergens*, *C. furcatus*, *C. arcuicornis*, *C. parapergens*, *C. jobei*, *C. lividus*, and *C. mastigophorus*) in the Mediterranean Sea and the Atlantic Ocean at different temporal and spatial scales, with the aim of characterizing the ecological niches of the most abundant *Clausocalanus* species co-occurring in these basins.

Material and methods

In the Mediterranean Sea (Figure 10.1), the seasonal and vertical distributions of *Clausocalanus* spp. in epipelagic oligotrophic waters were analysed in 2002 at an offshore site (Stn L20; 40°41′N 14°15′E; >300 m depth) in the open Gulf of Naples (Tyrrhenian Sea, western Mediterranean) by collecting samples in discrete layers in the upper 200 m water column. The annual cycle in the upper 50 m was compared with the annual cycle observed in parallel at the coastal eutrophic Stn MC (40°48′30″N 14°15′E; ~80 m depth), the site of a long-term zooplankton time-series since 1984. This comparison allowed the study of the seasonal distribution of *Clausocalanus* spp. under different trophic conditions.

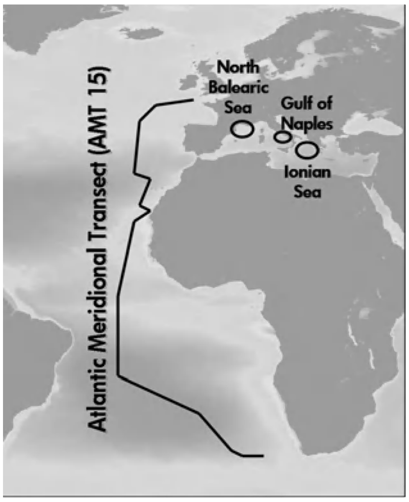

Figure 10.1. Map of regions visited during the present investigation: Atlantic Ocean (AMT 15) and Mediterranean Sea (north Balearic Sea and Gulf of Naples in the western basin; Ionian Sea in the eastern basin).

The spring *Clausocalanus* assemblages were investigated in the upper 100 m water column at numerous stations in the oligotrophic Ionian Sea (spring 2002) and in the eutrophic north Balearic Sea (spring 2003). This allowed the comparison of *Clausocalanus* assemblages in the open sea in the same season, but in very different trophic conditions.

In the Atlantic Ocean (Figure 10.1), the distribution of *Clausocalanus* spp. at a wider latitudinal scale was addressed during the Atlantic Meridional Transect cruise AMT 15 in September–October 2004.

The sampling methods always consisted of vertical tows performed with WP-2 (Stn L20 and AMT) or Nansen (Stn MC, Ionian and Balearic Seas) nets with 200 µm mesh, and the results were, therefore, comparable. The specific results presented here are based only on female abundance. Copepodites were much more abundant, but were not distinguished at the species level, whereas males were identified at the species level, but were rare.

Results

During the annual cycle in the Gulf of Naples, *Clausocalanus* was more abundant offshore, although total copepods were less numerous there than at the coastal station (Figure 10.2).

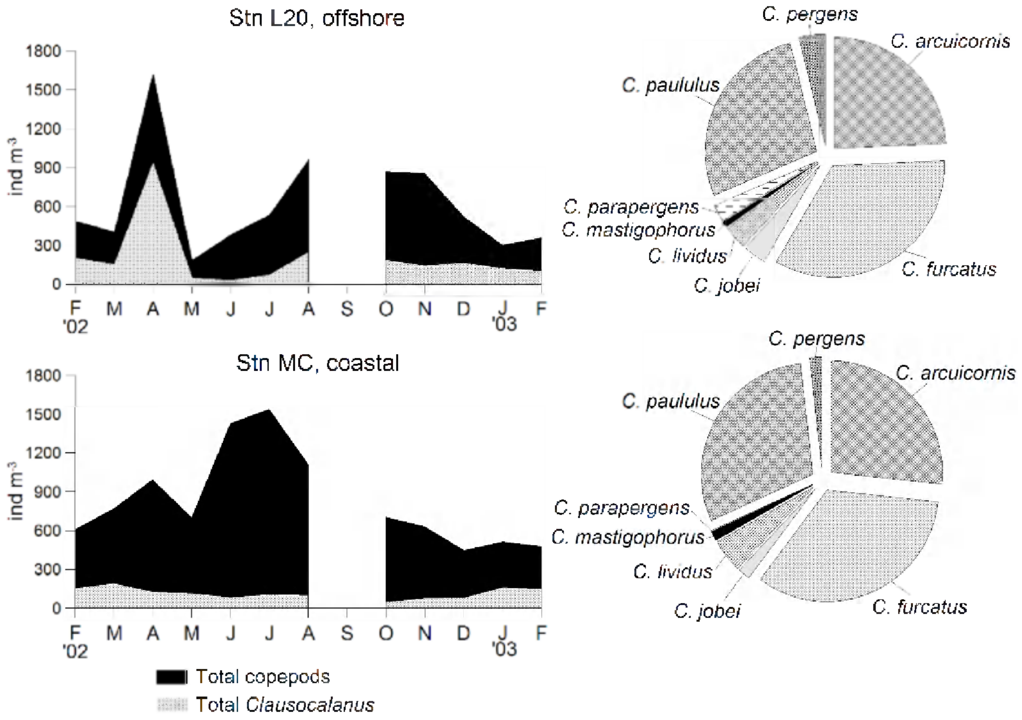

Figure 10.2. Abundance of the genus *Clausocalanus* and total copepods at offshore (Stn L20) and coastal (Stn MC) sites in the Gulf of Naples (Tyrrhenian Sea, western Mediterranean; left panels), and relative contributions of the occurring species to total *Clausocalanus* female abundance (right panels).

Also, the relative contribution of *Clausocalanus* to total copepods was higher offshore, but all species contributed very similarly to total *Clausocalanus* abundance in both offshore and coastal waters.

The annual cycle was characterized by a succession of peaks of different abundant species, from *C. arcuicornis* in spring, *C. furcatus* in summer–autumn, and *C. paululus* in winter–early spring. The comparison with the patterns recorded at Stn MC for a decade in the 1980s (Mazzocchi and Ribera d'Alcalà, 1995) demonstrated that the succession is maintained, but that *C. pergens* was more abundant in those years.

In the vertical space of the epipelagic water column, the small *C. paululus* and *C. pergens* were uniformly distributed in winter, concentrated in the upper 100 m in spring, and below 50 m depth (below the thermocline at the deep chlorophyll maximum) from June to mid-October. The medium-size *C. jobei*, *C. parapergens*, and *C. arcuicornis* also avoided the upper 25–50 m layer from June to mid-October. In winter, *C. jobei* was uniformly distributed in the water column, *C. parapergens* occurred deeper in winter–spring, and *C. arcuicornis* was concentrated in the upper layer. The small *C. furcatus* and the large *C. mastigophorus* were always concentrated in the upper 50 m layer, above the thermocline in summer. *C. lividus* was generally concentrated in the upper layer, similar to *C. mastigophorus* (Peralba and Mazzocchi, 2004).

In the open Mediterranean Sea in spring, the genus *Clausocalanus* was much more abundant in the Balearic than in the Ionian Sea, but its relative contribution to total copepod abundance was very similar (Figure 10.3).

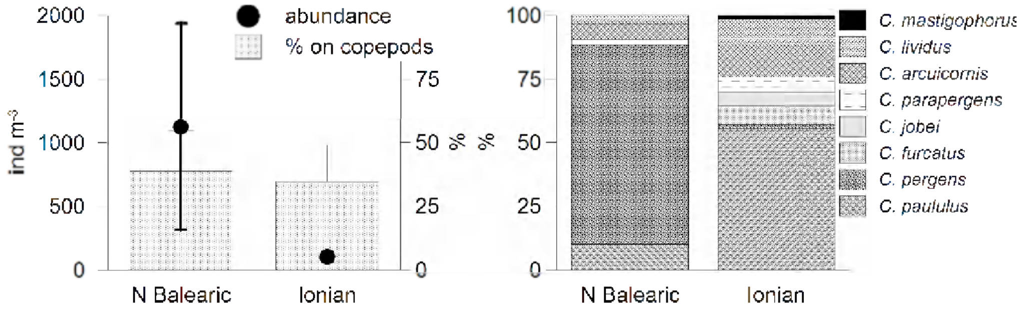

Figure 10.3. Average abundance of the genus *Clausocalanus* (black dots, ± stdev) and its relative contribution (columns, ± stdev) to total copepod abundance in spring in the northern Balearic Sea and the Ionian Sea (Mediterranean Sea; left panel), and average relative contribution of species to total *Clausocalanus* female abundance (right panel).

A remarkable difference occurred between the two *Clausocalanus* communities in terms of composition. *C. paululus*, similarly abundant in both regions, was relatively more important in the Ionian Sea, whereas *C. pergens* was very abundant and also contributed more in the north Balearic Sea and was only present in small numbers in the Ionian.

In the Atlantic Ocean in autumn, the percentage contribution of the genus *Clausocalanus* to total copepod abundance revealed latitudinal differences that largely corresponded to the biogeochemical provinces described by Longhurst (2007). The three smallest *Clausocalanus* species were the most abundant and demonstrated differences in their distribution. *C. paululus* predominated in temperate oligotrophic waters, *C. pergens* in cold eutrophic waters, and *C. furcatus* in warm oligotrophic waters.

Pooling together the *Clausocalanus* female abundance in the Mediterranean Sea and in the Atlantic Ocean reveals that the ranges of conditions under which the *Clausocalanus* species can persist (i.e. the niche breadth) largely overlap regarding both temperature and fluorescence (here used as a proxy of autotrophic biomass). Only *C. furcatus* and *C. mastigophorus* have thermal niches statistically different from

C. paululus and *C. pergens* (ANOVA test, *p* <0.01). Nevertheless, populations peak under different conditions (Figure 10.4).

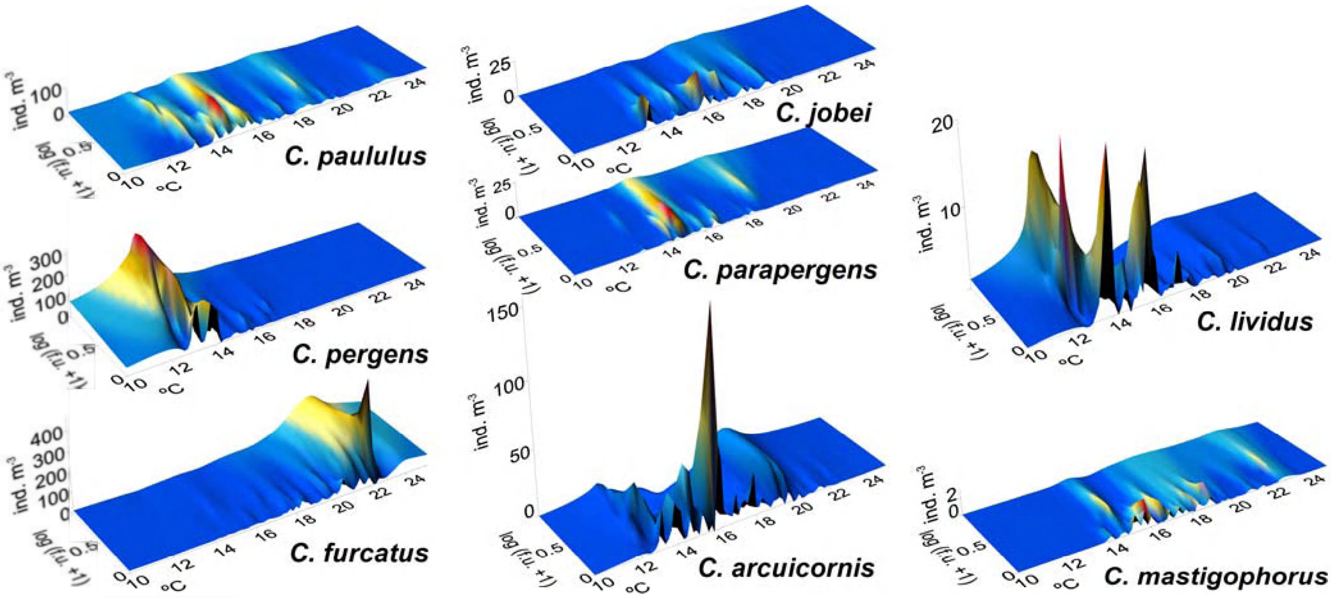

Figure 10.4. Abundance distribution (individuals m^{-3}, *z*-axis) of eight *Clausocalanus* species in relation to temperature (°C, *x*-axis) and fluorescence (log (f.u.+1), *y*-axis), based on data collected in the regions of the Mediterranean Sea and the Atlantic Ocean investigated during the present study.

This is particularly clear among the small species. *C. paululus* peaks in cold oligotrophic waters, *C. pergens* in colder eutrophic waters, and *C. furcatus* in warm oligo-mesotrophic conditions. The three medium-sized species, *C. arcuicornis*, *C. parapergens*, and *C. jobei*, peak in cold oligotrophic waters, but the former outnumbers the other two. The two larger species are less abundant; *C. lividus* peaks in cold oligotrophic and eutrophic conditions, whereas *C. mastigophorus*, which is very rare, is slightly more abundant in warm oligotrophic waters. The optimal conditions for occurrence are, indeed, more distinguishable among small congeners and among large congeners, whereas medium-sized species have a very similar optimum occurrence.

Conclusions

Eight *Clausocalanus* species widely co-occur in most regions of the Mediterranean Sea and the Atlantic Ocean on different spatial and temporal scales. However, their distinctive ecological traits can be clearly discerned. Niches seem to be clearly separated among congeners of similar size but largely overlap in congeners of different size.

The *Clausocalanus* assemblages are more diversified in oligotrophic than in eutrophic regions, but small-size species (sac spawners) prevail in all regions considered in the present study. Owing to their importance in zooplankton communities in both coastal and open waters of low to mid-latitudes, and their diverse ecological traits, the small *Clausocalanus* species should be more accurately monitored as good indicators of environmental conditions and sentinels of climate change.

References

Frost, B. W., and Fleminger, A. 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bulletin of the Scripps Institution of Oceanography, 12: 1–235.

Longhurst, A. 2007. Ecological Geography of the Sea, 2nd edn. Academic Press, Amsterdam. 542 pp.

Mazzocchi, M. G., and d'Alcalà, M. R. 1995. Recurrent patterns in zooplankton structure and succession in a variable coastal environment. ICES Journal of Marine Science, 52: 679–691.

Mazzocchi, M. G., and Paffenhöfer, G-A. 1998. First observations on the biology of *Clausocalanus furcatus* (Copepoda, Calanoida). Journal of Plankton Research, 20: 331–342.

Mazzocchi, M. G., and Paffenhöfer, G-A. 1999. Swimming and feeding behaviour of the planktonic copepod *Clausocalanus furcatus*. Journal of Plankton Research, 21: 1501–1518.

Peralba, À. 2008. Niche separation of *Clausocalanus* species in the Mediterranean Sea and in the Atlantic Ocean. PhD thesis, Open University, UK.

Peralba, À., and Mazzocchi, M. G. 2004. Vertical and seasonal distribution of eight *Clausocalanus* species (Copepoda: Calanoida) in oligotrophic waters. ICES Journal of Marine Science, 61: 645–653.

Saiz, E., and Calbet, A. 1999. On the free-spawning reproductive behaviour of the copepod *Clausocalanus lividus* (Frost and Fleminger, 1968). Journal of Plankton Research, 21: 599–602.

Uttieri, M., Paffenhöfer, G-A., and Mazzocchi, M. G. 2008. Prey capture in *Clausocalanus furcatus* (Copepoda: Calanoida). The role of swimming behaviour. Marine Biology, 153: 925–935.

11. The 2003 heat wave and marine plankton communities

Sergey A. Piontkovski, Serena Fonda-Umani, Antonio Olita, Alessandra de Olazabal, Lars Stemmann, Carmen G. Rubio, Stéphane Gasparini, Maria G. Mazzocchi, Ioanna Siokou-Frangou, Soultana Zervoudaki, Alexandra Gubanova, and Denis Altukhov

Introduction

It is believed that, as global temperature continues to increase because of climate change, the intensity of extreme atmospheric anomalies will also increase (WMO, 2003). One of these atmospheric anomalies is the heat wave. These waves are generally associated with atmospheric circulation patterns represented by large-scale anticyclonic forcing (Black *et al.*, 2004). They are perfect examples of extreme atmospheric events that have dramatic consequences for social and ecological ecosystems (Beniston, 2004).

In August 2003, most of Europe suffered the hottest heat wave ever recorded. The average air temperatures exceeded the previous record set in 1757. During its peak, in the two first weeks of August, the mortality rate increased by 54% in France (Hémon and Jougla, 2004). Indeed, in that summer, between 22 000 and 35 000 heat-related deaths were registered across Europe (Koppe and Jendritzky, 2004). The financial loss caused by crop failure over southern, central, and eastern Europe has been estimated at US $12.3 billion. Towards the end of the 21st century, every second summer could be as warm or warmer than 2003 (Schär *et al.*, 2004). The period during which maximum temperatures in excess of 30°C can be expected will be extended by one month at the end of the century (Beniston, 2004).

The impact of heat waves on marine ecosystems has yet to be understood. The aim of the present study was to look for signs of the 2003 heat wave in monthly fluctuations of zooplankton abundance throughout the Mediterranean basin. It was hypothesized that the propagation of the heat wave should weaken windstress and generate thermal water stratification. In the case of a low-nutrient scenario, enhanced stratification could lead to depleted phyto- and zooplankton abundance or biomass. Owing to indirect links between atmospheric processes and the zooplankton community, a time-lag should be observed in the response of zooplankton abundance or biomass to the extremes in atmospheric temperature (characterized by the heat wave).

Material and methods

Monthly time-series (atmospheric temperature, sea surface temperature (SST), chlorophyll *a*, and copepod species abundance) were assembled over five geographically different regions affected by the heat wave propagation (Figure 11.1). For the Chlorophyll *a* (Chl *a*) measurements, satellite ocean colour and SST time-series were obtained from the SeaWIFS and JAXA databases (http://oceancolor.gsfc.nasa.gov/; http://www.eorc.jaxa.jp), along with SST measurements carried out on board vessels. Data on zooplankton for all the regions were available from the data-holders. The abundance of species of copepods (gen. *Acartia, Paracalanus, Clausocalanus, Temora, Centropages, Oithona),* the cladoceran *Penilia avirostris,* and total copepod abundance were analysed for 2002–2005, allowing a comparison of the 2003 events with the monthly variations recorded during the years before and after the heat wave.

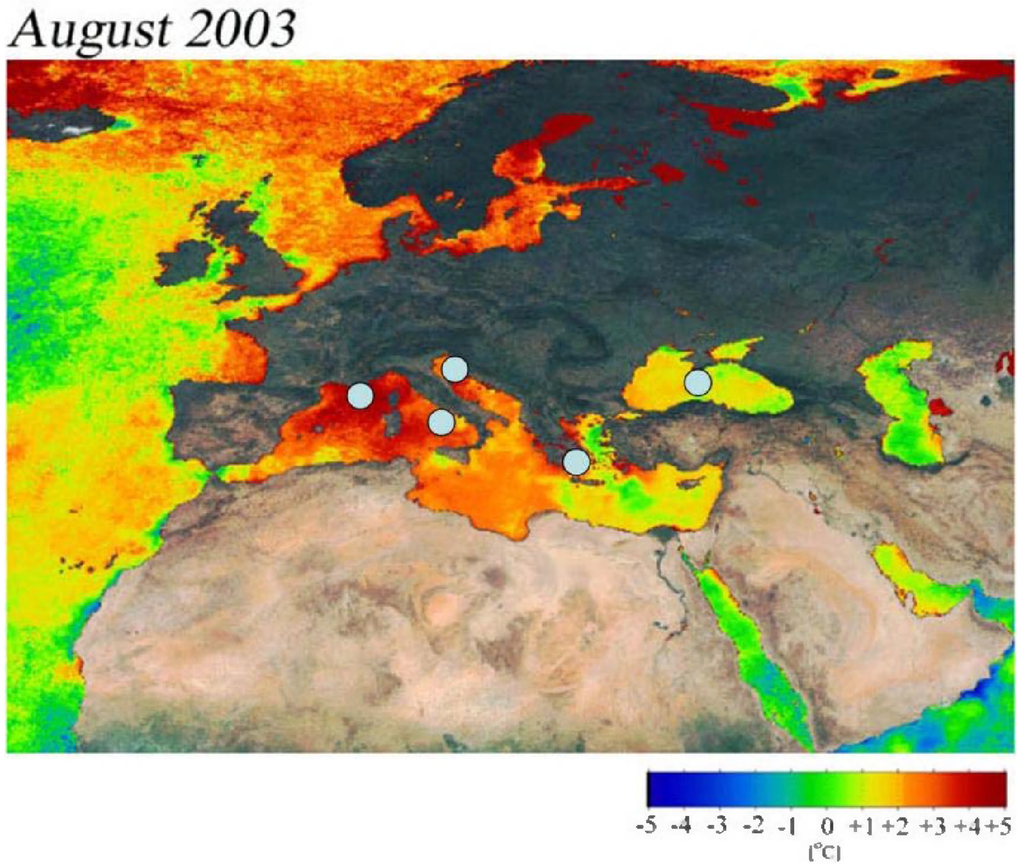

Figure 11.1. The European heat wave in August 2003 and the project sampling sites (http://www.eorc.jaxa.jp/en/imgdata/topics/2003/tp031127.html). The image shows the differences in SST around Europe between the monthly mean values in August 2003 and the nominal value (i.e. the average of SSTs in August from 1971 to 2000).

Results and discussion

Figure 11.1 shows the differences in SST around Europe between the monthly mean values in August 2003 and the nominal value (i.e. the average of SSTs in August from 1971 to 2000). Most areas had SSTs above the nominal value. For example, in the Mediterranean Sea, across southern France to western Italy, temperatures were 3–4°C higher than average.

SeaWIFS Chl *a* time-series demonstrated absolute minima in summer 2003 for Naples, Sevastopol, and Trieste (this last with a longer period signal), whereas no evident footprints of the heat wave on remotely sensed Chl *a* were found for the other sites.

In the sampled regions, the 2003 SST was 1–4°C higher than in "standard" years (2001, 2002, and 2004).

Zooplankton time-series from Villefranche Bay (Ligurian Sea), Gulf of Naples (Tyrrhenian Sea), Gulf of Trieste (Adriatic Sea), Saronic Gulf (Aegean Sea), and Gulf of Sevastopol (Black Sea) demonstrated no pronounced response of total copepod abundance to the heat-wave propagation (Figures 11.2 and 11.3). In some regions however (e.g. Trieste and Sevastopol), "typical" summer populations (*Penilia avirostris*) were less abundant in August–December 2003 than in the same periods in 2001, 2002, and 2004. In the Gulf of Naples, the same lesser abundance was noticed for *Centropages typicus*, which is a key summer species for the region.

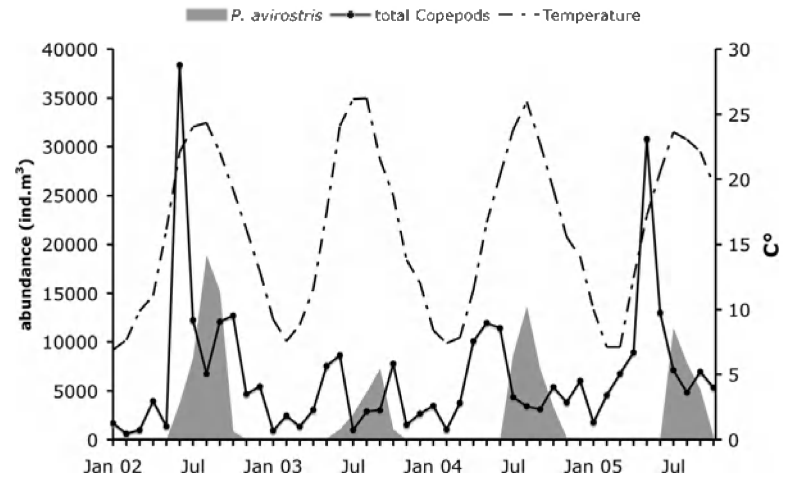

Figure 11.2. Monthly changes in SST and total copepod abundance in the Gulf of Trieste, 2002–2005.

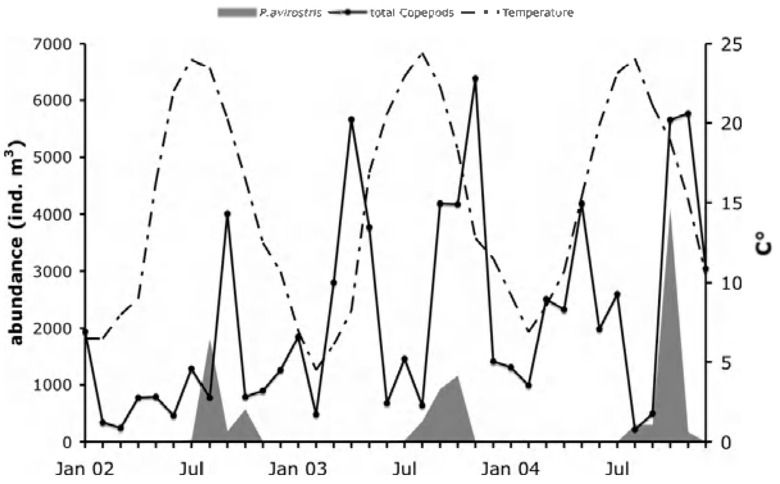

Figure 11.3. Monthly changes in SST and total copepod abundance in the Gulf of Sevastopol, 2002–2004.

In the Mediterranean basin, *P. avirostris* is an abundant herbivore species that ingests primarily smaller phytoplankton in the surface layer (Fonda-Umani *et al.*, 1992, 2005; Lipej *et al.*, 1997). In the Gulf of Trieste, for example, *P. avirostris* exhibits clear coupling with monthly changes in Chl *a* concentration, and its population peak follows the summer peak of phytoplankton, lasting for several weeks. In 2003, the year of the heat wave, there was a reduction in the summer chlorophyll peak. This was reflected in the abundance of *P. avirostris*, whose population peak was half as pronounced in summer 2003 as in 2002 or in 2004 and 2005.

The comparison of responses of zooplankton communities over a broad range of spatio-temporal scales demonstrated that global-scale atmospheric anomalies (exemplified for the region by the North Atlantic Oscillation) tend to affect zooplankton communities as a whole, which is exhibited by changes in integrative characteristics, such as total zooplankton abundance (Piontkovski *et al.*, 2006). On the other hand, regional atmospheric anomalies (exemplified by the 2003 heat wave) tend to affect zooplankton communities only partly. In this case, changes in integrative characteristics (i.e. total zooplankton abundance) were not very pronounced, but the community has responded through changes in the abundance of "typical" summer populations (i.e. *Penilia avirostris*) most susceptible to these atmospheric anomalies.

References

Beniston, M. 2004. The 2003 heat wave in Europe: a shape of things to come? An analysis based on Swiss climatological data and model simulations. Geophysical Research Letters, 31, L02202, doi: 10.1029/2003GL018857.

Black, E., Blackburn, M., Harrison, G., and Methven, J. 2004. Factors contributing to the summer 2003 European heat wave. Weather, 59: 217–223.

Fonda-Umani, S., Franco, P., Ghirardelli, E., and Malej, A. 1992. Outline of oceanography and the plankton of the Adriatic Sea. *In* Marine Eutrophication and Plankton Dynamics, pp. 347–365. Ed. by G. Colombo, I. Ferrari, V. U. Ceccherelli, and R. Rossi. Olsen and Olsen, Fredensborg, Denmark.

Fonda-Umani, S., Tirelli, V., Beran, A., and Guardiani, B. 2005. Relationships between microzooplankton and mesozooplankton: competition vs. predation on natural assemblages in the Gulf of Trieste (northern Adriatic Sea). Journal of Plankton Research, 27: 973–986.

Hémon, D., and Jougla, E. 2004. Surmortalité liée à la canicule d'août 2003. L'Institut National de la Santé et de la recherche Médicale (INSERM), Paris. 265 pp.

Koppe, C., and Jendritzky, G. 2004. Auswirkungen der Hitzewellen 2003 auf die Mortalität in Baden-Württemberg [Impacts of the 2003 heat wave on mortality in Baden-Württemberg]. *In* Gesundheitliche Auswirkungen der Hitzewelle im August 2003, pp. 5–18. Baden-Württemberg Ministry for Social Affairs, Stuttgart.

Lipej, L., Mozetic, P., Turk, V., and Malej, A. 1997. The trophic role of the marine cladoceran *Penilia avirostris* in the Gulf of Trieste. Hydrobiologia, 360: 197–203.

Piontkovski, S. A., O'Brien, T. D., Fonda-Umani, S. F., Krupa, E. G., Stuge, T. S., Balymbetov, K. S., Grishaeva, O. V., *et al.* 2006. Zooplankton and the North Atlantic Oscillation: a basin scale analysis. Journal of Plankton Research, 28: 1039–1046.

Schär, C., Vidale, P. L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A., and Appenzeller, C. 2004. The role of increasing temperature variability in European summer heat waves. Nature, 427: 332–336.

WMO (World Meteorological Organization). 2003. According to the World Meteorological Organization, extreme weather events might increase. Press Release 695, 2 July 2003, WMO, Geneva. Available online at http://www.wmo.ch/web/Press/Press695.doc.

12. A new fine-mesh zooplankton time-series from the Dove sampling station (North Sea)

Sophie G. Pitois

Introduction

The Dove Marine Laboratory (Cullercoats, North Shields, UK) plankton sampling station lies approximately 5.5 nautical miles east of Blyth on the Northumberland coast (Figure 12.1). The Dove time-series in the North Sea are some of the longest running coastal zooplankton time-series in the UK. Samples have been collected at approximately monthly intervals since 1971, using WP-3 (1000 µm mesh), WP-2 (200 µm mesh), and fine-mesh (65 µm mesh) ringnets. Previous studies have focused on the dynamics of the mesozooplankton using data from 1000 µm and 200 µm mesh ringnet samples (Clark and Frid, 2001; Clark *et al.*, 2003).

However, the fine-mesh (65 µm) samples are of particular interest because of the increasing awareness of the ecology of smaller copepod species, which are under-represented in samples collected by coarser mesh nets.

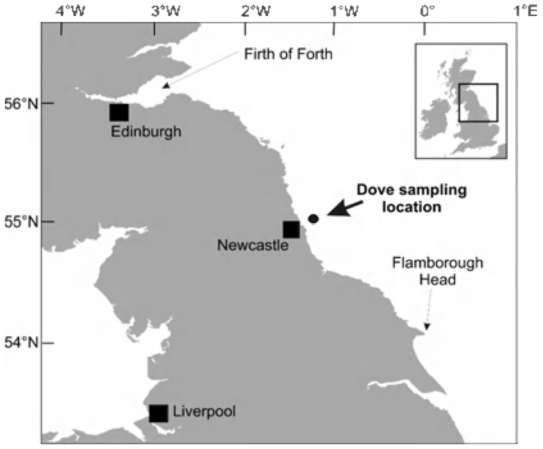

Figure 12.1. The Dove Marine Laboratory (Cullercoats, North Shields, UK) plankton sampling station lies approximately 5.5 nautical miles east of Blyth on the Northumberland coast in the North Sea.

Analysis of the fine-mesh samples will:

- extend the range of species whose dynamics in this region have been documented over the past four decades;
- provide information on the early life stages of some of the species recorded as adults in the previously analysed Dove series, thus allowing a fuller understanding of their population dynamics;
- provide additional information on the production of copepod nauplii, which are not quantitatively sampled by WP-2 or WP-3 nets.

Material and methods

Sampling at the Dove location was carried out monthly from 1971 to 2002, weather permitting, except for 1989, when no samples were taken. In addition to the WP-2 and WP-3 sampling described by Evans (1977), Evans and Edwards (1993), and Roff *et al.* (1988), vertical plankton hauls were made using a fine-mesh, conical ringnet (65 mm mesh, 46 cm mouth diameter). This net was deployed in four vertical hauls from 50 m to the surface (speed of gear was approximately 1.25 m s^{-1}), and the hauls were pooled so that each sample represented approximately 200 m^3 of filtered water. The samples were immediately preserved in 4% buffered formaldehyde solution and stored at the Dove Marine Laboratory. In 2002, the archived fine-mesh samples were transferred to Cefas, Lowestoft, for enumeration (Pitois *et al.*, 2009).

Results

Visual comparison with previously published results for WP-2 and WP-3 time-series

Neither of the two time-series (200 and 1000 µm mesh) from the Dove location displays any significant long-term trend (Figure 12.2). Visual comparison of the trends of individual species, using our results and previously published results from the coarse-mesh series (Clark *et al.*, 2003), seems to indicate similar trends in both time-series for *Oikopleura* spp., *Acartia* spp., *Temora* spp., and *Sagitta* spp. However, the respective efficiencies of the fine and coarse meshes vary substantially for most other species. Not surprisingly, the smallest organisms tend to be collected more efficiently by the fine-mesh net (i.e. Lamellibranch larvae, gastropod larvae, polychaete larvae, *Oikopleura* spp., *Fritillaria* spp., *Oithona* spp., and other cyclopoid copepods, which all have a mean width <150 µm). Consequently, the fine-mesh Dove dataset, taken on its own, might alter our perception of species abundance gained from previously published work on the Dove dataset.

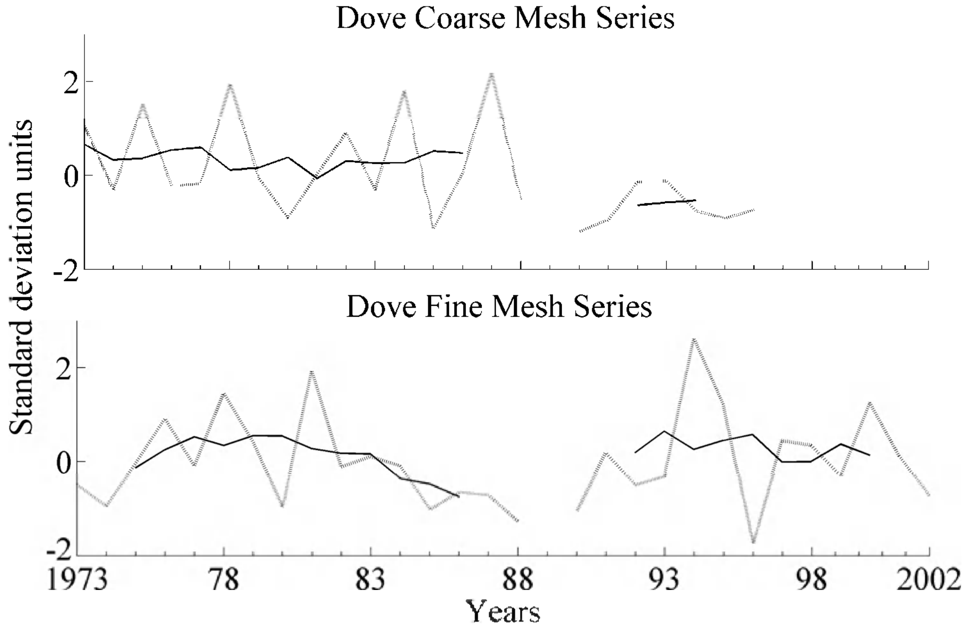

Figure 12.2. Total annual zooplankton abundance from Dove coarse- and fine-mesh series. Dotted line = standardized abundance; plain line = standardized abundance with five-year moving average.

Abundance and trends

For the analysis of trends, only those zooplankton taxa or groups of taxa identified in at least 10% of the samples analysed were considered. Copepod nauplii were the most abundant group of organisms identified, followed in decreasing order by *Oithona* spp., Lamellibranch larvae, Harpacticoid copepods, *Acartia* spp., polychaete larvae, gastropod larvae, *Paracalanus* spp., *Pseudocalanus* spp., *Oikopleura* spp., *Fritillaria* spp., *Evadne* spp., *Temora* spp., echinoderm larvae, Cirripedia, *Centropages* spp., other cyclopoid copepods, Bryozoa, *Microcalanus* spp., *Calanus* spp., and *Sagitta* spp. (Table 12.1).

Table 12.1. Mean annual abundance of zooplankton analysed from the Dove fine-mesh series for the period 1971–2002 (identified in at least 10% of the samples; column 3) and from the coarse-mesh series obtained from published work (Clark *et al.*, 2003; column 4). For each taxon (column 1), the stage of development is indicated (column 2: X = mixed; L = larva; C = copepodite I–V; A = unsexed adult; N = nauplius I–VI). Columns 6 and 7 indicate the most appropriate time-series to use for recording each taxon, based on a comparison between the abundances yielded by the Dove fine-mesh and coarse-mesh series (column 6), and as calculated from the model of mesh selectivity described by Nichols and Thompson (1991; column 7: C = coarse mesh; F = fine mesh). The model is based on 75% of the copepod carapace width ± s.d. (column 5).

TAXON	STAGE	MEAN ANNUAL ABUNDANCE FROM FINE-MESH SERIES (IND. M^{-3})	MEAN ANNUAL ABUNDANCE FROM COARSE-MESH SERIES (IND. M^{-3})	75% OF CARAPACE WIDTH (MM) ± S.D.	MOST APPROPRIATE TIME-SERIES FROM	
					ABUNDANCE COMPARISON	MODEL
Fritillaria spp.	X	144.42	37.35	–	F	–
Oikopleura spp.	X	213.97	86.48	–	F	–
Polychaeta	X	171.87	33.27	–	F	–
Tomopteris spp.	X	1.87	1.76	–	F	–
Bryozoa	L	20.74	9.73	–	F	–
Evadne spp.	X	125.84	439.85	–	C	–
Podon spp.	X	6.21	31.82	–	C	–
Hydroida	X	2.30	3.06	–	C	–
Sagitta spp.	X	7.60	13.09	–	C	–
Acartia spp.	C	575.69	760.92	131 ± 37	C	C
	A	90.49	489.84	207 ± 116	C	C
Calanus spp.	C	20.09	66.19	305 ± 127	C	C
	A	1.43	7.28	518 ± 80	C	C
Centropages spp.	C	63.17	18.49	145 ± 22	F	C
	A	5.51	26.0	268 ± 42	C	C
Corycaeus spp.	X	0.13	0.64	140 ± 39	C	C
Cyclopoida	X	19.97	No data*	74 ± 28	F	F
Harpacticoida	X	362.64	No data*	72 ± 14	F	F
Metridia spp.	C	0.05	No data*	233	–	C
Microcalanus spp.	C	13.59	No data**	115 ± 33	–	F
	A	0.21	8.5	156 ± 36	C	C
Nauplii	N	5117.00	No data*	68 ± 20	F	F
Oithona spp.	C	1272.7	930.18	110 ± 29	F	F
	A	7.68		116 ± 28	F	F
Oncaea spp.	C	0.09	0.11	81 ± 25	C	F
Paracalanus spp.	C	212.59	No data**	123 ± 33	–	F
	A	8.53	33.18	184 ± 36	C	C
Pseudocalanus spp.	C	182.87	No data**	170 ± 38	–	C
	A	24.12	155.33	239 ± 39	C	C
Temora spp.	C	81.57	323.57 (all stages incl.)	180 ± 62	C	C
	A	7.27		303 ± 68	C	C
Echinodermata	L	57.59	5.7	–	F	–
Decapoda	L	0.82	No data*	–	–	–
Brachyura	X	0.87	No data*	–	–	–
Euphausiacea	X	10.67	24.25	–	C	–
Hyperiidea	X	0.42	No data*	–	–	–
Isopoda	X	0.17	No data*	–	–	–
Mysidacea	X	0.16	No data*	–	–	–
Lamellibranchia	L	711.26	73.45	–	F	–
Gastropoda	L	119.29	38.54	–	F	–
Cirripedia	X	33.19	63.25	–	C	–
Phoronids	X	0.55	1.44	–	C	–

* No information was available in Clark *et al.* (2003).

** The taxon was included in a wider taxonomic group and no information could be extracted from the publication.

Amalgamation of coarse-mesh (200 µm and 1000 µm) and fine-mesh (65 µm) time-series

The previously analysed Dove time-series is an amalgamation of the data from the 1000 µm and 200 µm mesh series, the abundance of individual taxa being derived from the net that provides the most reliable estimate of abundance for that taxon. Here, we suggest combining the coarse-mesh data and the fine-mesh data by applying the criteria developed by Evans and Edwards (1993). We compared annual mean abundance from the coarse-mesh series, obtained from published results (Clark *et al.*, 2003), with that from the fine-mesh series and selected, as best for a particular species, the mesh size that resulted in the highest catch rate.

For most organisms, there was at least one order of magnitude difference in catch rates between nets, so it was clear which was the better sampling device. However, for a few organisms, the recorded annual mean abundance was similar in both series. This scenario usually applied to taxa with low abundance. In these situations, the net with the higher overall catch rate was selected as the better sampling device. As a validation tool for copepods, we used the model of mesh selectivity described by Nichols and Thompson (1991), which demonstrated that a mesh size of 75% of the copepod carapace width catches ca. 95% of the individuals of that size present in the seawater (Table 12.1).

Conclusions

The Dove fine-mesh series analysed here provides a new and unique resource for understanding long-term zooplankton dynamics and the potential to link nauplii and small larvae to the patterns seen in the adults/larger zooplankton. There is an urgent need for a better understanding of marine ecosystem functioning, particularly how climate change may affect primary and secondary production. Such climate-induced changes may affect ecosystem functioning by cascading up the foodweb from the lowest to the higher trophic levels. Therefore, the samples from the fine-mesh net are of particular interest because they provide quantitative abundance estimates for an extended range of species and life stages. This dataset complements the mesozooplankton Dove time-series and has the potential to assist in the creation of a stronger time-series with a wider range of efficiently sampled organisms. In combination with other time-series, such as the ones obtained from the Continuous Plankton Recorder and Helgoland, this should provide a useful tool to help further our understanding of zooplankton ecology in the North Sea.

Acknowledgements

This study was supported by funding (M0431, M1101) from the Department of Environment, Food and Rural Affairs (Defra, UK): "Impact of environmental change on the recruitment of commercial fish stocks — an examination of potential mechanistic links through temperature and prey". Special thanks are extended to the masters and crew of RV "Bernicia" for sample collection, and Frank Evans is acknowledged as originator of the time-series.

References

Clark, R. A., and Frid, C. L. J. 2001. Long-term trends in the central-west North Sea. Senckenbergiana Maritima, 31: 117–124.

Clark, R. A., Frid, C. L. J., and Nicholas, K. R. 2003. Long-term, predation-based control of a central-west North Sea zooplankton community. ICES Journal of Marine Science, 60: 187–197.

Evans, F. 1977. Seasonal density and production estimates of the commoner planktonic copepods of Northumberland coastal waters. Estuarine and Coastal Marine Science, 5: 223–241.

Evans, F., and Edwards, A. 1993. Changes in the zooplankton community off the coast of Northumberland between 1969 and 1988, with notes on changes in the phytoplankton and benthos. Journal of Experimental Marine Biology and Ecology, 172: 11–29.

Nichols, J. H., and Thompson, A. B. 1991. Mesh selection of copepodite and nauplius stages of four calanoid copepod species. Journal of Plankton Research, 13: 661–671.

Pitois, S. G., Shaw, M., Fox, C. J., and Frid, C. L. J. 2009. A new fine-mesh zooplankton time series from the Dove sampling station (North Sea). Journal of Plankton Research, 31: 337–343.

Roff, J. C., Middlebrook, K., and Evans, F. 1988. Long-term variability in North Sea zooplankton off the Northumberland coast: productivity of small copepods and analysis of trophic interactions. Journal of the Marine Biological Association of the UK, 68: 143–164.

13. Overview of epipelagic mesozooplankton in the open Mediterranean Sea

Ioanna Siokou-Frangou and Maria Grazia Mazzocchi

Introduction

The Mediterranean Sea is connected by shallow, narrow straits or canals with the Atlantic Ocean (in the west) and the Black Sea, from which it receives less saline waters, and with the Red Sea–Indian Ocean (in the east), from which it receives more saline waters. West–east gradients of increasing temperature (15–26 °C in the surface layer) and salinity (36.2–39) are observed across the Mediterranean, owing to its warm-temperate to subtropical character. This basin is also characterized by a west– east gradient of increasing oligotrophy (Bethoux *et al.*, 1992; Antoine *et al.*, 1996), which affects phytoplankton biomass and production and microzooplankton standing stock (Pitta *et al.*, 2001). The Mediterranean Sea has a narrow continental shelf (except in the Gulf of Lions, the Gulf of Syrte, the northern Adriatic Sea, and the northern Aegean Sea), great depths (mean depth of 3000 m), and several straits or other geomorphological constraints that delimit different regions within the two major sub-basins, i.e. the western (WMed) and the eastern (EMed) Mediterranean.

The latest overviews of Mediterranean zooplankton date back almost 20 years (Gaudy, 1985; Moraitou-Apostolopoulou, 1985; Champalbert, 1996). During the past two decades, the number of mesozooplankton studies in the Mediterranean has increased, especially in the EMed, and two of them were performed throughout the entire basin (Dolan *et al.*, 2002; Siokou-Frangou *et al.*, 2004).

In this paper, we attempt to provide an overview of this enriched literature on the spatial variability of mesozooplankton standing stock and community composition in the epipelagic layer (0–200 m).

Results and discussion

The standing stock of mesozooplankton rarely exceeds 1500 individuals m^{-3} and 20 mg dry wt m^{-3} (for the upper 200 m), reflecting the oligotrophic character of the Mediterranean Sea (Table 13.1). Exceptionally high values are observed in areas influenced by Atlantic Ocean and Black Sea waters: up to 5000 copepods m^{-3} during spring in the Alboran Sea (Seguin *et al.*, 1994) and up to 5248 total zooplankton m^{-3} in the northeastern Aegean Sea in the same season (Siokou-Frangou *et al.*, 2009). The general west–east trend of increasing oligotrophy was also found to be true for mesozooplankton, based on the results of synoptic cruises throughout the entire Mediterranean Sea (Dolan *et al.*, 2002; Siokou-Frangou *et al.*, 2004).

Superimposed on this general trend, a marked spatial variability appears in the distribution of mesozooplankton standing stock within each geographic area. This is mainly the result of the influence of local mesoscale hydrological and circulation features: (i) fronts in the Catalan and Ligurian seas (Alcaraz *et al.*, 2007); (ii) cyclonic and anticyclonic gyres in the Ligurian Sea, the Algerian basin, and the Ionian and Levantine seas (Pinca and Dallot, 1995; Mazzocchi *et al.*, 1997; Christou *et al.*, 1998; Riandey *et al.*, 2005); (iii) upwellings in the Sicily Strait (Mazzocchi *et al.*, 1997); and (iv) the influence of poor or rich water masses in the Balearic Sea (Fernández de Puelles *et al.*, 2004).

Results from a few studies based on sampling with fine-mesh nets (45–80 μm) have indicated the significance of the small-sized zooplankters within the Mediterranean pelagic ecosystem (Böttger-Schnack, 1997; Krsinic, 1998; Youssara and Gaudy, 2001; Zervoudaki *et al.*, 2006); this has also been observed in other oceanic regions.

Table 13.1. Mesozooplankton biomass (dry weight) and total abundance values collected by 200–250 µm mesh nets in several areas of the Mediterranean Sea.

Area	Author	Season	Column	Biomass (mg m^{-3})	Total abundance (ind. m^{-3})
Alboran Sea	Seguin *et al.* (1994) Thibault *et al.* (1994)	April–May 1991	0 - 200 m	3.6 - 18.3	*
Alboran Sea	Youssara and Gaudy (2001)	Winter 1997	0 - 200 m	5.5 - 25	400 - 1 150
Catalan Sea	Calbet *et al.* (2002)	Winter 1999	0 - 200 m		400 - 1 400
Gulf of Lions	Gaudy *et al.* (2003)	Spring 1998	0 - 200 m	3 - 13.5	
Mallorca Channel	Fernández de Puelles *et al.* (2004)	Spring 1991	0 - 100 m		400 - 1 800
Ligurian Sea (nets 200 + 500 µm pooled)	Pinca and Dallot (1995)	Spring 1986	0 - 200 m		50 - 2 000
Tyrrhenian Sea	Scotto di Carlo *et al.* (1984)	Annual mean	0 - 200 m		113
Adriatic Sea (central)	Benovic *et al.* (2005)	Spring 2002	0 - 100 m		275 - 800
Ionian Sea (north)	Mazzocchi *et al.* (2003)	Spring 1999	0 - 200 m		145 - 499
Ionian (east)	Mazzocchi *et al.* (1997)	October 1991	0 - 200 m		50 - 131
Aegean Sea (north)	Siokou-Frangou *et al.* (2004)	Spring 1997	0 - 200 m	5.5 - 13.3	338 - 1273
Aegean Sea (south)	Mazzocchi *et al.* (1997)	November 1991	0 - 200 m	2.5 - 5.1	32 - 77
	Siokou-Frangou *et al.* (2004)	Spring 1997			190 - 296
Levantine Sea (northwest)	Mazzocchi *et al.* (1997)	November 1991	0 - 200 m		64 - 81
	Christou *et al.* (1998)	Spring 1992			94 - 221
Rodos gyre	Mazzocchi *et al.* (1997)	November 1991	0 - 200 m		65 - 130
	Christou *et al.* (1998)	Spring 1992			230 - 367
Algerian Basin	Riandey *et al.* (2005)	July–August 1997	0 - 200 m		35 - 844
Sicily Channel	Mazzocchi *et al.* (1997)	October 1991	0 - 200 m		212 - 311
Levantine Sea (central)	Mazzocchi *et al.* (1997)	October 1991	0 - 200 m		97 - 13
	Pasternak *et al.* (2005)	May 2002	0 - 150 m		150 - 387
Offshore Egypt	Zakaria (2006)	Annual range 1984	0 - 100 m		200 - 1 100

* Copepods (individuals m^{-3}): 500–5000

Indeed, species of small copepods (<1 mm) dominate the epipelagic layer all over the Mediterranean Sea, as they do in the neighbouring subtropical Atlantic (Huskin *et al.*, 2001). *Clausocalanus* spp. (mostly *C. furcatus*, *C. pergens*, *C. paululus*, and *C. arcuicornis*) are the most abundant calanoid species, accompanied by the cyclopoids *Oithona* spp. (mainly *O. plumifera*, *O. similis*, and *O. setigera*) and *Oncaea* spp. (Seguin *et al.*, 1994; Siokou-Frangou *et al.*, 1997; Youssara and Gaudy, 2001; Gaudy *et al.*, 2003; Mazzocchi *et al.*, 2003; Andersen *et al.*, 2004; Fernández de Puelles *et al.*, 2004; Riandey *et al.*, 2005). The juveniles of the above genera dominate mesozooplankton communities throughout the year, whereas the adults of different congeneric species peak successively throughout the seasons (Siokou-Frangou *et al.*, 1997; Mazzocchi *et al.*, 2003; Peralba and Mazzocchi, 2004). The following copepod species (listed in order of abundance) appear to be spatially distributed. Thus, *Centropages typicus*, *Temora stylifera*, *Paracalanus parvus*, and *Acartia clausi* are more abundant in the WMed and in the Adriatic and northern Aegean seas (Hure *et al.*, 1980; Kouwenberg, 1994; Seguin *et al.*, 1994; Saiz *et al.*, 1999; Andersen *et al.*, 2004; Gaudy *et al.*, 2003; Fernández de

Puelles *et al.*, 2004; Zervoudaki *et al.*, 2006), while *Corycaeus* spp., *Farranula rostrata, Haloptilus longicornis,* and *Calocalanus* spp. seem to prefer the EMed (Weikert and Trinkaus, 1990; Siokou-Frangou *et al.*, 1997, 2004; Mazzocchi *et al.*, 2003).

The community composition and structure was found to be affected significantly by the mesoscale hydrological and circulation features. The copepods *Centropages typicus* and *Clausocalanus furcatus* in the Alboran Sea reveal a preference for the frontal area (Youssara and Gaudy, 2001), and different assemblages characterize the two sides of the front formed between the modified Black Sea water and the Aegean Sea water in the northeastern Aegean Sea (Zervoudaki *et al.*, 2006; Siokou-Frangou *et al.*, 2009). Community composition differs among cyclonic and anticyclonic gyres both in the eastern and western basins (Siokou-Frangou *et al.*, 1997; Riandey *et al.*, 2005) as well as across the front and the anticyclonic gyre of the Ligurian Sea (Pinca and Dallot, 1995).

Conclusions

The increased number of zooplankton studies in the Mediterranean Sea (especially in the EMed) during the past two decades has improved our knowledge of the distribution of pelagic communities in this "miniature ocean". The EMed is indeed poorer than the WMed, but within the former, there are areas presenting more similarities with the latter (both as standing stock and community composition), owing to similarities in environmental parameters (lower salinity and depth than the EMed). The influence of hydrology and circulation on mesozooplankton distribution contributes significantly to their spatial heterogeneity. This variability should be reflected in the structure of the planktonic foodweb in the open Mediterranean Sea, and argues for the need to address future integrated studies on the topic in the basin.

References

Alcaraz, M., Calbet, A., Estrada, M., Marrase, C., Saiz, E., and Trepat, I. 2007. Physical control of zooplankton communities in the Catalan Sea. Progress in Oceanography, 74: 294–312.

Andersen, V., Devey, C., Gubanova, A., Picheral, M., Malnikov, V., Tsarin, S., and Prieur, L. 2004. Vertical distributions of zooplankton across the Almeria–Oran frontal zone (Mediterranean Sea). Journal of Plankton Research, 26: 275–293.

Antoine, D., André, J-M., and Morel, A. 1996. Oceanic primary production 2. Estimation at global scale from satellite (coastal zone color scanner) chlorophyll. Global Biogeochemical Cycles, 10: 57–69.

Benovic, A., Lucic, D., Onofri, V., Batistic, M., and Njire, J. 2005. Bathymetric distribution of medusae in the open waters of the middle and south Adriatic Sea during spring 2002. Journal of Plankton Research, 6: 78–89.

Bethoux, J. P., Morin, P., Madec, C., and Gentili, B. 1992. Phosphorus and nitrogen behaviour in the Mediterranean Sea. Deep Sea Research, 39: 1641–1654.

Böttger-Schnack, R. 1997. Vertical structure of small metazoan plankton, especially non-calanoid copepods. II. Deep eastern Mediterranean (Levantine Sea). Oceanologica Acta, 20: 399–419.

Calbet, A., Saiz, E., and Alcarez, M. 2002. Copepod egg production in the NW Mediterranean: effects of winter environmental conditions. Marine Ecology Progress Series, 237: 173–184.

Champalbert, G. 1996. Characteristics of zooplankton standing stock and communities in the western Mediterranean Sea: relations to hydrology. Scientia Marina, 60(Suppl. 2): 97–113.

Christou, E. D., Siokou-Frangou, I., Mazzocchi, M. G., and Aguzzi, L. 1998. Mesozooplankton abundance in the E. Mediterranean during spring 1992. Rapport Commission Internationale pour la Mer Méditerranée, 35: 410–411.

Dolan, J. R., Claustre, H., Carlotti, F., Plouvenez, S., and Moutin, T. 2002. Microzooplankton diversity: relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic coast of Morocco to the eastern Mediterranean. Deep Sea Research Part I, 49: 1217–1232.

Fernández de Puelles, M-L., Valencia, J., Jansa, J., and Morillas, A. 2004. Hydrographical characteristics and zooplankton distribution in the Mallorca Channel (western Mediterranean): spring 2001. ICES Journal of Marine Science, 61: 654–666.

Gaudy, R. 1985. Features and peculiarities of zooplankton communities from the western Mediterranean. *In* Mediterranean Marine Ecosystems, pp. 297–303. Ed. by M. Moraitou-Apostolopoulou and V. Kiortsis. Plenum Press, New York and London.

Gaudy, R., Youssara, F., Diaz, F., and Raimbault, P. 2003. Biomass, metabolism and nutrition of zooplankton in the Gulf of Lions (NW Mediterranean). Oceanologica Acta, 26: 357–372.

Hure, J., Ianora, A., and Scotto di Carlo, B. 1980. Spatial and temporal distribution of Copepod communities in the Adriatic Sea. Journal of Plankton Research, 2: 295–316.

Huskin, M. E., Anadon, R., Medina, G., Head, R. D., and Harris, R. P. 2001. Mesozooplankton distribution and copepod grazing in the subtropical Atlantic near the Azores: influence of mesoscale structures. Journal of Plankton Research, 23: 671–691.

Kouwenberg, J. 1994. Copepod distribution in relation to seasonal hydrographics and spatial structure in the north-western Mediterranean (Golfe du Lion). Estuarine and Coastal Marine Science, 38: 69–90.

Krsinic, F. 1998. Vertical distribution of protozoan and microcopepod communities in the South Adriatic Pit. Journal of Plankton Research, 20: 1033–1060.

Mazzocchi, M. G., Christou, E. D., Fragopoulou, N., and Siokou-Frangou, I. 1997. Mesozooplankton distribution from Sicily to Cyprus (eastern Mediterranean) I. General aspects. Oceanologica Acta, 20: 521–535.

Mazzocchi, M. G., Nervegna, D., D'Elia, G., Di Capua, I., Aguzzi, L., and Boldrin, A. 2003. Spring zooplankton communities in the epipelagic Ionian Sea in relation to the eastern Mediterranean Transient. Journal of Geophysical Research, 108(C9), 8114, doi: 10.1029/2002JC001640.

Moraitou-Apostolopoulou, M. 1985. Zooplankton communities in the eastern Mediterranean Sea. *In* Mediterranean Marine Ecosystems, pp. 303–332. Ed. by M. Moraitou-Apostolopoulou and V. Kiortsis. Plenum Press, New York and London.

Pasternak, A., Wassmann, P., and Riser, C. W. 2005. Does mesozooplankton respond to episodic P inputs in the Eastern Mediterranean? Deep Sea Research Part II, 52: 2975–2989.

Peralba, À., and Mazzocchi, M. G. 2004. Vertical and seasonal distribution of eight *Clausocalanus* species (Copepoda: Calanoida) in oligotrophic waters. ICES Journal of Marine Science, 61: 645–653.

Pinca, S., and Dallot, S. 1995. Meso- and macrozooplankton composition patterns related to hydrodynamic structures in the Ligurian Sea (Trophos-2 experiment, April–June 1986). Marine Ecology Progress Series, 126: 49–65.

Pitta, P., Giannakourou, A., and Christaki, U. 2001. Planktonic ciliates in the oligotrophic Mediterranean Sea: longitudinal trends of standing stocks, distributions and analysis of food vacuole contents. Aquatic Microbial Ecology, 24: 297–311.

Riandey, V., Champalbert, G., Carlotti, F., Taupier-Letage, I., and Thibault-Bothac, D. 2005. Zooplankton distribution related to the hydrodynamic features in the Algerian basin (western Mediterranean Sea) in summer 1997. Deep Sea Research Part I, 52: 2029–2048.

Saiz, E., Calbet, A., Irigoien, X., and Alcaraz, M. 1999. Copepod egg production in the western Mediterranean: response to food availability in oligotrophic environments. Marine Ecology Progress Series, 187: 179–189.

Scotto di Carlo, B., Ianora, A., Fresi, E., and Hure, J. 1984. Vertical zonation patterns for Mediterranean copepods from the surface to 2000 m at a fixed station in the Tyrrhenian Sea. Journal of Plankton Research, 6: 1031–1036.

Seguin, G., Errhif, A., and Dallot, S. 1994. Diversity and structure of pelagic copepod populations in the frontal zone of the eastern Alboran Sea. Hydrobiologia, 292/293: 369–377.

Siokou-Frangou, I., Christou, E. D., Fragopoulou, N., and Mazzocchi, M. G. 1997. Mesozooplankton distribution from Sicily to Cyprus (eastern Mediterranean) II. Copepod assemblages. Oceanologica Acta, 20: 537–548.

Siokou-Frangou, I., Shiganova, T., Christou, E. D., Kamburska, L., Gubanova, A., Konsulov, A., Musaeva, E., *et al.* 2004. Zooplankton communities in the Aegean and Black seas: a comparative study. Marine Biology, 144: 1111–1126.

Siokou-Frangou, I., Zervoudaki, S., Christou, E. D., Zervakis, V., and Georgopoulos, D. 2009. Variability of mesozooplankton spatial distribution in the north Aegean Sea, as influenced by the Black Sea waters outflow. Journal of Marine Systems, doi: 10.1016/j.jmarsys.2008.12.025.

Thibault, D., Gaudy, R., and Le Fèvre, J. 1994. Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria–Oran Front, western Mediterranean Sea). Significance of pelagic food webs. Journal of Marine Systems, 5: 297–313.

Weikert, H., and Trinkaus, S. 1990. Vertical zooplankton abundance and distribution in the deep eastern Mediterranean Sea SE of Crete. Journal of Plankton Research, 12: 601–628.

Youssara, F., and Gaudy, R. 2001. Variations of zooplankton in the frontal area of the Alboran Sea (Mediterranean Sea) in winter 1997. Oceanologica Acta, 24: 361–376.

Zakaria, H. Y. 2006. The zooplankton community in Egyptian Mediterranean waters: a review. Acta Adriatica, 47: 195–206.

Zervoudaki, S., Nielsen, T. G., Christou, E. D., and Siokou-Frangou, I. 2006. Zooplankton distribution and diversity in a frontal area of the Aegean Sea. Marine Biology Research, 2: 149–168.

14. Temporal fluctuations of zooplankton communities in Varna Bay (western Black Sea) and Sevastopol Bay (northern Black Sea): a comparative study

Kremena Stefanova, Lyudmila Kamburska, Alexandra Gubanova, and Denis Altukhov

Introduction

Human activities tend to be concentrated mainly in coastal regions, which have a limited ability to assimilate their adverse effects. In the coastal areas of Europe and the Black Sea, the consequences of these activities, e.g. water pollution, eutrophication, loss of biological diversity, introduction of non-indigenous species, overfishing, land use and landscape deterioration, and coastal erosion, are already well known (Moncheva *et al.*, 2001; Prodanov *et al.*, 2001; Gubanova *et al.*, 2002; Kideys, 2002; Kamburska, 2004; Oguz, 2005; Kamburska *et al.*, 2006).

Even so, the lack of comparable time-series data for the coastal areas of the Black Sea is a problem when attempting to make a consistent assessment of the marine environment. In this study, we attempt to trace the ecological features of the zooplankton communities in two vulnerable coastal areas: Sevastopol Bay (northern Black Sea, NBS) and Varna Bay (western Black Sea, WBS). Our aims were (i) to assess the state and trends of zooplankton communities in both regions; and (ii) to contrast temporal zooplankton variability in the NBS and WBS coastal regions relative to long-term changes.

Material and methods

Study area

The zooplankton information collated in this study is derived from two coastal sites: (i) Stn 301 at Cape Galata, Varna Bay (WBS), depth 21 m, monitored by the Institute of Oceanology (IO-BAS), Bulgaria; and (ii) Stn 2 in Sevastopol Bay (NBS), maximum depth 14 m, monitored by the Institute of Biology Southern Seas (IBSS), Ukraine (Figure 14.1). The data were obtained using similar methodologies, with sampling taking place during comparable months, seasons, and years (1976, 1979–1980, 1989–1990, 1995–1996, 2002–2003, and 2004–2007). Published historical data were used to elucidate long-term trends (Konsulov, 1986, 1991a, 1991b; Konsulov and Kamburska, 1997, 1998; Gubanova *et al.*, 2001, 2002; Kamburska and Stefanova, 2002; Gubanova, 2003; Kamburska *et al.*, 2003, 2006).

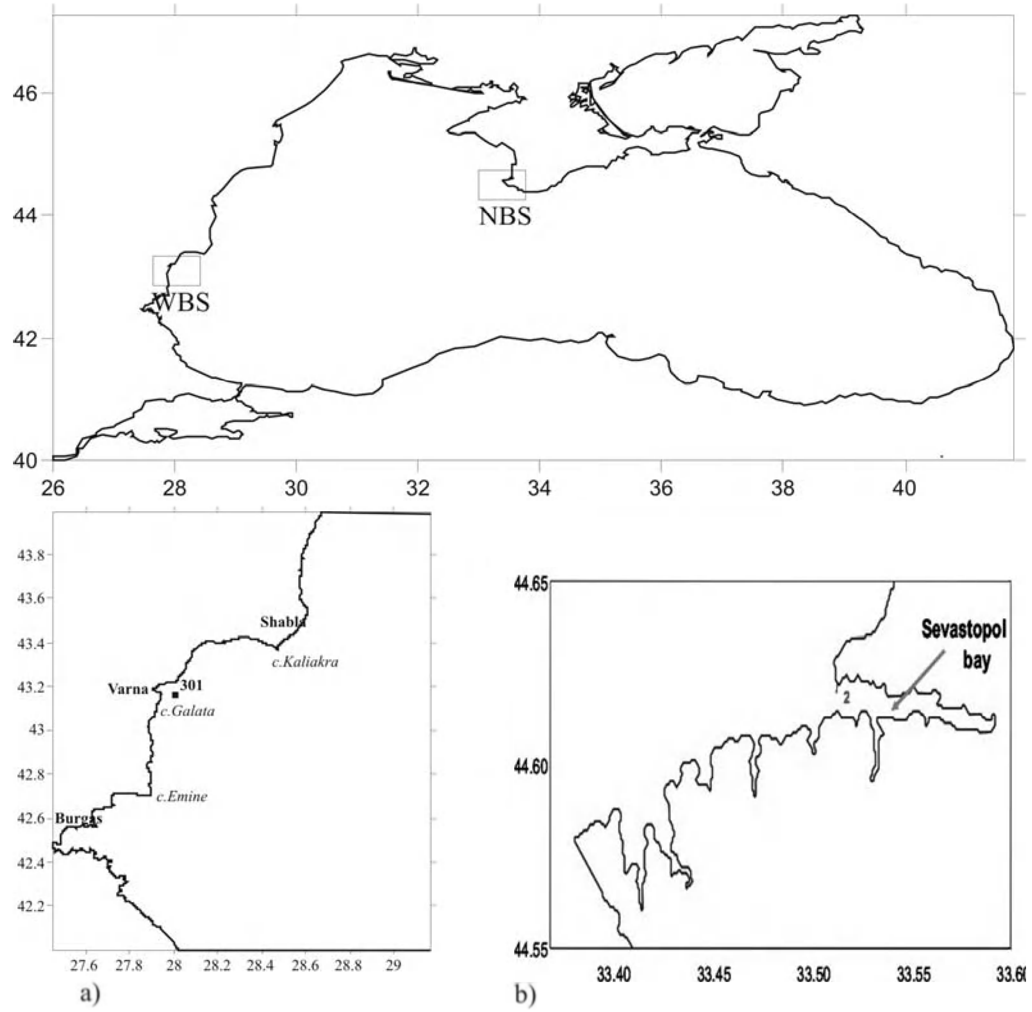

Figure 14.1. Maps of survey areas: (top panel) location of stations in the Black Sea; (a) Stn 301 at ca. Galata–Varna Bay (WBS); and (b) Stn 2 Sevastopol Bay (NBS).

Sampling method and analysis

Samples were collected using vertical Juday nets (0.1 m^2 mouth area, 150 μm mesh) towed from 2 m above the seabed and to the surface at a speed of 0.5 m s^{-1}. The volume of water passing through the net was estimated by multiplying the towing distance by the mouth area of the net. Before preservation in buffered 4% formalin solution, gelatinous species were sorted, counted, and measured. The numerical abundance (individuals m^{-3}) was calculated for each sample.

Statistical analyses were performed using the statistical software PRIMER.

Results and discussion

Interannual fluctuations

Plankton abundance and species composition are characterized by a very high degree of spatial and temporal variability, especially in coastal and shelf waters (Ribera d'Alcalà *et al.*, 2004). Ecosystem changes in the Black Sea basin were most pronounced in the NBS and WBS, where regional hydrochemical characteristics are primarily governed by nutrient enrichment supplied by run-off from the Danube, Dniester, and Dnieper rivers (BSC, 2008). Zooplankton communities have previously revealed high interannual variability at both sites.

In the WBS, total zooplankton numerical abundance generally ranged from ca. 1100 to ca. 53 000 individuals m^{-3}, with high values observed during the 1980s and 1990s (period of eutrophication), whereas, in the NBS, values ranged from ca. 300 to ca. 14 500 individuals m^{-3}. During the period 1976–1980, the amount of zooplankton in Sevastopol Bay (NBS) was two- to twelvefold greater than in Varna Bay (WBS; Figure 14.2). Most probably, the plankton fauna in the NBS was affected earlier than the WBS by eutrophication. Initially, the ecosystem responded favourably to the eutrophication and enhanced primary production by an increase in mesozooplankton and fish stocks during the late 1970s and early 1980s. Since the mid-1980s, a fivefold decrease in mesozooplankton in the Black Sea has been observed as a result of severe grazing pressure by the opportunistic species *Noctiluca scintillans*, *Aurelia aurita*, and *Mnemiopsis leidyi* (Oguz *et al.*, 2004). For both sites, the critical period was 1990–1996, when strong ecosystem changes continued to prevail.

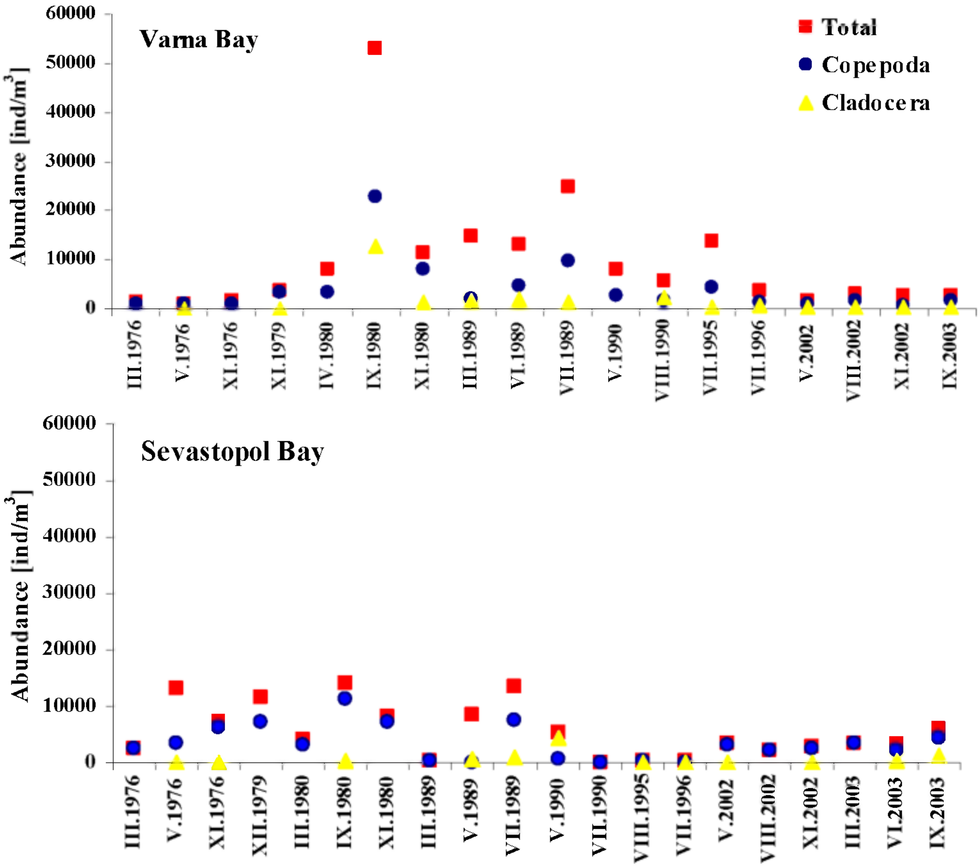

Figure 14.2. Abundance of total zooplankton, copepods, and cladocerans (individuals m^{-3}) from 1976 to 2003 in (top) Varna Bay (WBS) and (bottom) Sevastopol Bay (NBS).

Species composition

The structure of the community has changed significantly over the decades, mainly as a result of reorganization of the dominant groups and species. The most important change in the zooplankton community after the 1970s was in diversity. The changes in species composition of the phytoplankton, together with mass development of mixotrophic algae, triggered the expansion of phytophagous and detritophagous zooplankters (Zaitzev and Aleksandrov, 1997). As a result, the total abundance of the opportunistic copepod *Acartia clausi* increased significantly. The long-term dynamics of *Acartia*, which was generally dominant, demonstrated two periods of exceptionally great abundance, first during the late 1970s (clearer in the NBS) to early 1980s (the

WBS), and second from the end of the 1980s. Furthermore, species such as *Oithona nana* maintained a noteworthy quantity during 1976–1980 in both regions.

Cladocerans were represented by *Pleopis polyphemoides*, a component of the plankton fauna, with similar annual and interannual dynamics, in both regions. The extension of warm-water species, such as *Centropages ponticus*, *Evadne tergestina*, *E. spinifera*, and *Penilia avirostris*, after 2002 could be attributed to the impact of climate change, because there was no evidence of concurrent increases in eutrophication within the interior basin (Figure 14.3a and 14.3b).

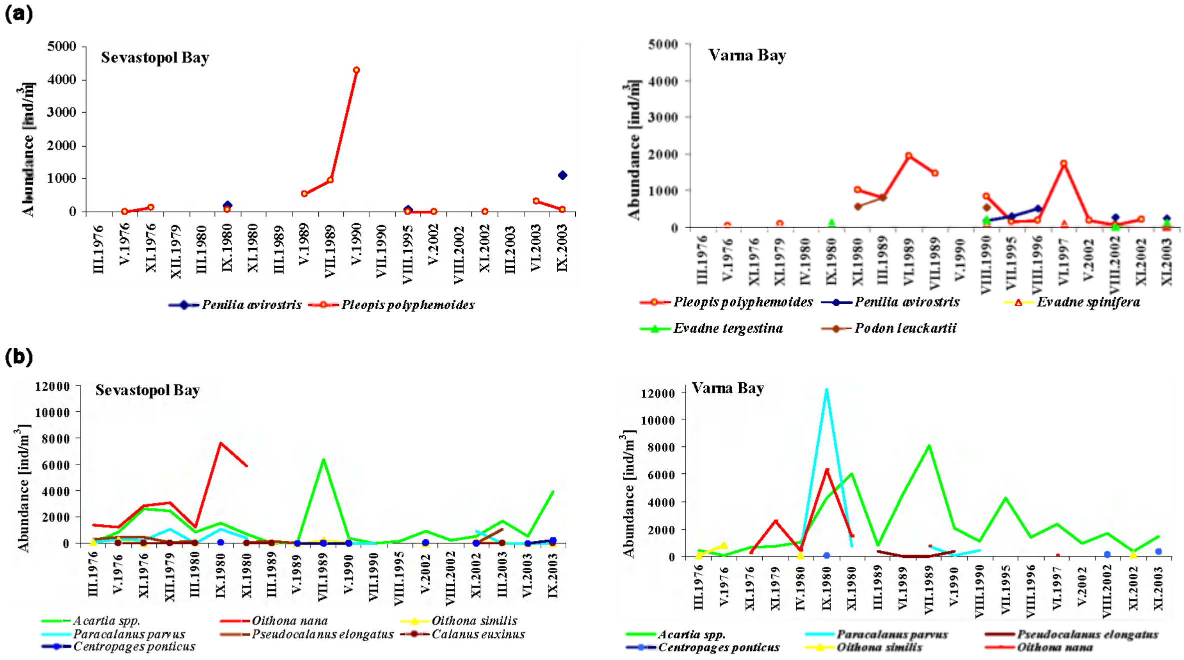

Figure 14.3. Abundance of (a) the most dominant cladocerans and (b) the most dominant copepods in Sevastopol and Varna bays from 1976 to 2003.

The heterotrophic dinoflagellate *N. scintillans*, although decreasing in abundance from the 1980s, occurred regularly in Sevastopol Bay (NBS), but at lower densities than in Varna Bay (WBS), where it appeared frequently in bloom concentrations (maximum of ca. 150 000 individuals m^{-3}).

The striking variability in zooplankton abundance and species assemblages, although not synchronized, is a peculiar attribute of the communities in the NBS and WBS coastal areas.

Cluster analysis was applied to the data in order to identify homogeneous subgroups by similarity of taxonomic composition and abundance. This analysis differentiated two main groups, but with a very high percentage similarity by the Bray–Curtis index (almost 73%; figure not shown). The results suggest great integrity in plankton communities during the 1970s, when the community was characterized by the dominance of copepods, mainly *Oithona nana* and *A. clausi*. However, the cluster analysis further demonstrates that, since 1990, the two areas have diverged. Seven species and taxa discriminated the groups. The main contributors (descriptors) to the dissimilarity were *E. spinifera*, *E. tergestina*, and *P. avirostris*, which prevailed in the WBS coastal areas. The brackish species *Podon leuckartii* and the rotifer *Synchaeta vorax*, which were only present in Varna Bay (WBS), also contributed to the differentiation of the sites.

Conclusions

The following similarities were observed in the plankton fauna of the WBS and NBS coastal areas during the study period.

- a significant variability in community structure
- an overall decreasing trend in total numerical abundance
- a shift in abundance during the 1980s, possibly in response to the combined impacts of eutrophication, overfishing, and introduction of non-indigenous species

The following dissimilarities between the WBS and NBS were observed.

- regular occurrence of *N. scintillans* in the NBS, but at a lower level than in the WBS (frequently in "bloom" concentrations)
- large interannual variability of mesozooplankton abundance in the WBS (Varna Bay), but a rather insignificant variability in the NBS (Sevastopol Bay)
- a generally greater zooplankton abundance in the WBS than in the NBS (except during the 1970s)
- the mesozooplankton community pattern (concentration, taxonomic structure, and interannual dynamics) appeared more vulnerable and unstable in WBS than in the NBS

The differences between the two Black Sea sites suggest that local driving forces play an essential role in the dynamics of the coastal ecosystems, which, furthermore, could obscure the implication of climate changes.

References

BSC (Black Sea Commission). 2008. State of the Environment of the Black Sea (2001–2006/7). Black Sea Commission Publications 2008-3, Istanbul, Turkey. 419 pp.

Gubanova, A. D. 2003. Long-term changes in the species composition and abundance of copepods of genera Acartia DANA in the Sevastopol Bay. *In* Modern Condition of Biological Diversity in Near-shore Zone of Crimea (the Black Sea Sector), pp. 94–100. Ed. by V. N. Eremeev and A. V. Gaevskaya. Ekosi-Gidrophizika, Sevastopol. 511 pp. [In Russian.]

Gubanova, A. D., Prusova, I. Yu., Nierman, U., Shadrin, N. V., and Polikarpov, I. G. 2001. Dramatic change in the copepod community in Sevastopol Bay (Black Sea) during two decades (1976–1996). Senckenbergiana Maritima, 31: 17–27.

Gubanova, A. D., Polikarpov, I. G., Saburova, M. A., and Prusova, I. Yu. 2002. Long-term dynamic of mesozooplankton community in the Sevastopol Bay (1976–1996) as exemplified by Copepoda. Oceanology, 42: 537–545. [In Russian and English.]

Kamburska, L. 2004. Effects of *Beroe* cf. *ovata* on gelatinous and other zooplankton along the Bulgarian Black Sea coast. *In* Aquatic Invasions in the Black, Caspian, and Mediterranean Seas, pp. 137–154. Ed. by H. Dumont, T. A. Shiganova, and U. Niermann. NATO ASI Series, 2 Environment, Vol. 35. Kluwer Academic Publishers, Dordrecht. 313 pp.

Kamburska, L., and Stefanova, K. 2002. Ecological state of zooplankton community in the system Beloslav Lake–Varna Lake–Varna Bay. *In* Proceedings of the Sixth International Conference on Marine Science and Technology, Varna, Bulgaria, 1: 336–341.

Kamburska, L., Doncheva, V., and Stefanova, K. 2003. On the recent changes of zooplankton community structure along the Bulgarian Black Sea coast – a post invasion effect of exotic ctenophores interactions. *In* Proceedings of the First International Conference on

Environmental Research and Assessment, 23–27 March 2003, Bucharest, Romania, pp. 69–85.

Kamburska, L., Shiganova, T., Stefanova, K., Moncheva, S., and Dowell, M. 2006. Interannual variations in the summer distribution of the invasive ctenophore *Mnemiopsis leidyi* A. Agassiz in the Black Sea. *In* Proceedings of the Workshop on Understanding and Modelling the Black Sea Ecosystem in Support of Marine Conventions and Environmental Policies, pp. 8–14. Ed. by A. K. Stips and W. Schrimpf.

Kideys, A. E. 2002. Fall and rise of the Black Sea ecosystem. Science, 297: 1482–1483.

Konsulov, A. 1986. Seasonal and annual dynamics of zooplankton in the Black Sea along the Bulgarian coast for the 1974–1984 period. Oceanology, 16: 23–33.

Konsulov, A. 1991a. Recent state of zooplankton community in Varna and Beloslav Lakes. *In* Proceedings of the Second Scientific Conference, Varna, Bulgaria, pp. 98–108. 246 pp. [In Bulgarian.]

Konsulov, A. 1991b. Study of biology, ecology and zooplankton significance along the Bulgarian Black Sea coast. PhD thesis. 302 pp.

Konsulov, A., and Kamburska, L. 1997. Sensitivity to anthropogenic factors of the plankton fauna adjacent to the Bulgarian coast of the Black Sea. *In* Sensitivity to Change: Black Sea, Baltic Sea and North Sea, pp. 95–104. Ed. by E. Ozsoy and A. Mikaelyan. NATO ASI Series, 2 Environment, Vol. 27. Kluwer Academic Publishers, Dordrecht. 516 pp.

Konsulov, A., and Kamburska, L. 1998. Black Sea zooplankton structural dynamic and variability off the Bulgarian Black Sea coast during 1991–1995. *In* Ecosystem Modelling as a Management Tool for the Black Sea, pp. 281–293. Ed. by L. Ivanov and T. Oguz. NATO ASI Series, 2 Environment, Vol. 47. Kluwer Academic Publishers, Dordrecht. 516 pp.

Moncheva, S., Doncheva, V., Shtereva, G., Kamburska, L., Malej, A., and Gorinstein, S. 2001. Application of eutrophication indices for assessment of the Bulgarian Black Sea coastal ecosystem ecological quality, pp. 71–82. *In* Proceedings of the Third Black Sea International Conference on Environmental Protection Technologies for Coastal Areas, 6–8 June 2001, Varna, Bulgaria.

Oguz, T. 2005. Long-term impacts of anthropogenic forcing on the Black Sea ecosystem. Oceanography, 18(Special issue: Black Sea Oceanography): 112–121.

Oguz, T., Tugrul, S., Kideys, A., Ediger, V., and Kubilay, N. 2004. Chapter 33. Physical and biogeochemical characteristics of the Black Sea. *In* The Sea: Ideas and Observations on Progress in the Study of Seas, Vol. 14, pp. 1331–1369. Ed. by A. R. Robinson and K. H. Brink. Harvard University Press, Cambridge, MA.

Prodanov, K., Moncheva, S., Konsulov, A., Kamburska, L., Konsulova, T., and Dencheva, K. 2001. Recent ecosystem trends along the Bulgarian Black Sea coast. Oceanology, 3: 110–128.

Ribera d'Alcalà, M., Conversano, F., Corato, F., Licandro, P., Mangoni, O., Marino, D., Mazzocchi, M. G., *et al.* 2004. Seasonal patterns in plankton communities in a pluriannual time-series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. Scientia Marina, 68(Suppl. 1): 65–83.

Zaitsev, Y., and Aleksandrov, B. 1997. Recent man-made changes in the Black Sea Ecosystem. *In* Sensitivity to Change: Black Sea, Baltic Sea and North Sea, pp. 25–32. Ed. by E. Ozsoy and A. Mikaelyan. NATO ASI Series, 2 Environment, Vol. 27. Kluwer Academic Publishers, Dordrecht. 516 pp.

15. Study of the copepod communities of Tangier and M'Diq (Atlantic and Mediterranean Moroccan coast, Strait of Gibraltar)

Amal Zaafa, Omar Ettahiri, Amina Berraho, Laila Somoue, Najat Elkhiati, and Mohamed Ramdani

Introduction

The Strait of Gibraltar is characterized by complex circulation in both directions, from the Atlantic to the Mediterranean and vice versa, in surface and deeper layers. Given the close relationship between the marine environment and the various biological components, the ecosystem of the Strait is constrained by this circulation.

As pointed out by Harris *et al*. (2000), the zooplankton community is very sensitive and very reactive to variations in the environment. In most cases, a change in the structure of the zooplankton populations reflects a change in the hydrological and climatic conditions. For this reason, many authors have suggested using zooplankton as an indicator of change in marine systems (Fromentin and Planque, 1996; Beaugrand *et al*., 2000, 2002; Edwards *et al*., 2002).

In this context, a preliminary study of the Strait of Gibraltar was carried out during 2006–2007 to detect the characteristics of the copepod communities of this ecosystem.

Material and methods

Zooplankton sampling was carried out during three months in two consecutive years: March, May, and December 2006, and May, July, and November 2007. Three stations were sampled along two transects: one off the Atlantic coast (the marine area off Tangier) and one off the Mediterranean coast (the M'Diq coastal region). The depth of the sampling locations off the Atlantic and Mediterranean coasts varied between 30 and 400 m and between 90 and 500 m, respectively (Figure 15.1).

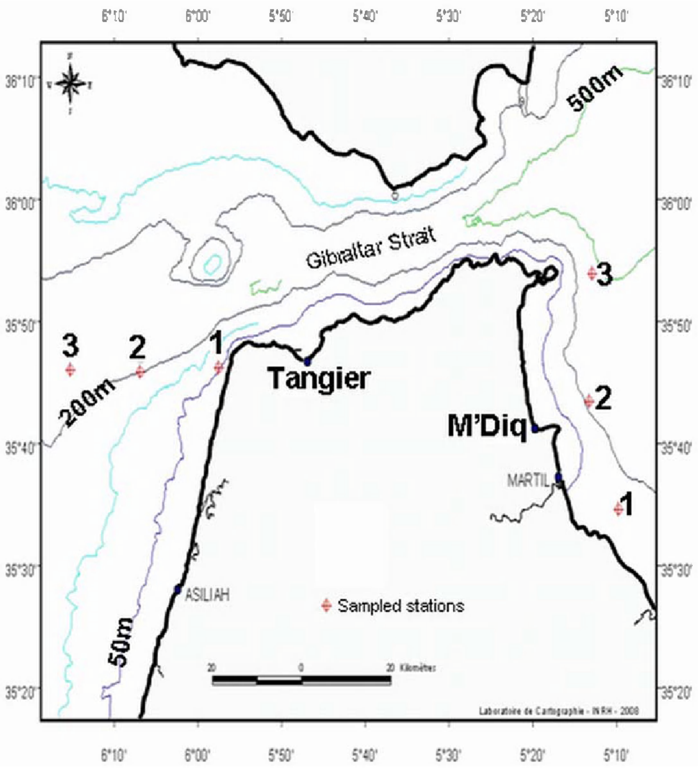

Figure 15.1. Map of the Strait of Gibraltar showing the location of the sampled stations.

Zooplankton samples were collected with a small bongo net (20 cm mouth diameter and 145 μm mesh) fitted with a flowmeter for the measurement of the water volume filtered. For identification and counting of the zooplankton, samples were separated into several fractions using the Motoda splitter (Motoda, 1959). Species were identified using appropriate taxonomic keys (Rose, 1933; Trégouboff and Rose, 1957; Frost and Fleminger, 1968; Crisafi and Mazza, 1966; Bradford *et al.*, 1983).

Data analysis included the calculation of biological indices (species richness, density, and Shannon index) using the software "Statistica", based on the "average linkage" method (Lance and Williams, 1967; Legendre and Demers, 1984).

Results

Qualitative analysis of all the zooplankton samples demonstrated a clear predominance of copepods, which accounted for 93% and 87% of the zooplankton on the Atlantic and Mediterranean transects, respectively. On the specific level, 85 species were recorded on the Atlantic transect and 82 on the Mediterranean transect, and 64 species were common to both transects.

The temporal variability (total number of species) was similar on both transects, with a maximum in autumn (December 2006 and November 2007; Figure 15.2). However, the between-station variability in species abundance was less marked on the Mediterranean than on the Atlantic transect.

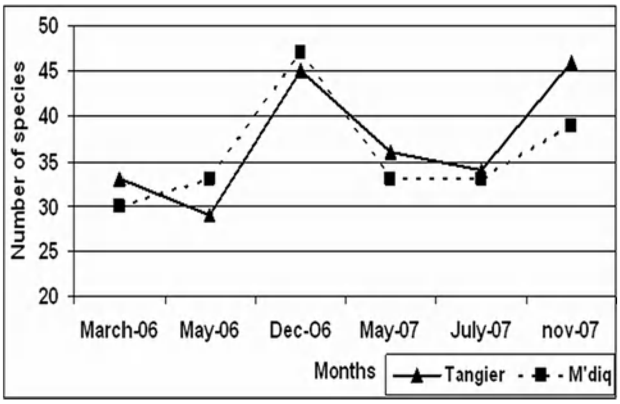

Figure 15.2. Variation in the specific richness of copepods in Tangier and M'Diq, March 2006–November 2007.

Regarding the quantitative evaluation of the copepods in the studied areas, contrary to the species richness, autumn was characterized by a low average density on both transects. Moreover, in 2007, the abundance of copepods increased earlier in the Mediterranean (May) than in the Atlantic (July). Maximum density was recorded at a relatively shallow coastal station on the Atlantic transect (ca. 1100 individuals m^{-3}) and at a relatively deep station on the Mediterranean transect (ca. 800 individuals m^{-3}). The state of the copepod populations, determined by the Shannon index, demonstrated stable and balanced populations in autumn on both transects. However, during 2007, the populations were even more stable in the Atlantic, compared with 2006 and the Mediterranean populations (Figure 15.3).

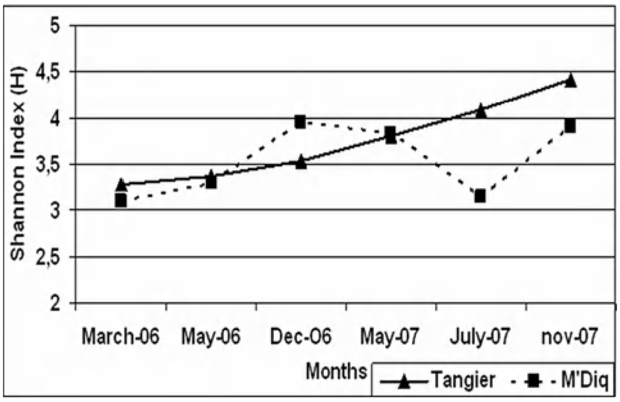

Figure 15.3. The Shannon index variation, March 2006–November 2007.

Discussion and conclusion

This study of the copepod community, undertaken off the Atlantic and Moroccan coasts, revealed similar numbers of species on both sites of the Strait of Gibraltar (82–85, including 64 species common to both regions). Giron (1963) related the zooplankton richness to the topography of the Alboran Sea, which is characterized by a narrow continental shelf and its geographical location near Atlantic water, where both neritic and pelagic species, and species of Atlantic origin, were present.

The temporal variation in the average densities demonstrated a seasonal cycle, more marked in the Atlantic than in the Mediterranean region. Indeed, in the Tangier area, the average density started to increase in spring (May), reached its maximum in summer (July), and decreased in autumn (November–December). However, in M'Diq, the peak of copepod abundance occurred in May (2007), with a minimum in November–December. According to Larnicol *et al.* (1995), the seasonal cycle of the Mediterranean water mass is not preserved on a time-scale, following the change in flow entering and leaving through the Strait of Gibraltar. Planktonic activity on the Mediterranean transect may be related to this cycle, which generates differences compared with the zooplankton production cycle in the Atlantic region. Moreover, Fernández de Puelles *et al.* (2003) demonstrated a seasonal cycle in zooplankton abundance, with a maximum during the first six months of the year.

In spite of a certain amount of variability between both sectors, the copepod populations were relatively stable and balanced in autumn 2006 and 2007. These results agreed with those of Chiahou and Ramdani (1997) and Somoue *et al.* (2005), who noted, in the northern and southern Moroccan Atlantic, a low diversity of copepods during the hot season. On the other hand, Roy (1992) underlined the role of hydrological conditions in affecting the structural variability of the zooplankton communities between warm and cold months. Indeed, the presence of upwelling during the warm months in the North Atlantic (Wooster *et al.*, 1976; Binet, 1991) and along the Alboran coast (García-Gorriz and Carr, 1999, 2001; Sarhan *et al.*, 2000; Gomez and Gorsky, 2002) supports the development of certain species and explains the imbalance in the copepod population structure in both the studied areas during these periods.

In conclusion, the Strait of Gibraltar is a very complex ecosystem whose various components are the result of exchanges between two completely different systems. An understanding of the functioning of this ecosystem requires the identification of the exchange elements and the magnitude of the exchange.

References

Beaugrand, G., Reid, P. C., Ibañez, F., and Planque, B. 2000. Biodiversity of North Atlantic and North Sea calanoid copepods. Marine Ecology Progress Series, 204: 299–303.

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692–1694.

Binet, D. 1991. Dynamique du plancton dans les eaux côtières ouest-africaines: écosystèmes équilibré et déséquilibrés. *In* Pêcheries ouest-africaines: variabilité, instabilité et changement, pp. 117–136. Ed. by P. Cury and C. Roy. ORSTOM, Paris. 525 pp.

Bradford, J. M., Haakonssen, L., and Jillett, J. B. 1983. The marine fauna of New Zealand: pelagic calanoid copepods: families Euchaetidae, Phaennidae, Scolecithricidae, Diaixidae, and Tharybidae. Memoir of the New Zealand Oceanographic Institute, 90. 149 pp.

Chiahou, B., and Ramdani, M. 1997. Systématique et distribution saisonnière des copépodes pélagiques de la côte atlantique marocaine (région d'El Jadida). Journal de Recherche Océanographique, 22: 75–80.

Crisafi, P., and Mazza, J. 1966. Revisione del genere *Sapphirina* J. V. Thompson, 1829. Atti della Società Peloritana di Scienze Fisiche, Matematiche e Naturali, 12: 561–618.

Edwards, M., Beaugrand, G., Reid, C., Rowden, A., and Jones, M. 2002. Ocean climate anomalies and the ecology of the North Sea. Marine Ecology Progress Series, 239: 1–10.

Fernández de Puelles, M. L., Pinot, J. M., and Valencia, J. 2003. Seasonal and interannual variability of zooplankton community in waters off Mallorca Island (Balearic Sea, western Mediterranean): 1994–1999. Oceanologica Acta, 26: 673–686.

Fromentin, J. M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. 2. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 111–118.

Frost, B. W., and Fleminger, A. 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bulletin of the Scripps Institution of Oceanography, 12: 1–235.

García-Gorriz, E., and Carr, M. E. 1999. The climatological annual cycle of satellite-derived phytoplankton pigments in the Alboran Sea. Geophysical Research Letters, 26: 2585–2988.

García-Gorriz, E., and Carr, M. E. 2001. Physical control of phytoplankton distributions in the Alboran Sea: a numerical and satellite approach. Journal of Geophysical Research, 106: 16 795–16 805.

Giron, F. 1963. Copépodes de la mer d'Alboran (Compagne du Président "Théodore-Tessier" juin 1957). Revue des Travaux de l'Institut des Pêches Maritimes, 27: 355–402.

Gomez, F., and Gorsky, G. 2002. Annual microplankton cycles in Villefranche Bay, Ligurian Sea, NW Mediterranean. Journal of Plankton Research, 25: 323–339.

Harris, R., Wiebe, P., Lenz, J., Skjoldal, H. R., and Huntley, M. 2000. ICES Zooplankton Methodology Manual. Academic Press, San Diego. 684 pp.

Lance, G. N., and Williams, W. T. 1967. A general theory of classificatory sorting strategies. 1. Hierarchical systems. Computer Journal, 9: 60–64.

Larnicol, G., Le Traon, P. Y., Ayoub, N., and De Mey, P. 1995. Mean sea level and surface circulation variability of the Mediterranean Sea from 2 years of TOPEX/POSEIDON altimetry. Topex/Poseidon data. Journal of Geophysical Research (Oceans), 100: 25 163–25 177.

Legendre, L., and Demers, S. 1984. Towards dynamic biological oceanography and limnology. Canadian Journal of Fisheries and Aquatic Sciences, 4: 2–19.

Motoda, S. 1959. Devices of simple plankton apparatus. Memoirs of the Faculty of Fisheries, Hokkaido University, 7: 73–94.

Rose, M. 1933. Copépodes pélagiques. Faune de France, Vol. 26. Fédération Française des Societés de Sciences Naturelles, Lechevalier, Paris. 374 pp.

Roy, C. 1992. Réponses des stocks de poissons pélagiques à la dynamique des upwellings en Afrique de l'ouest: analyse et modélisation. Collection Etudes et Thèses, ORSTOM, Paris. 146 pp.

Sarhan, T., Garcia Lafuente, J., Vargas, M., Vargas, J. M., and Plaza, F. 2000. Upwelling mechanisms in the northwestern Alboran Sea. Journal of Marine Systems, 23: 317–331.

Somoue, L., Elkhiati, N., Ramdani, M., Lam Hoi, T., Berraho, Am., and Do Chi, T. 2005. Abundance and structure of copepod communities along the Atlantic coast of southern Morocco. Acta Adriatica, 46: 63–76.

Trégouboff, G., and Rose, M. 1957. Manuel de planctonologie méditerranéenne. Tome I et II. Centre National de la Recherche Scientifique, Paris. 794 pp.

Wooster, W. S., Bakun, A., and McLain, D. R. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. Journal of Marine Research, 34: 131–141.

16. Seasonal and spatial variability of *Farranula rostrata* (Copepoda, Cyclopoida) in the Mediterranean Sea

Soultana Zervoudaki, Epaminondas D. Christou, Stamatina Isari, Davor Lucic, Maria Grazia Mazzocchi, Maria Luz Fernández de Puelles, Mohamed Nejib Daly Yahia, Alexis Ramfos, Nina Fragopoulou, and Ioanna Siokou-Frangou

Introduction

Non-calanoid copepods (i.e. Cyclopoida) have been reported to be numerically important in oligotrophic seas, playing relevant ecological roles in epipelagic communities (Calbet *et al.*, 2001; Turner, 2004; Zervoudaki *et al.*, 2007).

In the Mediterranean Sea, epipelagic zooplankton are characterized by diversified copepod assemblages in which numerous species of both temperate and subtropical origin co-occur (Razouls and Durand, 1991). Among cyclopoids, F*arranula rostrata* has been reported as one of the most abundant species among smaller copepods in the eastern Mediterranean (Siokou-Frangou *et al.*, 1997), whereas, in the western Mediterranean, its presence seems to be less important (Razouls and Kouwenberg, 1993; Youssara and Gaudy, 2001; Gaudy *et al.*, 2003; Riandey *et al.*, 2005). Despite these findings, the spatial distribution and seasonal variability of this species in the Mediterranean has been very poorly investigated (Siokou-Frangou *et al.*, 1997; Ramfos *et al.*, 2005, 2006; Isari *et al.*, 2006). To fill this gap, we present here the first comparative overview of the spatial and seasonal variability of *F. rostrata* in different offshore and coastal waters of the Mediterranean Sea.

Table 16.1. Sampling locations and methods used in data collection.

SITE	SAMPLING METHOD	DEPTH (M)	SAMPLING FREQUENCY	YEAR	SOURCE
Mallorca Channel	Bongo, 250 µm, oblique	75	Monthly	1994 – 2001	Fernández de Puelles *et al.* (2003)
Bay of Bizerte	WP-2, 200 µm, vertical	25	Monthly	2004	Daly-Yahia (pers. comm.)
Gulf of Naples	Nansen, 200 µm, vertical	50	Biweekly until 1990, weekly from 1995 onwards	1984 – 2006	Mazzocchi and Ribera d'Alcalà (1995), Ribera d'Alcalà *et al.* (2004)
N. Adriatic	WP-2, 200 µm, vertical	35	Monthly	1999 – 2006	Lučić, unpublished
S. Adriatic (Lokrum)	Nansen, 200 µm, vertical	90	Monthly	1996 – 1997	Lučić, unpublished
Saronic Gulf	WP-2, 200 µm, vertical	90	Seasonal	1997 – 2004	Siokou-Frangou *et al.* (1998)
Balearic Sea	WP-2, 200 µm, vertical	75, 100, 200	Monthly	1999	Fernández de Puelles (pers. comm.)
N. Aegean Sea	WP-2, 200 µm, vertical	200	March and September	1997, 1998, 2000, 2003	Siokou-Frangou *et al.* (2002); Zervoudaki *et al.* (2006); Isari *et al.* (2006)
S. Aegean Sea	WP-2, 200 µm, vertical	200	March and September	1997	Siokou-Frangou *et al.* (2002)
Ionian Sea	WP-2, 200 µm, vertical	200	March and September	2000	Ramfos *et al.* (2006)
Mediterranean Sea	WP-2, 200 µm, vertical	100	June	1999	Siokou-Frangou *et al.* (2004)
E. Mediterranean (POEM)	WP-2, 200 µm, vertical	300	October–November	1991	Siokou-Frangou *et al.* (1997)

Material and methods

The present study is based on a large dataset that includes quantitative information provided by weekly, monthly, and/or seasonal sampling of zooplankton performed in different offshore and coastal areas of the Mediterranean Sea. Table 16.1 summarizes the information on sampling stations, methods used, and periods of data analysed. Samples were taken by vertical or oblique hauls in water columns ranging from 35 to 90 m depth at the coastal areas and from 100 to 300 m depth at the offshore areas. The comparison between areas is based on the average values of *F. rostrata* abundance over seasons and/or stations and the percentage contribution of this species to total copepod abundance. The study areas are presented in detail in the references given in Table 16.1.

Results

The percentage contribution of *F. rostrata* to total copepod abundance was found to be low at the coastal areas (Figure 16.1). The contribution varied seasonally, and the temporal variability was more pronounced in the Gulf of Naples, the northern Adriatic Sea, and in the Bay of Bizerte than in the southern Adriatic and the Saronic Gulf, whereas it was minor in the Mallorca Channel. The minima of the contribution of *F. rostrata* generally occurred during summer, and the maxima in autumn–winter. Data from the offshore areas of the Aegean and Ionian seas (eastern Mediterranean) demonstrated that the relative abundance of this species among copepods was greater offshore than in coastal waters. However, in the western Mediterranean, the contribution of this species was low. In offshore waters of the eastern Mediterranean, *F. rostrata* dominated mainly during the warm period, whereas in the Balearic Sea, higher percentages were found during spring (Figure 16.1).

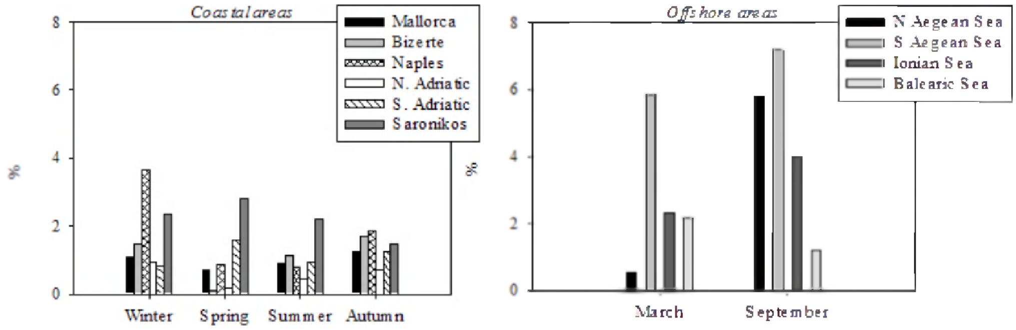

Figure 16.1. Relative abundance of *Farranula rostrata* in coastal and offshore waters of the Mediterranean Sea.

At a basin scale, during June 1999, *F. rostrata* accounted for 30% of the total copepod community in the oligotrophic Levantine Sea, and its contribution decreased towards the western Mediterranean (Figure 16.2). In autumn 1991, *F. rostrata* ranked among the eight most abundant species in the eastern Mediterranean, although its relative contribution was generally low (<10%).

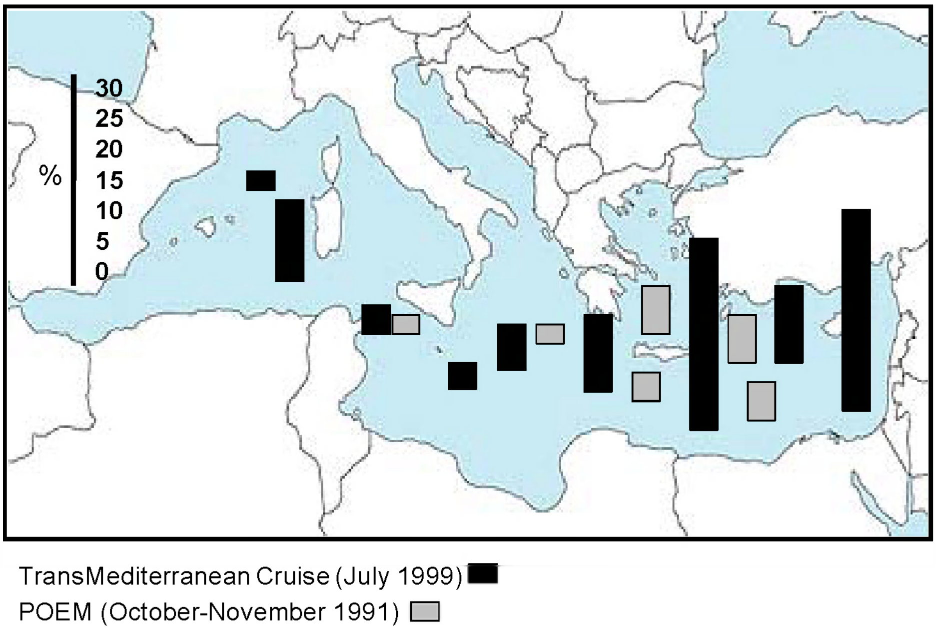

Figure 16.2. Relative abundance of *Farranula rostrata* in offshore areas of the Mediterranean Sea during July 1999 and October–November 1991.

Discussion

The sites of relatively great abundance are related to offshore areas of the eastern Mediterranean Sea and especially to the Levantine Sea. These results support the hypothesis of the species' subtropical character, given that the eastern Mediterranean is distinguished by a high percentage of thermophile and subtropical elements (Basescu, 1985), and that the Levantine Sea is the warmer and more saline area within the basin (Theocharis *et al.*, 1999). In addition, the greater abundance of *F. rostrata* in the offshore areas, compared with the coastal areas, confirms the pelagic character of the species (Raymont, 1983).

In the Mediterranean coastal waters, *F. rostrata* has not been found among the abundant or even common species in the studied areas nor in other Mediterranean coastal areas, according to the literature (Gaudy, 1985; Mazzocchi and Ribera d'Alcalà, 1995; Gaudy and Champalbert, 1998; Calbet *et al.*, 2001; Kamburska and Fonda-Umani, 2006). The low values of relative abundance in both coastal and offshore waters, however, should be considered cautiously because the zooplankton samples were collected with nets of 200 µm mesh or even larger. It is well known that the small copepods (such as *Farranula* spp.) have historically been undersampled because of the use of nets with a mesh of 200 µm or larger. The use of finer nets, especially in the Mediterranean Sea, has demonstrated that small copepods are more abundant than larger ones (Calbet *et al.*, 2001; Zervoudaki *et al.*, 2006).

Regarding seasonal fluctuations, *F. rostrata* demonstrated a preference for autumn and winter in the coastal areas, when the influence of the open sea becomes more intensive (Scotto di Carlo *et al.*, 1985; Siokou-Frangou *et al.*, 1998). This is confirmed by the observation that no clear seasonal pattern was observed in the Mallorca Channel, an area largely and continuously affected by offshore waters (Fernández de Puelles *et al.*, 2003). In the offshore areas, *F. rosrata* predominated during the warm period (June and September), corroborating the thermophilic character of the species. Studies of the seasonal cycle of *F. rostrata* have revealed that, in the Sargasso Sea, this species attained large numbers during April, June, and July and was among the five most abundant species (Georgiana and Deevey, 1971). In the Bermuda time-series station, *F. rostrata* was found mainly in spring, comprising approximately 20–25% of the overall non-calanoid copepod abundance (Al-Mutairi and Torres, 2006).

These first comparative observations on the spatial and seasonal distribution of *F. rostrata* suggest that this species is probably a key component in the eastern Mediterranean Sea. Its reproductive strategy, trophic modes, and population dynamics should be investigated in order to understand the ecological role of this species within the pelagic foodweb of oligotrophic areas.

References

Al-Mutairi, H. A., and Torres, J. J. 2006. Non-calanoid copepods at the Bermuda Atlantic Time-Series Study (BATS) Station: community structure and ecology, 1995–1999. American Society of Limnology and Oceanography (ASLO), 13th Ocean Sciences Meeting, 20–24 February 2006, Honolulu, HA.

Basescu, M. 1985. Geological determinants of marine plants and animals. *In* Mediterranean Marine Ecosystems, pp. 195–212. Ed. by M. Moraitou-Apostolopoulou and V. Kiortsis. Plenum Press, New York.

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., and Duarte, C. M. 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. Journal of Plankton Research, 23: 319–331.

Fernández de Puelles, M. L., Grás, D., and Hernádez-León, S. 2003. Annual cycle of zooplankton biomass, abundance and species composition in the neritic area of the Balearic Sea, western Mediterranean. Marine Ecology, 24: 123–139.

Gaudy, R. 1985. Features and peculiarities of zooplankton communities from the western Mediterranean. *In* Mediterranean Marine Ecosystems, pp. 279–301. Ed. by M. Moraitou-Apostolopoulou and V. Kiortsis. Plenum Press, New York.

Gaudy, R., and Champalbert, G. 1998. Space and time variations in zooplankton distribution south of Marseilles. Oceanologica Acta, 21: 793–802.

Gaudy, R., Youssara, F., Diaz, F., and Raimbault, P. 2003. Biomass, metabolism and nutrition of zooplankton in the Gulf of Lions (NW Mediterranean). Oceanologica Acta, 26: 357–372.

Georgiana, B., and Deevey, G. B. 1971. The annual cycle in quantity and composition of the zooplankton of the Sargasso Sea off Bermuda. I. The upper 500 m. Limnology and Oceanography, 16: 219–240.

Isari, S., Ramfos, A., Somarakis, S., Koutsikopoulos, C., Kallianiotis, A., and Fragopoulou, N. 2006. Mesozooplankton distribution in relation to hydrology of the northeastern Aegean Sea, eastern Mediterranean. Journal of Plankton Research, 27: 1–15.

Kamburska, L., and Fonda-Umani, S. 2006. Long-term copepod dynamics in the Gulf of Trieste (northern Adriatic Sea): recent changes and trends. Climate Research, 31: 195–203.

Mazzocchi, M. G., and Ribera d'Alcalà, M. 1995. Recurrent patterns in zooplankton structure and succession in a variable coastal environment. ICES Journal of Marine Science, 52: 679–691.

Ramfos, A., Somarakis, S., Koutsikopoulos, C., and Fragopoulu, N. 2005. Summer mesozooplankton distribution in coastal waters of central Greece (eastern Mediterranean). II. Species assemblages. Journal of the Marine Biological Association of the UK, 85: 765–774.

Ramfos, A., Isari, S., Somarakis, S., Georgopoulos, D., Koutsikopoulos, C., and Fragopoulou, N. 2006. Mesozooplankton community structure in offshore and coastal waters of the Ionian Sea (eastern Mediterranean) during mixed and stratified conditions. Marine Biology, 150: 29–44.

Raymont, J. E. G. 1983. Plankton and Productivity in the Oceans. 2nd Edition. Vol. 2: Zooplankton. 2nd edn. Pergamon Press, Oxford. 824 pp.

Razouls, C., and Durand J. 1991. Inventaire des copepods planctoniques mediterraneens. Vie Milieu, 41: 73–77.

Razouls, C., and Kouwenberg, J. H. M. 1993. Spatial-distribution and seasonal-variation of mesozooplankton biomass in the Gulf-of-Lions (northwestern Mediterranean). Oceanologica Acta, 16: 393–401.

Riandey, V., Champalbert, G., Carlotti, F., Taupier-Letage, I., and Thibault-Botha, D. 2005. Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. Deep Sea Research Part I, 52: 2029–2048.

Ribera d'Alcalà, M., Conversano, F., Corato, F., Licandro, P., Mangoni, O., Marino, D., Mazzocchi, M. G., *et al.* 2004. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. Scientia Marina, 68(Suppl. 1): 165–183.

Scotto di Carlo, B., Tomas, C. R., Ianora, A., Marino, D., Mazzocchi, M. G., Modigh, M., Montresor, M., *et al.* 1985. Uno studio integrato dell'ecosistema pelagic costriero del Golfo di Napoli. Nova Thalassia, 7: 99–128.

Siokou-Frangou, I., Christou, E. D., Fragopoulou, N., and Mazzocchi, M. G. 1997. Zooplankton distribution from Sicily to Cyprus (eastern Mediterranean) II. Copepod assemblages. Oceanologica Acta, 20: 537–547.

Siokou-Frangou, I., Papathanassiou, E., Lepretre, A., and Frontier, S. 1998. Zooplankton assemblages and influence of environmental parameters upon them in a Mediterranean coastal area. Journal of Plankton Research, 20: 847–870.

Siokou-Frangou, I., Bianchi, M., Christaki, U., Christou, E. D., Giannakourou, A., Gotsis, O., Ignatiades, L., *et al.* 2002. Organic carbon partitioning and carbon flow along a gradient of oligotrophy in the Aegean Sea (Mediterranean Sea). Journal of Marine Systems, 33/34: 325–353.

Siokou-Frangou, I., Zervoudaki, S., and Christou, E. D. 2004. Epipelagic mesozooplankton and copepod grazing along an east–west transect in the Mediterranean Sea. CIESM, Barcelona, 37th CIESM Congress, 7–11 June 2004, Barcelona, Spain.

Theocharis, A., Balopoulos, E., Kioroglou, S., Kontoyiannis, H., and Iona, A. 1999. A synthesis of the circulation and hydrography of the south Aegean Sea and the Straits of the Cretan Arc (March 1994–January 1995). Progress in Oceanography, 44: 511–530.

Turner, J. T. 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies, 43: 255–266.

Youssara, F., and Gaudy, R. 2001. Variations of zooplankton in the frontal area of the Alboran Sea (Mediterranean Sea) in winter 1997. Oceanologica Acta, 24: 361–376.

Zervoudaki, S., Nielsen, T. G., Christou, E. D., and Siokou-Frangou, I. 2006. Zooplankton distribution and diversity in a frontal area of the Aegean Sea. Marine Biology Research, 2: 149–168.

Zervoudaki, S., Christou, E. D., Nielsen, T. G., Siokou-Frangou, I., Assimakopoulou, G., Giannakourou, A., Maar, M., *et al.* 2007. The importance of smaller copepods in a frontal area of the Aegean Sea. Journal of Plankton Research, 29: 317–338.

Author contact information

Denis Altukhov, Sections 11, 14
Institute of Biology of the Southern Seas
National Academy of Sciences of Ukraine
2 Nakhimov Prospect
99011 Sevastopol
Ukraine
E-mail: dennalt@gmail.com

Elvire Antajan, Section 6
IFREMER Laboratoire Environnement Ressources
BP 699
62200 Boulogne-sur-Mer
France
E-mail: elvire.antajan@ifremer.fr

Mirna Batistic, Section 2
Institute for Marine and Coastal Research
University of Dubrovnik
Kneza Damjana Jude 12
20000 Dubrovnik
Croatia
E-mail: mirna.batistic@unidu.hr

Radhouan Ben-Hamadou, Section 1
Centro de Ciências do Mar do Algarve (CIMAR/CCMAR)
Universidade do Algarve
Campus de Gambelas
8005–139 Faro
Portugal
E-mail: bhamadou@ualg.pt

Amina Berraho, Section 15
Institut National de Recherche Halieutique
2 Rue de Tiznit
Casablanca 01
Morocco
E-mail: amina_berraho@yahoo.fr

Luis Chícharo, Section 1
Centro de Ciências do Mar do Algarve (CIMAR/CCMAR)
Universidade do Algarve
Campus de Gambelas
8005–139 Faro
Portugal
E-mail: lchichar@ualg.pt

Maria Alexandra Chícharo, Section 1
Centro de Ciências do Mar do Algarve (CIMAR/CCMAR)
Universidade do Algarve
Campus de Gambelas
8005–139 Faro
Portugal
E-mail: mchichar@ualg.pt

Epaminondas D. Christou, Section 16
Institute of Oceanography
Hellenic Centre for Marine Research
Athens-Souniou Avenue
PO Box 712
19013 Anavissos-Attikis
Greece
E-mail: edc@ath.hcmr.gr

Joana Cruz, Section 1
Centro de Ciências do Mar do Algarve (CIMAR/CCMAR)
Universidade do Algarve
Campus de Gambelas
8005–139 Faro
Portugal
E-mail: jcruz@ipimar.pt

Mohamed Nejib Daly Yahia, Sections 2, 16
University 7 November – Carthage
Faculty of Sciences of Bizerte
Laboratory of Aquatic Systems Biodiversity and Functioning
7021 Zarzouna
Bizerte
Tunisia
E-mail: nejib.daly@gmail.com; nejib_daly@yahoo.fr; nejib.daly@fsb.rnu.tn

Ons Daly Yahia–Kéfi, Section 2
Institut National Agronomique de Tunisie
Avenue Charles Nicolle 43
1082 Tunis-Mahrajene
Tunisia
E-mail: dalyyahya.ons@inat.agrinet.tn; onsdaly@yahoo.fr

Alessandra de Olazabal, Section 11
Department of Biological Oceanography
Instituto Nazionale di Oceanografia e Geofisica Sperimentale (OGS)
Via A. Piccard 54
34014 Trieste, Italy
E-mail: adeolazabal@ogs.trieste.it

Najat Elkhiati, Section 15
Faculté des Sciences Aïn Chock
Université Hassan II
Route d'El Jadida
5466 Casablanca
Morocco
E-mail: Amina_berraho@yahoo.fr

Omar Ettahiri, Section 15
Institut National de Recherche Halieutique
2 Rue de Tiznit
Casablanca 01
Morocco
E-mail: ettahiri@yahoo.fr

Maria Luz Fernández de Puelles, Sections 2, 3, 16
Centro Oceanográfico de Baleares (Spanish Institute of Oceanography)
Muelle de Poniente s/n.
07015 Palma de Mallorca
Spain
E-mail: mluz.fernandez@ba.ieo.es

Serena Fonda-Umani, Section 11
Department of Life Sciences
University of Trieste
Via A. Valerio 28/A
34127 Trieste
Italy
E-mail: s.fonda@units.it

Nina Fragopoulou, Section 16
Laboratory of Zoology
Department of Biology
University of Patras
26500 Patras
Greece
E-mail: nfrago@upatras.gr

Constantin Frangoulis, Section 4
Institute of Oceanography
Hellenic Centre for Marine Research
Gournes Pediados
PO Box 2214
71003 Heraklion
Crete
Greece
E-mail: cfrangoulis@her.hcmr.gr

Stéphane Gasparini, Section 11
Université Pierre et Marie Curie – Paris VI
Laboratoire d'Océanographie de Villefranche (LOV), UMR 7093
Observatoire Oceanologique de Villefranche (OOV)
BP.28
06234 Villefranche-sur-Mer, Cedex
France
E-mail: gasparini@obs-vlfr.fr

Astthor Gislason, Editor
Marine Research Institute
Skulgata 4
121 Reykjavik
Iceland
E-mail: astthor@hafro.is

Gabriel Gorsky, Editor
Université Pierre et Marie Curie – Paris VI
Laboratoire d'Océanographie de Villefranche (LOV), UMR 7093
Observatoire Oceanologique de Villefranche (OOV)
BP.28
06234 Villefranche-sur-Mer, Cedex
France
E-mail: gorsky@obs-vlfr.fr

Jacqueline Goy, Section 2
Institut Océanographique
195 Rue St Jacques
75005 Paris
France
E-mail: j.goy@oceano.org

Alexandra Gubanova, Sections 11, 14
Institute of Biology of Southern Seas
National Academy of Sciences of Ukraine
2 Nakhimov Prospect
99011 Sevastopol
Ukraine
E-mail: adgubanova@gmail.com

Aziz Hafferssas, Section 5
Faculty of Biological Sciences
University of Sciences and Technology Houari Boumedienne
El Alia 16
111 Algiers
Algeria
E-mail: hafferssas@yahoo.fr

Claudia Halsband-Lenk, Section 6
Plymouth Marine Laboratory
Prospect Place
Plymouth
PL1 3DH
UK
E-mail: clau1@pml.ac.uk

Cecelia Hannides (née Sheridan), Section 7
Energy, Environment and Water Research Center
The Cyprus Institute
20 Kavafi Street
PO Box 27456
1645 Nicosia
Cyprus
E-mail: c.hannides@cyi.ac.cy

Roger P. Harris, Section 10
Plymouth Marine Laboratory
Prospect Place
Plymouth
PL1 3DH
UK
E-mail: r.harris@pml.ac.uk

Jean-Henri Hecq, Section 4
MARE Centre
Laboratory of Oceanology
University of Liège, B6
4000 Liège
Belgium
E-mail: jh.hecq@ulg.ac.be

Stamatina Isari, Section 16
Laboratory of Zoology
Department of Biology
University of Patras
26500 Patras
Greece
E-mail: misari@upatras.gr

Lyudmila Kamburska, Section 14
Institute for Environment and Sustainability, EC, DG-JRC
Via E. Fermi 2749
TP 272
21027 Ispra (VA)
Italy
E-mail: lyudmila.kamburska@jrc.it

Benjamin Kürten, Section 8
School of Marine Science and Technology
Newcastle University
Newcastle upon Tyne
NE1 7RU
UK
Tel: +44 191 2225607
E-mail: kuertenb@web.de

Michael Landry, Section 7
Scripps Institution of Oceanography
University of California San Diego
9500 Gilman Drive
La Jolla, CA 92093
USA
E-mail: mlandry@ucsd.edu

Priscilla Licandro, Section 2
Sir Alister Hardy Foundation for Ocean Science
Walker Terrace
Plymouth
PL1 3BN
UK
E-mail: prli@sahfos.ac.uk

Davor Lucic, Sections 2, 16
Institute for Marine and Coastal Research
Kneza Damjana Jude 12
University of Dubrovnik
20000 Dubrovnik
Croatia
E-mail: lucic.davor@unidu.hr

Cristina Madeira, Section 1
Centro de Ciências do Mar do Algarve (CIMAR/CCMAR)
Universidade do Algarve
Campus de Gambelas
8005–139 Faro
Portugal
E-mail: cristina_madeira@hotmail.com

Alenka Malej, Section 2
Marine Biology Station Piran
National Institute of Biology
Fornace 41
6330 Piran
Slovenia
E-mail: alenka.malej@mbss.org

Maria Grazia Mazzocchi, Sections 3, 10, 11, 13, 16
Stazione Zoologica Anton Dohrn
Villa Comunale
80121 Naples
Italy
E-mail: grazia.mazzocchi@szn.it

Juan-Carlos Molinero, Section 2
Leibniz Institute of Marine Science (IFM-GEOMAR)
Wischofstrasse 1–3
24148 Kiel
Germany
E-mail: jmolinero@ifm-geomar.de

Pedro Morais, Section 1
Centro de Ciências do Mar do Algarve, (CIMAR/CCMAR)
Universidade do Algarve
Campus de Gambelas
8005–139 Faro
Portugal
E-mail: pmorais@ualg.pt

Erhan Mutlu, Section 9
Institute of Marine Sciences and Technology
Dokuz Eylul University
Haydar Aliyev Bulvan No. 100
35340 Inciralti
Izmir
Turkey
E-mail: erhan.mutlu@deu.edu.tr

Antonio Olita, Section 11
Istituto per l'Ambiente Marino Costiero
c/o IMC Loc. Sa Mardini
09170 Oristano
Italy
E-mail: Antonio.Olita@iamc.cnr.it

Suzanne J. Painting, Section 8
Centre for Environment, Fisheries and Aquaculture Science (Cefas)
Pakefield Road
Lowestoft
NR33 0HT
UK
E-mail: suzanne.painting@cefas.co.uk

Àurea Peralba, Section 10
Stazione Zoologica Anton Dohrn
Villa Comunale
80121 Naples
Italy
E-mail: aureaperalba@gmail.com

Sergey A. Piontkovski, Section 11
Institute of Biology of the Southern Seas
2 Nakhimov Prospect
99011 Sevastopol
Ukraine
Tel: +968 99834832
E-mail: spiontkovski@gmail.com

Sophie G. Pitois, Section 12
Centre for Environment, Fisheries and Aquaculture Science (Cefas)
Pakefield Road
Lowestoft, NR33 0HT, UK
E-mail: sophie.pitois@cefas.co.uk

Brian Popp, Section 7
University of Hawaii
Department of Geology and Geophysics
1680 East–West Road
Honolulu, HI 96816
USA
E-mail: popp@hawaii.edu

Laura Prieto, Section 2
Instituto de Ciencias Marinas de Andalucia (ICMAN, CSIC)
Avenida Republica Saharaui 2
Rio San Pedro s/n
11519 Puerto Real, Cadiz
Spain
E-mail: laura.prieto@icman.csic.es

Mohamed Ramdani, Section 15
Institut Scientifique
Avenue Ibn Battota
Rabat–Agdal
10106 Rabat
Morocco
E-mail: ramdanimohamed@yahoo.fr

Alexis Ramfos, Section 16
Department of Aquaculture and Fisheries
Technological Educational Institute of Messolonghi
Nea Ktiria
Messolonghi 30200
Greece
E-mail: ramfos@teimes.gr

Carmen Garcia-Comas Rubio, Section 11
Université Pierre et Marie Curie – Paris VI
Laboratoire d'Océanographie de Villefranche (LOV), UMR 7093
Observatoire Oceanologique de Villefranche (OOV)
BP.28
06234 Villefranche-sur-Mer, Cedex
France
E-mail: carmencomas@gmail.com

Rabia Seridji, Section 5
Faculty of Biological Sciences
University of Sciences and Technology Houari Boumedienne
El Alia 16
111 Algiers
Algeria
E-mail: r_seridji@yahoo.fr

Ioanna Siokou-Frangou, Sections 2, 11, 13, 16
Institute of Oceanography
Hellenic Centre for Marine Research
Athens-Souniou Avenue
PO Box 712
19013 Anavyssos-Attikis
Greece
E-mail: isiokou@ath.hcmr.gr

Laila Somoue, Section 15
Institut National de Recherche Halieutique
2 Rue de Tiznit
Casablanca 01
Morocco
E-mail: s_laila2005@yahoo.fr

Kremena Stefanova, Section 14
Institute of Oceanology
Bulgarian Academy of Sciences
PO Box 152
9000 Varna
Bulgaria
E-mail: stefanova@io-bas.bg

Lars Stemmann, Section 11
Université Pierre et Marie Curie – Paris VI
Laboratoire d'Océanographie de Villefranche (LOV), UMR 7093
Observatoire Oceanologique de Villefranche (OOV)
BP.28
06234 Villefranche-sur-Mer, Cedex
France
E-mail: stemmann@obs-vlfr.fr

Ulrich Struck, Section 8
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin
Invalidenstraße 43
10115 Berlin
Germany
Tel: +49 30 20938552
E-mail: ulrich.struck@mfn-berlin.de

Amal Zaafa, Section 15
Faculté des Sciences Aïn Chock
Université Hassan II
Route d'El Jadida
5466 Casablanca
Morocco
E-mail: Amina_berraho@yahoo.fr

Soultana Zervoudaki, Sections 2, 11, 16
Institute of Oceanography
Hellenic Centre for Marine Research
Athens-Souniou Avenue
PO Box 712
19013 Anavyssos-Attikis
Greece
E-mail: tanya@ath.hcmr.gr

Abbreviations and acronyms

AA	amino acid
AAT	atmospheric average annual temperature
AL	aboral length
ATD	annual temperature deviation
CIESM	Mediterranean Science Commission
CSIA	compound-specific isotope analysis
DCM	deep chlorophyll maximum layer
EUR-OCEANS	European Network of Excellence for Ocean Ecosystems Analysis
HPLC	high-performance liquid chromatography
IFREMER	French Research Institute for Exploitation of the Sea
LW	length–weight
MAW	Modified Atlantic Water
NAO	North Atlantic Oscillation
NBS	northern Black Sea
NHT	northern hemisphere temperature
NPSG	North Pacific Subtropical Gyre
PLFA	phospholipid-derived fatty acid
POM	particulate organic matter
PUFA	polyunsaturated fatty acid
RAI	regional atmospheric index
SIA	stable isotope analysis
SML	surface mixed layer
SMW	Surface Mediterranean Water
SST	sea surface temperature
TAP	total annual precipitation
TOM	terrestrial organic matter
UNESCO	United Nations Educational, Scientific and Cultural Organization
WBS	western Black Sea
WCO	Western Channel Observatory
WGZE	ICES Working Group on Zooplankton Ecology
WKZEM	Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic

Titles published in the ICES Cooperative Research Report series

No.	Title	Price (Danish Kroner)
299	Alien species alert: *Crassostrea gigas* (Pacific oyster)	50
298	ICES Report on Ocean Climate. 66 pp.	100
297	Effects of extraction of marine sediments on the marine environment 1998–2004. 180 pp.	120
296	Definition of standard data-exchange format for sampling, landings, and effort data from commercial fisheries. 43 pp.	60
295	Manual of recommended practices for modelling physical–biological interactions during fish early life. 111 pp.	70
294	Hake age estimation: state of the art and progress towards a solution. 43 pp.	50
293	The effect of climate change on the distribution and abundance of marine species in the OSPAR Maritime Area. 46 pp.	170
292	ICES Zooplankton Status Report 2006/2007. 164 pp.	150
291	ICES Report on Ocean Climate 2007. 60 pp.	30
290	Changes in surface CO_2 and ocean pH in ICES shelf sea ecosystems. 35 pp.	70
289	ICES Report on Ocean Climate. 56 pp.	70
288	Structure and dynamics of the North Sea benthos. 258 pp.	350
287	Collection of acoustic data from fishing vessels. 83 pp.	60
286	Acoustic seabed classification of marine physical and biological landscapes. 183 pp.	130
285	Results of the spring 2004 North Sea ichthyoplankton surveys. 59 pp.	60
284	Status of introductions of non-indigenous marine species to the North Atlantic and adjacent waters 1992–2002. 149 pp.	80
283	Alien Species Alert: *Undaria pinnatifida* (wakame or Japanese kelp). 36 pp.	60
282	Incorporation of process information into stock–recruitment models. 152 pp.	90
281	Zooplankton Monitoring Results in the ICES Area: Summary Status Report 2004/2005. 43 pp.	90
280	ICES Report on Ocean Climate. 47 pp.	70
279	Protocol for the Use of an Objective Mesh Gauge for Scientific Purposes. 8 pp.	40
278	Description of the ICES HAC Standard Data Exchange Format, Version 1.60. 86 pp.	60
277	The intentional introduction of the marine red king crab Paralithodes camtschaticus into the Southern Barents Sea. 18 pp.	60
276	Zooplankton Monitoring Results in the ICES Area: Summary Status Report 2003/2004. 34 pp.	80
275	The Annual ICES Ocean Climate Status Summary 2004/2005. 2005. 37 pp.	80
274	Spawning and life-history information for North Atlantic cod stocks. 152 pp.	90
273	Guidance on the Application of the Ecosystem Approach to Management of Human Activities in the European Marine Environment. 22 pp.	40
272	Ecosystem Effects of Fishing: Impacts, Metrics and Management Strategies. 177 pp.	70
271	Vector Pathways and the Spread of Exotic Species in the Sea. 25 pp.	60
270	The *Nephrops* fisheries of the Northeast Atlantic and Mediterranean – A review and assessment of fishing gear design. 38 pp.	50

These publications can be ordered from ICES Secretariat, H. C. Andersens Boulevard 44–46, DK-1553 Copenhagen V, Denmark; fax: +45 33 93 42 15; e-mail: info@ices.dk. An invoice including the cost of postage and handling will be sent. Publications are usually dispatched within one week of receipt of payment. Further information about ICES publications, including ordering and payment by credit card, cheque, and bank transfer, can be found at www.ices.dk under "Publications".