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Mucilages and climatic changes in the Tyrrhenian Sea

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ABSTRACT

1. Pelagic mucilage aggregates are composed of phytoplankton and bacteria, whilst macro- and micro-phytobenthos and bacteria make up the benthic ones. During the summer of 1991 massive mucilage aggregates, both pelagic and benthic, appeared in the Tyrrhenian Sea, seriously damaging fisheries, tourism and the benthic biocoenoses. Only a few, loose benthic mucilages have persisted during the last decade although the pelagic ones have shown a great resurgence during the last autumn.

2. ^{14}C autoradiographies show that the mucilage is photosynthesized and excreted by the micro- and macroalgae it contains. The mucilage aggregates are a microecosystem with biological and chemical composition, and a functionality that is different from the surrounding waters. The mucilages cannot be the result of a gelification of the Dissolved Organic Matter (DOM) in the water trapping the free algae present in the water.

3. Since 1991 up to the present, variations of Dissolved Inorganic Nitrogen (DIN) and Dissolved Inorganic Phosphorous (DIP) and of their ratio have been observed in the surface waters. These variations could be assumed as the cause of mucilages, however, the mucilage occurrence cannot be directly related to the change of nutrient concentrations and ratios because: i) the higher N:P ratio was persistent also during years without mucilages; ii) nutrients and their ratios have a continuous spatial distribution while mucilages have a discontinuous spatial and temporal distribution. It is suggested that mucilage aggregates are the result of a hyperproduction as a pathological response of the algae to a microbial infection. This hypothesis is also supported by some laboratory experiments.

4. The observed trophic changes in the surface Tyrrhenian waters have been related to the Levantine Intermediate Waters (LIW) as they are the main source of nutrients for the surface ones. Data collected from several areas between 1982 and 1998 show that changes in the temperature, salinity and nutrient concentrations and ratios took place in the LIW, so changing the Tyrrhenian climate.

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KEY WORDS: bacterial infection; Levantine Intermediate Waters; mucilages; N:P ratio; nutrient deficiency; Tyrrhenian climate change

INTRODUCTION

Mucilages heavily affect marine ecosystems, mainly when the massive development of aggregates covers large areas of the rocky substrate, suffocating and destroying benthic biocoenoses. Furthermore, fisheries

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and tourism are seriously damaged. A wide literature of laboratory and field studies about mucilages is available, but little is still known about the factors triggering the phenomenon (review in Vollenweider and Rinaldi, 1995). There is laboratory evidence that many environmental stresses cause the hyperproduction of exudates (high irradiance, temperature, nutrient availability). Nutrient deficiency is one of the main causes thus far investigated, particularly when the N/P ratio shifts toward the phosphorus deficiency (Mykkestad, 1977; Jensen, 1984; Fogg, 1990; Mykkestad, 1995). Biological causes too have been hypothesized: viral or bacterial infections could lead, more or less directly, to the abnormal production of mucilages (Innamorati, 1992; Murray, 1995; Azam *et al.*, 1999).

In the Tyrrhenian waters both benthic and pelagic mucilages occurred, although these differed not only in their location but also in their biological features (Innamorati, 1995). Massive mucilages excreted by planktonic and benthic marine algae in the Tyrrhenian Sea have been observed since 1991, but previous observations of scuba divers and fishermen oral tradition reveal their presence in earlier decades too (Innamorati, 1995). The Tyrrhenian phenomenon was readily recognized as the same that occurred in the Adriatic Sea, where it was well known since 1800 (Fonda Umani *et al.*, 1989). From analyses of the relationships between the trophic status of the water inside and outside the mucilages, there was evidence that during 1991 the N/P ratio was higher (> 30) than in the previous years, both in the surface (0–100 m) and intermediate (> 100 m) waters (Innamorati *et al.*, 1993, 1994, 1995b). The Northern Tyrrhenian waters were previously characterized by a general nitrogen deficiency, showing a quite different pattern from the eutrophic northwestern Adriatic waters (Innamorati and Giovanardi, 1992; Innamorati *et al.*, 1995a). These results led us to re-examine all our physical and chemical data collected in the Northern Tyrrhenian from 1982 to 1998, to recognize if some trophic changes really occurred (Innamora *et al.*, 1998). Furthermore, as the Levantine Intermediate Waters (LIW) constitute the main source of nutrients for surface Tyrrhenian waters; river and terrestrial runoff and the oligotrophic North Atlantic Waters (NAW) contribute very little, it was supposed that any trophic change would be caused by a more general change in the LIW. To verify this hypothesis, we focused our attention on the layer 200–1000 m (Melley *et al.*, 2000), examining data from the last two decades and from different Mediterranean areas.

In this paper we summarize our results on Tyrrhenian mucilages production together with a synthesis of our researches on the temporal trend of trophic conditions in the Mediterranean waters.

MATERIAL AND METHODS

Benthic mucilages were collected by scuba divers in different sites of the Archipelago Toscano (Capo d'Uomo dell'Argentario, August 1991; Montecristo Island, August 1991, July–August 1992, July 1993; Formiche di Grosseto, August 1991, July–August 1992, July 1993 and from May to October 1995). Pelagic mucilages have been collected at Procida Island (September 1991, 1992; October 2000) from nets (300 × 20 m) left in the sea overnight, by wringing them out and dripping them in a bucket. On each cruise Conductivity Temperature Depth (CTD) profiles were measured (Idronaut Ocean Seven). In the samples of both mucilages and water column, the latter collected with Niskin bottles, the analysis of nutrients (nitrites plus nitrates and orthophosphates), phytoplankton biomass (chlorophyll) and composition (inverted microscope counting), Coloured Dissolved Organic Matter (CDOM) concentrations and ^{14}C incubations for primary production measurement (Riemann and Möller Jensen, 1991) and autoradiography (Becciolini and Balzi, 1992), were performed following standards methods.

For the analysis of the thermohaline and trophic conditions in the Tyrrhenian Sea and in the LIW of different Mediterranean areas, data collected during 28 cruises have been examined (Table 1). At first we analysed temperature, salinity and nutrients in the layers 0–99 m and 100–400 m from 16 cruises (Table 1) carried out in the Tyrrhenian Sea from 1982 to 1995; subsequently, we took in account the layer 200–1000 m (LIW) from cruises until 1998 and from other data available from the Mediterranean Sea

Table 1. Sampling period and area of the cruises. The number of samples used in this paper are indicated

Cruises	Sampling period	Area	Samples used	
			0-400 m	200-1000 m
Marsili 82 ^a	6/6-19/1982	Southern Tyrrhenian Sicily Channel Western Ionian		87
Elba1	10/2-8/1982	Archipelago Toscano	74	
Elba2	7/5-12/1983	Corsica Channel Archipelago Toscano	223	29
ATT1	9/3-12/1985	Corsica Channel	154	21
ATT2	11/21-28/1986	Corsica Channel Archipelago Toscano	131	18
ATT3	3/12-23/1987	Corsica Channel Archipelago Toscano	216	30
ATT4	4/6-18/1988	Corsica Channel Eastern Ligurian	171	27
ATT5	7/5-11/1988	Eastern Ligurian	166	14
ATT6	11/22-12/4/88	Corsica Channel Eastern Ligurian	171	8
ATT7	2/15-3/2/1989	Corsica Channel Eastern Ligurian	250	15
ATT8	7/25-8/3/1989	Corsica Channel	91	14
Tempo1 ^b	9/22-10/9/1989	Northern Tyrrhenian		49
Tempo2 ^b	2/16-23/1990	Northern Tyrrhenian		48
Arci1	6/19-7/2/1990	Archipelago Toscano	92	
Arci2	5/7-17/1991	Archipelago Toscano Corsica Channel	100	4
Arci3	9/3-22/1991	Corsica Channel Northern Tyrrhenian	69	10
POEMBC 091 ^c	10/1991	Western Ionian		99
MUCINUTRI*	12/28/91-7/28/92	Archipelago Toscano	30	
MARET	5/26-6/1/1993	Northern Tyrrhenian	63	23
EOCUMM94	7/7-12/1994	Southern Tyrrhenian		26
EOCUMM95	7/22-28/1995	Southern Tyrrhenian		34
ARCIPICO*	3/16-12/6/1995	Archipelago Toscano	77	
SYMPLEX96	4/15-5/15/1996	Sicily Channel		76
SYMPLEX97	7/20-8/10/1997	Sicily Channel		27
SALE2	8/14-25/1997	Southern Tyrrhenian Sicily Channel Western Ionian		79
SYMPLEX98	3/27-4/20/1998	Sicily Channel		23
NUGLOB*	6-9/1998	Archipelago Toscano	20	14
Fronti 98	7/14-26/1998	Western Mediterranean		7

^a See Faranda (1985).^b Cruise carried out by ISDGM (CNR) and CRAM (ENEA), La Spezia (Astraldi *et al.*, 1995).^c Cruise carried out by CNR, Trieste (Civitaresse *et al.*, 1996).

* Two stations monthly sampled.

(Table 1). Vertical profiles of temperature and salinity were performed with multiparametric probes (Idronaut Oc. Seven, KMS Meerestechnik, Neil Brown). The samples for analysis (Strickland and Parsons, 1972) of dissolved nitrogen (nitrites plus nitrates) and phosphorus (orthophosphates) were collected with Niskin bottles at fixed depths (0, 10, 25, 50, 75, 100 m and every 100 m until the bottom).

For the cruises carried out by other research groups, see Faranda (1985), Astraldi *et al.* (1995), Civitarese *et al.* (1996). The identification of the LIW was made from CTD vertical profiles, T-S diagrams and nutrient concentrations. From the total of stations sampled (~2000) those with a bottom depth of <100 m and affected by rivers input were discarded, the arithmetic means of nutrient concentrations and N/P ratios are for the samples listed in Table 1.

RESULTS

The first signs of Tyrrhenian benthic mucilages were visible in spring, with the development of isolated and discontinuous metaphytic aggregates (Round, 1981), dominated by the filamentous algae *Nematochryopsis marina* (= *Tribonema marimum* J. Feldmann) and/or *Acinetospora crinita* (Carmichael) Kornmann, and benthic pennate diatoms (Sartoni and Sonni, 1992; Innamorati *et al.*, 1995b). Afterwards the mucilage spread out over the rocky bottom, reaching a maximum expansion and covering the erectile organisms at the height of summer. In the same period (July–August) mucilages showed the peak of chlorophyll, orthophosphates, total phosphorus, CDOM concentration and cell density (Melley *et al.*, 1998). After the largest development, the mucilages buried the benthic biocoenoses under a layer of degrading material, which afterwards changed into a fine light-grey powdery layer covering the bottom with dead benthos remnants (Cinelli, 1992).

Even assuming that the mucilage incorporates debris and organisms from surrounding waters, the autoradiography revealed (Plate 1) that the phytocoenose inside is the mucilage producer. Radioactivity both inside and outside of the cells showed a dense and insoluble mucopolysaccharides matrix (confirmed with alcian blue PAS reaction) spreading out from the cell towards the surrounding medium, synthesized after the ^{14}C assimilation and then excreted.

The biological and trophic characteristics inside the mucilages (Table 2) are quite different from the surrounding waters (Innamorati *et al.*, 1995b; Melley *et al.*, 1998). The biomass, the carbon production and the cell density were higher, while the carbon assimilation per biomass unit (C/Chl or C/cell) was lower. Nutrient concentrations were higher too, mostly phosphorus, while the N/P ratio was lower. The ratio was lower than the Redfield's one (N/P = 16) while, in the pelagic environment during 1991, a higher N/P ratio ($\gg 16$) was noted, if compared to the previous data obtained until 1990 in the Northern Tyrrhenian waters (Innamorati *et al.*, 1992, 1995b), when the ratio was $\ll 16$. The variation of the mean values of nutrients and N/P ratio from 1982 to 1995 (Figure 1), showed the evident decrease of phosphorus, the increase of nitrogen and the consequent increase of N/P from 1991, not only in the surface but also in the deeper layers. The trend of N/P ratio showed a nitrogen deficiency (N/P = 6.1) in the layer 0–99 m and a higher value (N/P = 19.9) in the deeper waters (100–400 m) until 1990. In the following years the data were distributed towards higher mean values (N/P = 19.6 in the layer 0–99 m and N/P = 36.0 in the layer 100–400 m), revealing the shift to phosphorus deficiency.

The summer physical structure of the water column before and after 1990 (Figure 2) was different with higher salinity in the surface layers after 1990 and the increase both in temperature (0.6°C) and salinity (0.15‰) of the LIW (Figure 2(b)). Furthermore, examining the nutrient concentrations from 1982 to 1995 vs. temperature in the LIW (Figure 3) there was evidence that the phosphorus decreased and the nitrogen increased, following the temperature increment and causing consequently the increase of the N/P ratio.

In Figure 4 the means of nutrients and N/P ratio obtained from the samples of the LIW of various Mediterranean areas (Table 1), vs. time are shown. Dissolved nitrogen (Figure 4(a)) showed an initial increase at the end of the 1980s followed by a decrease, similar to the phosphorus (Figure 4(b)). The effect of these fluctuations on the variation of N/P ratio (Figure 4(c)) results in an increase until the mid-1980s before stabilizing at a relatively high range.

(a)

(b)

Plate 1. Autoradiographies of a pennate diatom (a) and of *Nematochryopsis marina* (= *Tribonema marinum* J. Feldmann) (b).

Table 2. Biological and trophic characteristics of the Tyrrhenian mucilages (M) compared with the surrounding water (W)^a

Characteristics		Montecristo		Procida		Formiche		Formiche 1995*	
		W	M	W	M	W	M	W	M
Chlorophyll	mg m ⁻³	0.047	11.09	0.182	510	0.075	33.87	0.263	24.65
Cell density	cell litre ⁻¹	8 × 10 ⁴	8 × 10 ⁶	2 × 10 ⁵	6 × 10 ⁸	1 × 10 ⁵	3 × 10 ⁷	6.5 × 10 ⁴	8 × 10 ⁶
Chl./cell	pg cell ⁻¹	0.59	1.42	0.96	0.79	0.72	1.30	4.03	5.50
Phaeop./Chl	%	~0	18	~0	32	~0	56	40	46
C production	mg m ⁻³ h	0.13	14.30	0.79	173.00	0.46	48.30		
C/Chl	h ⁻¹	2.82	1.29	4.30	0.34	6.13	1.43		
C/cell	pg cell h ⁻¹	1.66	1.80	4.20	0.27	4.40	1.86		
NO ₂ + NO ₃	µM	0.55	5.13			0.46	1.03	0.545	0.854
PO ₄	µM	0.02	12.84			0.02	0.07	0.039	0.481
N/P		33.14	0.63			29.50	1.41	15.41	1.78

^a Chl = chlorophyll. Phaeop. = phaeopigments.

* Means of monthly sampling from May to October 1995.

DISCUSSION

The results show that the producers of mucilage are the same algae, that are contained inside them (Plate 1; Table 2). The unicellular phytoplankters, during excretion, aggregate among them, or with filamentous algae, to form respectively the pelagic or the benthic mucilages. The latter must be considered as the metaphyton defined by Behere (Round, 1981) in order to distinguish the assemblage of cells kept around a macroalga by mucilage from the epiphytic cells firmly attached to a macrophyta. Both in the benthic and in the pelagic form the individuals (micro and macrophyta) and their relationships inside mucilage, constitute a true phytocoenose and can be named metaphytocoenose (or mucophytocoenose). They are a quite different system from the surrounding water, as the biological composition, the physical and chemical properties and the activities of production, decomposition together with the presence of massive numbers of bacteria indicate.

The abnormal mucilages hyperproduction, the high bacterial activity inside the aggregates and their patchy distribution, emphasizes the hypothesis of a biological cause, a microbial infection, as the triggering factor inducing the pathological response of the enhanced mucilages excretion (Innamorati, 1992, 1995). Some preliminary experiments (Innamorati *et al.*, 1996) on axenic phytoplankton cultures show that the majority of the cultures inoculated with filtrates from mucilages produced mucopolysaccharides. Therefore the role of bacteria for mucilage production must be clarified by further investigations.

The increase of the N/P ratio in the Tyrrhenian surface waters with the abnormal mucilage formation may suggest the relationship between the two phenomena. But, while the distribution of dissolved nutrients is continuous, mucilages have spatially and temporally discontinuous distributions. Furthermore, it is known that in the Adriatic Sea the mucilages are a sporadic recurrent phenomenon also scientifically well documented since the latest 1880 and during 1900. In the last 30 years the Adriatic waters have been always characterized by phosphorus deficiency as have the Tyrrhenian waters from 1991 up to the present. Therefore, since in the sea the mucilages have always been found with high N/P ratio — but more often, high N/P ratio can be found without mucilages — it seems that in nature the P deficiency, can be considered as a necessary condition for the appearance of mucilages, but not the only factor.

Figure 1. Mean concentrations of P- PO_4 (a), N-($\text{NO}_3 + \text{NO}_2$) (b) and mean N:P values (c) in all the cruises carried out in the Northern Tyrrhenian Sea and in the two layers. General means for the periods 1982–1990 and 1991–1995 are indicated.

The recent Tyrrhenian phosphorus deficiency (since 1991, Nair *et al.*, 1994), is quite different from that of Adriatic. In the latter, the high N:P ratio is a chronic characteristic also related to the high nutrient supply from rivers. The increase of the N:P ratio in the surface Tyrrhenian waters appears independent from anthropic sources and related to the increase of N:P in the LIW due to a variation of dissolved nitrogen, phosphorus and N:P ratio and related to temperature variations.

Detailed examination of the spatial distribution of temperature, salinity, nutrients and N:P ratio in the core of the LIW from 1982 up to 1998, was carried out in the different Mediterranean areas (Table 1). The variation is mostly evident between 1991 and 1995, even though it is complicated by the superimposition of temporal and spatial variability. Nevertheless, the great number of data allows us to hypothesize a thermohaline and trophic change along a temporal scale (Figure 4), produced in the LIW that, originated in the Levantine basin and circulating from Eastern to Western Mediterranean, could affect surface and intermediate layers all over the Mediterranean Sea.

Figure 2. T-S diagrams (σ_t is also reported). Data from 1982 to 1995 summer cruises: (a) before 1990 (June–September); (b) after 1990 (May–September). S‰ = salinity.

Figure 3. Nutrient concentrations vs. temperature in the LIW in the Northern Tyrrhenian Sea during 1982–1995. Correlation coefficients (r) of N and P regressions are respectively 0.69 and -0.35 .

It seems possible to relate the transient variation suggested by the shape of the fluctuations (Figure 4) and mostly evident in the Central Mediterranean, to the change that occurred in the Levantine Basin between 1987 and 1995 (Roether *et al.*, 1996). In these waters there was the sinking of denser waters and the consequent raising of the deep and intermediate layers, with a perturbation of the water circulation at a wider spatial scale (Malanotte-Rizzoli *et al.*, 1999) that could affect the characteristics of the Tyrrhenian Sea.

Figure 4. Temporal distribution of the means of N-($\text{NO}_2 + \text{NO}_3$) (a), P- PO_4 (b) and of the N:P ratio (c) in the LIW from various Mediterranean areas. (Manual fitting curves).

No direct relationship exists between mucilage invasion and the observed changes in marine environment, unless it is that they are natural events without anthropic interference. The challenge for nature conservation is that of the preservation of all environmental conditions, as they are or can be, as are necessary for humankind. The natural destruction of ecosystems must be stopped: no matter if mucilages and consequential changes are for ages recurrent natural events. The future goal is to avoid the damage they cause, even though our present knowledge does not suggest anything to restore the previous properties of these enormous water masses.

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REFERENCES

- Astraldi M., Borghini M., Galli C., Gasparini G.P., Lazzoni E. 1995. La circolazione nel Canale di Corsica durante l'estate. *Atti della Società Toscana di Scienze Naturali, Memorie Serie A, Suppl. CII*: 9–21.
- Azam F., Fonda Umani S., Funari E. 1999. Significance of bacteria in the mucilage phenomenon in the northern Adriatic Sea. *Annali dell'Istituto Superiore di Sanità* **35**: 411–419.
- Becciolini A., Balzi M. 1992. I parametri di cinetica cellulare e la determinazione del 'labeling index' nei tumori umani. In *Argomenti di laboratorio per l'oncologia*. Bombardieri E., Caravatti M., Gion M., Landolfo S. (eds). Clus International: Brescia: 35–36.
- Cinelli F. 1992. Il caso Argentarola. In *La crisi del Mediterraneo in seguito alla fioritura di masse algali*. Accademia Internazionale di Scienze e Tecniche Subacquee Ustica, vol. 9: 33–36.

- Civitaresse G, Crise A, Crispi G, Mosetti R. 1996. Circulation effect on nitrogen dynamics in the Ionian Sea. *Oceanologica Acta* **19** (6): 609–622.
- Faranda FM (a cura di). 1985. Studio globale delle interrelazioni dell'ecosistema pelagico dei mari meridionali italiani. Dip.to di Biologia Animale ed Ecologia Marina, Università di Messina, Rapporti 1: 1–54.
- Fogg GE. 1990. Massive phytoplankton gel production. In *Eutrophication-related Phenomena in the Adriatic Sea and in Other Mediterranean Coastal Zones*. Water Pollution Research Report, 16. Barth H, Fegan I (eds). Commission of the European Communities: Brussels: 207–212.
- Fonda Umani S, Ghirardelli E, Specchi M (a cura di). 1989. *Gli episodi di 'mare sporco' nell'Adriatico dal 1729 ai giorni nostri*. Regione Autonoma Friuli-Venezia Giulia: Trieste.
- Jensen A. 1984. Excretion of organic carbon as function of nutrient stress. In *Lectures Notes on Coastal and Estuarine Studies* 8°, *Marine Phytoplankton and Productivity*. Holm Hansen O, Bolis L, Gilly R (eds). Springer-Verlag: Berlin: 61–72.
- Innamorati M. 1992. Mucillaggini e fitoplancton. In: *'La crisi del Mediterraneo in seguito alla fioritura di masse algali'*. Accademia Internazionale di Scienze e Tecniche Subacquee Ustica, vol. 9: 61–80.
- Innamorati M. 1995. Hyperproduction of mucilages by micro and macro algae in the Tyrrhenian Sea. *The Science of the Total Environment* **165**: 65–81.
- Innamorati M, Bernacchioni S, Nuccio C, Balzi M, Melley A. 1996. Le mucillaggini fitoplanctoniche come epidemia infettiva batterica. *Biologia Marina Mediterranea* **3**: 607–610.
- Innamorati M, Giovanardi F. 1992. Interrelationships between phytoplankton biomass and nutrients in the eutrophicated areas of the North-Western Adriatic Sea. *The Science of the Total Environment Suppl.*: 235–250.
- Innamorati M, Lazzara L, Nuccio C, Mori G, Massi L, Cherici V. 1992. Il fitoplancton dell'Alto Tirreno: condizioni trofiche e produttive. *Atti IX Congr AIOL*, S. Margherita Ligure 20–23/11/1990, Genova: 199–205.
- Innamorati M, Raddi E, Buzzichelli S, Melley A, Balzi M. 1993. Le mucillaggini nel Mar Tirreno. *Biologia Marina, supplemento al notiziario della Società Italiana di Biologia Marina* **1**: 23–26.
- Innamorati M, Melley A, Castelli C, Gorini C, Balzi M. 1994. Mucillaggini tirreniche, nutrienti, cenosi fitoplanctoniche. *Biologia Marina Mediterranea* **1**: 189–193.
- Innamorati M, Lazzara L, Nuccio C, Mori G, Massi L. 1995a. Nutrienti, biomassa e produzione fitoplanctonica nell'Alto Tirreno Toscano. *Atti della Società Toscana di Scienze Naturali, Memorie Serie A, Suppl. CII*: 137–150.
- Innamorati M, Melley A, Nuccio C, Castelli C, Balzi M. 1995b. Le mucillaggini tirreniche. *Atti della Società Toscana di Scienze Naturali, Memorie Serie A, Suppl. CII*: 293–307.
- Innamorati M, Melley A, Nuccio C. 1998. Cambiamento generale delle caratteristiche trofiche del Mar Tirreno. *Biologia Marina Mediterranea* **5**: 35–40.
- Malanotte-Rizzoli P, Manca B, Ribera D'Alcalà M, Theocharis A, Brenner S, Budillon G, Ozsoy E. 1999. The Eastern Mediterranean in the 80s and in the 90s: the big transition in the intermediate and deep circulations. *Dynamics of Atmospheres and Oceans* **29**: 365–395.
- Melley A, Innamorati M, Nuccio C, Piccardi R, Benelli M. 1998. Caratterizzazione e stagionalità delle mucillaggini tirreniche. *Biologia Marina Mediterranea* **5**: 203–213.
- Melley A, Innamorati M, Mori G. 2000. Cambiamenti termoclinici e delle risorse trofiche delle Acque Intermedie Levantine nel Mediterraneo. *Biologia Marina Mediterranea* **7**: 93–100.
- Murray AG. 1995. Phytoplankton exudation: exploitation of the microbial loop as a defence against algal viruses. *Journal of Plankton Research* **17**: 1079–1094.
- Myklestad SM. 1977. Production of carbohydrates by marine planktonic diatoms. II Influence of the N/P ratio in the growth medium on the assimilation ratio, growth rate, and production of cellular and extracellular carbohydrates by *Chaetoceros affinis* var. *willei* (Gran) Husted and *Skeletonema costatum* (Grev.) Cleve. *Journal of Experimental Marine Biology and Ecology* **29**: 161–179.
- Myklestad SM. 1995. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. *The Science of the Total Environment* **165**: 155–164.
- Nair R, Cattini E, Gasparini GP, Rossi G. 1994. Circolazione ciclonica e distribuzione dei nutrienti nel Tirreno Settentrionale. *Atti X Congr AIOL*, Allassio 4–6/11/1992, Genova: 65–76.
- Riemann B, Möller Jensen L. 1991. Measurement of primary production by means of acidification and bubbling method. *Journal of Plankton Research* **13**: 853–862.
- Roether W, Manca B, Klein B, Bregant D, Georgopoulos D, Beitzel V, Kovacevic V, Luchetta A. 1996. Recent changes in Eastern Mediterranean Deep Waters. *Science* **271**: 333–335.
- Round FE. 1981. *The Ecology of Algae*. University Press: Cambridge.
- Sartoni G, Sonni C. 1992. *Tribonema marinum* J. Feldmann e *Acinetospora crinita* (Carmichael) Sauvageau nelle formazioni mucillaginose bentoniche osservate sulle coste toscane nell'estate 1991. In *La crisi del Mediterraneo in*

- seguito alla fioritura di masse algali*. Accademia Internazionale di Scienze e Tecniche Subacquee Ustica, vol. 9: 37–46.
- Strickland JDH, Parsons TR. 1972. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board, Canada* **167**: 49–90.
- Vollenweider RA, Rinaldi A (eds). 1995. *Marine Mucilages. Proceedings of an International Workshop on Marine Mucilage Phenomena*, Cesenatico, Italy 10–12 September 1992. In: *The Science of the Total Environment*, Special Issue, vol. 165.