ELSEVIER

Deep-Sea Research II 53 (2006) 1314–1328

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Distribution of TEP in the euphotic and upper mesopelagic zones of the southern Iberian coasts

L. Prieto[a,*], G. Navarro[a], A. Cózar[b], F. Echevarría[b], C.M. García[b]

[a]*Instituto de Ciencias Marinas de Andalucía (CSIC), 11510 Puerto Real, Cádiz, Spain*
[b]*Área de Ecología, Facultad de Ciencias del Mar, Universidad de Cádiz, 11510 Puerto Real, Cádiz, Spain*

Received 1 February 2005; accepted 21 March 2006
Available online 2 August 2006

Abstract

The spatial and temporal distributions of transparent exopolymer particles (TEP) were studied for the Gulf of Cádiz, by analyzing its abundance in the euphotic and upper mesopelagic zones. Both layers of the water column should reflect a distinct pattern in TEP distribution, as production of TEP is mainly linked to phytoplankton activity, which is sited in the euphotic zone, while losses of TEP due to aggregation-sinking and degradation occur from the surface to further below in the water column. Concentration of TEP in the euphotic zone reflected the varied oceanographic characteristics of the studied region. It was higher in coastal upwellings, fronts and such areas of topographic forcing, suggesting that TEP were being produced by active growing phytoplankters. A comparison with a well-known ecosystem, the coastal upwelling in the northwestern Alboran Sea, showed that the TEP:Chl *a* ratio at stations with clear eutrophic characteristics was several orders of magnitude lower than in the area southwest of the anticyclonic current of the Gulf. This ratio in the highly dynamic system of the Strait of Gibraltar seems to have a much clearer relation with the stage of a bloom and, at a basin scale, to the trophic condition of the ecosystem than TEP concentrations alone. Throughout the area studied in the Gulf of Cádiz, the role of TEP for aggregation processes was analyzed based on two aggregation models. Both approximations pointed to the importance of TEP in the export of matter from the euphotic zone to deeper waters in the Gulf of Cádiz.

Keywords: Gulf of Cádiz; Strait of Gibraltar; North Alboran Sea; Transparent exopolymeric particles; Euphotic zone; Upper mesopelagic zone

1. Introduction

Trying to match the abundance of aggregates observed in nature to that predicted using aggregation theory models, the abundance of particles in the ocean appeared to be excessively low (McCave, 1984; Jackson, 1990; Hill, 1992), until the presence of transparent exopolymeric particles (TEP) was recognized. TEP, first identified and named by Alldredge et al. (1993), are visible when stained and are present in natural waters at a concentration of 10^4–$10^6\,l^{-1}$. TEP are formed from polysaccharides exuded mainly by phytoplankton under conditions of nutrient limitation (Obernosterer and Herndl, 1995; Penna et al., 1999). This exuded matter collides to form particles large enough to be

---

*Corresponding author. Tel.: +34 956 832612; fax: +34 956 834701.
E-mail address: laura.prieto@uca.es (L. Prieto).

0967-0645/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2006.03.009

retained on a 0.4-μm filter, this being the methodological requirement to consider these particles as TEP (Passow, 2000).

The significant role of TEP in the oceanic carbon cycle is manifold (Passow, 2002). TEP are key constituents of marine aggregates, the fast-sinking vehicles for biogenic carbon transport to beneath the mixed layer, where they are isolated from contact with the atmosphere for decades to millennia. Also, due to their abundance and sticky nature, TEP can be key for coagulation of diatom blooms (Alldredge and Jackson, 1995; Prieto et al., 2002), in as well as scavenging mineral particles (Kumar et al., 1998) or trace elements (Quigley et al., 2002; Guo et al., 2002) from the water column. Moreover, TEP represent a link between dissolved and particulate organic matter and their exudation by nutrient-limited cells is interpreted as the consequence of carbon overflow. Thus, the presence of TEP increases the average Redfield C:N molar ratio of particulate organic matter (Mari et al., 2001).

Despite its importance in the oceanic biogeochemical cycle, studies that analyze the distribution of TEP in the pelagic ecosystem, spanning distinct layers of the water column and covering an extensive geographical area, are scarce. The varying light distribution with depth marks a distinct set of processes implied in the resulting TEP concentrations. Within the euphotic zone (EZ), these exopolymers are produced by phytoplankton. Within this layer the eventual aggregation process of phytoplankton blooms is initiated, with TEP being transported below as aggregates. In the EZ, the dominant process is TEP production. The base of the EZ extends to the beginning of the upper mesopelagic zone (UMZ), where TEP concentrations are affected by aggregation–sedimentation processes as well as the degradation by bacteria, which occurs throughout the water column.

In this study we present the temporal and spatial variability of TEP in the euphotic and upper mesopelagic zones along the Gulf of Cádiz, an area defined by its varying oceanographic features, which range from coastal upwelling, fronts, and zones influenced by topographical forcing to anticyclonic currents. Some of these features of the Gulf of Cádiz, while being described from an hydrodynamic point of view (Stevenson, 1977; Folkard et al., 1997), until now had not been analyzed in detail in situ employing biological variables (Navarro et al., 2006). A previous cruise studied part of the region analyzing TEP distribution in the first 75 m of the water column, east of 7°00′W (García et al., 2002). This study suggested that the distribution of TEP was the result of phytoplankton biomass maxima occurring either locally or upstream of the main anticyclonic current and pointed out the necessity to intensify the knowledge of the hydrodynamics in the Gulf of Cádiz and its relation to biochemistry patterns. The present study, which includes a more extensive set of data, is aimed to explore the connection between TEP distribution and the physical and biologic structure of the Gulf of Cádiz, in an attempt to analyze the role of TEP in aggregation processes in the region. To achieve the second objective, two models were applied to evaluate the importance of TEP in this environment. One approach was the two particle-type coagulation model for diatoms of Ruiz et al. (2002) based on empirical data. The other approach used was model of Jackson (1990) of the theoretical initial process for aggregate formation of individual similar size particles. In parallel and owing to the diverse conditions found in the wide area sampled, we explored the relation of the trophic state of the ecosystem and the phase of the growing phytoplankton with the ratio between TEP and Chlorophyll and TEP abundance in isolation, being closer with the former than with the latter. In order to compare the results with known eutrophic areas, data from a well developed coastal upwelling (northwest Alboran Sea) and from a highly dynamic system (the Strait of Gibraltar) are also presented.

2. Material and methods

Samples were taken during the GOLFO-01 cruise on R.V. "*Hespérides*" (May 17–24, 2001) in the Gulf of Cádiz (SW Iberian Peninsula, Fig. 1). TEP were sampled in the first 200 m of the water column (fixed depths of 10, 25, 50, 75, 100 and 200 m), covering both the euphotic (EZ) and upper mesopelagic zones (UMZ). The division of the water column between EZ and UMZ was carried out when photosynthetic available radiation (PAR) profiles were performed (stations sampled during the day) with a spectroradiometer PRR-600. Temperature, conductivity, turbidity, chlorophyll fluorescence, and dissolved oxygen profiles were made in each sampling site with an Idronaut MK 317 CTD probe fitted with oceanographic bottles.

TEP samples were fixed with filtered (0.2 μm) formalin at a final concentration of 1%. The

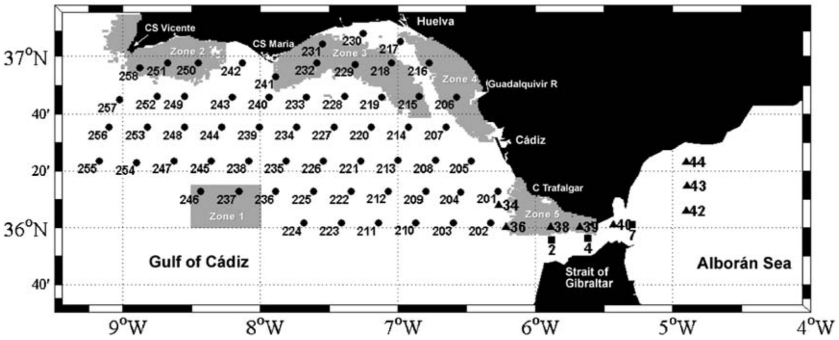

Fig. 1. Map showing location of stations sampled for TEP during the GOLFO-01 (circles), ICTIOALBORAN-CADIZ 97 (triangles) and CANIGO IV cruises (squares). Shadow areas correspond to the five zones distinguished based on EOF decomposition of SeaWiFS images by Navarro and Ruiz (2006). Zone 1 (anticyclonic current): stations 237 and 246; Zone 2 (Cape San Vicente): 250, 251 and 258; Zone 3 (Huelva Front): 215, 218, 229, 231 and 232; Zone 4 (coast Huelva-Cádiz): 206 and 216; Zone 5 (Cape Trafalgar): 36, 38 and 39.

fixation with formalin does not interfere with the stained procedure (Passow and Alldredge, 1994; Schuster and Herndl, 1995). In the laboratory, samples were filtered (100–160 ml) through a polycarbonate Poretics membrane (0.4 μm) using a constant filtration pressure (~95 mmHg). The samples were immediately stained with alcian blue. The concentration of TEP was estimated by spectrophotometry following Passow and Alldredge (1995a). Gum xanthan was the reagent used to build the standard curve. The sensitivity of the method was estimated at $3\,\mu g\,l^{-1}$. The triplicate measurements indicated a mean coefficient of variation of 22% (with a range of 1–49%) in TEP concentrations. The concentration of solid particles (in total volume concentration, ppm) was measured with a Coulter Counter (Multisizer II), using a pore size aperture size of 140 μm. The effective counting range was estimated to be 2–60% of the orifice size (around 2.8 and 84 μm). The Coulter Counter cannot detect TEP due to its gel nature (Alldredge et al., 1993).

TEP data of the northwestern Alboran Sea and the Strait of Gibraltar were obtained during the ICTIOALBORÁN-Cádiz 97 cruise (June 29–July 2, 1997) in the upper 75 m as described by García et al. (2002). In winter, TEP concentration down to the lower mesopelagic zone (<820 m) in the Strait of Gibraltar were measured during the CANIGO IV cruise (February 10–23, 1999). Both cruises were on board R.V. "*Cornide de Saavedra*" and TEP analysis procedure was the same as during the GOLFO-01 cruise. Chlorophyll *a* (Chl *a*) data were measured by standard fluorometric methods (Parsons et al., 1984) in the three cruises and in the same depths as TEP.

The Strait of Gibraltar is a very active channel where the pattern of Atlantic surface currents flowing to the Mediterranean and deep counter current is strongly affected by tidal dynamics and meteorological forcing, leading to pulsating upwelling events at the sill forced by topography (Bruno et al., 2002; Echevarría et al., 2002). The northwest Alboran Sea is characterized by the existence of active coastal upwelling and a frontal zone defined by the Atlantic jet entering the Mediterranean, with a marked gradient and a central relatively oligotrophic gyre (Sarhan et al., 2000).

Statistical analyses were performed on the data using Kaleidagraph^{TM} software. Correlation coefficients (Pearson correlation coefficients, Zar 1984) and significance levels were calculated following confirmation that the data set showed a normal distribution. For the comparison of TEP and TEP:Chl *a* among different zones, the non-parametric Wilconxon–Mann–Whitney test was carried out.

3. Results

3.1. TEP abundance in the Gulf of Cádiz

The sampling carried out in the Gulf of Cádiz in Spring 2001 showed that TEP maxima occurred always in the first meters of the water column (Fig. 2), associated to the nutrient enrichment of coastal areas. Indeed, distribution of TEP at 10 m was very similar to the pattern for chlorophyll. At this depth, chlorophyll (Chl *a*) and TEP concentrations were highly correlated ($r = 0.60$, $n = 58$, $p < 0.0001$), reflecting the phytoplankton origin of TEP. The correlation between the two variables was

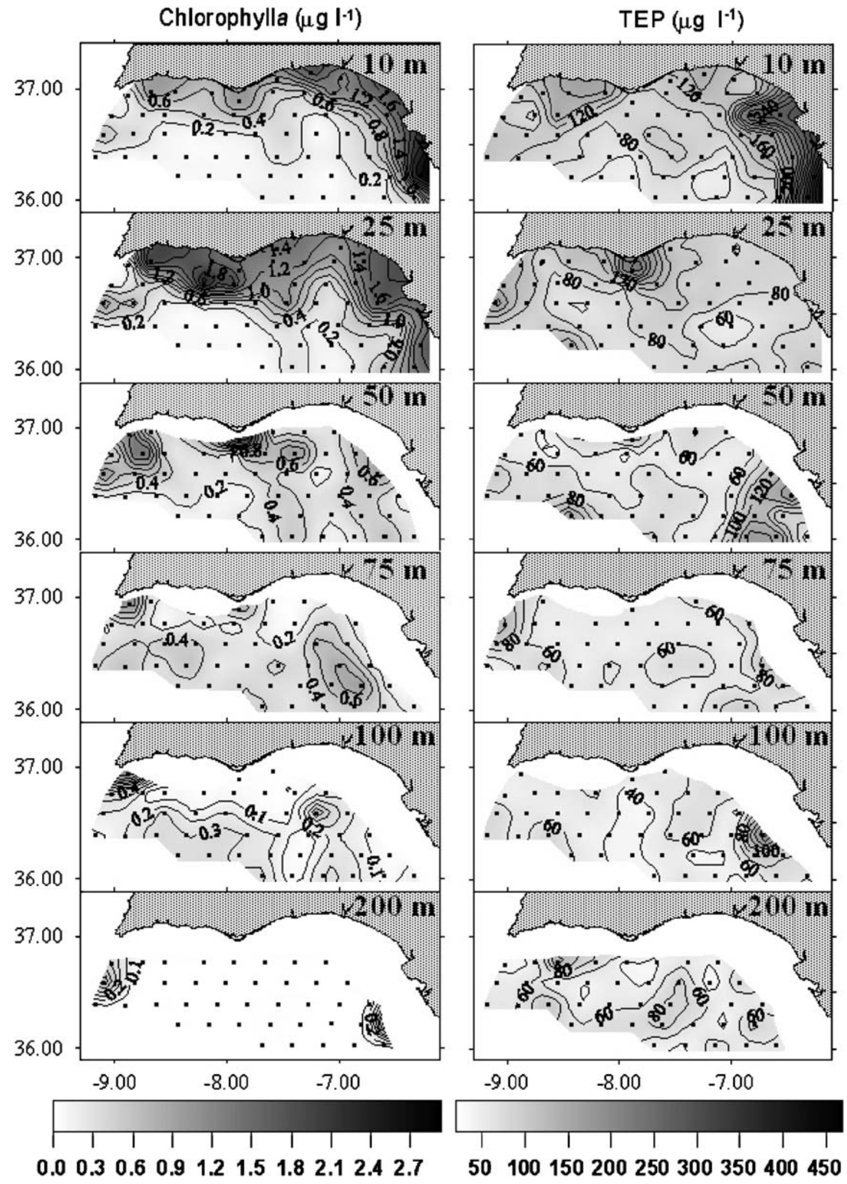

Fig. 2. Chlorophyll *a* ($\mu g\,l^{-1}$) and TEP ($\mu g\,l^{-1}$, average) at 10, 25, 50, 75, 100 and 200 m depths in the Gulf of Cádiz during GOLFO-01.

smaller but still statistically significant at 25 m ($r = 0.33$, $n = 53$, $p < 0.02$). The correlation between TEP and Chl *a* was significant for all samples from the euphotic zone considered together ($r = 0.29$, $n = 91$, $p < 0.01$). There was not a statistically significant correlation between TEP and Chl *a* deeper in the water column.

The differentiation of these nutrient enriched coastal areas during GOLFO-01 is supported by an Empirical Orthogonal Function (EOF) based regionalization derived from satellite images analysis (Navarro and Ruiz, 2006). The first region (Zone 1) represents the open ocean influenced by anticyclonic circulation in the center of the Gulf and is characterized by high temperatures and the lowest chlorophyll values of the cruise (Fig. 1). The Cape San Vicente region (Zone 2) is a quasi-permanent upwelling zone, characterized by cold surface waters and high nutrient concentrations along with a relatively high phytoplankton biomass registered during GOLFO-01. A similar region of upwelling that includes a frontal structure (Huelva Front), with eastward currents that are especially active when westerlies blow is Zone 3, influenced by Cape

Santa Maria. Zone 4 is a coastal area between Cádiz and Huelva with elevated chlorophyll and nutrient values and warmer water temperatures. Navarro and Ruiz (2006) observed the meteorological forcing of chlorophyll values in this zone, where westerlies and rainfall induce elevated values, while easterlies force a decrease in chlorophyll. As for Zones 2 and 3, Cape Trafalgar (Zone 5) was typified by cold waters, which here is a more permanent feature (this being related to topography and tidal fluctuations; Vargas-Yañez et al., 2002).

An analysis of differences in TEP concentrations among these five regions described by Navarro and Ruiz (2006) is presented here for both the euphotic (EZ) and upper mesopelagic zones (UMZ). Mean concentrations of TEP were significantly higher (Wilcoxon–Mann–Whitney test) in the EZ in Zones 2–4 (Cape San Vicente, Huelva Front and coast between Huelva and Cádiz) than in Zone 1, the anticyclonic current (Fig. 3). TEP abundance in the EZ were 120.3 ± 35.5 ($n = 18$), 122.43 ± 63.6 ($n = 36$), and $202.43 \pm 169.2\,\mu g\,l^{-1}$ ($n = 6$), in Zones 2, 3 and 4, respectively. In Zone 1, TEP concentrations were $63.8 \pm 24.8\,\mu g\,l^{-1}$ ($n = 36$), being relatively uniform with depth, with similar values being found in the EZ and the UMZ (Wilcoxon–Mann–Whitney test). Within the other zones, significant differences were found between the EZ and the UMZ, with TEP concentrations being higher in the EZ than in UMZ, indicating the importance of TEP production in those regions (Fig. 3) (Wilcoxon–Mann–Whitney test). However, TEP concentrations in the UMZ were not significantly different between regions (Wilcoxon–Mann–Whitney test). Unfortunately, no station was situated clearly within Zone 5 (Cape Trafalgar), so data from there are not included in Fig. 3. Nevertheless, stations near Trafalgar (stations 201 and 202) were most likely under the same influences and had high TEP concentrations of $261.3 \pm 196.3\,\mu g\,l^{-1}$ ($n = 12$) in the shallowest 25 m. The only available TEP data within Zone 5 were collected during the ICTIOAL-BORÁN-CÁDIZ97 cruise (stations 36, 38 and 39, Fig. 1); they also showed an elevated TEP abundance of $139.6 \pm 139\,\mu g\,l^{-1}$ ($n = 7$). This TEP concentration should be considered as characteristic of the mixed layer (ML) rather than the euphotic zone, as PAR profiles were not available. The criterion used to estimate the depth of the ML was a density gradient $\leqslant 0.005\,kg\,m^{-4}$. Beneath the ML, TEP values were below detection. TEP:Chl *a* values in the ML were low (52.0 ± 31.6), suggesting early stages in phytoplankton growth.

At Cape Trafalgar, TEP:Chl *a* values in Zones 2, 3 and 4 were relatively low (Fig. 4). The only TEP:Chl *a* ratio shown is that of the EZ since phytoplankton growth occurs mainly in this layer of the water column, where the relationship between TEP production and phytoplankton growth stage is meaningful. Zone 1 has markedly higher TEP:Chl *a* ratios, with a value of 854.2 ± 773.9, suggesting an elevated TEP production in low-nutrient waters compared to the enriched areas defined by Zones 2, 3 and 4.

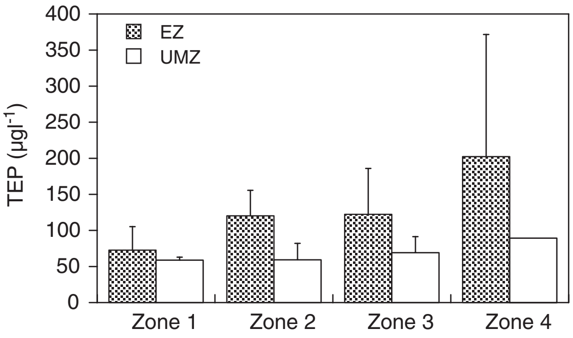

Fig. 3. TEP concentration ($\mu g\,l^{-1}$, average and standard deviation) during GOLFO-01 cruise in the areas distinguished through satellites images analysis by Navarro and Ruiz (2006). The water column was divided in two compartments: the euphotic zone (EZ) and the upper mesopelagic zone (UMZ), based in PAR profiles. In the case of Zone 1, stations were sampled during the night and PAR profiles were not available, considering the PAR profile of a similar characteristic station (St. 236) as guide to divided the water column in EZ and UMZ.

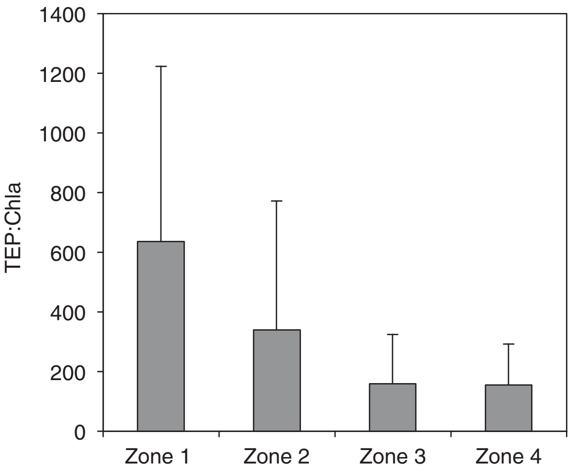

Fig. 4. TEP:Chl *a* ratio in the euphotic zone in the same zones as Fig. 3.

3.2. TEP distribution in an upwelling frontal region in the northwestern Alboran Sea

Fig. 5 shows profiles along a transect from a coastal area clearly defined by upwelling to the poorer waters offshore in the northwestern Alboran Sea. This upwelling was clearly delineated by the inclination of the isotherms as well as the decrease in chlorophyll fluorescence in the offshore direction. High TEP concentrations of 533.6 ± 38.0 $\mu g\,l^{-1}$ were present for the first 25 m in the upwelling area, while offshore a abundance of TEP in the water column were reduced and relatively uniform ($<25\,\mu g\,l^{-1}$). TEP concentrations were strongly correlated to chlorophyll *a* concentrations for all samples in the Alboran Sea ($r = 0.92$, $n = 13$, $p < 0.0001$).

3.3. Spatial and temporal variability of TEP in the Strait of Gibraltar

Due to tidal and topographic forcing, chlorophyll fluorescence is usually high eastward of Camarinal Sill and in immediately-adjacent surface waters of the NW Alboran Sea (Fig. 6). In summer, TEP was again correlated with that of chlorophyll ($r = 0.73$, $n = 12$, $p < 0.01$), with relatively high concentrations of TEP, 169.3 ± 127.4 $\mu g\,l^{-1}$ ($n = 4$), in the ML of the sill and Mediterranean stations (Fig. 6A). In the

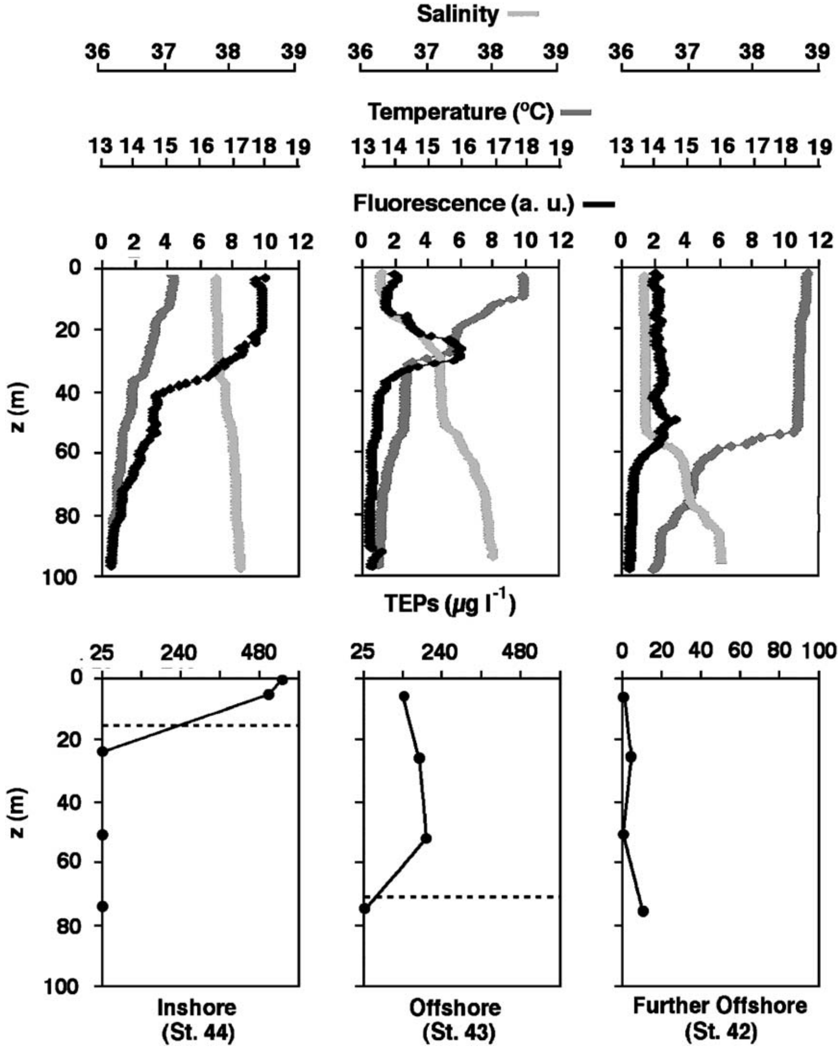

Fig. 5. Vertical profiles of salinity (light gray), temperature (°C, dark gray), fluorescence (a.u., black) and TEP ($\mu g\,l^{-1}$) in the Alboran Sea. Dashed lines indicated the position of the interface (IT) between Atlantic and Mediterranean waters. In station 42, IT was at 105 m (below the sampled depths). Note in Station 42 the changes in TEP scale (all the data are under the detection limit).

winter cruise, when the upper and lower mesopelagic zones were sampled, TEP distribution in the Strait was distinct (Fig. 6B). TEP concentration was reduced and uniform along the Strait and deep in the water column, with a mean value of 41.0 ± 15.4 μg l^{-1} ($n = 96$). The maximum TEP concentration over winter (87.5 ± 8.2 μg l^{-1}, $n = 6$) was found in the UMZ on the Atlantic side, a region affected by the influx of Mediterranean waters. This value was, however, low compared to TEP concentrations in summer. TEP and chlorophyll concentrations were not correlated during this cruise.

4. Discussion

4.1. TEP distribution in the southern Iberian coasts

TEP abundance in the euphotic zone, but not in the upper mesopelagic zone, along the southern Iberian coasts appears to be closely related to oceanographic features that modulate phytoplankton growth, such as coastal upwellings, fronts, topographical forcing or anticyclonic currents.

This general pattern suggests that maximum TEP concentrations coincide with the regions where biomass of phytoplankters is higher due to favorable growing conditions. Upwelling, fronts and regions of mixing caused by topographical forcing are oceanographic features where nutrients and shear increase in the euphotic zone, with the consequent positive effect on phytoplankton populations (Mann and Lazier, 1996). The nutricline (nitrate plus nitrite) was observed at shallower depths in all these regions compared to the rest of the Gulf (Navarro et al., 2006). Indeed, the coincident maxima for TEP and Chl *a* are consistent with TEP production by active growing phytoplankton without their accumulation in the Gulf of Cádiz. Certainly, both variables were positively correlated in the euphotic zone of the Gulf of Cádiz, as occurring in the Alboran Sea and during summer in the Strait of Gibraltar. Such correlations have been observed in other ecosystems (Hong et al., 1997; Passow and Alldredge, 1995a, b).

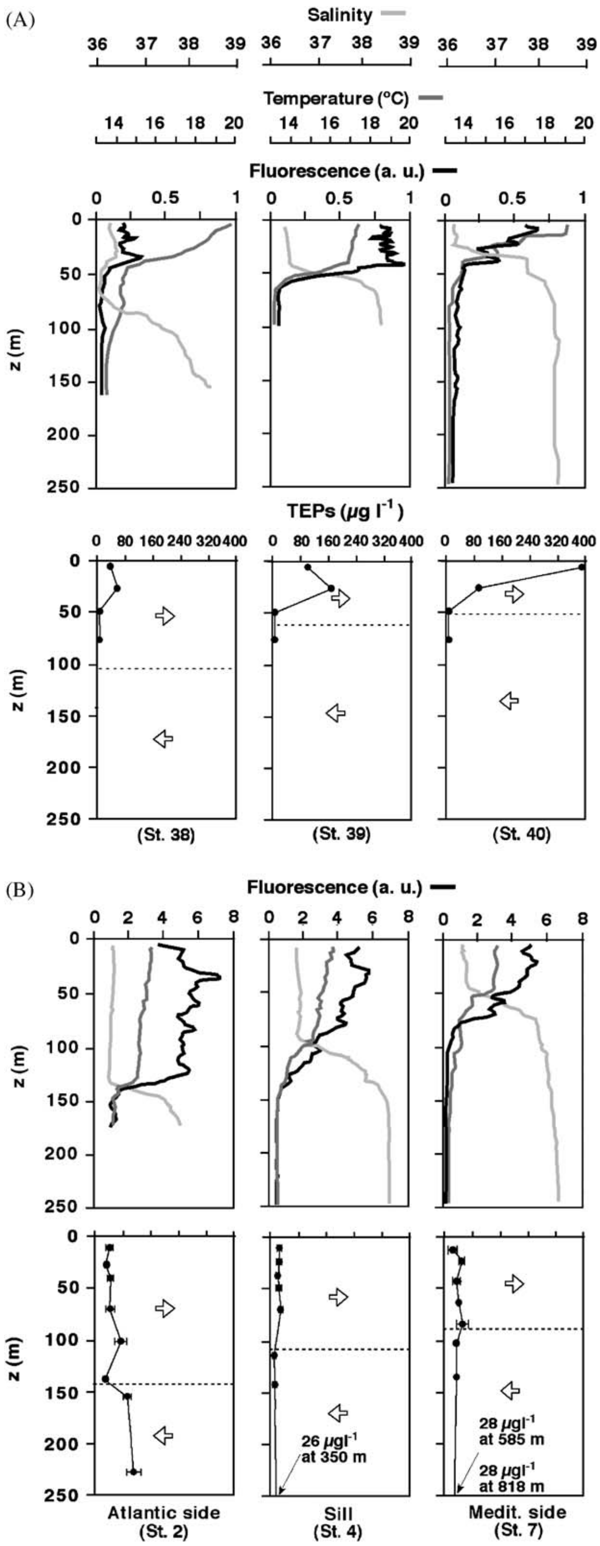

Fig. 6. Vertical profiles of salinity (light gray), temperature (°C, dark gray), fluorescence (a.u., black) and TEP (μg l^{-1}) in the Strait of Gibraltar. (A) Summer of 1997. (B) Winter of 1999. Dashed lines indicate the position of the interface (IT) between Atlantic and Mediterranean waters. Empty arrows show the main direction of the current.

Nevertheless, the absence of a positive correlation between TEP and Chl *a* is also a common feature both in coastal (Schuster and Herndl, 1995; Passow et al., 1995) and oceanic ecosystems (Engel, 2004; Prieto et al., 2002).

However, TEP and Chl *a* were not correlated in the Strait of Gibraltar over winter. Sampling of Mediterranean waters westwards of the sill provided a slight increase in TEP concentrations during the winter. These waters were not sampled during the summer cruise. East of the sill, Mediterranean waters gave reduced TEP concentration relative to Atlantic waters during both cruises (Fig. 6). This result suggests a possible increase in particle concentration in the water mass having passed through the shallow and narrow Camarinal Sill, an inference that requires further research to be confirmed. This change within de Mediterranean deep poor-chlorophyll waters in particle concentration that probably is mirrored in higher TEP concentration is the reason of the lack of correlation between both variables during this cruise. TEP and Chl *a* were not correlated in the Gulf of Cádiz during a previous study (García et al., 2002). In this last case, the absence of a direct correlation was attributed to the effect of advection in the direction of the main current and may be explained by possible bloom stages. In the present study, the alternative dominance of winds (Navarro et al., 2006) meant that the distribution of variables had no clear spatial structure over the length of the current. García et al. (2002) suggested that the TEP maxima close to Cape Trafalgar may be a local phenomenon, although stating that the possibility of other sources should not be discarded. A posteriori studies based on temporal variability analysis using satellite images (Navarro and Ruiz, 2006) together with TEP distribution analyses in this study have confirmed the local origin of this TEP patch.

The reduced TEP:Chl *a* values in Cape Trafalgar are indicators of early stages of a bloom, since the quantity of TEP exuded by unit phytoplankton biomass depends on physiological conditions. In the first stages of a bloom, TEP may be relatively low as a result of the increased number of phytoplankters whose production of TEP is minor (Corzo et al., 2000). As the bloom develops, the concentration of nutrients declines with a subsequent decrease in phytoplankton biomass, increasing the TEP:Chl *a* ratio. Following this, the individual rate of TEP production increases, influenced by an elevated C/N ratio (Penna et al., 1999), TEP:Chl *a* being much higher.

An elevated TEP concentration together with low Chl *a* values in the mixed layer is a "short-life" situation. As soon as enough particulate matter (phytoplankton cells, mineral particles or detritus) are present, TEP will form aggregates with this material (Prieto et al., 2002), probably increasing the aggregates' weight allowing them to be flushed out to deeper waters (Kumar et al., 1998). For instance, in the case of bloom termination, as TEP cells and detritus coincide with time, TEP possibly plays an important role in transporting the biological matter generated downward during the bloom. To illustrate this, we can focus on the northwestern Alboran Sea section, which covers the different stages of a bloom (Fig. 5). TEP and chlorophyll *a* concentrations had coincident maxima, suggesting that TEP concentrations were the result of an elevated number of cells, perhaps having a lower individual rate of exudation per cell. Those maxima appeared inshore, the area most affected by the upwelling, where average TEP:Chl *a* values were lowest, while further offshore TEP:Chl *a* values increased in the mixed layer by one order of magnitude (Table 1). A similar pattern of TEP:Chl *a* with bloom development was observed in a mesocosm experiment, with the displacement from nutrient enrichment instead of being in space, was in time (Prieto et al., 2002). In that case, TEP:Chl *a* values increased from 37.1 ± 12.0 to 510.2 ± 641.1, i.e. from diatom blooming to post-blooming conditions, an increment of the same order as that of Alboran.

Likewise TEP:Chl *a* is related to the stage of the bloom; at basin scale this ratio may be associated to the trophic state of the ecosystem. In Table 1 TEP:Chl *a* ratios of different oceanographic ecosystems are summarized. The trend shown is for areas favorable to phytoplankton growth to have a lower ratio and for TEP production per individual cell to increase otherwise. In agreement with this, for the more oligotrophic stations from the Gulf of Cádiz, the TEP:Chl *a* ratio was remarkably high (Table 1, Fig. 4). Similarly high values of exopolymer to Chl *a* ratio also were found in the same most pronounced oligotrophic region of the Gulf of Cádiz during summer (García et al., 2002) as well as at the ALOHA station (Prieto, unpublished data). Meanwhile, in the eutrophic region of the northwestern Alboran Sea the TEP:Chl *a* ratio was two orders of magnitude lower than that of

Table 1
Data of TEP concentration ($\mu g\,l^{-1}$) over the entire water column and the ratio TEP:Chl *a* only in the euphotic zone (EZ), the layer where this ratio is meaningful from a trophic point of view for an ecosystem. Beneath this layer, the ratio is more affected by the lack of chlorophyll

Season	Geographic site		Zone	TEP ($\mu g\,l^{-1}$)	TEP: Chl *a*	References
Spring	Balsfjord		0–18 m	100–255	29–500	Riebesell et al. (1995)
			21–63 m	125–250	40–500	
Spring	East sound		Surface	50–160	3–80	Kiørboe et al. (1996)
Summer	Ross Sea (Antarctica)		Surface	0–2800	Mean 89.1	Hong et al. (1997)
Autumn	Mecklenburg bight (Baltic Sea)		Bottom (16–26 m)	267–471		Jähmlich et al. (1998)
Spring	Otsuchi Bay (Subartic Pacific Ocean)		0–15 m	24–2321^{a}	125–144^{a}	Ramaiah et al. (2001)
Summer	Central Baltic Sea		4–20 m	145–322	Mean 130	Engel et al. (2002)
Summer	Gulf of Cadiz		ML	$<$ 25–717^{a}	ud-340^{a}	García et al. (2002)
			ML	$<$25–628^{b}	ud-11952^{b}	
Summer	NE Atlantic Ocean		10–70 m	10–120	49–104	Engel (2004)
Winter	ALOHA		ML	86–468^{b}	804–5335^{b}	Prieto, unpub.
			BML	63–477^{b}		
Spring	Gulf of Cadiz		EZ	83^{a}	57^{a}	This study
			UMZ	82–89^{a}		
			EZ	24–205^{b}	63–2708^{b}	
			UMZ	26–137^{b}		
Summer	SG	Atlantic side	ML	27–49	57–88	This study
		Sill	ML	90–152^{a}	42–69^{a}	
		Medit. side	ML	354	181	
Winter	SG	Atlantic side	EZ	43–70	53–88	This study
			UMZ	82–93		
		Sill	EZ	32–38	62–97	
			UMZ	25–26		
			LMZ	26		
		Medit. side	EZ	27–43	51–82	
			UMZ	28–42		
			LMZ	28		
Summer	Alboran Sea	Inshore	ML	507–560^{a}	28–29*	This study
		offshore	ML	$<$ 25–121	ud-130	

To calculate TEP:Chl *a*, only TEP data over the detection limit were considered. UMZ: upper mesopelagic zone; LMZ: lower mesopelagic zone; ML: mixed layer; BML: below mixed layer; SG: Strait of Gibraltar; ud: undetected.

[a] Eutrophic sites (average chl $a > 2\,\mu g\,l^{-1}$).

[b] Oligotrophic sites (average chl $a < 0.2\,\mu g\,l^{-1}$).

ALOHA and the oligotrophic area in the Gulf of Cádiz (Table 1). Also, in the highly dynamic ecosystem of the Strait of Gibraltar, the lowest TEP:Chl *a* values were found close to the Camarinal Sill in the summer sampling (Table 1), where the generation of mixing processes favor pulsating nutrient enrichments at surface waters (Echevarría et al., 2002). Thus, at basin scale a TEP:Chl *a* ratio in the order of 10^3 in the EZ is related to ecosystems with oligotrophic characteristics while a low TEP:Chl *a* ratio is associated with eutrophic environments (Table 1). Despite this, TEP concentrations alone do not define these trophic conditions.

Primary production rates were only estimated in nine samples during the GOLFO-01 cruise by Navarro et al. (2006). Nevertheless, TEP:Chl *a* and primary production rates show a negative significant correlation ($r = -0.50$, $n = 9$, $p < 0.2$). Moreover, average TEP:Chl *a* ratio in the EZ showed a negative significant correlation with silicate concentrations ($r = -0.55$, $n = 10$, $p < 0.1$) among the different zones and ecosystems sampled during the GOLFO-01 and ICTIOALBORÁN-CÁDIZ 97 cruises (no nutrient data available for the CANIGO-IV cruise). Both correlations of TEP:Chl *a* make stronger the argument of the ratio as a valuable descriptor of the ecosystem.

4.2. *Significance of TEP in aggregation processes in the Gulf of Cádiz*

Since TEP was not seen to accumulate in the EZ, this suggested that losses of TEP in the Gulf of

Cádiz must be elevated. TEP disappears from the EZ by two main processes: degradation by bacteria and the aggregation-sinking process associated with other particles. The former has been already considered as less important than aggregation-sinking due to the refractory nature of TEP (Obernosterer and Herndl, 1995; Stoderegger and Herndl, 1999). This leads to the suggestion that aggregation rates in the Gulf of Cádiz must be elevated. In order to quantify these aggregation processes in the system, two distinct models were explored.

Implementing the coagulation model for diatoms of Ruiz et al. (2002), employing the minimum and maximum aggregation kernel (β) estimated empirically (0.59 and $13.08\,\mathrm{l\,mg\,C^{-1}\,d^{-1}}$, respectively), a first result (Model 1) was estimated by calculating the range of time needed to reduce the concentration of particles by half ($t_{1/2}$) due to coagulation. The model considered a two particle-type representation of seston dynamics by

$$\frac{\mathrm{d}C_{\mathrm{small}}}{\mathrm{d}t} = \text{Primary Production} - \beta\,\frac{\mathrm{TEP}}{\mathrm{TEP}+850}\,C_{\mathrm{agg}}C_{\mathrm{small}} - \lambda_{\mathrm{small}}C_{\mathrm{small}}$$

$$\frac{\mathrm{d}C_{\mathrm{agg}}}{\mathrm{d}t} = \beta\,\frac{\mathrm{TEP}}{\mathrm{TEP}+850}\,C_{\mathrm{agg}}C_{\mathrm{small}} - \lambda_{\mathrm{agg}}C_{\mathrm{agg}}, \qquad (1)$$

where TEP is the TEP concentration ($\mu\mathrm{g\,l^{-1}}$), which modulates the aggregation kernel, C_{small} and C_{agg} are the carbon concentrations of particles and aggregates, respectively ($\mathrm{mg\,C\,l^{-1}}$), and λ represents the loss rates by sedimentation (set to 0.7 and $2.537\,\mathrm{d^{-1}}$ for particles and aggregates, respectively). The modulation by TEP of the aggregation kernel is done by multiplying it by a Michaelis–Menten type of factor with a half saturation of $850\,\mu\mathrm{g\,l^{-1}}$ for the process, since the overcoming of this concentration during the mesocosm experiment used to develop the Model 1 seemed to trigger the aggregation process (Ruiz et al., 2002). The loss rates by sedimentation were derived entirely from the same experimental data.

The Primary Production was estimated as laid out by Ruiz et al. (2002), using Jassby and Platt (1976), formulations, photosynthetic parameters of Fasham et al. (1990), and Michaelis–Menten factors for limitation of nitrogen and phosphorous. PAR and nutrient values included in the primary production estimations were measured during the cruise. Further information on PAR and nutrient data are given by Navarro et al. (2006). C_{small} was estimated through the Chlorophyll values assuming the ratio Chl *a*:C of 0.4 mg Chl *a* mmol $\mathrm{C^{-1}}$ (Tett et al., 2002). We considered the concentration of solid particles measured with the Coulter Counter as the concentration of aggregates in the water. The mean particle size measured by the Coulter Counter was then transformed into its carbon equivalent by applying the expression of Alldredge (1998). Some of the particles counted with the Coulter Counter were probably included in the Chl *a* determinations, but following conversion of both aggregates concentration and Chlorophyll values, to their corresponding carbon concentrations, the percent of carbon able to be counted twice was less than 1% (average 0.15%).

The second approximation (Model 2) used was the theoretical model of Jackson (1990) of the initial process for aggregate formation of individual similarly sized particles, based on the assumptions of Kiørboe et al. (1990)

$$\frac{\mathrm{d}C}{\mathrm{d}t} = -7.824 \quad \alpha\frac{\phi}{\pi}\,\mathrm{shear}\ C, \qquad (2)$$

where α is the stickiness, ϕ is the volume fraction of suspended particles (ppm), shear is the fluid shear rate ($\mathrm{s^{-1}}$), and C is the particle concentration. The calculated volume fraction ϕ coincided with the concentration of solid particles (SP) measured with the Coulter Counter. The effect of TEP in the aggregation process in this model was incorporated in the stickiness values. Therefore, values for stickiness were estimated using the α and TEP:SP $\mu\mathrm{g\,\mu l^{-1}}$ relationship given by the formula $\alpha = 9.1\times10^{-4}$ (TEP:SP), where TEP:SP is the ratio of TEP to the total volume of Coulter Counter detectable particles (see Engel, 2004, for details). Using TEP:SP to estimate α is considered to be a better indicator for the coagulation efficiency of bulk particles compared to TEP:Chl *a* (Engel, 2004). TEP:SP is less dependent on the relative abundance of phytoplankton or their physiological state since phytoplankton cells represent only a fraction of particles that coagulate. To compare $t_{1/2}$ results to the first approximation (Model 1), the maximum and minimum values of *shear* in nature were considered (3.16 and $0.03\,\mathrm{s^{-1}}$, respectively) that coincided with those utilized to set bounds to the empirical aggregation kernel (β) used in Model 1.

Considering the entire range of half-life values based on the minimum and maximum shear values in nature, Model 1 provides a much narrower range of $t_{1/2}$ than Model 2 (Table 2). An important distinction between the empirical Model 1 and the

Table 2
Estimated aggregation of particles within the euphotic zone (EZ) in the Gulf of Cadiz

Station	Model 1		Model 2	
	$t_{1/2}$ (d) Shear min	$t_{1/2}$ (d) Shear max	$t_{1/2}$ (d) Shear min	$t_{1/2}$ (d) Shear max
207	0.28	0.02	24.96	0.24
208	1.89	0.04	67.49	0.64
209	1.03	0.03	65.35	0.62
215[a]	0.53	0.03	29.16	0.28
216[b]	0.63	0.02	123.23	1.17
217	0.51	0.03	90.41	0.86
218[a]	0.75	0.04	103.58	0.98
219	2.2	0.13	148.07	1.41
225	5.46	0.12	89.66	0.85
226	5.01	0.08	100.02	0.95
228	0.77	0.07	107.43	1.02
233	0.71	0.05	128.34	1.22
234	1.42	0.07	108.23	1.03
235	1.97	0.53	166.15	1.58
236	3.81	0.37	170.41	1.62
241[a]	0.73	0.04	70.84	0.67
242	0.88	0.03	67.83	0.64
243	0.68	0.05	94.30	0.90
244	3.17	0.27	151.88	1.44
245	1.23	0.17	156.63	1.49
249	1.77	0.06	137.09	1.30
250[c]	0.60	0.02	40.84	0.39
251[c]	0.89	0.03	108.34	1.03
252	0.80	0.06	117.95	1.12
253	0.53	0.02	72.16	0.69
257	6.01	0.04	74.03	0.70
258[c]	0.39	0.02	194.44	1.85

The mean half-lives ($t_{1/2}$) of particle concentration were calculated according to Model 1 and Model 2 (see text for details), considering a minimum and maximum shear of 0.03 and 3.16 s^{-1}, respectively. Only stations sampled during the day are showed. In these stations photosynthetic active radiation profiles were performed, thus permitting estimations of primary production used in the Model 1.

[a] Zone 3, Huelva Front.

[b] Zone 4, coast between Huelva and Cadiz.

[c] Zone 2, Cape San Vicente.

theoretical Model 2 is that the former model assumes that the important interactions occur between small and large particles, while the latter considers that the prevalent interactions are the ones between particles of the same size and that the suspension is mono-disperse. For this reason, Model 1 Chl *a* and SP values are used to represent the two size classes involved in the aggregation process while in Model 2 only one size class is needed, SP being used in concordance with previous implementations of the Jackson Model in nature (Engel, 2004).

Added to this, the aggregation kernels used in Model 1 equations are comprised of the mechanisms of coagulation (mainly differential sedimentation and turbulent shear) as well as the effect of the entire set of parameters active in the process of aggregation (stickiness, aggregates porosity and curvilinear trajectories), being obtained from phytoplankton derived particles (Ruiz et al., 2002). Ruiz et al. (2002) obtained aggregation kernels of the same magnitude (3.741 and 2.7361 $mgC^{-1} d^{-1}$) during two aggregation events led by distinct diatom species in the experimental aquarium. Thus, the aggregation kernel seems to be robust to changes in the nature of the interacting particles. As this kernel is also affected by turbulence shear and differential sedimentation, and since the range of turbulence in nature is known, limits can be set to the empirical aggregation kernel considering the maximum changes in the kernel, assuming that it is affected by turbulence in its entirety, while in reality only one part is affected and the portion proportional to the differential sedimentation remains unaffected. It follows therefore that the range of values used in this study for the empirical aggregation kernel actually must be narrower. Nevertheless, the exact value of the kernel at a level of turbulence distinct to that at which the experimental determination was made, cannot be calculated. It was preferable to provide the whole range of estimations rather than simply assume a single value.

Even for the minimum shear rate, Model 1 points out the importance of aggregation in the Gulf of Cádiz. Prior to the occurrence of marine snow aggregates $t_{1/2}$ is of the order of 1 day, as was observed both in field data (Logan et al., 1995) and experiments in the laboratory (Prieto et al., 2002). Setting this value of half-life as the limit for considering aggregation as a relevant process, the proportion of stations potentially affected by coagulation within the EZ at the low range of shear rates following Model 1 approximation is higher than the ones that are not (Fig. 7). From this analysis, we also observed that coastal stations, including Zones 2–4, showed the lowest $t_{1/2}$. Consequently, this result indicates that the excess material from primary production is being probably vertically transported by marine aggregates to deeper waters. Using minimum shear values, it is actually in the first few meters of the water column where the broadest range of $t_{1/2}$ is predicted (Fig. 8). This indicates that when seston dynamics are less influenced by turbulent shear, Model 1 is more sensitive to TEP concentrations (whose maxima were registered in the first 10 m) and to the effect of the PAR forcing function in primary production.

Engel (2004) estimated northeast Atlantic Ocean aggregation rates using the Model 2 approximation, assigning a shear value of $0.84\,s^{-1}$ as per Kriest and Evans (1999), obtaining $t_{1/2}$ values in the order of weeks to months (38–105 d). An estimated shear value in the Gulf of Cádiz during the GOLFO-01 cruise was performed from wind speed calculated based on the environmental data collected aboard the research vessel (for details see Navarro et al., 2006). The wind-induced turbulence at the bottom of the mixed layer was calculated from the daily averages of wind speed from the empirical relationship proposed by MacKenzie and Leggett (1991)

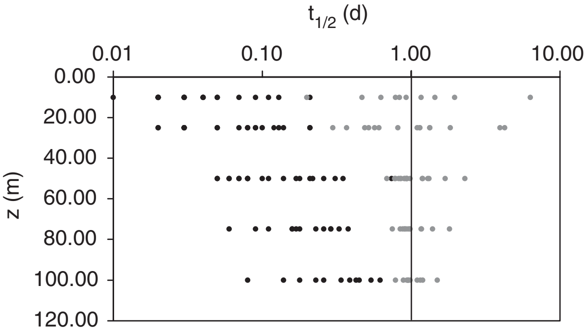

Fig. 8. Depth distribution of estimated half-lives ($t_{1/2}$) of particle concentration due to aggregation in the Gulf of Cádiz. Values were calculated after Model 1 considering a minimum (gray circles) and maximum aggregation kernel (black circles) of 0.59 and $13.08\,d^{-1}$ mg C, respectively.

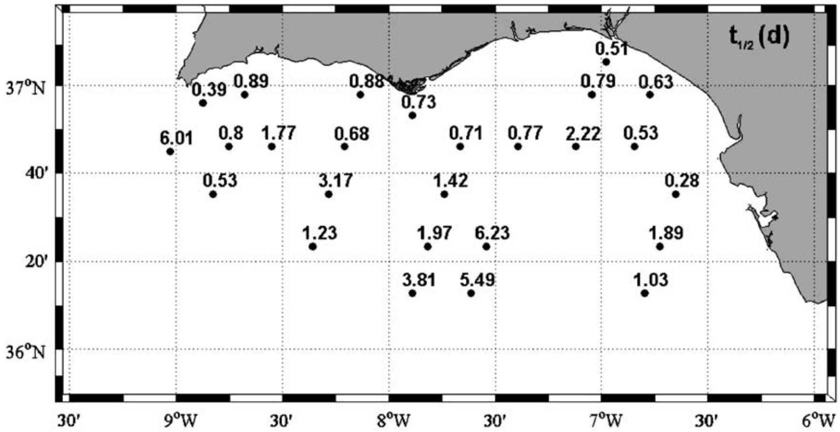

Fig. 7. Estimated mean half-lives ($t_{1/2}$) of particle concentration due to aggregation in the Gulf of Cádiz within the euphotic zone (EZ). The aggregation process was simulated according to Ruiz et al. (2002) approximation (Model 1), considering a minimum aggregation kernel of 0.59 mg C, result of the low range of shear in nature. Only in stations sampled during the day photosynthetic active radiation profiles were performed, thus permitting estimations of primary production used in the Model 1.

and the depth of the mixed layer. This estimation gave an average shear value in the Gulf of Cádiz of $0.48\,s^{-1}$. Even when applying this shear value using the Model 2 approximation, half-life values are still low, ranging from 1.6 to 12 d in the EZ. This estimate confirms again the potential importance of TEP in aggregation processes in the Gulf of Cádiz, framing this ecosystem within the adjacent ocean basin.

TEP has a dual role in the coagulation process, increasing both particle abundance and stickiness, but thus far in the Model 2 approximation only the effect of stickiness was considered. To estimate the influence of TEP abundance on aggregation rates in the Gulf of Cádiz using the Model 2, the volume concentration of TEP was also included in ϕ. Hence, the TEP-volume fraction (ppm) was estimated from colorimetric determination by first calculating TEP–carbon assuming a carbon conversion factor of TEP–carbon = 0.7 TEP_{color}(Passow, 2002); the volume fraction was then estimated from TEP–carbon assuming a carbon density of $17.4\,g\,carbon\,l^{-1}$ (Engel and Passow, 2001). This conversion yielded a range of 0.9–20 ppm, which once included in the calculation of ϕ, slightly reduced $t_{1/2}$, e.g. from 1.6 to 1.4 d at the EZ of station 207 where TEP was maximum, indicating that varying stickiness was the dominant effect of TEP in aggregation rates in the Gulf of Cádiz.

We can conclude that aggregation should play an important role in the Gulf of Cádiz to export matter from the euphotic zone to the UMZ, importance that probably could not have been achieved without the registered concentrations of TEP.

Combining the measurements of TEP in all the ecosystems studied, we can summarize by saying that the spatial and temporal variability of TEP in the euphotic zone are mediated both by the hydrodynamics of the studied area as well as by the environmental conditions of the water column. When local hydrology is characterized by either a quasi-permanent coastal upwelling, as is the case in the Alboran Sea and Cape San Vicente, a front (Huelva Front) or a topographic forcing (Cape Trafalgar), TEP and chlorophyll distributions are closely related, while when topographic and hydrographic characteristics of the studied area generate strong advection, as in the Strait of Gibraltar, phytoplankton and TEP concentration increase but showed a less evident spatial pattern. The ratio between TEP and photosynthetic pigments emerges as an improved descriptor of the trophic state of the system (and to the stage of a bloom) compared to TEP abundance alone, this being very low in eutrophic sites and on the order of 10^3 in oligotrophic environments such as the center of the Gulf of Cádiz, situated southwest of the anticyclonic current. It is in this oligotrophic environment where half-life values were highest, suggesting a possibly low organic material vertical flux as could be expected in this environment.

Acknowledgements

We thank the captains, crews and technicians of the R.V. *Cornide de Saavedra* and *Hespérides* for support in the field. We acknowledge scientific fellows involved in the three campaigns for their assistance. ICTIOALBORÁN-Cádiz 97 data were acquired under the specific co-operation agreement between the ‘‘Instituto Español de Oceanografía’’ (IEO) and the University of Cádiz. This work was financially supported by Spanish National Program CICYT (Projects MAR96 1837, MAR99-0643-C03-02, CTM2005-01091/MAR and REN2001-2733-C02-02/MAR), the EU MAST CANIGO project (Contract no. MAS3-CT96-0060), a doctoral fellowship to L.P. provided by Spanish MECD and a research grant to L.P. by the ‘‘Consejería de Educación y Ciencia’’ (Junta de Andalucía).

References

Alldredge, A.L., 1998. The carbon, nitrogen and mass content of marine snow as a function of aggregate size. Deep-Sea Research I 45, 529–541.

Alldredge, A.L., Jackson, G.A. (Eds.), 1995. Aggregation in marine systems. Deep-Sea Research II 42, 274pp.

Alldredge, A.L., Passow, U., Logan, B.E., 1993. The abundance and significance of a class of large, transparent organic particles in the ocean. Deep-Sea Research I 49, 1131–1140.

Bruno, M., Alonso, J.J., Cózar, A., Vidal, J., Ruiz-Cañavate, A., Echevarría, F., Ruiz, J., Gómez, F., 2002. The boiling water phenomena at Camarinal Sill, the Strait of Gibraltar. Deep-Sea Research II 49, 4097–4113.

Corzo, A., Morillo, J.A., Rodríguez, S., 2000. Production of transparent exopolymer particles (TEP) in cultures of *Chaetoceros calcitrans* under nitrogen limitation. Aquatic Microbial Ecology 23, 63–72.

Echevarría, F., García-Lafuente, J., Bruno, M., Gorsky, G., Goutx, M., González, N., García, C.M., Gómez, F., Vargas, J.M., Picheral, M., Striby, L., Varela, M., Alonso, J.J., Reul, A., Cózar, A., Prieto, L., Sarhan, T., Plaza, F., Jiménez-Gómez, F., 2002. Physical–biological coupling in the Strait of Gibraltar. Deep-Sea Research II 49, 4115–4130.

Engel, A., 2004. Distribution of transparent exopolymer particles (TEP) in the northeast Atlantic Ocean and their potential significance for aggregation processes. Deep-Sea Research I 51, 83–92.

Engel, A., Passow, U., 2001. Carbon and nitrogen content of transparent exopolymer particles (TEP) in relation to their Alcian Blue adsorption. Marine Ecology Progress Series 219, 1–10.

Engel, A., Meyerhöfer, M.v., Bröckel, K., 2002. Chemical and biological composition of suspended particles and aggregates in the Baltic Sea in summer (1999). Estuarine, Coastal and Shelf Sciences 55, 729–741.

Fasham, M.J.R., Ducklow, H.W., McKelvie, S.M., 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. Journal of Marine Research 48, 591–639.

Folkard, A.M., Davies, P., Fiúza, A.F.G., Ambar, I., 1997. Remotely sensed sea surface thermal patterns in the Gulf of Cádiz 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., 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.

Guo, L., Hung, C.C., Santschi, P.H., Walsh, I.D., 2002. ^{234}Th scavenging and its relationship to acid polysaccharide abundance in the Gulf of Mexico. Marine Chemistry 78 (2–3), 103–119.

Hill, P.S., 1992. Reconciling aggregation theory with observed vertical fluxes following phytoplankton blooms. Journal of Geophysical Research 97, 2295–2308.

Hong, Y., Smith, W.O., White, A.M., 1997. Studies on transparent exopolymeric particles (TEP) produced in the Ross Sea (Antarctica) and by *Phaeocystis antartica* (Prymnesiophyceae). Journal of Phycology 33, 368–376.

Jackson, G.A., 1990. A model of the formation of marine algal flocs by physical coagulation processes. Deep-Sea Research I 37, 1197–1211.

Jähmlich, S., Thomson, L., Graf, G., 1998. Factors controlling aggregate formation in the benthic boundary layer of the Mecklanburg Bight (Western Baltic Sea). Journal of Sea Research 41, 245–254.

Jassby, A.T., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnology and Oceanography 21, 540–547.

Kiørboe, T., Andersen, K.P., Dam, H.G., 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. Marine Biology 107, 235–245.

Kiørboe, T., Hansen, J.L.S., Alldredge, A.L., Jackson, G.A., Passow, U., Dam, H.G., Drapeau, D.T., Waite, A., García, C.M., 1996. Sedimentation of phytoplankton during a diatom bloom: rates and mechanisms. Journal of Marine Research 54, 1123–1148.

Kriest, I., Evans, G.T., 1999. Representing phytoplankton aggregates in biogeochemical models. Deep-Sea Research I 46, 1841–1859.

Kumar, M.D., Sarma, V.V.S.S., Ramiaah, N., Gauns, M., Sousa, deS.N., 1998. Biogeochemical significance of transparent exopolymeric particles in the Indian Ocean. Geophysical Research Letters 25, 81–84.

Logan, B.E., Passow, U., Alldredge, A.L., Grossart, H.P., Simon, M., 1995. Rapid formation and sedimentation of large aggregates is predictable from the coagulation rates (half-lives) of transparent exopolymeric particles (TEP). Deep-Sea Research II 42, 215–238.

MacKenzie, B.R., Leggett, W.C., 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Marine Ecology Progress Series 73, 149–160.

Mann, K.H., Lazier, J.R.N., 1996. Dynamics of marine ecosystems. Biological-Physical Interactions in the Oceans, second ed. Blackwell Science, Cambridge, 394pp.

Mari, X., Beauvais, S., Lemee, R., Pedrotti, M.L., 2001. Non-Redfield C:N ratio of transparent exopolymeric particles in the northwestern Mediterranean Sea. Limnology and Oceanography 46, 1831–1836.

McCave, I.N., 1984. Size spectra and aggregation of suspended particles in the deep ocean. Deep-Sea Research I 31, 329–352.

Navarro, G., Ruiz, J., 2006. Spatial and temporal variability of phytoplankton in the Gulf of Cádiz through remote sensing images. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.04.014].

Navarro, G., Ruiz, J., Huertas, I.E., García, C.M., Criado Aldeanueva, F., Echevarría, F., 2006. Basin scale structures governing the position of the deep fluorescence maximum in the Gulf of Cádiz. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2006.04.013].

Obernosterer, I., Herndl, G.J., 1995. Phytoplankton extracellular release and bacterial growth: dependence on inorganic N:P ratio. Marine Ecology Progress Series 116, 247–257.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, Oxford, 173pp.

Passow, U., 2000. Formation of transparent exopolymer particles, TEP, from dissolved precursors. Marine Ecology Progress Series 192, 1–11.

Passow, U., 2002. Transparent exopolymer particles (TEP) in aquatic environments. Progress in Oceanography 55, 287–333.

Passow, U., Alldredge, A.L., 1994. Distribution, size and bacterial colonization of transparent exopolymer particles. Marine Ecology Progress Series 113, 185–198.

Passow, U., Alldredge, A.L., 1995a. A dye-binding assay for the spectrophotometric measurement of transparent exopolymer particles (TEP) in the ocean. Limnology and Oceanography 40, 1326–1335.

Passow, U., Alldredge, A.L., 1995b. Aggregation of a diatom bloom in a mesocosm: the role of transparent exopolymeric particles (TEP). Deep-Sea Research II 42, 99–109.

Passow, U., Kozlowski, W., Vernet, M., 1995. Palmer LTER: temporal variability of transparent exopolymeric particles in Arthur Harbor during the 1994–1995 growth season. Antarctic Journal—Review, 265–266.

Penna, A., Bertuli, S., Penna, N., Magnani, M., 1999. Influence of nutrient ratios on the in vitro extracellular polysaccharide production by marine diatoms from the Adriatic Sea. Journal of Plankton Research 21, 1681–1690.

Prieto, L., Ruiz, J., Echevarría, F., García, C.M., Gálvez, J.A., Bartual, A., Corzo, A., Macías, D., 2002. Scales and processes in the aggregation of diatom blooms. High time resolution and wide size range records in a mesocosm study. Deep-Sea Research I 49, 1233–1253.

Quigley, M.S., Santschi, P.H., Hung, C., Guo, L., Honeyman, B.D., 2002. Importance of acid polysaccharides for ^{234}Th complexation to marine organic matter. Limnology and Oceanography 47, 367–377.

Ramaiah, N., Yoshikawa, T., Furuya, K., 2001. Temporal variations in transparent exopolymer particles (TEP) associated with a diatom spring bloom in a subarctic ria in Japan. Marine Ecology Progress Series 212, 79–88.

Riebesell, U., Reigstad, M., Wassmann, P., Noji, T., Passow, U., 1995. On the trophic fate of Phaeocystis-derived mucus for vertical flux. Netherlands Journal of Sea Research 33, 193–203.

Ruiz, J., Prieto, L., Ortegón, F., 2002. Diatom aggregate formation and fluxes: a modelling analysis under different size-resolutions schemes and with empirically determined aggregation kernels. Deep-Sea Research I 49, 495–515.

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

Schuster, S., Herndl, G.J., 1995. Formation and significance of transparent exopolymer particles in the northern Adriatic Sea. Marine Ecology Progress Series 124, 227–236.

Stevenson, R.E., 1977. Huelva Front and Malaga, Spain, Eddy Chain as defined by Satellite and Oceanographic Data. Deutsche Hydrographische Zeitschrift 30 (2).

Stoderegger, K., Herndl, G.J., 1999. Production of exopolymer particles by marine bacterioplankton under contrasting turbulence conditions. Marine Ecology Progress Series 189, 9–16 (Armi, L., Farmer, D.M., 1988. The flow of Mediterranean water through the Strait of Gibraltar. Progress in Oceanography 21, 1–105).

Tett, P., Arístegui, J., Barton, D., Basterretxea, G., De Armas, J.D., Escámez, J.E., Hernández León, S., Lorenzo, L.M., Montero, N., 2002. Steady-state DCM dynamics in Canaries waters. Deep-Sea Research II 49, 3543–3559.

Vargas-Yañez, M., Sarhan, T., Plaza, F., Rubín, J.P., García-Martínez, M.C., 2002. The influence of tide–topography interaction on low-frequency heat and nutrient fluxes. Application to Cape Trafalgar. Continental Shelf Research 22, 115–139.

Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice Hall International Editions, Englewood Cliffs, NJ, 718pp.