Flujos de partículas y biodisponibilidad de la materia orgánica en ecosistemas profundos: el cañón submarino de Blanes

Pilar López Fernández

UNIVERSITAT DE BARCELONA

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PARTICLE FLUXES AND THE BIOAVAILABILITY OF THE ORGANIC MATTER IN DEEP ECOSYSTEMS: BLANES SUBMARINE CANYON

Memoria de la Tesis Doctoral presentada por

Pilar López Fernández

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La gran ola de Kanagawa, *Hokusai, 1830*

Maestro, quisiera saber
cómo viven los peces en el mar.

Como los hombres en la tierra: los grandes
se comen a los pequeños.

(William Shakespeare)

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SINOPSIS

Los márgenes continentales representan una zona de fuertes interacciones entre el continente, el océano y la atmósfera. Las condiciones hidrodinámicas de estos márgenes a su vez controlan la dispersión de los sedimentos en la plataforma continental y de estas hacia mar abierto. Dentro de los márgenes continentales, los cañones submarinos representan una de las zonas de intercambio más intenso entre el talud continental y la cuenca profunda, ya que actúan como un importante conducto del material hacia esta. Investigaciones anteriores han mostrado que los márgenes continentales son un importante depósito de material orgánico particulado, en gran parte debido a los aportes de ríos, que al ser transportados a través de los cañones, representan una fuente de alimento clave para las comunidades bentónicas profundas. Por este motivo, los cañones submarinos son lugares de especial interés para investigaciones interdisciplinares sobre la interacción geosfera-biosfera en el océano.

Dentro de este contexto y asociado principalmente al proyecto de investigación español PROMETEO se ha realizado la presente tesis, sobre el estudio de los flujos anuales de material particulado en la columna de agua dentro del sistema del cañón submarino de Blanes, el cañón submarino y su talud sur adyacente. El objetivo del presente trabajo es caracterizar la variabilidad temporal y espacial de los flujos de partículas y materia orgánica, así como la biodisponibilidad y el valor nutricional de dicha materia orgánica para las comunidades bentónicas de aguas profundas del margen catalán.

El estudio, se ha centrado en un período de muestreo de un año de duración, de Noviembre de 2008 a Noviembre de 2009. La medida directa de los flujos se ha realizado mediante el fondeo de 8 líneas instrumentadas dotadas de trampas de sedimento y correntímetros a lo largo de dos transectos, uno en el eje del cañón de Blanes y otro en su talud adyacente, a las mismas profundidades.

La evolución temporal de los flujos de partículas muestra tres períodos distintos determinados por: i) la presencia de tormentas; ii) la convección del mar abierto y el florecimiento primaveral de fitoplancton; y iii) las entradas de aerosoles.

Los resultados obtenidos muestran que los flujos de masa fueron más altos en el cañón (un orden de magnitud), en comparación con los del talud, en gran medida gracias a las entradas laterales por las cárcavas en los flancos del cañón que canalizan el material re-suspendido en la plataforma continental.

Ambos hábitats estuvieron fuertemente influenciados por las fuerzas atmosféricas y mostraron un aumento de los flujos totales de masa durante los meses de otoño e invierno. La distribución espacial de los flujos de masa total y sus componentes principales (materia orgánica, carbonatos, ópalo y litogénicos) pone de manifiesto los contrastes entre los dos dominios fisiográficos del área de estudio (cañones vs. talud).

Los flujos de carbono orgánico (OC) en el cañón y en el talud adyacente variaron en el periodo investigado, aunque no de manera simultanea en los dos ambientes. Mientras que la concentración de partículas de OC en el talud fue consistentemente más alta que en el cañón, los flujos de materia orgánica son relativamente altos dentro del cañón a pesar de que la fracción litogénica domina los flujos de masa total (hasta 80%), lo que confirma su eficacia en la canalización de partículas orgánicas desde la plataforma continental hasta el fondo.

En este estudio se muestra que la materia orgánica recogida por trampas de sedimentos en la primavera tuvo un valor nutricional más alto que a finales de otoño-invierno, y esta característica es compartida tanto por el cañón como por la plataforma continental. Esta diferencia probablemente sea debido a la floración del fitoplancton en el área de estudio. Durante este período la composición bioquímica del carbono polimérico (BPC) se caracteriza por un aumento en la contribución de lípidos en comparación con la misma observada durante el período de tormenta, que está caracterizado por un mayor contenidos de proteínas en los sedimentos recolectados por las trampas.

De acuerdo con la teoría del aprovechamiento (alimentación, aprovisionamiento o forrajeo) óptimo -optimum foraging theory de MacArtur and Pianka (1966), los resultados de este estudio sugieren que, después de los eventos episódicos de invierno, los detritívoros de aguas profundas tendrían que ingerir más detritus para cumplir con sus requerimientos de alimento lábil que durante la primavera, cuando hay más material fresco de las partículas en sedimentación, asociado con las floraciones de fitoplancton. Llegamos a la conclusión que, si bien los cañones submarinos, como el cañón submarino de Blanes actúan como conductos principales para el material exportado fuera de la plataforma continental después de eventos episódicos de alta energía, el suministro de alimentos lábil al ecosistema bentónico de aguas profundas está conectado mayoritariamente a los procesos biológicos que ocurren en la superficie del mar.

Nuestros resultados confirman el papel clave ecológico de los cañones submarinos para el funcionamiento de los ecosistemas de aguas profundas, y pone de manifiesto la importancia de los cañones en la vinculación de las tormentas episódicas y la producción primaria que ocurren en la superficie del mar hasta el fondo del mar profundo.

ABSTRACT

Continental margins represent areas of strong interactions between the continent, the ocean and the atmosphere. The hydrodynamic conditions of these margins control the dispersion of particles fluxes toward the platform to the open sea. In continental margins, submarine canyons represent one of the most intense exchange zones between the upper slopes to the deep sea, because canyons can act as an important channel for the material to the seabed. Many previous studies have shown that the continental margins may represent a reservoir of particulate organic matter, often derived from river discharge, which, while being transported downslope, represent a key food source for the benthos. Therefore, submarine canyons are places of special interest for interdisciplinary research on geosphere-biosphere interactions in the ocean.

Within this context and mainly associated to the Spanish research project PROMETEO, has conducted a study, presented in this thesis mode, of the annual particulate fluxes in the water column in the Blanes canyon system, which includes the submarine canyon and adjacent open slope. The objective of this work is to characterize the temporal and spatial variability of total mass fluxes and bioavailability of organic matter to the deep-sea benthos in the margin Catalan Western Mediterranean Sea.

In this study, for the first time, we have investigated the particles fluxes and their contents, the biochemical composition and bioavailability of particulate organic matter during a sampling period of one year (November 2008-November 2009) into the Blanes canyon and adjacent slope (Catalan margin, northwestern Mediterranean Sea). Direct fluxes measurements were performed by the deployment of 8 mooring lines equipped with sediment traps and currentmeters along two transect, one along the axis of the Blanes canyon and another along the adjacent slope at the same depth.

The temporal evolution of particle fluxes shows three different periods determined by the storms, open ocean convection and phytoplankton bloom and aerosol inputs.

The results show that the mass fluxes were higher in the canyon (an order of magnitude), than in the open slope, largely thanks to the lateral inputs by the gullies on the canyon flanks, that serve as channel for re-suspended material from the shallower platform.

Both habitats were strongly influenced by atmospheric forces and showed an increase of total mass fluxes during autumn and winter. The spatial distribution of total mass fluxes and its main components (organic matter, carbonates, opal and lithogenic) shows the contrasts between the two domains physiographic features of the study area (canyon vs. open slope).

Within the organic carbon (OC) fluxes, in the canyon and adjacent slope varied in the investigated period, although not consistently in both environments. While the concentration of OC particles in the open slope was consistently higher than in the canyon the organic matter fluxes are relatively high within the barrel although lithogenic fraction dominates the total mass flows (up 80%), confirming their efficacy in channeling organic particles from the shelf to the bottom.

In this study we show that the organic matter collected by sediment traps in spring had a higher nutritional value than in late autumn-winter, and this feature was shared by both the canyon and the adjacent open slope. This difference is likely to be due to the typical spring plankton bloom in the study area. During this period the biochemical composition of BPC was characterized by increasing lipid contributions compared with those observed during the storm period, characterized by higher protein contents

According to the theory of optimum utilization, the results of this study suggest that after episodic events winter detritivores deepwater detritus would have to eat more to meet their food requirements labile than in spring, when more fresh material in particle sedimentation associated with phytoplankton blooms. We conclude that while submarine canyons, like the barrel of Blanes act as

major conduits for material exported from the continental shelf after episodic high energy events, food supply labile deepwater benthic ecosystem is connected to the biological processes occurring at the surface of the sea.

Our results confirm the ecological role of submarine canyons for the functioning of deep-sea ecosystems, and highlight the importance of canyons in linking episodic storms and primary production occurring at the sea surface to the deep sea floor.

PRESENTACIÓN DE LA TESIS: ESTRUCTURA, HIPÓTESIS Y OBJETIVOS

La presente tesis de doctorado, se enmarca dentro del proyecto nacional de investigación titulado: "Estudio integrado de Cañones Submarinos y Taludes profundos del Mediterráneo Occidental: Un hábitat esencial (PROMETEO)", realizado entre los años 2009 y 2011. Dicho proyecto, planteaba una investigación multidisciplinar en el cañón submarino de Blanes y su talud sur adyacente con especial atención a los factores y procesos que configuran el ambiente físico y las comunidades biológicas determinadas por éste.

Proyectos anteriores, en colaboración con equipos europeos y norteamericanos (proyectos EUROMARGE-NB, EUROSTRATAFORM Y HERMES), en el margen nor-catalán y del Golfo de León, han demostrado el elevado nivel energético de los eventos de "cascading" de aguas frías y densas de plataforma. El "cascading" de aguas densas de plataforma es un fenómeno conocido en otros márgenes continentales del mundo (Ivanov et al., 2004; Durrieu de Madron et al., 2005), pero no así sus efectos sobre el ecosistema profundo y la modelación del relieve submarino. Tales eventos conllevan la exportación masiva de materia orgánica fresca hasta los niveles más profundos del margen, con la subsiguiente influencia, apenas entrevista hasta la fecha (Béthoux et al., 2002), en el funcionamiento de los ecosistemas profundos a escala de cuenca (Canals et al., 2006).

A su vez, en las dos últimas décadas se ha avanzado mucho en la descripción de la biología de algunas especies y de las comunidades del talud profundo (Gage y Tyler, 1991; Tyler, 2003). El Mediterráneo nor-occidental ha sido reconocido como una de las cinco regiones más bien descritas del planeta en cuanto a la biología de sus grandes profundidades. Aún así, la investigación de las grandes profundidades está en una fase muy preliminar, ya que la gran mayoría de los estudios son de carácter descriptivo, con un elevado desconocimiento de cuales son los procesos que ocurren en estas profundidades, y los factores que los controla.

El proyecto PROMETEO estaba orientado al establecimiento de las relaciones entre las condiciones hidrográficas, los flujos de materia (su composición y biodisponibilidad de la materia orgánica) y los ecosistemas profundos. La estrategia diseñada contempló la adquisición simultánea, durante un ciclo anual completo, de datos de hidrografía y de flujos de agua y partículas, y el recurso alimentario disponible para el bentos. El proyecto incluía el fondeo de sistemas de registro oceanográfico y sedimentológico (correntímetros y trampas de sedimento) en relación con la variabilidad estacional de dichas condiciones abióticas y de la dinámica de los ecosistemas.

ESTRUCTURA

Esta Tesis Doctoral, ha sido confeccionada según la modalidad de compilación de artículos publicados y/o enviados a revistas, consta de 6 capítulos, referencias bibliográficas y anexos.

En el Capitulo 1 de introducción, se presenta la zona de estudio incluyendo una visión general de trabajos realizados en esta zona de Mediterráneo y se describe la metodología utilizada para la realización de la Tesis Doctoral.

Los capítulos 2, 3 y 4 contienen el grueso de los resultados de la Tesis Doctoral que se presenta e incluye 3 artículos publicados.

El capitulo 2 es el primer artículo científico de esta Tesis Doctoral titulado: "*Multiple drivers of particle fluxes in the bathyal zone of the North Catalan margin: Blanes submarine canyon and adjacent slope" by Pilar Lopez-Fernandez, Antonio Calafat, Anna Sanchez-Vidal, Miquel Canals, Mar Flexas, Jordi Cateura and Joan B: Company and (2013) Progress in Oceanography*, Volume 118, Pages 95–107. En este capítulo se presenta la distribución de los flujos de sedimentos tanto dentro del cañón de Blanes como en su talud continental adyacente, así como la composición de los mismos. En él se pone de manifiesto las diferencias en la masa de los flujos de partículas y su composición biogeoquímica, entre los dos habitas y las diferentes reacciones de los mismos frente a los mismos procesos.

El capítulo 3, es el segundo artículo científico de esta Tesis Doctoral titulado: "*Bioavailability of sinking organic matter in the Blanes canyon and the adjacent open slope (NW Mediterranean Sea)" by Pilar Lopez-Fernandez, Silvia Bianchelli; Antonio Pusceddu; Antoni Calafat; Anna Sanchez-Vidal; Roberto Danovaro (2013) Biogeosciences,* Volume 10, Pages 3405-3420. En este capítulo se estudia la diferencia en la biodisponibilidad de la materia orgánica entre el cañón de Blanes y el talud adyacente, haciendo una descripción de los factores ambientales que pueden influir en dicha diferencia, así como las repercusiones para los ecosistemas profundos.

El capitulo 4, es el tercer artículo científico de esta Tesis Doctoral titulado: "*Bioavailable compounds in sinking particulate organic matter, Blanes Canyon, NW Mediterranean Sea: effects of a large storm and sea surface biological processes" by Pilar Lopez-Fernandez, Silvia Bianchelli; Antonio Pusceddu; Antoni Calafat; Roberto Danovaro; Miquel Canals (2013) Progress in Oceanography* Volume 118, Pages 108–121. En este artículo se analiza el cañón de Blanes como vía de transporte de materia orgánica lábil desde la plataforma continental hacia los sistemas bentónicos profundos, y como el suministro de alimentos lábil al ecosistema bentónico de aguas profundas está conectado a los procesos biológicos que ocurren en la superficie del mar, en particular la influencia de tormentas sobre el transporte y la calidad de esta materia orgánica.

El Capitulo 5, se ha concebido como un resumen general de los resultados y una discusión integradora de los resultados obtenidos y presentado en los capítulos anteriores.

Finalmente el Capitulo 6, contiene las principales conclusiones obtenidas en la Tesis Doctoral

HIPÓTESIS Y OBJETIVOS PRINCIPALES

La hipótesis de partida del presente trabajo es "la existencia de una diferencia significativa entre la cantidad y composición biogeoquímica de los flujos de partículas en dos ambientes marinos: el cañón submarino de Blanes y su talud continental sur adyacente".

Para demostrar esta hipótesis se establecieron como objetivos principales:

a) Cuantificar y caracterizar el flujo de partículas de la zona batial (desde 300 hasta 1800 m) del sistema del cañón submarino de Blanes (Cañón de Blanes y su talud sur adyacente)

b) Cuantificar el flujo de materia y energía que llega al fondo (materia orgánica biodisponible) con el fin de contribuir a determinar la interacción de las condiciones ambientales con los ecosistemas del Cañón de Blanes.

Dichos objetivos permitirían caracterizar el comportamiento del cañón submarino de Blanes como conductor del transporte de sedimento desde la zona de cabecera hasta la zona batial y evaluar el impacto en el ecosistema profundo de los materiales transportados, con especial atención a la zona centrada en 1200 metros de profundidad, donde se sitúa un máximo relativo de biomasa.

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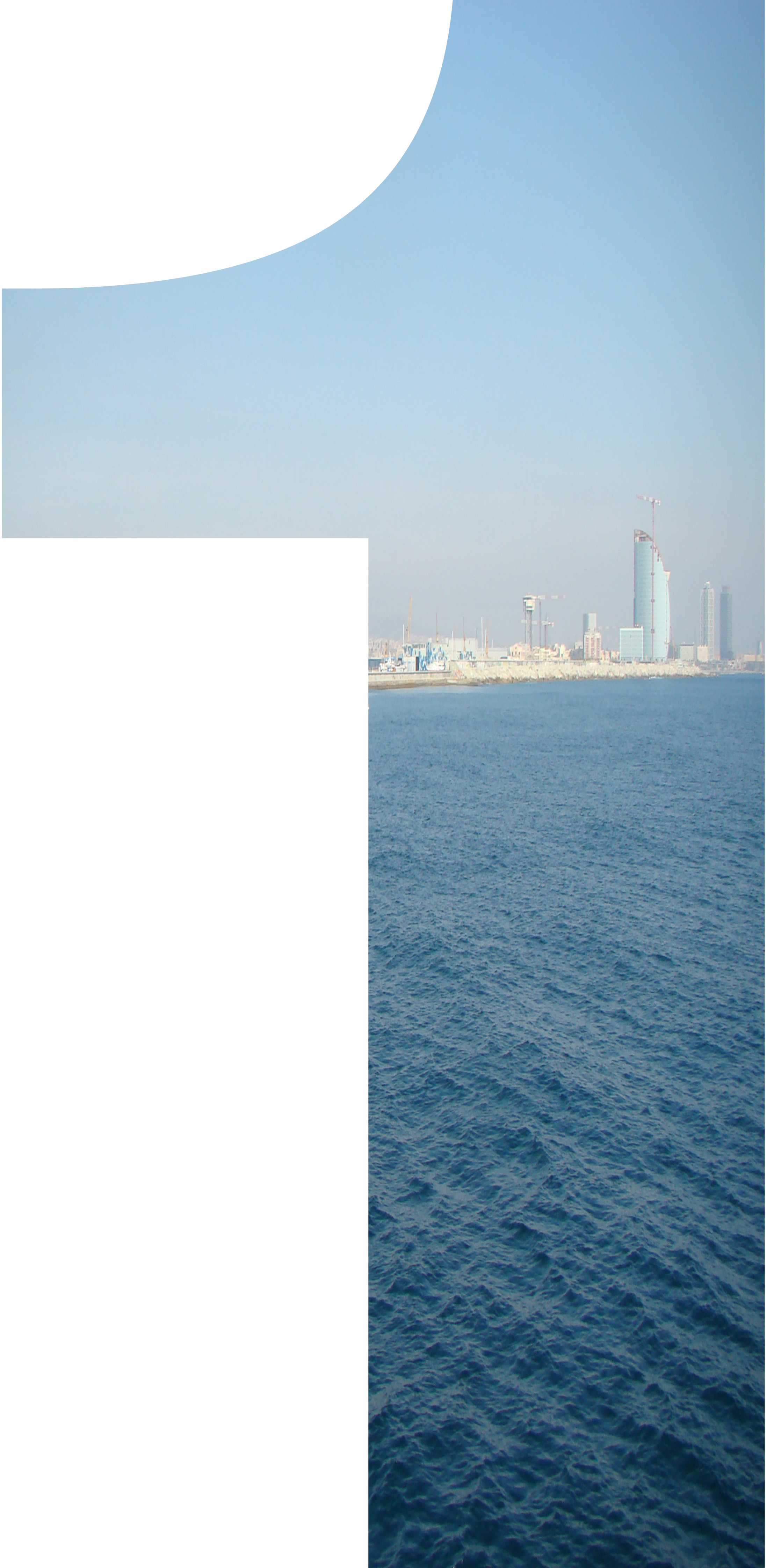

CAPÍTULO 1
INTRODUCCIÓN

1.1. INTRODUCCIÓN

En el presente trabajo se estudia el trayecto que sigue la materia orgánica desde las zonas más someras, hacia el fondo del océano, en particular las fracciones de carbono orgánico, generado en las aguas superficiales o aportadas desde la costa y su biodisponibilidad (grado de una sustancia que se hace fisiológicamente disponible a los tejidos del organismo, dependiendo de los índices de absorción, distribución, metabolismo y excreción) para los organismos bentónicos. Este estudio se ha llevado a cabo en el Mediterráneo Occidental y concretamente en el cañón submarino de Blanes y su talud continental adyacente.

1.1.1. Márgenes continentales

Los márgenes continentales ocupan apenas un 7% de la superficie mundial del océano, sin embargo, en las últimas décadas se han ido acumulando evidencias de que los márgenes continentales, juegan un papel importante en los ciclos biogeoquímicos marinos (Bauer y Druffel 1992, Weaver et al. 2004). Los márgenes continentales comprenden diferentes provincias geomorfológicas que incluyen, la plataforma continental, el talud continental, que puede estar inciso por los cañones submarinos y/o presentar deslizamientos en masa (Fig. 1.1) y el ascenso continental o la fosa oceánica.

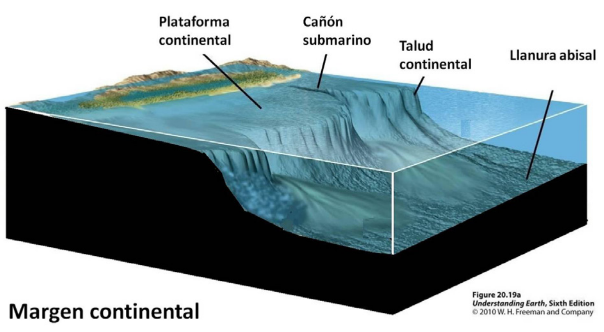

Fig. 1.1. Esquema de las diferentes provincias geomorfológicas de los márgenes continentales. Modificada de " Understanding Earth, Grotzinger and Jordan, 2010. W.H. Freeman and Company"

Los márgenes continentales representan una zona de fuertes interacciones entre el continente, el océano y la atmósfera (Weaver et al., 2004). Las condiciones hidrodinámicas de los márgenes a su vez controlan la dispersión de los flujos de partículas sedimentarias en la plataforma y hacia el mar abierto (Levin y Dayton, 2009).

La dinámica de los sedimentos de la plataforma continental depende de la interacción entre la llegada de sedimento, principalmente de origen fluvial, su transporte, distribución y deposición por diferentes procesos hidrodinámicos (oleaje, corrientes...). Procesos de alta energía o corta duración, como las grandes tormentas, las corrientes oceánicas y las corrientes de aguas densas de plataforma, desempeñan un papel importante en la resuspensión y transporte de sedimentos a través de la plataforma continental y hacia la parte superior del talud continental (Puig et al., 2003; Ogston et al., 2000; Bourrin et al., 2008). Los márgenes continentales son las regiones críticas de amortiguamiento entre la tierra y el océano abierto. La alta productividad biológica de las aguas costeras ligadas a los aportes de nutrientes de origen terrestre hacen de esta zona una zona de deposición preferencial de materia orgánica (Walsh, 1991). La materia orgánica se forma, inicialmente, como biomasa autótrofa y se transforma a través de las múltiples vías tróficas en cada nivel de la cadena alimentaria marina (Wassmann et al., 1998; Gehlen, et al., 2006).

El transporte de la materia orgánica particulada en los márgenes continentales se realiza a través de flujos advectivos de partículas, los cuales, a su vez, están influidos por el clima general (Heussner et al., 2006), condiciones hidrodinámicas locales (Bonnin et al., 2008) y la presencia de diferentes hábitats bentónicos (Pusceddu et al., 2010a). Dentro de los márgenes continentales, los cañones submarinos representan una de las zonas de intercambio más intenso entre la plataforma, el talud continental y las cuencas profundas, ya que actúan como un importante conducto de material hacia el fondo del mar (Canals et al., 2006; Sanchez-Vidal et al., 2012).

1.1.2. Cañones submarinos

Los cañones submarinos son incisiones profundas en la plataforma y el talud continentales. Están presentes en la mayoría de los márgenes continentales, van desde ambientes costeros a la llanura abisal (> 5000 m de profundidad). El número total de cañones submarinos aún no está claro. Algunas zonas de la plataforma continental, como el Mediterráneo noroccidental, se caracterizan por la presencia de una extensa red de cañones submarinos. Los cañones submarinos son conocidos desde hace siglos por los pescadores, especialmente aquellos con la cabecera del cañón próxima a la costa. Este es el caso del cañón Blanes, cuya cabecera se encuentra situada a 4 km de la costa. La presencia del cañón determina variaciones tridimensionales de las corrientes y provoca el aumento del intercambio de agua y sedimentos entre la plataforma y el talud continentales.

Los cañones se caracterizan por flancos con una pendiente más o menos pronunciada y un canal central. Los cañones son considerados como canales rápidos de transporte de material entre el continente y la plataforma continental a los ambientes de profundidad. El transporte de sedimentos a través de los cañones submarinos no es constante ni unidireccional, caracterizándose por periodos de transporte y resuspensión, alternando con intervalos pasivos durante los cuales el sedimento se puede acumular en el fondo del canal central, principalmente. En determinados cañones y debido a episodios meteorológicos locales, el transporte hacia el fondo a través de cañones submarinos se asocia a la presencia de corrientes de aguas densas de plataforma ("cascading"), estas pueden ser altamente energéticas y ocasionar importantes consecuencias sobre la estructura y el funcionamiento de la cadena alimentaria, desde el fitoplancton hasta los más grandes metazoos (Canals et al., 2006; Company et al., 2008; Pusceddu et al., 2010a).

El transporte de materia a través de los cañones, no solo se realiza por el eje principal, también tienen lugar aportes laterales desde la plataforma, que pueden ocasionar un aumento con la profundidad del flujo de masa transportado. En un reciente trabajo de Pusceddu et al. (2010a), llevado a cabo a lo largo del Mar Mediterráneo, se señala que no todos los cañones submarinos son canales activos de transporte de materia orgánica a la cuenca profunda y en ocasiones no presentan diferencias significativas en el contenido de materia orgánica sedimentaria y composición bioquímica, con las plataformas adyacentes a profundidades similares. La entrada de materia orgánica al interior del océano a través de cañones es sobre todo de periodicidad estacional (Fabres et al., 2008), con los máximos flujos de transporte asociados con las floraciones de fitoplancton en las capas superiores de la columna de agua (Pasqual et al., 2011) o con procesos episódicos, como las tormentas (Palanques et al., 2008; Sánchez Vidal et al., 2012) y el cascading (Canals et al., 2006; Pasqual et al., 2010).

Las características hidrodinámicas (por ejemplo "upwellings" o afloramientos) de los cañones submarinos, pueden prolongar la residencia de los nutrientes y las comunidades de plancton en los alrededores del cañón. Esto provoca un aumento de la producción primaria, teniendo un efecto positivo en la población de zooplancton que atraen a las larvas de peces y cetáceos (Pusceddu et al., 2010a; 2010b). Los cañones del Mediterráneo occidental han sido identificados como puntos calientes o "hot spots" de biodiversidad, ya que muchos procesos biológicos son alterados o intensificados por ellos (Hickey, 1995; Gili et al., 1999). Además, los cañones submarinos sirven como refugios y áreas de reclutamiento de juveniles (Gili et al., 1999) y son clave para el mantenimiento de los recursos vivos (Cartes et al., 1994; Sardà et al., 1994; Stefanescu et al., 1994; Sardà and Cartes, 1997).

1.1.3. Transporte de materia orgánica

La mayoría de los animales que viven en el fondo marino profundo se basan en una cadena alimentaria que comienza a cientos o miles de metros por encima, en las capas superficiales del océano. La fotosíntesis, impulsada por la luz solar, sustenta la vida vegetal microscópica (fitoplancton) en la superficie del mar, que a su vez alimenta a las comunidades de origen animal y microbiano a través de la columna de agua hasta el océano profundo (Margalef, 1985). Durante el hundimiento de la materia orgánica al fondo del mar, el transporte es mediado por flujos advectivos de partículas, los cuales, a su vez, están influidos por el clima general (Smith et al., 2008), las condiciones hidrodinámicas locales y la presencia de diferentes hábitats bentónicos (Pusceddu et al., 2010a). El resultado final es la acumulación de materia orgánica en la interfase entre el agua y el sedimento. Se ha estimado que solo del 1 al 3 % del carbono orgánico producido por la fotosíntesis en la capa fótica es exportado al fondo del mar (Lampitt and Antia, 1997). Este hecho, ha llevado a la mayoría de los estudios sobre aguas profundas a concebir las profundidades del mar como un medio ambiente "a dieta", debido a la falta de productividad primaria local y siendo alimentado por cantidades muy bajas de partículas orgánicas pobres nutricionalmente (Druffel and Robison, 1999). Desde un punto de vista biogeoquímico, evaluar cómo las plataformas continentales exportan y concentran las partículas de materia orgánica hacia la cuenca profunda es un paso necesario para estimar su influencia en los ecosistemas de aguas profundas (Smith et al., 2008).

La materia orgánica está compuesta por un restringido conjunto de elementos, cuatro de los cuales (C, H, N y O) constituyen aproximadamente el 99% de su peso. Estos átomos se unen formando cadenas y anillos para generar moléculas orgánicas (monómeros). Ciertas combinaciones simples de átomos ($-CH_3$, -OH, -COOH y $-NH_2$) se presentan repetidamente en las moléculas biológicas dando diferentes propiedades físicas y químicas a éstas. Las pequeñas moléculas a su vez se asocian entre ellas para formar moléculas más grandes denominadas macromoléculas (polímeros). Podemos decir que la materia orgánica está compuesta por cuatro grandes familias de macromoléculas: las proteínas, los carbohidratos, los lípidos y los ácidos nucleicos.

El valor nutricional de la materia orgánica (su calidad) no es más que el potencial nutritivo o la cantidad de nutrientes que el alimento aporta al organismo. Es un valor difícil de medir, carente de unidad de medición, y que depende de diversos factores tales como la aportación energética, la proporción de los macro y micronutrientes que contienen -carbohidratos, proteínas, lípidos…, y la capacidad de asimilación de dichos nutrientes (biodisponibilidad).

La calidad y cantidad de la materia orgánica en los sedimentos superficiales se han considerado de importancia en la determinación de las cantidades de material potencialmente disponible para los organismos de consumo, lo que afecta la estructura de la comunidad bentónica y el metabolismo (Buchanan y Longbottom, 1970; Graf et al., 1983;. Grant y Hargrave, 1987; Thompson y Nichols, 1988). En efecto, la cantidad total de materia orgánica o carbono orgánico que se deposita en el fondo, no son totalmente representativos de la calidad de los alimentos, y dice muy poco acerca de su disponibilidad para los consumidores (Newell y Field, 1983; Bianchi y Levinton, 1984; Misic y Covazzi-Harrigue, 2008; Pusceddu et al., 2009). Por lo que en primer lugar, es útil realizar una clasificación de la materia orgánica de acuerdo a la disponibilidad biológica. Podemos separar la materia orgánica en diferentes tipos o fracciones: 1) Fracción refractaria (ácidos húmicos y fúlvicos y carbohidratos estructurales) que representan moléculas de materia orgánica adherida a partículas inorgánicas no aptas para el consumo, resistentes a la descomposición biológica y por tanto, de bajo valor nutritivo. Es el depósito de carbono más persistente, con potencial para ser almacenados durante miles de años en el interior del océano, y 2) Fracción biopolimérica de importancia para la nutrición heterótrofa (Fabiano y Pusceddu, 1998), compuesta de biopolímeros (carbohidratos simples, lípidos y proteínas). Sólo esta fracción de la materia orgánica es directamente utilizable como fuente de alimento por los consumidores bentónicos con un alto valor nutritivo. Pero no toda la fracción biopolimérica de las partículas pueden ser rápidamente digerida por los consumidores, generalmente menos del 15-50% del carbono orgánico particulado (POC) se compone de moléculas que son enzimáticamente digeribles (Fabiano y Pusceddu, 1998). De ahí que podamos dividir las moléculas en: a) moléculas semilábiles, las moléculas que pueden persistir durante meses o años y son responsables de la mayor parte de la materia orgánica biodisponible que se exporta desde la zona fótica hacia mayores profundidades, y b) moléculas lábiles, moléculas que pueden ser utilizadas por los microorganismos heterótrofos en cuestión de días o incluso horas (Bauer et al., 1992; Kirchman et al., 1993).

Para cuantificar los componentes que potencialmente son más fácilmente disponibles para los consumidores (es decir, compuestos semilábiles o lábiles sensu Pusceddu et al., 2009), se utiliza el carbono biopolimérico (BPC "biopolymeric carbon"), que no es más que la suma de carbohidratos, proteínas y lípidos convertidos en equivalentes de carbono (mg C mg^{-1}) utilizando los factores de conversión de 0,40, 0,49 y 0,75, respectivamente. Ya que solo una fracción de BPC es rápidamente reactiva a la digestión heterotrófica (Pusceddu et al., 2003; Pusceddu et al., 2009), la concentración de carbono orgánico biodisponible (BAOC "Bioavailable organic carbon") se calculó como la suma de proteínas y carbohidratos digeribles convertidos en equivalentes de carbono mediante el uso de los mismos factores que para sus cantidades totales (Danovaro et al., 2001; Pusceddu et al., 2003).

De acuerdo con Pusceddu et al. (2010), hemos utilizado las relaciones de fitopigmentos:/BPC y de proteína/carbohidrato como descriptores de la frescura y la calidad nutricional de las partículas orgánicas, respectivamente (Pusceddu et al., 2009; Pusceddu et al., 2010b).

El concepto de calidad y frescura o descomposición, están relacionados, porque la calidad de la materia orgánica cambia progresivamente con la degradación, es decir, el envejecimiento y los cambios en la calidad están vinculadas a una resistencia cada vez mayor de las reservas de carbono orgánico hacia la degradación o mineralización microbiana.

Ya que los pigmentos fotosintéticos y sus productos de degradación se supone que son compuestos lábiles en una perspectiva trofodinámico cuanto menor es su contribución al OC en el sedimento, mayor será la edad del material orgánico. Por otra parte, ya que la fracción o porcentaje de OC asociado con fitopigmentos también se asocia típicamente con una mayor fracción de compuestos enzimáticamente digeribles, es decir, inmediatamente disponible para los animales heterótrofos (Pusceddu et al., 2003), los valores más altos de esta relación también serán indicativos de una mayor calidad nutricional (Dell'Anno et al., 2002). Además, puesto que el nitrógeno es el factor más limitante para la nutrición heterótrofa y las proteínas (que se degradan más rápido que los carbohidratos) son compuestos ricos en nitrógeno, por lo que la relación proteína/ carbohidrato será indicativa del envejecimiento y del valor nutricional de la materia orgánica (Danovaro et al., 1993; Dell 'Anno et al., 2002; Tselepides et al., 2000;. Pusceddu et al ., 2009).

Según Danovaro et al., (1995, 2000) la distribución de la meiofauna está controlada por la calidad del alimento que reciben (expresado como porcentajes de partículas lábiles frente al total de partículas de materia orgánica). Los organismos que buscan alimento deciden el tipo de alimento o el tiempo que permanecen en un mismo lugar en función de la cantidad de energía que obtienen, la energía que gastan y el tiempo que invierten en el proceso (Pianka, 1966).

La teoría de la alimentación Óptima de MacArthur y Pianka (1996) propone que la serie de estrategias que presentan los animales para capturar, manipular, asegurar y consumir su alimento, la seleccionan de forma que se maximice la tasa costes/beneficios para la especie (MacArthur y Pianka, 1966; Kamil et al., 1987).

Begon et al. (1988) resume este concepto diciendo que si un animal hace lo correcto al aprovisionarse, explotando el alimento y obteniendo energía de un modo económico, entonces será favorecido por la selección natural ya que dispondrá de más tiempo y energía para reproducirse con éxito, y podrá dejar más descendientes: y si sus capacidades son heredables se extenderán, en el tiempo evolutivo, a toda la población.

Para los organismos bentónicos del ecosistema de aguas profundas, dependientes de la producción primaria en las capas superiores del agua, es crucial la cantidad y calidad de alimentos que llegan al fondo del mar (Bühring and Christiansen, 2001; Smith et al., 2008). En el Mediterráneo, la producción primaria se caracteriza por una discontinuidad estacional con un periodo corto de floración de fitoplancton entre finales de invierno y principios de primavera (Estrada et al., 1996). Además de la sedimentación de las capas superiores de agua, las corrientes de fondo (distribución horizontal o advectiva) juegan un papel importante en la distribución de la materia orgánica en el fondo (Sokolova, 1997). En el Mediterráneo, en general, existe una disminución de la abundancia del bentos desde la plataforma hacia profundidades abisales que se correlaciona con una disminución de la diversidad local (Rex, 1981; Hilbig et al., 2006). Esta diversidad, parece estar regulada por la disponibilidad de materia orgánica (biodisponibilidad) (Danovaro et al., 1995). Sin embargo, los mecanismos que están detrás de esta relación, diversidad/biodisponibilidad de la materia orgánica, no son tan obvios. Desde principios de los años 90, Rucabado et al. (1991) y, en estudios posteriores (Sardá et al., 2004) han detectado de forma persistente un máximo de biomasa, alrededor de 1200 m de profundidad, en la zona del Mediterráneo noroccidental. A su vez, Bianchelli et al., (2008) ponen de manifiesto que los cañones submarinos, por norma general albergan mayor biomasa y biodiversidad que los taludes continentales adyacentes. Existe un gran desconocimiento de las causas de la zonación de estas comunidades y los estudios disponibles en el Mediterráneo en los que se aborda esta problemática son muy escasos.

En el presente trabajo, damos información de los patrones de circulación y de transporte de la materia orgánica hacia la cuenca profunda, así como de su biodisponibilidad a lo largo del tiempo, en dos hábitat continuos pero con diferentes características tanto hidrodinámicas como morfológicas, el cañón submarino de Blanes y el talud continental sur adyacente.

1.2. ZONA DE ESTUDIO

1.2.1. El Mar Mediterráneo

El agua del Mediterráneo noroccidental, región que comprende la mitad norte de la Cuenca Algero-Balear y que incluye el Mar Provenzal, el Golfo de León y el Mar Catalán, está formada principalmente por tres masa de agua de diferente temperatura y salinidad. Estas masas de agua son:

Agua Atlántica (AW, Atlantic water), agua superficial de origen atlántico, con una temperatura que oscila entre los 15º-20ºC y una salinidad entre 36% y 36.5% según la época del año.

Por debajo de la AW, aproximadamente a 200-400 m, se encuentra el Agua Levantina Intermedia (LIW, Levantine Intermediate Water) más salada y caliente. Se origina en la cuenca oriental del Mediterráneo. La LIW tienen valores promedio de temperatura de alrededor de 13.2ºC y de salinidad de 38,50% y marca un máximo de la temperatura y la salinidad en la mayor parte de la cuenca occidental (Font et al., 1987)

La masa de agua más profunda es el agua profunda del Mediterráneo occidental (WMDW, Weatern mediterranean Deep Water), se forma en el Golfo de León por la convección profunda de mar abierto durante los meses de invierno (Millot, 1999). La WMDW tiene valores medios de temperatura y salinidad de 12.80ºC y 38.45%.

La circulación de las corrientes marinas a lo largo del margen continental del Mediterráneo noroccidental no es simple (Fig. 1.2). En general, las corrientes muestran una variabilidad estacional en su intensidad ligada al carácter estacional de la circulación general en toda la cuenca (Font et al., 1995; Vidal- Vijande et al., 2011). Esta complejidad se debe a varios mecanismos como las variables atmosféricas, los efectos topográficos y procesos dinámicos internos, que conducen a fuertes corrientes costeras limítrofes, chorros inestables que arrojan vórtices, giros de subcuenca permanentes y recurrentes y los remolinos de mesoescala energéticos. Todas estas estructuras interactúan y dan lugar a una variabilidad significativa de escalas temporales (sub-mesoescala, mesoescala, estacional e interanual) (Pascual et al., 2013).

La circulación general de Mediterráneo noroccidental, se rige por la corriente del Norte, una corriente baroclina formada por la AW, que fluye sobre la LIW. La corriente del Norte describe un flujo general ciclónico (anti-horario) a lo largo del talud continental del noroeste del Mediterráneo (Millot, 1999). Esta corriente llega al mar Catalán desde el Golfo de León, siguiendo el talud en dirección sudoeste. Además de este flujo baroclino, la corriente del Norte, tiene una componente barotrópica que involucra toda la columna de agua, incluyendo la LIW y la subyacente WMDW (Conan y Millot, 1995).

La corriente del Norte es una corriente asociada a un frente de densidad cuya base se encuentra entre 300 y 400 m. Tiene una estratificación débil por debajo de 600 m (Jordá et al., 2013), además de la variabilidad espacio temporal, la corriente del Norte presenta unas estructuras de mesoescala tales como meandros y remolinos (Font et al.; 1995; Flexas et al.; 2002; Casella et al., 2011)

Las observaciones realizadas por Conan & Millot (1995) frente a la costa de Marsella sugieren que las variaciones estacionales en el transporte asociado a la Corriente del Norte están ligadas a los procesos de formación de aguas profundas en el Golfo de León (Rubio et al., 2005). Durante la primavera y el verano, la columna de agua de todo el Mediterráneo occidental está bien estratificada con la termoclina situada entre los 20 y los 50 metros de profundidad. En invierno, la columna de agua se homogeneiza por el efecto de la mezcla, factores como los vientos, la presencia de masas de agua densa y la compleja topografía de la plataforma junto con los numerosos cañones submarinos, provocan unos patrones de circulación complicados. La interacción de la corriente del Norte con la topografía local como los cañones submarinos es relevante, ya que puede causar movimientos verticales sig-

Fig. 1.2. Esquema de la circulación general superficial del mar Mediterráneo (modificada de Millot et al., 1990; Durrier de Madron et al., 2010). La zona de estudio, marcada con un círculo rojo, se situa en la trayectoria de la denominada corriente del Norte /CN-CLPC)o corriente Liguro-Provenzal_Catalana.

nificativos (Boyer et al., 2006; Flexas et al., 2008).

La presencia de los cañones submarinos ejerce una gran influencia sobre la corriente superficial, que junto a los fenómenos de mesoescala cómo la aparición de eddies anticiclónicos, provenientes del norte, producen cambios en la circulación de la corriente (Rubio et al., 2005).

Los cañones submarinos son sistemas complejos en los que la interacción con la topografía modifica la circulación local. Por ejemplo, la interacción corriente-topografía que tiene lugar en el borde del cañón produce estructuras hidrodinámicas locales y contribuyen al intercambio de aguas entre la plataforma y el talud (Schoenher, 1991; Allen et al., 2001; Sobarzoa et al., 2001; Boyer et al., 2006a; Flexas et al., 2008), esta interacción asociada con movimientos verticales de flujo afectan en el afloramiento o deposición de nutrientes, teniendo grandes implicaciones para el ecosistema de las cuencas profundas (Sardá et al., 1994).

1.2.2. Hidrografía del cañón submarino de Blanes

La cabecera del cañón submarino de Blanes se encuentra a 4 km frente a la costa catalana. El Cañón es uno de los más destacados en el Mediterráneo noroccidental, potencialmente afecta a la trayectoria de la corriente Catalana, la continuación de la corriente del Norte que fluye a lo largo de la costa de Cataluña. La plataforma continental de Blanes es una amplia llanura que llega a una distancia de costa aproximada de unos 35 km desde la orilla y alcanza una profundidad de unos 200 m. El cañón submarino de Blanes, por lo tanto divide el camino de la corriente Catalana (Fig. 1.3).

Fig. 1.3. Situacion del cañón de Blanes. Obsérvese cómo la cabecera del cañón de Blanes se hace paralela a la costa. Más al norte se sitúa el cañón de La Fonera o de Palamós.

Características de mesoescala tales como meandros y remolinos son recurrentes en la zona del cañón de Blanes y producen patrones de circulación tridimensionales altamente fluctuantes dentro del cañón. En particular, los meandros y remolinos anticiclónicos de la corriente del Norte tienden a ser profundos y , por lo tanto , sus efectos se extienden hacia la parte más profunda del cañón (Flexas et al., 2008).

La circulación en la zona de estudio está dominada por un flujo general hacia el sur ciclónico sobre el talud continental. La Corriente del Norte presenta de 30 a 50 km de ancho, y se caracteriza por un perfil de velocidad vertical de 30 a 50 cm s^{-1} en superficie, disminuyendo de forma casi lineal con la profundidad, hasta una velocidad de 10-15 cm s^{-1} en el comienzo el talud (Lapouyade y Durrieu, 2001, Flexas et al., 2002).

El patrón principal de la circulación profunda (por debajo de 600 m) en el cañón puede ser explicado por el ajuste de la corriente a la batimetría cañón, que se ve favorecida por la baja estratificación a profundidades inferiores y cerca de la pendiente. Cuando la corriente pasa sobre el cañón, la columna de agua se estira y gana vorticidad ciclónica, por lo que el flujo sigue la batimetría. En el eje del cañón, cerca de la parte inferior, el flujo está fuertemente limitado por las paredes del cañón. La fuerza de Coriolis no puede equilibrar el gradiente de presión barotrópico a gran escala y el flujo es en la dirección de la fuerza del gradiente de presión (es decir, fuera del cañón) que conduce al hundimiento de la masa de agua. Las aceleraciones de la corriente entrante desde el talud podrían entonces traducirse directamente en intensificaciones del patrón de velocidad en el cañón (Jordá et al., 2013)

En el cañón de Blanes, se observa un cambio en la dirección del flujo entre las aguas costeras y las aguas de alta mar, las aguas costeras que fluyen hacia al este y las aguas de alta mar que fluyen hacia el suroeste. Esto crea una región de alto esfuerzo cortante horizontal que junto a la reducción de las velocidades del este en el cañón producen una extensa región de circulación anticiclónica, desencadenando el hundimiento en la capa superior como resultado del vórtice (Granata et al., 1999). Esta corriente, característica en esta región, puede tener efectos relevantes sobre el ecosistema marino debido a la interacción con la topografía del fondo. Estudios anteriores han demostrado que el cañón de Blanes tiene un pronunciado efecto en la vorticidad del flujo, causando al flujo meandros con una rotación anticiclónica en las aguas superiores del cañón y a continuación una vez dentro del mismo adquirir una rotación ciclónica (Maso et al., 1990;. Maso y Tintore, 1991). Sin embargo, este patrón típico de flujo, después del desarrollo de una fuerte picnoclina en primavera, puede ser alterado por un flujo de inversión en la capa superior (Rojas et al., 1995).

1.2.3. Morfología del cañón submarino de Blanes.

La cabecera del cañón de Blanes se encuentra paralela a la costa intercalando cárcavas en forma de V y de U mediante divisiones lineales en la parte superior de las paredes y con gradientes de pendiente inferior a 15 ° (Lastras et al., 2011). En la pared del sudoeste, las cárcavas tienden a ramificarse rápidamente, convirtiéndose en omnipresentes y desde el borde hacia el fondo con respecto al eje del cañón. Por el contrario las cárcavas en la pared noreste siguen estando limitadas a la parte inferior de la pared debido a afloramientos de capas sub-horizontales en la parte superior del cañón, los cuales pueden ser identificados más de 5 km, a partir de la isobata de 500 m (Lastras et al., 2011). Estos afloramientos crean una parte empinada de la pared de más de 50 ° de pendiente entre 420 y 600 m de profundidad. Al aumentar la profundidad (>600 m), las cárcavas en la pared noreste aumentan su tamaño y al alcanzar una profundidad de más de 750 m, las cárcavas en forma de V empiezan a ocupar las dos paredes, con gradientes de pendiente a menudo superior a 35º (Lastras et al., 2011). El predominio de procesos de deposición en contra de los procesos erosivos favorece la presencia de meandros en la morfología del cañón y el ensanchamiento en la base del canal. Sin embargo en el curso medio del área este del cañón de Blanes, se han identificado conjuntos de cicatrices que sugiere una interacción entre ambos procesos (sedimentación y erosión) (Amblas et al., 2006)

1.3. MATERIAL Y MÉTODOS

Con el fin de responder a los objetivos planteados se realizo un diseño experimental basado en el muestreo de la zona de estudio mediante la utilización de las denominadas trampas de sedimento o de partículas de tipo secuencial. Dichas trampas son contenedores para recoger las partículas que caen hacia el fondo del mar, colocadas a diferentes profundidades de la columna de agua en líneas instrumentadas fondeadas.

1.3.1. Diseño experimental

Se fondearon ocho líneas instrumentadas durante un año en dos transectos diferentes. Cuatro líneas fueron depositadas a lo largo del eje del cañón submarino de Blanes y cuatro en el talud continental sur adyacente al cañón (BC y OS, respectivamente) (Fig. 1.4). Las líneas de muestreo fueron fondeadas a diferentes profundidades desde 300 hasta 1800 metros de profundidad, así en el cañón submarino se distribuyeron en las profundidades siguientes: 300, 900, 1200 y 1500 m (BC300, BC900, BC1200 y BC1500). Mientras en el talud continental se distribuyeron en las profundidades siguientes: 900, 1200, 1500 y 1800 m (OS 900, OS1200, OS1500 y OS1800) (figura 1.4).

Las ocho líneas de muestreo fueron equipadas con trampas de sedimento Technicap PPS3/3 y correntímetros Aanderaa RCM7/9 a 30 metros por encima del fondo marino. Las trampas de sedimento presentan una forma cilíndrico-cónica con unas dimensiones de 2 m de altura y una boca con un diámetro de 40 cm, lo que da un índice de altura/diámetro de 2.5 y un área de recogida de material de 0.125 m^2. Cada trampa de sedimento estaba equipada con 12 tubos colectores programados para recoger muestras a intervalos de 15 días durante 6 meses. Con el objetivo de aumentar la resolución de muestreo de las trampas del cañón y del talud a 1200 metros de profundidad, fueron programadas con intervalo de muestreo de 7-8 días. El experimento tuvo un éxito del 82 %, recogiendo 197 muestras de las 240 totales.

1.3.2. Procedimiento analítico

Antes de su utilización, el material de las trampas es limpiado en profundidad. El colector rotante fue limpiado con detergente y puesto en remojo en una solución de HNO_3 0.5 M durante una noche y aclarado varias veces con agua destilada.

Para evitar la degradación de los posibles organismos recolectados en los tubos colectores e inhibir la actividad bacteriana, estos fueron rellenados con una solución de agua marina filtrada y formol al 5%, neutralizada a pH 7.5-8 con perborato de calcio.

Una vez recuperadas las muestras de las líneas de fondeo, los tubos colectores fueron almacenados en oscuridad a 2-4ºC hasta su posterior procesado. Una vez en el laboratorio las muestras fueron visualmente controladas y se extrajo el sobrenadante. Cada muestra fue filtrada con una malla de 1mm para retirar los organismos nadadores ("swimmers") (aquellos organismos que no caen gravitacionalmente a través de la columna de agua). Los organismos inferiores a 1mm fueron retirados a mano mediante el uso de una lupa microscópica.

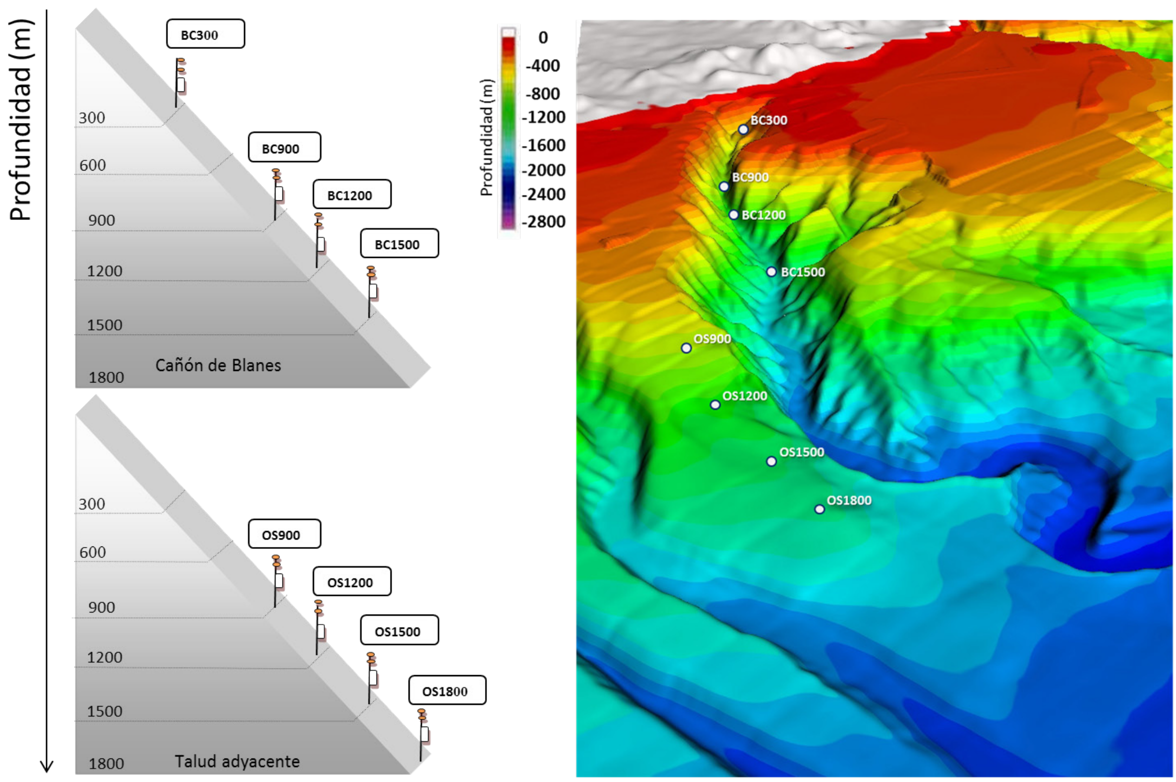

Fig. 1.4. Mapa batimétrico tridimensional del cañón de Blanes (fuente GRCGM), con la localización de las estaciones de muestreo. La nomenclatura de las estaciones de muestreo es el siguiente: Cañón de Blanes (BC); talud adyacente (OS) y profundidad.

Para obtener sub-muestras de igual volumen, se utilizo una bomba peristáltica de alta precisión, a través de la división repetida de las muestras. Finalmente las muestras se liofilizaron para su almacenamiento antes de su análisis.

El flujo total de las muestras se calculo utilizando la masa total, el área de la boca recolectora de la trampa y el intervalo de muestreo aplicando la siguiente fórmula:

$TMF = MT / A \times D = (g) / (m^2) \times (d) = g.m^{-2}.d^{-1}$

Donde calculado de esta manera, un flujo es el resultado de la velocidad de caída por la concentración de material.

$F: V \times C: (m.d^{-1}) \times (g.m^{-3}): g.m^{-2}.d^{-1}$ (Honjo,1996)

TMF= Flujo total de partículas;

MT= masa total

A= área del tubo recolector (0.120 m^2);

D= días de muestreo

1.3.2.1. Analisis de los componentes principales de las partículas recogidas (Materia orgánica, Carbonatos, Sílice biogénico y litogénicos)

Los análisis de carbono total, nitrógeno total y carbono orgánico se realizaron en los Servicios Científico-Técnicos de la Universidad de Barcelona mediante un analizador elemental (EA Flash series 1112 and NA2100).

Se colocaron aproximadamente 10 mg de muestra liofilizada en capsulas de estaño. El funcionamiento del analizador está basado en la combustión de las muestras por encima de 1000ºC, esta combustión produce la rotura de los componentes de la muestra. Los gases formados son conducidos mediante helio a través de catalizadores que reducen el número de especies gaseosas resultantes. A continuación los gases de CO_2 resultantes, son analizados por un cromatógrafo de gases por conducción térmica.

Para la obtención de carbono orgánico, se sigue el mismo protocolo con la diferencia que previamente al análisis, la muestra fue atacada con repetidas adiciones de 100 µl de HCl 6M para la eliminación completa del carbanato cálcico y posteriormente secada en la estufa, en cápsulas de plata. Para el cálculo de materia orgánica (OM) en la muestra se adopto el factor de conversión 2, respecto al contenido de carbono orgánico.

El contenido de carbono inorgánico (IC) se calculo mediante la diferencia entre el carbono total y el carbono orgánico. El contenido de carbonato cálcico se obtuvo a partir del carbono inorgánico utilizando la relación de masa molecular 8.33 y asumiendo que todo el carbono inorgánico se encontraba en forma de carbonato cálcico.

El contenido de sílice biogénica (ópalo) fue analizado en dos pasos separados con extracciones de carbonato sódico siguiendo el procedimiento descrito por Fabres et al., (2000). El silicio y el aluminio fueron medidos mediante un espectrómetro de emisión atómica-acoplado a un plasma de inducción “Inductive Coupled Plasma Atomic Emission Spectrometer” (ICP-AES). Este proceso consiste en la vaporización, disociación, ionización y posterior excitación en el interior de un plasma de los diferentes elementos químicos.

El contenido de sílice fue corregido de la primera disolución usando la relación Si/Al de la segunda disolución, siguiendo el protocolo descrito por Kamatani and Oku (2000). El sílice corregido fue transformado en ópalo utilizando el factor de corrección 2.4 descrito por Mortlock and Froelich (1989).

La fracción litogénica se obtuvo asumiendo la siguiente relación:

% litogénico =100-(% material orgánica+ % carbonato cálcico+%+ópalo).

1.3.2.2. Composición bioquímica (Proteinas, Carbohidratos, Lípidos y Feopigmentos)

El uso de conservantes en las trampas de sedimento para minimizar la influencia microbiana (Gardner et al., 1989) puede causar algunos problemas analíticos en la determinación de algunas clases de compuestos orgánicos, pero trabajos previos demostraron que el uso de formaldehido como conservante no afecta a la determinación del contenido de proteína, carbohidratos y lípidos, en comparación con las muestras sin tratar (Wakeham et al., 1993; Dell’Anno et al., 2002). Todos los análisis se realizaron por triplicado usando aproximadamente 10 mg de muestra liofilizada y siguiendo los protocolos descritos por Danovaro (2010). Se utilizó un espectrofotómetro (340>λ>750 nm), este análisis se basa en la diferencia de radiación absorbida por una solución que contiene una cantidad desconocida de soluto, y una que contiene una cantidad conocida de la misma sustancia. Para la detección de proteínas, carbohidratos y lípidos las muestras pasaron por diversos procesos de coloración y se reportaron a valores equivalentes de albúmina de suero bovino (BSA, bovine serum albumin) para proteínas, glucosa para carbohidratos y tripalmitina para lípidos.

Proteínas

La evidencia experimental en el laboratorio ha demostrado que diversos protocolos proporcionan resultados similares en términos de equivalentes de BSA (Berges et al., 1993).

La cuantificación del contenido de proteínas se realizó mediante una modificación del protocolo descrito por Hartree (1972) después de las modificaciones de Rice (1982). Haciendo reaccionar las proteínas con tartrato de Na-K y el reactivo de Folin-Ciocalteu en medio básico (pH 10). La reacción proporciona una coloración azul, estable y cuya intensidad es proporcional a la concentración de proteína en la solución de reacción.

Carbohidratos

La concentración de carbohidratos totales se determino de acuerdo con Dubois et al. (1956) optimizado para sedimentos por Gerchacov y Hatcher (1972). Este análisis se basa en la reacción entre los azúcares y fenol en presencia de ácido sulfúrico concentrado. El método no es específico y determina las concentraciones de carbohidratos totales, incluyendo la celulosa.

Lípidos

La determinación de la concentración total de lípidos en muestras de sedimentos marinos se lleva a cabo generalmente según Bligh y Dyer (1959) y Marsh y Weinstein (1966), modificada para ser aplicada a la matriz de sedimento.

Pigmentos

Existen diferentes métodos para la evaluación de la concentración de clorofila-a y feopigmentos en sedimentos marinos, que pueden proporcionar diferentes sub o sobreestimaciones (Pinckney et al., 1994), en parte debido a la importancia relativa de los productos de degradación de las clorofilas "(Szymczak-Żyła y Kowalewska, 2007). Por esta razón, hemos sumado la concentración de clorofila-a y de feopigmentos y se describen como fitopigmentos totales (Pusceddu et al., 2010).

El análisis de los pigmentos se llevo a cabo de acuerdo con Lorenzen y Jeffrey (1980). Los pigmentos se extrajeron usando 3-5 ml de acetona al 90% como agente de extracción durante 12 horas a 4 ° C, en oscuridad. A continuación las muestras se analizaron mediante fluorometría. Para la estimación de los feopigmentos, se realizo una acidificación con 200 µl de HCl 0,1 N de la muestra con el objetivo de degradar la clorofila-a.

Proteínas enzimáticamente hidrolizables (lábil)

El protocolo fue desarrollado a partir del método propuesto por Mayer et al. (1995), originalmente basado en la evaluación de los aminoácidos liberados desde el sedimento después del tratamiento con enzimas proteolíticos. El procedimiento permite la evaluación de la fracción digestible de proteínas en sedimentos marinos. Esta se calcula como la diferencia entre las cantidades de proteína total y la proteína que resta tras la eliminación de la fracción enzimáticamente digerida. Las muestras fueron incubadas durante 3 hrs en una disolución de enzimas k-proteinasa y proteinasa en una matriz de fosfato potásico. Después de la incubación se sigue el mismo protocolo realizado para el análisis de proteínas totales.

Carbohidratos enzimáticamente hidrolizables (lábil)

El procedimiento permite la evaluación de la fracción de hidratos de carbono digeribles en sedimentos marinos, se estima como la diferencia entre los carbohidratos totales y los carbohidratos que quedan tras la eliminación de la fracción enzimáticamente digerida (Danovaro et al., 2001). Las muestras fueron incubadas durante 2 horas en una disolución de enzimas k-proteinasa, proteinasa, α-amilasa, β-glucosidasa y lipasa en una matriz de fosfato potásico. Tras la incubación se sigue el mismo protocolo realizado para el análisis de carbohidratos totales.

Carbono biopolimérico (semilábil)

El carbono biopolimérico (BPC) es un factor que se utiliza para estimar la fracción de carbono orgánico potencialmente disponible para la ingestión de los organismos. Proteínas, carbohidratos y lípidos fueron convertidos en equivalentes de carbono usando los factores de conversión 0.40, 0.49 y 0.75 mg C mg^{-1}, respectivamente. (Fabiano et al., 1995).

Carbono biopolimérico enzimáticamente hidrolizable (lábil)

El carbono biopolimérico enzimáticamente hidrolizable (BAOC) es una estimación de la fracción de carbono orgánico rápidamente asimilable por los consumidores bentónicos, se define como la suma de los equivalentes de carbono de hidratos de carbono y proteínas hidrolizables. Proteínas y carbohidratos enzimáticamente hidrolizables fueron convertidos en equivalentes de carbono usando los factores de conversión 0.40 y 0.49 mg C mg^{-1}, respectivamente (Danovaro et al., 2001). Suponiendo insignificante la contribución de los lípidos hidrolizables.

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CAPÍTULO 2

MULTIPLE DRIVERS OF PARTICLE FLUXES IN THE BLANES SUBMARINE CANYON AND SOUTHERN OPEN SLOPE: RESULTS OF A YEAR ROUND EXPERIMENT

RESUMEN

El capitulo 2 presenta la distribución de los flujos de partículas dentro del cañón de Blanes y en el talud adyacente, así como la composición de los mismos. Este capítulo pone de manifiesto la diferencia de flujos en cuanto cantidad y composición de los mismos en los dos hábitats.

Para caracterizar la variabilidad temporal y espacial de los flujos de masa total en el cañón submarino de Blanes y el talud adyacente, se colocaron ocho fondeos equipados con una trampa de sedimento cada uno, a las profundidades de 300, 900, 1200 y 1500 m a lo largo del eje del cañón, y a 900, 1200, 1500 y 1800 m de profundidad en el talud adyacente, entre noviembre de 2008 y noviembre de 2009. Los resultados obtenidos muestran que los flujos de masa fueron superiores en el cañón, desde 0,05 hasta 82,67 g m^2 d^{-1}, en comparación con los del talud, que variaron desde 0,01 hasta 9,91 g m^2 d^{-1}. Ambos hábitats estuvieron fuertemente influenciados por las agentes atmosféricos y mostraron un aumento de los flujos totales de masa durante los meses de otoño e invierno. La distribución espacial de los flujos de masa total y sus componentes principales (materia orgánica, carbonatos, ópalo y litogénicos) pone de manifiesto los contrastes entre los dos dominios fisiográficos del área de estudio (cañón frente talud). La evolución temporal de los flujos de partículas muestra tres períodos distintos controlados por la presencia de tormentas, la convección del mar abierto y el florecimiento de fitoplancton, y las entradas de aerosoles, respectivamente. A pesar de que la fracción litogénica domina los flujos de masa total (hasta un 80%), los flujos de materia orgánica son relativamente altos dentro del cañón, lo que confirma su eficacia en la canalización de partículas orgánicas desde la plataforma continental hasta el fondo.

MULTIPLE DRIVERS OF PARTICLE FLUXES IN THE BLANES SUBMARINE CANYON AND SOUTHERN OPEN SLOPE: RESULTS OF A YEAR ROUND EXPERIMENT

Pilar Lopez-Fernandez[a], Antoni Calafata[1], Anna Sanchez-Vidal[a], Miquel Canals[a], M. Mar Flexas[b],*, Jordi Cateura[b], and Joan B. Company[c]

a GRC Geociències Marines, Dept. d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, E-08028 Barcelona, Spain

b Laboratori d'Enginyeria Maritima (LIM), Universitat Politècnica de Catalunya, E-08034, Barcelona, Spain

c Institut de Ciències del Mar (ICM), CSIC, E-08003, Barcelona, Spain

1Corresponding author: Tel. +34 934021361, Fax. +34 934021340

Postal address: GRC Geociències Marines, Dept. d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, E-08028 Barcelona, Spain

E-mail: antonicalafat@ub.edu (Antoni Calafat)

* Now at: Jet Propulsion Laboratory, JPL/Caltech, California

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ABSTRACT

To characterize the temporal and spatial variability of total mass fluxes in the Blanes submarine canyon and the nearby southern open slope, eight near-bottom sediment traps were deployed at 300, 900, 1200 and 1500 m along the canyon axis, and at 900, 1200, 1500 and 1800 m of water depth on the southern open slope from November 2008 to November 2009. The results obtained show that mass fluxes were higher into the canyon, ranging from 0.05 to 82.67 g m^{-2} d^{-1}, compared with those from the open slope that ranged from 0.01 to 9.91 g m^{2} d^{-1}. Both environments were highly influenced by atmospheric forcing and showed increased total mass fluxes during autumn and winter months. The spatial distribution of total mass fluxes and major constituents (organic matter, carbonate, opal and lithogenics) highlights the contrasts amongst the two physiographic domains in the study area (canyons vs. open slope). The temporal evolution of particle fluxes shows three distinct situations succeeding each other along the year. These are determined by: 1) storms in autumn and winter, driving 60% of the annual total mass flux in Blanes Canyon and 44% in the open slope stations, and also 60% and 40% of the annual OC flux in Blanes Canyon and the southern open slope, respectively; 2) open sea convection in late winter and spring, which is accompanied by a phytoplankton bloom and drives 13% of the settling OC in the canyon and 34% in the open slope; and 3) dust inputs and resuspension by bottom trawling in late spring and –summer months, driving 17% of the annual OC flux in the canyon and 18% in the slope.

2.1. INTRODUCTION

Continental margins are regions of high sediment accumulation as they receive large amounts of terrestrial particles from fluvial discharges and biogenic particles from marine primary productivity (Monaco et al., 1990; Heussner et al., 1996). Continental margins are characterized by complex successions of open slope segments incised by submarine canyons (Weaver et al., 2004). The continental slope is a steep narrow fringe that separates the coastal zone and the continental shelf from the deep ocean. Submarine canyons are common features on the margins of continents worldwide (Harris and Whiteway, 2011 and references therein) and are well known as natural conduits of sediment from the deep margin and basin (Baker and Hickey, 1986; Carson et al., 1986; Durrieu de Madron, 1994; Gardner, 1989; Granata et al., 1999; Hagen et al., 1996; Monaco et al., 1999; Durrieu de Madron et al., 2000; Schmidt et al., 2001; Epping et al., 2002; Van Weering et al., 2002; Canals et al., 2006; Liu et al., 2009; Zuñiga et al., 2009). Particle fluxes within canyons are usually orders of magnitude higher than in the open slope (Puig et al., 2003; Martin et al., 2006; DeGeest et al., 2008; Walsh and Nittrouer, 1999). Determining what drives the transport and deposition of natural sedimentary particles in submarine canyons including carbon is currently a major topic in marine geology and biogeochemistry.

The role of submarine canyons in transferring organic matter (OM) to the deep is especially relevant in oligotrophic systems like the Mediterranean Sea (Pasqual et al., 2010; Zuñiga et al., 2009; Tesi et al., 2008). OM transport to the deep is mediated by vertical and lateral (advection) fluxes of particles, which, in turn, are influenced by climate (Smith et al., 2009) and hydrodynamic conditions (Bonnin et al., 2008). In this frame, submarine canyons represent places of intense exchange between the shelf edge and upper continental slope and bathyal-to-hadal environments, eventually behaving as major forced conduits of matter and energy to the deep sea (Canals et al., 2006). Submarine canyons are also considered biodiversity hotspots, and as such are rich in endemisms and constitute preferential recruitment areas for many megafauna species (Gili et al., 1999, 2000; Sardà et al., 2009). Environmental and topographic variability are very high both within and between canyons (Hickey, 1995; Harris and Whiteway, 2011; Würtz, 2012), which translates into the structure and dynamics of biological communities (Gili et al., 1999). Measuring such variability is critical in understanding the dynamics of marine populations in submarine canyons (Sardà and Cartes, 1997).

The aim of this paper is twofold: first, to investigate the temporal and spatial variability of near bottom particle fluxes in the bathyal zone of the Blanes submarine canyon and the southern open slope from 300 to 1800 m of water depth and, second, determining the drivers and forcings driving that variability. To achieve this aim we used near-bottom sediment trap and current meter data obtained from instrumented moorings deployed along the canyon and adjacent open slope to the south during one entire year. Hydrodynamic (wave height)

and hydrological (river discharge) data are also considered as they provide information on external forcings affecting the study area and triggering events that influence particle fluxes to the deep.

2.2. GENERAL SETTING: PHYSIOGRAPHY AND METOCEANIC CONDITIONS

The N-S oriented Blanes submarine canyon is located in the North Catalan margin, where a narrow continental shelf is deeply incised by three main submarine canyons that are from N to S Cap de Creus, La Fonera and Blanes canyons (Amblas et al., 2006; Canals et al., 2013), the later being the target of this study. The head of the Blanes canyon, at a depth of 60 m, is less than 4 km from the coastline. The width of the canyon increases with depth up to a maximum of 20 km at its deepest point. The canyon displays a V-shaped cross section in the upper course, indicating the dominance of erosion processes, and a U-shaped cross section in the lower course, where depositional processes have prevailed at least for the last millennia (Lastras et al., 2011). Canyon wall height and morphology play an important role in the variability of near-bottom currents, with a highly variable flow at the eastern smoother wall, and a prevailing offshore-directed flow over the western wall forced by a shallower and sharper topography than the opposite wall (Zuñiga et al., 2009) (Fig. 1).

Both northern and eastern storms are common in the study area. Following Mendoza and Jimenez (2006), a storm in the study area is defined as a violent atmospheric disturbance accompanied by strong winds and other perturbations, such as changes in atmosphere pressure, resulting in a significant wave height (Hs) exceeding a threshold of 2 m for a minimum duration of 6 h. Most storms in the study area occur when winds blow from the northern or eastern quadrants. Cold and dry continental northern winds lead to 'dry' storms while warmer and humid marine eastern winds originate 'wet' storms (Guillen et al., 2006). Dry northern storms trigger high waves offshore as the wind pushes the seawater off the coast, whereas eastern wet storms push seawater against the coast while inducing heavy rains over the watersheds and subsequent increases in river discharge. High breaking waves during eastern wet storms often cause serious erosion and infrastructure damage along the coastline.

Circulation in the study area is dominated by a general southward cyclonic flow over the continental slope called the Northern Current (NC), which is forced by the entrance of Atlantic Water (AW) into the Mediterranean through the Strait of Gibraltar and the boundary conditions imposed by the coastline perimeter and the submerged physiography of the Western Basin. AW temperature ranges between 15 and 20ºC and salinity between 36 and 36.5 psu (Millot, 1999). Western Mediterranean Intermediate Water (WIW) forms in winter in the Northwestern part of the Western Mediterranean Basin, and is identifiable as a relative temperature minimum layer in Atlantic Water. Below the AW, at about 300-400 m, lies the saltier and warmer Levantine Intermediate Water (LIW), which originates in the Eastern Mediterranean Basin. LIW has mean values of about 14ºC and 38.75 psu and marks a maximum of temperature and salinity in most of the Western Basin (Font et al., 1988). The deepest water mass is the Western

Mediterranean Deep Water (WMDW), formed in the Gulf of Lion by deep open ocean convection during winter months (Millot, 1999). WMDW has mean temperature and salinity values of 13°C and 39 psu. The NC is associated to a shelf-slope density front that separates the continent-influenced fresher waters over the shelf from offshore saltier waters (Font et al., 1995).

2.2.1. Experimental design

Two transects of mooring lines were deployed from November 2008 to November 2009 in and out the Blanes submarine canyon. The first line included four moorings that were distributed along the axis of the canyon at 300, 900, 1200 and 1500 m of water depth (labeled BC300, BC900, BC1200 and BC1500) while the second transect consisted also of four moorings at 900, 1200, 1500 and 1800 m of water depth across the open slope to the south of the canyon (labeled OS900, OS1200, OS1500 and OS1800) (Fig. 1).

Each mooring was equipped with a Technicap PPS3 sediment trap and an Aanderaa RCM7/9 current-meter pair at 25 m above the bottom. Each sediment trap had 12 receiving cups and was programmed for a sampling interval of 15 days so that particles were continuously collected during 6 months. The only exception was the two sediment traps at 1200 m, which were programmed with a sampling interval of 7 to 8 days. The higher resolution data of these two sediment traps has been averaged over 14 to 16 days intervals to get an equivalent resolution for the whole set of samples. The success rate of the overall experiment was 82%, with 197 samples recovered from a theoretical maximum of 240 (Table 1). Gaps in the particle samples temporal series were caused by mechanical failures of different types. The Technicap PPS3 sequential sediment traps have a cylindrico-conical shape with a height-diameter ratio of 2.5 for the cylindrical part and a collecting area of 0.125 m2. Before the deployment, the rotary collector of every trap was soaked in HNO3 0.5 M overnight and rinsed several times with distilled water in the laboratory. Receiving cups were filled with a 5% formaldehyde solution in 0.45 μm filtered sea water buffered with sodium borate to avoid the degradation of the collected particles because of grazing and disruption by swimming organisms eventually captured. Each currentmeter, deployed 2 m below the sediment trap, recorded current speed and direction with a sampling interval of 30 minutes. For calibration purposes, SBE 911 Conductivity-Temperature-Depth (CTDs) profiles were obtained over each mooring site in October 2008, February, May, and September 2009.

2.2.2. Sample treatment and analytical procedures

After retrieving, the samples were stored in the dark at 2-4°C until processed in the laboratory. The supernatant was removed from each sam-

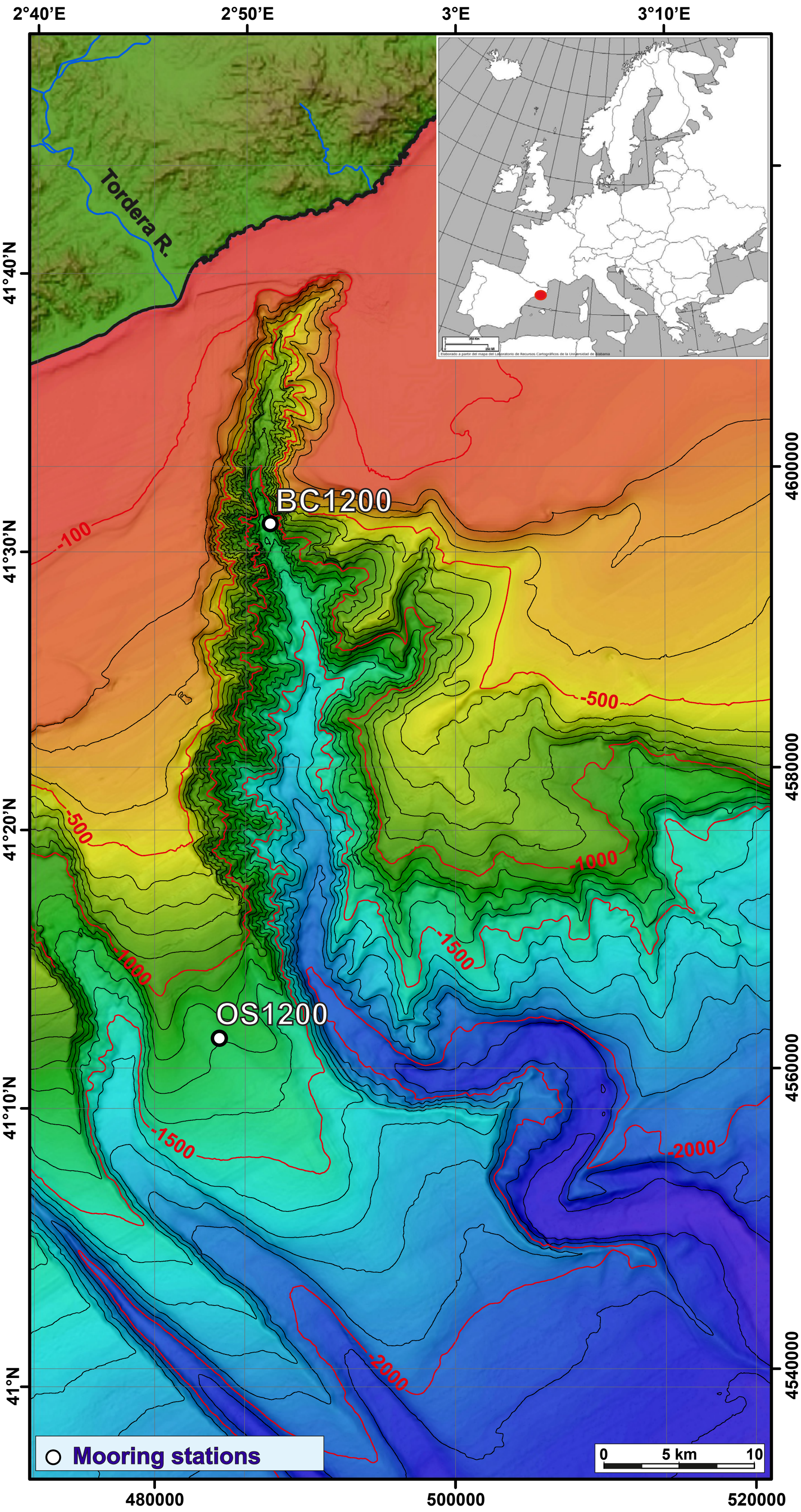

Fig. 2.1. Bathymetric map of Blanes Canyon area showing the location of mooring stations BC300 to BC1500 along the canyon axis and OS900 to OS1800 in the adjacent open slope to the south. The locations of Tordera River gauging station (Can Simó) and the metoceanic Blanes buoy are also shown. Depth in meters. BC stands for Blanes Canyon, indicating the moorings deployed along the canyon axis, and OS stands for Open Slope, indicating the moorings deployed across the adjacent open slope. Numbers to the right of BC or OS refer to water depth.

MOORING STATION	LONGITUDE	LATITUDE	WATER DEPTH (m)	SAMPLING PERIOD	SAMPLING INTERVAL (days)	SUCCESS RATE (%)
BC 300*[1]	2° 53' 43.38"	41° 39' 36.66"	300	28/11/08 - 12/04/09	15-16	42
BC 900	2° 54' 19.14"	41° 34' 12.72"	900	07/11/08 -01/11/09	15-16	100
BC 1200	2° 50' 49.26"	41° 31' 15.06"	1200	07/11/08 -26/10/09	7-8	100
BC 1500	2° 52' 58.00"	41°27' 28.80"	1500	07/11/08 -26/01/09	15-16	33
OS 900	2° 49' 7.80"	41° 16' 7.19"	900	07/11/08 -01/11/09	15-16	100
OS 1200	2° 48' 54.60"	41° 13' 8.99"	1200	07/11/08 -26/10/09	7-8	98
OS 1500	2° 53' 48.00"	41° 09' 0.59"	1500	13/05/09 - 01/11/09	15-16	50
OS 1800	2° 58' 9.00"	41° 04' 52.19"	1800	07/11/08 -01/11/09	7-16	100

Table 2.1. Location, water depths and sampling records of the moorings deployed in the Blanes Canyon (BC) and the adjacent southern open slope (OS). Numbers to the right of BC and OS refer to water depth.

ple, the swimmers >1 mm were separated by wet screening on a nylon mesh while those <1 mm were handpicked under a dissecting microscope. A high precision peristaltic pump was then used to obtain aliquots through repeated division of cleaned raw samples. Every sample was then centrifugated to eliminate salt and formaldehyde, freeze-dried and stored in the dark before analysis. Samples were then pounded to fine powder. Total mass fluxes (TMFs) expressed in g m-2 d-1 were calculated after the dry weight, the trap collecting area and the sampling interval of each sample. TMFs were calculated following the formula

TMF = Sample dry weight (mg) / collecting area (m2) x sampling interval (days).

Due to the loss of some sediment trap samples, time-weighted fluxes (TWFs) were calculated for periods with complete series. TWFs were calculated as

TWF= ΣFi / (collection area x Σdi),

being Fi the TMF in period i, and di, the number of collecting days of period i. This parameter eliminates the disturbances due to the loss of samples.

Total carbon (TC), organic carbon (OC) and total nitrogen (TN) concentrations were measured using an elemental analyzer EA Flash series 1112 and NA2100. Samples for OC determination were decarbonated with HCl 6M. Inorganic carbon (IC) was calculated as the difference between TC and OC from where calcium carbonate (CaCO3) contents were obtained using the molecular mass ratio of 8.33 and assuming that all IC was in the form of CaCO3. OM contents were calculated as twice the OC content. Opal (biogenic silica) was analyzed using a two-step extraction of 2.5 h with 0.5 M Na2CO3 following Fabres et al. (2002). Si and Al were measured with an Inductive Couple Plasma Atomic Emission Spectrometer (ICP-AES), with the Si contents of the first extraction corrected by the Si/Al ratio of the second one (Kamatani and Oku, 2000). Corrected Si concentrations were transformed to opal after multiplying by a factor of 2.4 according to Mortlock and Froelich (1989). The lithogenic fraction was obtained assuming that the percentage of lithogenics was equal to 100 - (%OM + %CaCO3 + %opal).

2.2.3. Data on external inputs and oceanographic conditions

Daily river discharge of the Tordera River, which opens near the Blanes canyon head, were obtained from the Can Simó gauging station located at Fogars de la Selva, 12 km upstream of the river mouth (Fig. 1). This gauging station is operated by Agència Catalana de l'Aigua (ACA).

Dry and wet dust deposition in mg m-2 were obtained from the Dust Regional Atmospheric Model BSC-DREAM8b (Nickovic et al., 2001; Pérez et al., 2006), which is run by the Barcelona Supercomputing Center, for the box 41.00º to 41.50º N and 2.40 to 3.10ºE, assuming no significant variation across the study area. Total particles in the air in µg m-3 was supplied by Institut de Diagnosi Ambiental i Estudis de l'Aigua (IDÆA-CSIC) from a station situated at 41.77º, 2.35ºE, at an altitude of 720 m in the Montseny massif, 25 km inland from the Tordera River

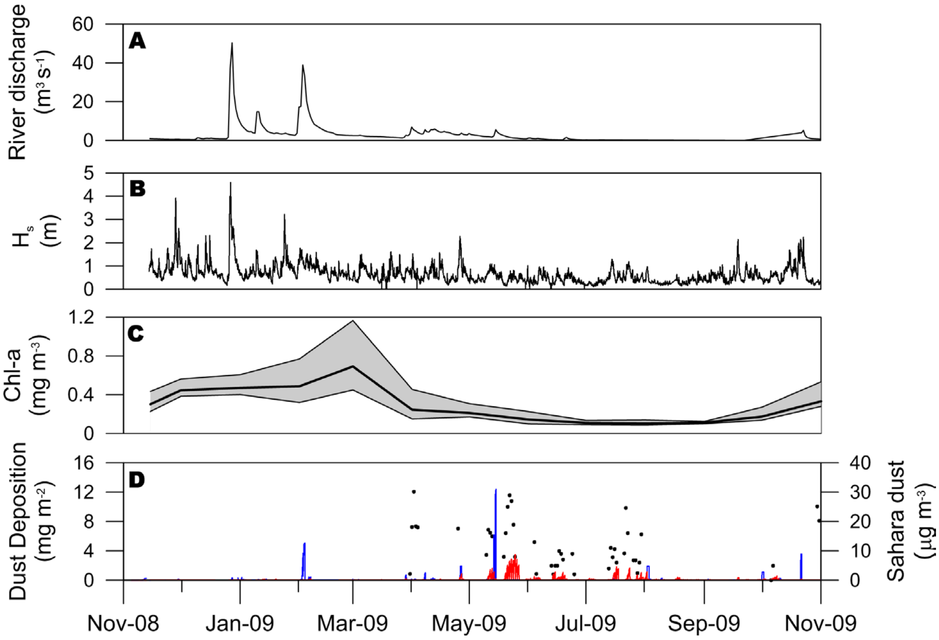

Fig. 2.2. Environmental conditions in the study area during the entire monitoring period from November 2008 to November 2009. (A) Daily Tordera River discharge (m3 s1) at Can Simó gauging station; (B) significant wave height Hs (m) at the Blanes metoceanic buoy; (C) monthly average and maximum and minimum MODIS Chlorophyll-a concentrations (mg m2); and (D) dry dust deposition (red line), wet dust deposition (blue line) and Sahara dust outbreaks (black dots). Location of gauging station and metoceanic buoy is shown in Fig. 1. For further details, see Section 3.3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

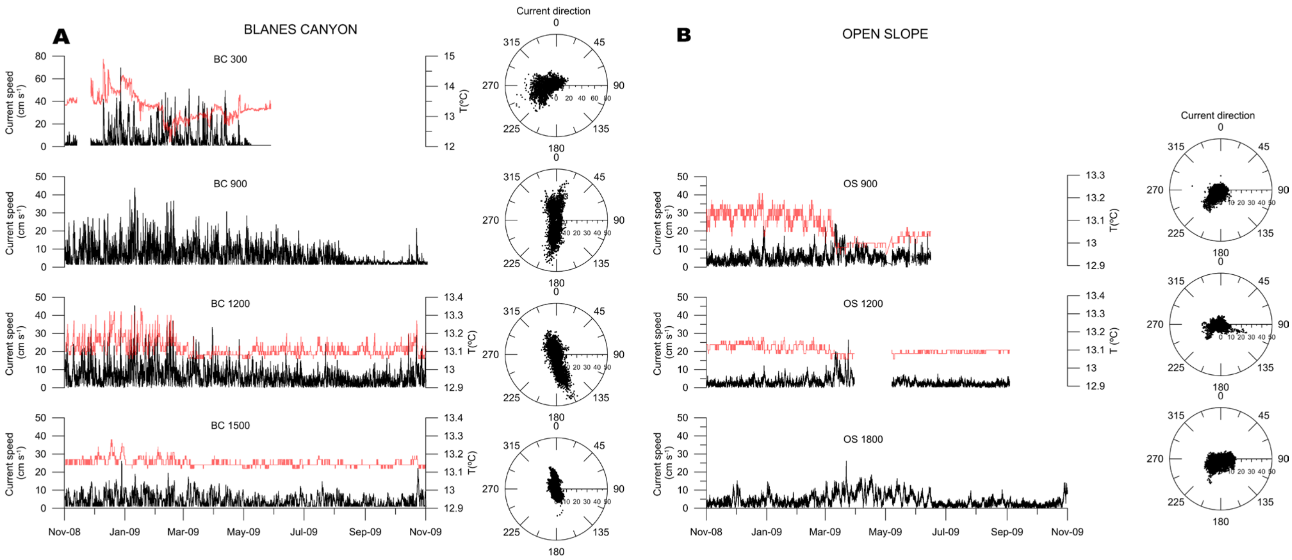

Fig. 2.3. Current speed and temperature x–y plots and current direction polar plots measured at 23 mab in all mooring stations in the Blanes Canyon (A) and in the adjacentopen slope (B). Note that the vertical scale for current speed in BC300 differs from the other stations. Radial scales in current direction polar plots are equivalent to the y-axisof x–y current speed plots.FIG 2.3.png

mouth. Levels of aerosols were measured continuously with optical counters (GRIMM 1107), and the integrated mass of particulate aerosols with diameters up to 10 μm was utilized to characterize the daily atmospheric scenarios influencing particulate matter levels, including the detection of African dust outbreaks, following the methodology reported by Pérez et al. (2008).

Significant wave height (Hs) was obtained from the Xarxa d'Instruments Oceanogràfics i Meteorològics (XIOM) Blanes metocean buoy situated in the inner shelf 1.8 km offshore the Tordera River mouth (Fig. 1).

Monthly averaged MODIS-Aqua estimated sea surface chlorophyll-a concentrations (Chl-a, mg m-3) were obtained through the European Commission Environmental Marine Information System (EMIS) for the box 41.00º to 41.50º N and 2.40 to 3.10ºE, assuming no significant variation across the study area (emis.jrc.ec.europa.eu/emis_1_0.php). Chlorophyll concentration is a standaproduct from satellite-based optical sensors, usually retrieved from empirical algorithms using reflectance ratios at two or more wavebands, and Aqua mission is a NASA-centered contribution to the Earth Observing System international program.

2.3. **RESULTS**

2.3.1. Storms and hydrodynamic conditions

Following Mendoza and Jimenez (2006), two major storms occurred during the study period from November 2008 to November 2009, the first at the end of November 2008 and the second by the end of December 2008.

Two moderate storms also occurred in late in January and April 2009. Finally, two milder events with Hs close to 2 m took place by mid September and late October 2009, thus totaling six noticeable events (Fig. 2).

The first major one was a dry northern storm starting the 28th of November 2008 with Hs higher than 2 m for 20 h and peak values of 4 m, with no river discharge increase (Fig. 2). This storm induced southeastward flowing (i.e. following the canyon axis) currents inside the canyon peaking at 22 cm s^{-1} at BC900, 23 cm s^{-1} at BC1200 and 14 cm s^{-1} at BC1500.

The second major was an eastern wet storm that initiated the 26th of December 2008 with Hs higher than 2 m for 65 hours, peak Hs of 4.6 m and maximum wave height in excess of 8 m. This was the most extreme storm ever recorded instrumentally in the area, with a return period in excess of 100 years (Sanchez-Vidal et al., 2012). Rainfall was intense and the Tordera River reached a peak discharge of 50 m3 s-1 (Fig. 2). The storm coincided with an increase in current speed in all stations within the canyon, i.e. BC300 (up to 70 cm s^{-1}), BC900 (27 cm s^{-1}), BC1200 (32 cm s^{-1}) and BC1500 (25 cm s^{-1}). Increased currents were directed SW (BC300) to SSE-SE following the canyon axis (Figs. 1 and 3). A few days delay in current peaks was observed for the deeper stations, including open slope stations where current increase because of the 26th of December 2008 storm was nonetheless lower.

The January and April 2009 moderate storms surpassed the 2 m threshold for a few hours only and Hs did not exceed 3.5 m. Both were noticed only in two mooring stations inside the canyon, which were BC900 (19 cm s^{-1}) and BC1200 (28 cm s^{-1}) for the end of January 2009 storm, and BC900 (23 cm s^{-1}) and BC1200 (27 cm s^{-1}) for the end of April 2009 storm. None of these two storms translated into noticeable near-bottom current speed increases in any of the open slope stations. While the January 2009 storm was a wet one accompanied by increased river discharge (up to 38 m3 s^{-1}) with a few days delay (Fig. 2), the April 2009 one did not record any increase in river discharge.

Besides storm-related current speed variations, currentmeter records in canyon stations showed up and down currents following the canyon axis, which is indicative of a strong bathymetric control (Fig. 3A). The annual mean current speed decreased with increasing water depth, from BC300 (7.7 cm s^{-1}) to BC900 and BC1200 (7.0 and 6.7 cm s^{-1}), and BC1500 (4.2 cm s^{-1}), while in the open slope stations a decrease was also observed from OS900 (5.5 cm s^{-1}) to OS1200 (3.0 cm s^{-1}) though a slight increase was noticed at OS1800 (4.4 cm s^{-1}). Such weak values might be close to the variability detection capability of the currentmeters.The moorings registered the local formation of Western Mediterranean Intermediate Water (WIW) in February 2009 inside the canyon and the arrival of new WMDW between March and May 2009 inside the canyon and at the open slope too. In February 2009 the instruments at 300 m inside the canyon recorded minimum water temperatures of 12.14 ºC coupled with an increased current speed up to 45 cm s^{-1} (Fig. 3). The arrival of new dense WMDW from March to May 2009 was observed as an increase in salinity (not shown) and a decrease in temperature, with minimum water temperatures of 13.05ºC and 12.95ºC At BC1200 and OS900 (Fig 3). During an hydrographic survey performed in May 2009 it could be observed that the plume of new WMDW arriving at the open slope affected the lower half of the water column, from about 600 m down to the bottom of the water column, where turbidity was high (Fig. 4).

2.3.2. Primary production and dust inputs

Primary production in the NW Mediterranean is markedly seasonal. Time series of Chl-a concentration during the monitored annual cycle show two distinct periods: a first one with an increasing trend from November 2008, when Chl-a started to go up, to March 2009, when Chl-a concentration peaked at 1.17 mg m-3, followed by a second period marked by a decreasing trend leading to very low Chl-a concentration from

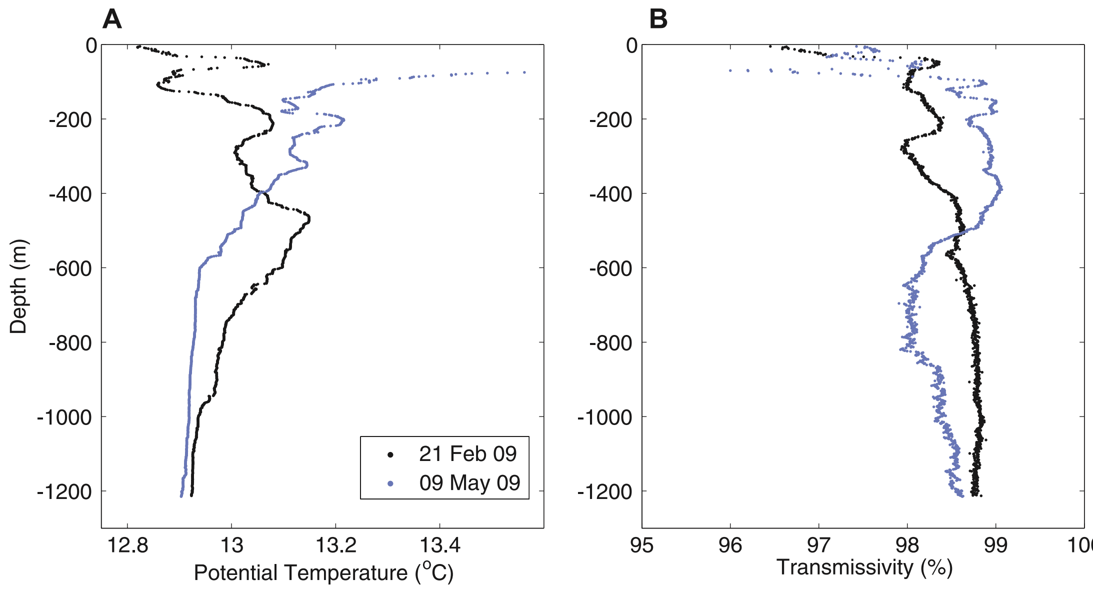

Fig. 2.4. (A) Potential temperature and (B) transmissivity profiles obtained from CTD casts performed at the location of OS1200 station in February 2009 and May 2009. Note the highly turbid layer of WMDW from about 600 m to the bottom (lower transmissivity values in the May 2009 profile), also corresponding to homogenized relatively cooler waters (potential temperature plot).

May to October 2009, with the highest year-round values occurring from early February to mid March 2009 (Fig. 2C).

Monthly total dust deposition was also highly variable (Fig. 2D). Relatively low dust inputs from November 2008 to mid February 2009 were followed by higher inputs until November 2009. Wet deposition had a maximum of 11.75 mg m^{-2} by mid May (blue line in Fig. 2D). Dry deposition presents four relative maximums in May, June and two in July 2009, with values up to 3.33, 1.07, 1.84, and 1.65 mg m^{-2}, respectively (red line in Fig. 2D). PM10 levels reached maximum values of 0.05 mg m^{-3} in late February-March 2009. 12% of the dust input was identified as Saharan dust, which outbreaks were especially evident during specific events from April to July 2009 (black dots in Fig. 2D).

2.3.3. Total mass fluxes

Basic statistics of TMFs (maximum, minimum and standard deviation) as well as time-weighted fluxes (TWFs) are shown in Table 2. TMFs and TWFs in the canyon axis were generally one order of magnitude higher than those from the adjacent open slope. Average TMFs were 18.35 and 1.88 g m^{-2} d^{-1} in the Blanes Canyon and the open slope, respectively. Higher fluxes that certainly occurred at BC300 and BC1200 in December 2008 are minimum estimates due to the overflow of the sediment traps by excess flux.

TWFs increased down canyon from 12.68 g m^{-2}

MOORING STATION		MASS FLUX g m^{-2} d^{-1}	ORGANIC MATTER %	OPAL %	$CaCO_3$ %	LITHOGENICS %
BC 300 n=10	AVERAGE	12.06	1.68	1.61	37.25	59.62
	MAX	82.67	3.84	4.19	43.05	78.27
	MIN	0.05	1.26	0.27	19.14	55.60
	S.D.	25.67	0.67	1.32	7.00	6.91
	TWF-TWC	12.68	1.68	1.45	37.25	59.62
BC 900 n=24	AVERAGE	14.75	1.96	0.36	24.96	72.73
	MAX	35.30	2.22	2.17	30.14	75.63
	MIN	0.17	1.82	0.01	22.12	67.76
	S.D.	10.63	0.10	0.59	1.87	1.87
	TWF-TWC	15.39	1.96	0.35	24.96	72.73
BC 1200 n=24	AVERAGE	22.52	2.11	1.25	24.38	72.47
	MAX	75.38	2.72	4.64	27.24	82.54
	MIN	0.07	1.73	0.11	14.18	70.59
	S.D.	16.59	0.22	1.47	2.35	2.28
	TWF-TWC	23.82	2.11	1.04	24.38	72.47
BC 1500 n=6	AVERAGE	26.57	2.21	4.36	24.69	68.74
	MAX	51.19	2.60	7.24	25.03	72.20
	MIN	6.07	1.98	0.92	23.31	69.66
	S.D.	20.11	0.23	2.74	0.66	2.66
	TWF-TWC	26.57	2.21	4.36	24.69	68.74
OS 900 n=24	AVERAGE	3.43	3.00	1.64	24.01	71.54
	MAX	9.91	5.15	3.39	26.24	74.01
	MIN	0.54	2.07	0.50	22.64	67.86
	S.D.	2.38	0.74	0.69	1.08	1.96
	TWF-TWC	3.53	2.82	1.64	24.01	71.54
OS 1200 n=24	AVERAGE	2.20	3.12	1.92	24.55	70.40
	MAX	5.91	5.57	5.63	27.31	75.30
	MIN	0.27	2.34	0.51	21.36	66.46
	S.D.	1.70	0.97	1.25	1.66	2.48
	TWF-TWC	2.29	3.12	1.92	24.55	70.40
OS 1500 n=11	AVERAGE	0.37	5.20	3.98	24.45	66.37
	MAX	0.81	8.91	7.27	28.37	72.06
	MIN	0.11	2.94	2.31	18.99	61.44
	S.D.	0.24	2.10	1.81	2.93	3.78
	TWF-TWC	0.34	5.20	3.98	24.45	66.37
OS 1800 n=24	AVERAGE	0.78	3.74	4.08	24.48	67.70
	MAX	2.50	10.66	9.68	27.64	72.66
	MIN	0.02	2.78	1.24	20.01	60.06
	S.D	0.84	2.26	2.27	2.05	4.22
	TWF-TWC	0.78	3.74	4.08	24.48	67.70

Table 2.2. Total Mass Fluxes (TMF) (g m2 d1) in La Fonera (from Martín et al., 2006), Lacaze-Duthiers (from Pasqual et al., 2010), Cap de Creus (from Pasqual et al., 2010) andBlanes canyons (year 2003–2004, from Zuñiga et al., 2009) compared to Blanes canyon in 2008–2009 (this study). Numbers after the canyon name correspond to the year ofsampling. Table 22.pdf

d^{-1} at BC300 to 15.39 g m^{-2} d^{-1} at BC900, 23.82 g m^{-2} d^{-1} at BC1200 and 26.57 g m^{-2} d^{-1} at BC1500, even though TWFs at BC300 and BC1500 likely are underestimated due to sediment trap clog-

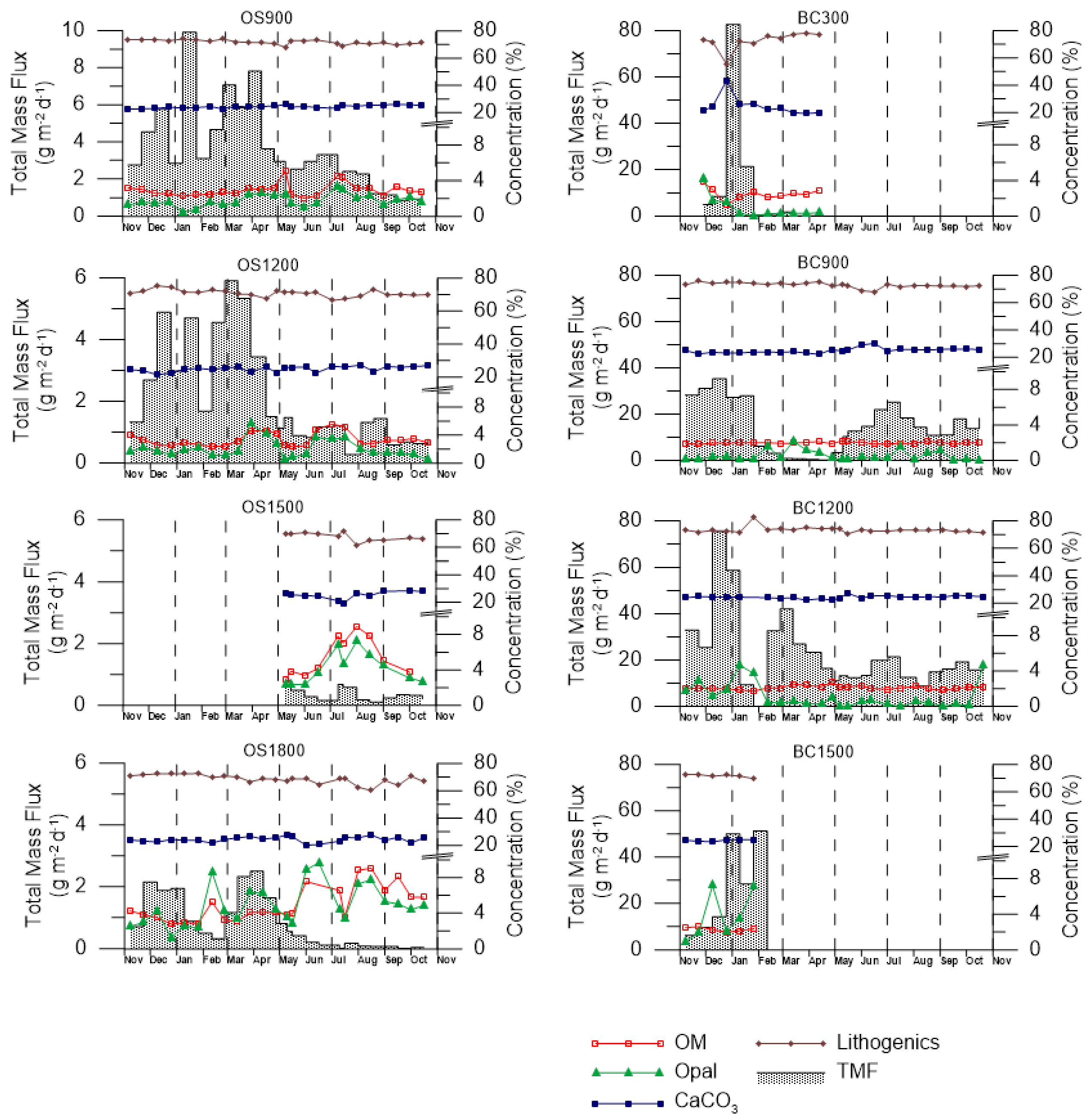

Fig. 2.5. Time-series of Total Mass Fluxes (TMF) (g m2 d1) (grey bars) and relative concentrations of major constituent as percentages of total weight, with organic matter(OM) in red, opal in green, CaCO3 in blue and lithogenics in brown. (For interpretation of the references to color in this figure legend, the reader is referred to the web versionof this article.).

ging after excess flux. In the open slope the lowest and highest TMFs were recorded at OS1800 (0.01 g m^{-2} d^{-1}) and OS900 (9.91 g m^{-2} d^{-1}). TWFs decreased down slope from 3.53 at OS900 to 0.78 g m^{-2} d^{-1} at OS1800. The temporal variability of TMFs is also worth of attention. At the BC300 station, which record extends from the beginning of December 2008 to the beginning of April 2009, maximum TMF values of 82.67 g m^{-2} d^{-1} were measured by the end of December 2009 and beginning of January 2009 (Fig. 5). From February to April 2009, fluxes decreased and remained significantly low (i.e. below 2 g m^{-2} d^{-1}). TMF at BC900 was also high in December 2008 (up to 35.29 g m^{-2} d^{-1}), decreased to 0.17 g m^{-2} d^{-1} in April 2009 and then increased again up to 25.15 g m^{-2} d^{-1} in July 2009 (Fig. 5). Deeper in the canyon axis, at BC1200, TMF was noticeably high. In November 2008 TMF was 32.97 g m^{-2} d^{-1}, increasing to 75.38 g m^{-2} d^{-1} in December 2008, then decreasing to 0.07 g m^{-2} d^{-1} in mid-January 2009 to increase again in March 2009 when it peaked at 42.21 g m^{-2} d^{-1}. From March 2009 onwards TMF at BC1200 decreased again showing a couple of minor relative increases in late June-early July and from late August to mid October 2009 (Fig. 5). TMF at BC1500, with data from November 2008 to February 2009 only, increased up to 50.03 g m^{-2} d^{-1} by the end of December 2008 and beginning of January 2009, and showed a second increase up to 51.19 g m^{-2} d^{-1} in February 2009.

In the open slope TMF were significantly lower. At OS900, two TMF relative increases were observed in November-December 2008 and March–April 2009, peaking at 5.76 g m^{-2} d^{-1} and 7.81 g m^{-2} d^{-1}, respectively. Then TMF decreased continuously down to values close to 1 g m^{-2} d^{-1}. At OS1200, TMF also increased up to 4.88 g m^{-2} d^{-1} in November - December 2008, 4.70 g m^{-2} d^{-1} in January 2009 and 5.91 g m^{-2} d^{-1} in March 2009. At OS1500 only samples from May 2009 to end of October 2009 were recovered. TMF showed slight augmentations in May 2009 (0.81 g m^{-2} d^{-1}) and July 2009 (0.68 g m^{-2} d^{-1}). Finally, TMF at OS1800 increased in December 2008 (2.15 g m^{-2} d^{-1}) and beginning of April 2009 (2.50 g m^{-2} d^{-1}).

2.3.4. Composition of settling particles

The lithogenic fraction was the dominant component of settling particles in both the canyon and the open slope, averaging 60-72% and 66-72% of the TMFs, respectively. In all stations the lithogenic fraction decreased in spring and summer (i.e. from May to August 2009), a tendency that was more pronounced in the open slope environment.

The CaCO3 fraction was the second dominant component of the settling particles in all stations, with average values close to 25% except in the shallowest station, BC300, with 37.25%. The CaCO3 content was slightly higher in canyon stations than in the open slope. Within the canyon, the maximum CaCO3 contribution to TMFs was found at BC300, with 43.05%, while the minimum was at BC1200, with 14.18%, both extreme values obtained in wintertime, in December 2008 and February 2009, respectively. The extreme values (18.99% and 28.37%) in the open slope were measured in summer (July 2009) and autumn (October 2009) at station OS1500 (Table 2).

The annual average OM content in the canyon stations ranged from 2.21% at BC1500 to 1.68% at BC300. Maximum and minimum contributions to the TMFs (3.84% and 1.26%) were recorded at BC300 in November and December 2008, respectively. In the open slope average OM values ranged from 5.20% at OS1500 to 3.00% at OS900, with a maximum value of 10.66% at the OS1800 station and a minimum of 2.07% at OS900 (Table 2). Two or more OM peaks were observed in the open slope stations for which the entire record was available, while no peaks were found in canyon stations (Fig. 5). OM average content showed an increasing trend with increasing water depth except for the deepest station OS1800 (Table 2).

Opal concentrations within the canyon were very low most of the time, with average values

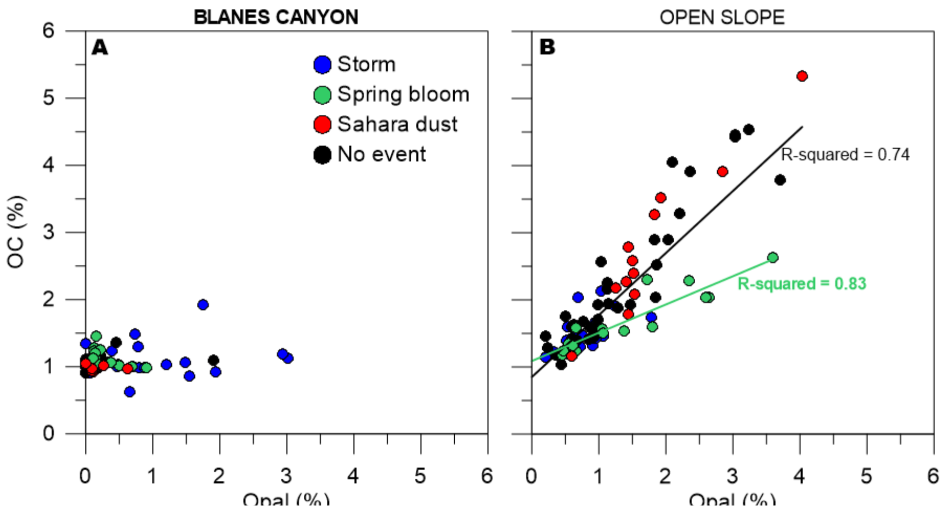

Fig. 2.6. Organic carbon contents (OC) to opal ratios for the particle trap samples recovered at the open slope (right) and inside the Blanes Canyon (left) during differentsituations driving mass fluxes: storms (blue dots), offshore convection with phytoplanktonic bloom (green dots), Saharan dust inputs (red dots) and in absence of any specificevent (black dots). Regression line between OC and opal during the spring bloom and when there is not any significant event are also shown. (For interpretation of thereferences to color in this figure legend, the reader is referred to the web version of this article.)

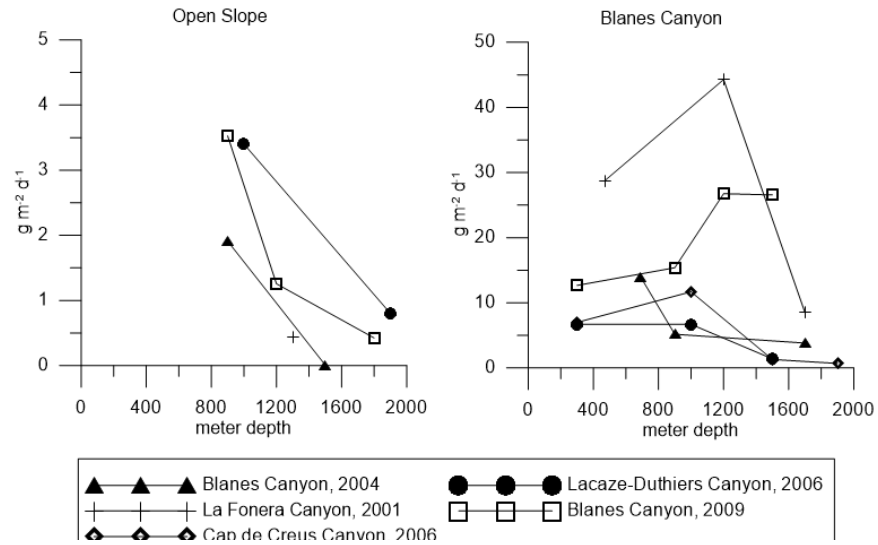

Fig. 2.7. Total Mass Fluxes (TMF) (g m2 d1) in La Fonera (from Martín et al., 2006), Lacaze-Duthiers (from Pasqual et al., 2010), Cap de Creus (from Pasqual et al., 2010) and Blanes canyons (year 2003–2004, from Zuñiga et al., 2009) compared to Blanes canyon in 2008–2009 (this study). Numbers after the canyon name correspond to the year ofsampling.

ranging from 0.36% to 4.36% (Fig. 5 and Table 2). The highest values within the canyon, 7.24% and 4.64%, were observed at BC1500 and BC1200 in wintertime, in December 2008 and January 2009, respectively. In the open slope stations opal concentrations were generally higher and more variable than within the canyon (Fig. 5), with increasing averages with depth going from 1.64% to 4.08% at OS900 and OS1800, respectively. The maximum opal concentration of 9.68% in the open slope was recorded in June 2009 at OS1800.

2.4. DISCUSSION

Temporal variability of particle fluxes at all stations during the monitoring period shows the occurrence of three periods with increased TMF caused by different types of drivers, which are storms, dense shelf water formation, open sea convection, dust inputs, phytoplanktonic blooms and bottom trawling.

2.4.1. Impact of storm events on particle fluxes

The months from November 2008 till the end of January 2009 were characterized by unstable weather leading to both dry and wet storms associated to strong winds, high seas and occasional heavy rainfall (Fig. 2). Usually the influence of storms is system-wide, affecting all aspects of particle remobilization, transport, and deposition (Liu and Lin, 2004). During storms, high wave energy mobilizes shelf sediments, leading to an increased supply of particles to the submarine canyon (Liu et al., 2006). In our study, for each of the storms, strong winds triggering high waves were likely to generate fast currents on the shelf (Pedrosa-Pàmies, 2013). Strong shoreward winds caused a surge of seawater over and along the coast that led to an intense, turbid alongshore flow that was captured by the Blanes Canyon head (Sanchez-Vidal et al., 2012). Such turbid coastal flow could also have had a contribution from the invasion of the shelf by the southwards flowing NC. Furthermore, bottom shear stress produced by high surface waves alone was enough to resuspend shelf sediments down to an abnormally large depth, thus increasing the density of the shelf water by particle loading thus easing its flowing into and down canyon. Inside the canyon, current speed increases up to 70 cm s^{-1} at BC300 and 32 cm s^{-1} at BC1200 following its axis were recorded. This demonstrates that the canyon acted as a major conduit for shelf sediment transport, as also shown by the high suspended sediment concentrations recorded by near-bottom transmissometers. The above-described situation was particularly well illustrated by the 26th of December 2008 exceptional eastern storm, as described by Sanchez-Vidal et al. (2012), and it was probably the case, though to a lesser extent, of the storms occurring in November 2008 (dry northern storm) and January 2009 (wet eastern storm) too (Figs. 2, 4). The down canyon transport of resuspended sediments continues until turbulence, current speed or density are unable to maintain the particle load in suspension, so that sand sized particles settle in the upper reaches of the canyon, while the clay sized particles are transported down canyon (Pedrosa-Pàmies et al., 2013). This is evidenced by the high particles fluxes recorded during the three stormiest months of November and December 2008, and January 2009. Concurrent relatively high TMFs were also recorded in the open slope stations, though of lower magnitude (Fig. 5), suggesting that particles were transported not only down canyon but also across and possibly along the open slope.

The measurement of fluxes at BC1200 inside the canyon higher than those in the shallower station BC900 suggest the lateral transfer of particles to the canyon axis along the gullies that indent the middle canyon walls (Fig. 1), possibly accompanied by smaller amounts released by resuspension taking place between those two stations. The marked increase of TMFs at the deepest station BC1500 as a result of the last storm in January 2009, compared to the shallower stations where fluxes were higher after the two previous storms, could be explained, first, by a pronounced exhaustion of resuspendable sediment in the shallowest system compartments after the earlier storms and, second, by the remobilization of sediments temporarily accumulated into the canyon at depths less than 1500 m. This explanation is somehow similar to the one given for the transport of suspended sediment in torrential rivers experiencing a progressive reduction of the suspended load after a succession of events (Alexandrov et al., 2003; Hudson, 2003; Moreno et al., 2005; Rovira and Batalla, 2006). This view is supported by the comparison of TMFs in late January and early February 2009 amongst all canyon axis stations: the shallower stations show lower fluxes while the deepest BC1500 station displays markedly higher fluxes (Fig. 5). The common initial source of particles and this step-by-step transport along the canyon involving the resuspension of particles previously accumulated in its shallower reaches (Pasqual et al., 2010) helps understanding the lack of significant compositional differences in between the fluxes associated to the various storms that occurred during the winter stormy period. During that period particle fluxes were mainly composed of lithogenics with very minor opal contributions at the canyon stations (Fig. 5). The low variability of OC contents and its lack of relationship with opal concentrations in the canyon stations (Fig. 6) suggest that opal came probably from resuspended silica skeletal fragments from the shelf.

Overall, the values measured during the winter stormy period represent 60% of the TWFs recorded in the Blanes canyon and 44% of the TWFs in the slope stations. Accordingly, the stormy period of 2008-09 contributed with 60% of OC flux in the Blanes Canyon and 40% in the open slope.

2.4.2. Impact of dense water formation and primary production on particle fluxes

In February 2009 a sudden drop in temperature down to 12.14 ºC and an increase in flow velocity up to 50 cm s^{-1} at BC300 indicate a WIW formation event, i.e., likely dense shelf water from the Gulf of Lions spreading into the Blanes Canyon as WIW. It is not the first time that dense shelf waters from the Gulf of Lion reach the Blanes Canyon (Zuñiga et al., 2009), a process that was numerically modeled by Ulses et al. (2008). In winter 2009, dense shelf waters cascading in the Gulf of Lion was not particularly intense (Puig et al., 2013), which is also reflected in the Blanes Canyon where the event was of short duration and did not reach the deeper station (i.e. it was not recorded at BC1200 and BC1500). The sediment traps did not present any increase in TMFs, though we cannot discard clogging of the receiving cups as a consequence of previous overflow of some traps, at least the BC300 one.

In March 2009 the recording of colder and saltier waters at the open slope reflects the arrival of new WMDW flowing along the continental slope (Fig. 3). The new WMDW tongue was recorded over the slope from March to early May 2009, with current speeds up to 26 cm s^{-1} and minimum water temperatures of 12.95ºC (Fig 3 and 4). New WMDW forms under extreme winter conditions in the Gulf of Lion and the Ligurian Sea causing strong heat losses that trigger either dense shelf water cascading or open-sea deep convection, or both, as it is often the case (Lopez-Jurado et al., 2005; Durrieu de Madron et al., 2013). In the most offshore stations OS1200 and OS1800 the maximum fluxes of the whole monitoring period were recorded in March 2009 (Fig. 5). We hypothesize that this was caused by resuspension of fine seafloor sediments by open-sea convection. Recent studies have shown that independently of resuspension and transport by dense shelf water cascading into deep water, high current velocities associated with open sea convection have also the ability to resuspend particles in the deep margin and basin (Martin et al., 2010; Stabholz et al., 2012). The occurrence of an open sea convection event in the Northwestern Mediterranean Sea in winter 2008-09 has been documented in CIESM (2009), Stabholz et al. (2012) and Tamburini et al. (2013). This situation translates into a decrease in the biogenic components (OC and opal) of particle fluxes at the onset of the event in March 2009. After vertical mixing, re-stabilization of the surface layer, and increased insolation, the marked phytoplanktonic bloom usually occurring in late winter-spring in the study area (Estrada et al., 1996; Rossi et al., 2003) caused enhanced Chl-a concentrations (Fig. 2) and increased the settling of bio-aggregates. Accordingly, settling particles were richer in OM and opal (Fig. 5). The influence of pelagic sedimentation is more noticeable in the open slope than inside the canyon where it gets diluted because of its own character as a dynamic preferential conduit of lithogenics escaping from the shelf. In the open slope opal concentrations explain 83% of OC variance (Type-I lineal-regression, $p<0.05$), while no correlation amongst these two variables is found in the canyon (Fig. 6). The persistent mixing and homogenization of the particulate matter inside the canyon due to its dynamic behavior involving stronger currents prevents the seasonal signal associated to pelagic sedimentation to appear clearly (Fig. 7B). Overall, the 2009 open sea convection event and associated primary production contributed with 13% of OC flux in the Blanes Canyon and 34% in the open slope.

2.4.3. Impact of atmospheric dust entries on particle fluxes

From June to September 2009 the traps located in the open slope recorded an increase in organic compounds (OC and biogenic opal) (Fig. 5) without any obvious augmentation of superficial chlorophyll-a concentration as observed from satellite imagery imagery (Fig. 2). The origin of fresh material inputs under this situation in summer months could be perhaps explained by the development of a deep chlorophyll maximum closely associated to the nutricline (Estrada, 1996). There are processes like windy events carrying dust to the Northwestern Mediterranean that may to a point compensate nutrient depletion due to water stratification and subsequently support secondary blooms (Goutx et al., 2000; Pasqual et al., 2011). These processes have been identified as the cause of increased sinking fluxes of biogenic particles by a number of authors working in the Northwestern Mediterranean Sea (Zuñiga et al., 2007; Lee et al., 2009; Ternon et al., 2010). Because of its proximity to North Africa and the Sahara desert, the Mediterranean Basin is recurrently affected by the arrival of dust from these areas. Large amounts of mineral dust are thus mobilized from the arid regions of North Africa and injected into the atmosphere under favorable weather conditions finally leading to deposition over land and sea surfaces, the later contributing to pelagic settling all across the Mediterranean Sea (Guerzoni et al., 1997, 1999; Ridame and Guieu, 2002). This dust brings new nutrients such as dissolved inorganic phosphorous and iron to Mediterranean surface waters, and holds the potential to stimulate primary production during summer periods even though the water column is stratified (i.e. no inputs of nutrients from deep waters as there is no vertical mixing).

By the end of spring and early summer 2009 there was a noticeable arrival of Saharan dust (Fig. 2) to the Northwestern Mediterranean area, which paralleled the increase in biogenic components that is visible in our open slope records. The arrival of new nutrients may have stimulated an early summer phytoplanktonic growth. Lopez-Fernandez et al. (2013) pointed out that during summer 2009 sediment trap samples showed an increase in both phytopigment contents and nutritional value of the particle fluxes comparable to the spring bloom increases. Even though the enhancement of the biological activity induced by the deposition of Saharan dust was not visible from MODIS (Fig. 2C), this should not be interpreted as a lack of marine biological response, as tested by Volpe et al. (2009). Instead, it could be caused by a lack of sensitivity of the satellite sensors in detecting small chlorophyll-a variations, or simply by the development of a subsurface deep chlorophyll maximum, as pointed out by Estrada et al. (1993). The biogenic particle flux increase was more evident in open slope stations due to their stronger pelagic influence and a weaker influence of advected resuspended sediments. In addition, the higher slope of the OC vs. opal correlation associated to the enhanced arrival of Saharan dust compared to that of the spring phytoplankton bloom (Fig. 6) suggests a different phytoplankton community developing due to dust fertilization, with less contribution of opal indicating a shift from siliceous (diatomaceous) to carbonate producing organisms. This idea is supported by high CaCO3 concentration in settling particles in the Blanes Canyon, pointing to the sedimentation of organisms with carbonated shells, which is supported by the visual inspection of the samples showing abundant pteropods (Fig.4). This fact prompts a combination of secondary production and settling of calcareous phytoplankton.

2.4.4. Impact of bottom trawling on particle fluxes

At the end of the spring and beginning of summer 2009 a relative increase in TMF poorly loaded with biogenic compounds was observed at 900 m depth in both domains, canyon and open slope and, to a lesser extent, at 1200 m depth. The influence of trawling has been hypothesized to be the cause of such unexpected high particle fluxes occurring in summer months under calm seas, low waves and weak river discharge (Puig and Palanques, 1998; Palanques et al., 2005; Puig et al., 2012). Indeed the Blanes Canyon and the adjacent open slopes contain fishing grounds where bottom trawling is commonly practiced. The local trawling fleet fishes down to 800 m depth (Ramirez-Llodra et al., 2010, their Fig. 1), with the main effort concentrated along the northern open slope from late winter to early summer and over the eastern canyon wall from late summer to mid-winter, with new fishing ground being opened in the canyon head axis (Company et al., 2008; Sarda et al., 2009). The western flank of the canyon is not or poorly fished because of its steep and rough topography (Ramirez-Llodra et al., 2010). We hypothesize that the increase in particle fluxes recorded at 900 and 1200 m in summer 2009 could have been caused by bottom trawling leading to the formation of resuspension clouds (Puig et al., 2012), followed by subsequent particle settling, mostly made by lithogenic material, directly over the fishing grounds themselves or at short distance due to lowered ocean dynamics during that time of the year. Under more dynamic conditions, like the winter ones, such man-induced resuspension and settling events are less obvious or unnoticeable likely due to either dilution amidst of naturally larger fluxes or to farther transport by faster and currents, or both.

Overall, the relative weight in the annual total OC flux by enhanced primary production linked to dust inputs and by resuspension due to bottom trawling, mostly occurring synchronously in otherwise quiet late spring and summer months, is 17% in the Blanes Canyon and 18% in the open slope. Obviously, the synchronic character of these two drivers, dust inputs and intensified bottom trawling, prevents separating the contribution of each of them to total OC fluxes.

2.4.5. The annual particle flux variability

Data obtained in the Blanes submarine canyon and the adjacent slope reveals clear differences in the amount and the composition of settling particles in canyon and slope environments. As found in other submarine canyons nearby such as La Fonera (Martin et al., 2006) and Cap de Creus (Pasqual et al., 2010), particle fluxes inside the Blanes submarine canyon were always higher (almost one order of magnitude) than the fluxes recorded in the open slope at the same depths (Fig. 5). This difference was stronger during and immediately after storm events, like the ones of November and December 2008 and January 2009 (Figs. 2 and 4). This reinforces the view of deeply incised submarine canyons as preferential conduits for particle fluxes because of their topography (Gardner, 1989; Durrieu de Madron, 1994) and enhanced hydrodynamics, mainly during storm events (Palanques et al., 2005; Liu et al., 2006; Martin et al., 2006; Sanchez-Vidal et al., 2012).

On an annual basis, TWFs increased down canyon to 1500 m of water depth (Table 2 and Fig. 7). However, clogging of the receiving cups at BC300 after the storm in late December 2008 may have biased TWF in this station, implying that the observed down canyon increase should be interpreted with caution for the upper canyon reaches. The results from the investigated annual cycle apparently contradicts previous work by Zuñiga et al. (2009), who found a down canyon particle flux decrease. In 2008-09 flux values were significantly higher than those measured by Zuñiga et al. (2009) for the annual cycle 2003-04. Our values range from 12.68 g m^{-2} d^{-1} at 300 m of water depth to 26.56 g m^{-2} d^{-1} at 1500 m in 2008-09, while those obtained by Zuñiga et al. (2009) vary from 13.98 g m^{-2} d^{-1} at 600 m to 3.82 g m^{-2} d^{-1} at 1700 m of water depth. Particle fluxes in the canyon and slope in 2008-09 were, therefore, one order of magnitude higher than those in 2003-04. The number of storm events in winter 2008-2009 that fed the canyon with high amounts of sedimentary particles from the shelf contrasts with a lonely storm in winter 2003-04. This reveals the high interannual variability of particle fluxes in the study area, mostly related to atmospheric forcing eventually involving high energy processes (see Section 5.1). A similar down canyon increase in TWF was also detected in the nearby La Fonera canyon where Martin et al. (2006) and Palanques et al. (2006) suggested an influence by storm events and bottom trawling activities too.

In the open slope, TWFs show the typical decrease with increasing distance from shore (Fig. 7). TWF values ranged from 3.53 g m^{-2} d^{-1} in the surface station OS900 to 0.77 g m^{-2} d^{-1} in OS1800. This evidences that the influence of hydrodynamic processes is much less in the southern open slope compared to the Blanes Canyon, which is in correspondence with a dominant hemipelagic origin of particles reaching the open slope floor.

The composition of TMFs was in general rather stable (Fig. 5), with a predominant (around 70%) lithogenic fraction. This tendency was more prominent inside the canyon (Fig. 6), where OC and opal contributions did not vary significantly with changing TMFs. This points to a strong homogenization of the particulate matter transported within the canyon during sediment resuspension and settling cycles, but it could also be that the resuspended particles are already made of old and refractory material. In contrast, OC and opal concentrations in settling particles in the open slope present higher variability and decrease with increasing TMFs (Figs. 5 and 6), suggesting again that the main influence on particle fluxes in the open slope are hemipelagic processes.

2.5. CONCLUSIONS

The spatial and temporal distribution of total mass fluxes and fluxes of major components allow differentiating two domains with distinct behavior in the study area: 1) the canyon domain, where particle fluxes are influenced by frequent lateral inputs from the continental shelf, the upper canyon reaches and the gullies carved in the canyon flanks, and 2) the open slope, where seasonal trends become predominant in determining the quantity and composition of settling particles, which carry a clear pelagic signal.

This study reinforces the view that submarine canyons act as preferential conduits for the transport of particles from the continental shelf to the deep margin and basin, in accordance with previous works in different canyons of the Western Mediterranean Sea such as Lacaze-Duthiers, Cap de Creus, La Fonera and Foix canyons (Heussner et al., 2006; Martin et al., 2006; Pasqual et al., 2010; Puig et al., 2000, among others). At the same depths, particle fluxes were one order of magnitude higher in the Blanes Canyon than in the open slope. The high amounts of sedimentary particles transported through the Blanes Canyon can be explained by the relatively large sediment drainage area (i.e. the wide continental shelf to the north) opening into the canyon, the incision length of the canyon into the shelf, the closeness of its head to the shoreline and the proximity of the Tordera River mouth. All this results in the release of continental and resuspended material mostly during weather-driven high-energy events, which drive the capture of high mass fluxes by the submarine canyon. The transfer of particles to the mid canyon and deeper can be further enhanced by lateral inputs from a dense network of gullies carved in the canyon flanks, including suspensates released by bottom trawling in canyon flanks themselves as shown by Puig et al. (2012) in the nearby La Fonera Canyon. Particle inputs by bottom trawling become evident especially in the environmentally quiet summer months, when they are not masked by the much higher inputs resulting from natural, high-energy drivers. In contrast, particle fluxes in the open slope are more influenced by other types of hydrodynamic forcing, such as (i) the arrival of recently formed deep waters in the open Northwestern Mediterranean Sea during convection events, which might resuspend slope sediments, and (ii) the sedimentation of biogenic particles produced during phytoplanktonic blooms and occasional dust events.

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CAPÍTULO 3

BIOAVAILABILITY OF SINKING ORGANIC MATTER IN THE BLANES CANYON AND THE ADJACENT OPEN SLOPE (NW MEDITERRANEAN SEA)

RESUMEN

En el capítulo 3, se estudia a diferencia en la biodisponibilidad de la materia orgánica entre el cañón submarino de Blanes y el talud adyacente. En este capítulo se hace una descripción de los factores ambientales que pueden influir en dicha diferencia y la repercusión que supone para los ecosistemas profundos.

Los cañones submarinos son lugares de intenso intercambio de energía y de material entre la plataforma y las cuencas adyacentes profundas. Para probar la hipótesis de que los cañones submarinos activos representan conductos preferenciales de alimentos disponibles para el bentos de aguas profundas, se colocaron dos líneas de fondeo a 1200 m de profundidad desde noviembre 2008 hasta noviembre 2009 en el interior del cañón de Blanes y en el talud adyacente (Margen catalán, Mar Mediterráneo noroccidental). Se investigaron los flujos de carbono orgánico (OC), la composición bioquímica y calidad de los alimentos en sedimentación. Los flujos de OC en el cañón y en el talud adyacente variaron entre los periodos de muestreo, aunque no de manera consistente en los dos sitios. En particular, mientras que en el talud adyacente los flujos mayores de OC fueron observados en agosto de 2009, en el cañón los flujos más elevados de se produjeron en abril-mayo de 2009. Durante casi todo el período de estudio, los flujos de OC en el cañón fueron significativamente mayores que los del talud adyacente, mientras que la concentración de partículas de OC en el talud fue consistentemente más alta que en el cañón. Este resultado confirma que los cañones submarinos son vias eficaces de OC a las profundidades del mar, las partículas transferidas son predominantemente de origen inorgánico. Utilizando análisis estadísticos multivariantes, fueron identificados dos grupos principales de periodos de muestreo: uno en el cañón que agrupa las muestras de trampas recogido en diciembre de 2008, coincidiendo con la aparición de una fuerte tormenta en la superficie del mar, y se asocia con el aumento de los flujos de partículas nutricionalmente disponibles de la plataforma superior; y un segundo grupo que incluye las muestras, tanto del cañón y del talud recogidas en marzo de 2009, conjuntamente con la ocurrencia de la floración de fitoplancton estacional en la superficie del mar, y se asocia con el aumento de los flujos de fitopigmentos totales. Nuestros resultados confirman el papel clave ecológico de los cañones submarinos para el funcionamiento de los ecosistemas de aguas profundas, y pone de manifiesto la importancia de los cañones en la vinculación de las tormentas episódicas y producción primaria que ocurren en la superficie del mar hasta el fondo del mar

BIOAVAILABILITY OF SINKING ORGANIC MATTER IN THE BLANES CANYON AND THE ADJACENT OPEN SLOPE (NW MEDITERRANEAN SEA)

P. Lopez-Fernandez[1], S. Bianchelli[2], A. Pusceddu[2], A. Calafat[1], A. Sanchez-Vidal[1], and R. Danovaro[2]

1GRC Geociències Marines, Dept. d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, 08028 Barcelona, Spain

2Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Via Brecce Bianche 60131 Ancona, Italy

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Correspondence to: A. Calafat (antonicalafat@ub.edu)

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ABSTRACT

Submarine canyons are sites of intense energy and material exchange between the shelf and the deep adjacent basins. To test the hypothesis that active submarine canyons represent preferential conduits of available food for the deep-sea benthos, two mooring lines were deployed at 1200 m depth from November 2008 to November 2009 inside the Blanes canyon and on the adjacent open slope (Catalan Margin, NW Mediterranean Sea). We investigated the fluxes, biochemical composition and food quality of sinking organic carbon (OC). OC fluxes in the canyon and the open slope varied among sampling periods, though not consistently in the two sites. In particular, while in the open slope the highest OC fluxes were observed in August 2009, in the canyon the highest OC fluxes occurred in April-May 2009. For almost the entire study period, the OC fluxes in the canyon were significantly higher than those in the open slope, whereas OC contents of sinking particles collected in the open slope were consistently higher than those in the canyon. This result confirms that submarine canyons are effective conveyors of OC to the deep sea. Particles transferred to the deep sea floor through the canyons are predominantly of inorganic origin, significantly higher than that reaching the open slope at a similar water depth. Using multivariate statistical tests, two major clusters of sampling periods were identified: one in the canyon that grouped trap samples collected in December 2008, concurrently with the occurrence of a major storm at the sea surface, and associated with increased fluxes of nutritionally available particles from the upper shelf. Another cluster grouped samples from both the canyon and the open slope collected in March 2009, concurrently with the occurrence of the seasonal phytoplankton bloom at the sea surface, and associated with increased fluxes of total phytopigments. Our results confirm the key ecological role of submarine canyons for the functioning of deep-sea ecosystems, and highlight the importance of canyons in linking episodic storms and primary production occurring at the sea surface to the deep sea floor

3.1. INTRODUCTION

Continental margins are the edges of continents and represent a zone of strong interactions between the continent, the open ocean, and the atmosphere (Weaver at al., 2004) These interactions drive margin's hydrodynamic conditions, which in turn control the dispersal of particulate matter fluxes on the shelf and towards the open sea (Levin and Dayton, 2009). Many previous investigations have shown that continental margins may represent a reservoir of particulate organic matter, often derived from river discharge, which, while transported downslope, represent a key food source for the benthos (Walsh, 1991). Organic carbon (OC) transport to the deep sea is mediated through vertical fluxes of particles, which, in turn, are influenced by the general climate (Smith et al., 2009), local hydrodynamic conditions (Bonnin et al., 2008) and the presence of different benthic habitats (Pusceddu et al., 2010a). Among these, the submarine canyons indent the continental margins all over the world (Harris and Whiteway, 2011) representing the more intense zone of exchange between the upper continental slope and bathyal-to-hadal depths. Submarine canyons may act as a major forced conduit of material to the deep sea (Canals et al., 2006).

A recent investigation carried out along the Mediterranean Sea pinpointed that not all submarine canyons are active conveyors of material to the deep adjacent basin nor are characterized by significant differences in sedimentary organic matter content and biochemical composition when compared with the adjacent open slopes at similar depths (Pusceddu et al., 2010a). Basically, such lack of consistency can be ascribed to a recurrently missing temporal (seasonal) replication of the data. It is indeed most likely that the input of particulate organic material to the ocean's interior through canyons can be seasonal (e.g., Fabres et al., 2008), with the highest peaks associated with phytoplankton blooms in the upper layers of the water column (Pasqual et al., 2011) or with episodic events, including storms (Palanques et al., 2008; Sanchez-Vidal et al., 2012) and dense shelf water cascading (Tesi et al., 2008; Pasqual et al., 2010; Pusceddu et al., 2010b). In addition, the chemical composition of organic particles changes during sinking because of the consumption by heterotrophic plankton (including prokaryotes) (Hedges et al. 2001). It has indeed been estimated that about 10% of the primary production falls to a depth of 400 m, whereas only about 1% reaches 5000 m (Murray, 1992). This, traditionally, has led most deep-sea ecologists to conceive the deep sea as "nutritionally deprived" environment, missing local primary productivity and being fuelled by very low amounts of nutritionally poor organic particles (Gage and Tyler, 1991; Druffel and Robinson, 1999).

In recent years, the debate about the food limitation of the deep-sea benthos has continued and led to less conservative theories (Smith et al., 2008; Glover et al., 2010; Soetaert and van Oevelen, 2010). This has been mostly due to the fact that several studies have pointed out that the total amount of organic matter is not fully representative of the food quality of particles (Grémare et al., 1998; Misic and Covazzi-Harrigue, 2008; Pusceddu et al., 2009). Total OC is indeed composed of a biopolymeric fraction, made of biopolymers (including protein, carbohydrate and lipids) of relevance for heterotrophic nutrition (Fabiano and Pusceddu, 1998) and a complex/geo-polymeric fraction, adhered to inorganic particles and mostly refractory to consumption (Mayer, 2004; Grémare et al., 2002; Pusceddu et al., 2009). Early studies indeed demonstrated that among biopolymeric compounds, total proteins and lipids often explain the largest proportion of variations in the macro- and meiofauna growth (Grémare et al., 1997; Grémare et al., 1998) Moreover, not the whole biopolymeric fraction of suspended particles can be rapidly digested by metazoan consumers, as, generally, less than 15-50% of particulate organic C is enzymatically digestible (Grémare et al., 2003; Pusceddu et al., 2003; Grémare et al, 2005; Dell'Anno et al., this issue).

To our best knowledge, information about the digestible fraction of sinking organic particles towards the deep sea is practically not existent. Indirect estimates have been made based on sedimentary data (Dell'Anno et al., 2000; Grémare et al., 2005; Mayer et al., 1995; Vandewiele et al., 2009), but direct measures on trap samples are not available, yet.

In this study, we investigated the biochemical composition of particulate organic matter and its bioavailability to benthic consumers (using an enzymatic approach enabling the determination of the potentially digestible fraction), settling down along the water column during one year-long (November 2008-November 2009)

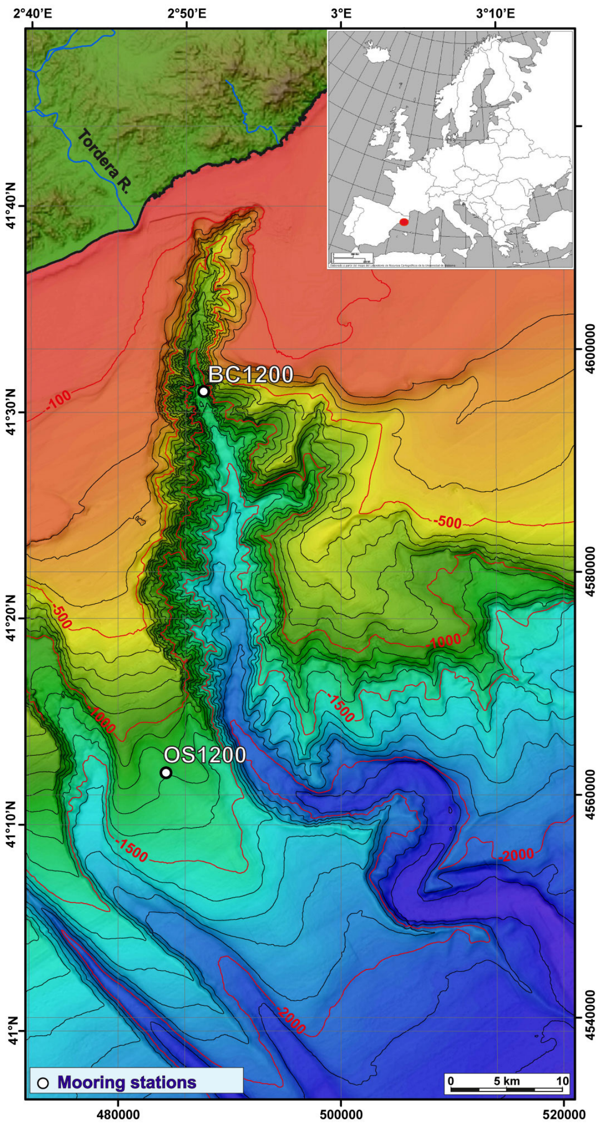

Fig. 3.1. Bathymetric map of Blanes canyon showing the location of the mooring station in Blanes canyon axis (BC1200) and in the adjacent southern open slope (OS1200). The location of Tordera River and the meteorological buoy is also shown. Depth in meters.

intensive (weekly) sampling activity carried out comparatively inside the Blanes canyon and on its adjacent open slope (Catalan Margin, NW Mediterranean Sea), at the same water depth.

3.2. **MATERIAL AND METHODS**

3.2.1. The study area

The Blanes canyon (Figure 1) is oriented in N-S direction and located in the northern Catalan margin (NW Mediterranean Sea). The Catalan margin is characterized by very complicated seafloor topography, showing a narrow continental shelf deeply incised by other canyons (Amblas et al., 2006). The head of Blanes canyon is less than 4 km from the coast, at 60 m depth. The Tordera River mouth is located near the head of the canyon. Occasionally, its main discharge corresponds to short-lived episodic floods (Rovira and Batalla, 2006). The canyon has a V-shaped cross section in the shoreward region characterized by a strong erosion, and a U-shaped cross section collecting sediment deposition from upper areas more offshore (Lastras et al., 2011; Figure 1). Currents inside the canyon are strongly influenced by the topography of the canyon walls, with a highly variable flow in the smooth wall at the East and a unidirectional offshore flow over the western wall forced by its shallow and sharp topography (Zuñiga et al., 2009).

3.2.2. Sampling of sinking particles

Two mooring lines were deployed for one year (November 2008-November 2009) at two stations located at 1200 m depth, one inside the canyon and one in the adjacent open slope (Figure 1). Each line was equipped with sediment trap-current meter pairs, positioned at 25 m above the sea bottom. Sediment traps (Technicap PPS3) were equipped with 12 receiving cups with a cylindrical–conical shape with a height/diameter ratio of 2.5 and a collecting area of 0.125 m^2. The traps were programmed with an interval of 7 to 8 days, which resulted in 48 sequential samples per station till the end of the monitoring period. Prior to the deployment, in the laboratory, the rotator collector was cleaned with detergent and rinsed several times with distilled water. Receiving cups were filled with a sodium borate buffered 5% formaldehyde solution in 0.45 μm pre-filtered sea water to avoid degradation of the collected particles.

In long term sediment traps, the use of preservative in the collecting cups is required to minimize microbial influence (Gardner, 1983). This may cause some analytical problems with the determination of some classes of organic compounds, but previous works demonstrated that the use of formaldehyde as preservative does not affect the determination of protein, carbohydrate and lipid contents when compared to untreated samples (Wakeham, 1993; Dell'Anno et al., 2002). The only possible problem is the lethal effect of the preservative on zooplankton that can lead to collections which do not represent vertical fluxes. For this reason larger swimmers (including all organisms that do not fall gravitationally through the water column but enter actively the traps) were removed before the analyses (Owens et al., 2013). After recovering, samples were stored in the dark at 2-4 ºC until they were processed in the laboratory.

Once in the laboratory, the samples were visually checked and the supernatant removed. Swimmers were removed by wet sieving (using sea water) on a 1-mm nylon mesh and hand-picking under a dissecting microscope. A high precision peristaltic pump was then used to obtain subsamples through repeated splitting of the rinsed raw samples. After that, formaldehyde and salt in excess were removed using centrifugation with cold Milli-Q water to avoid organic matter explosion, and were then freeze-dried and stored at 4°C in the dark until further analysis. After ground to a fine powder, samples were weighed and the total mass flux (TMF) calculated using the dry weight, the trap collecting area and the sampling interval. TMF were normalized to mg m^{-2} d^{-1}.

3.2.3. Biochemical composition and bioavailability of POM

Organic carbon (OC) concentrations in the sinking particles were measured using an elemental analyzer (EA Flash series 1112 and NA2100). Organic carbon (OC) was obtained by acid digestion with HCl 6M of the total carbon.

Biogenic silica (opal) was analyzed using two segmented step extractions with 0.5 M Na_2CO_3, according to Fabres et al. (2000). Si and Al were measured using an Inductively Couple Plasma Atomic Emission Spectrometer (ICP-AES).

Chlorophyll-a and phaeopigment analyses were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted (12 h at 4°C in the dark) from triplicate sub-aliquots of the trap material (about 10 mg of freeze dried material) and the sediment (10-20 mg lyophilized sediment), using 3-5 ml of 90% acetone as extractant. Extracts were analyzed fluorometrically to estimate chlorophyll-a, and, after acidification with 200 µl 0.1N HCl, to estimate phaeopigments. Different methods for assessing chlorophyll-a concentrations in marine particles can provide different under- or over- estimates (Pinckney et al., 1994), largely because of the relative importance of the chlorophylls' degradation products, which are particularly abundant in deep-sea sediments or particles sunk into traps (Szymczak-Żyła and Kowalewska, 2007). For this reason, Chlorophyll-a and phaeopigment concentrations were summed up and reported as total phytopigment concentrations (Pusceddu et al. 2009). These were then converted into C equivalents using a conversion factor of 40 µg C µg chlorophyll-a^{-1} (Witbaard et al., 2000; Van Oevelen et al., 2011). Protein, carbohydrate and lipid particle contents were analyzed spectrophotometrically as described in Danovaro (2010) according to Rice (1982), Gerchacov and Hatcher (1972) and Marsh and Weinstein 1966, respectively, and concentrations expressed as bovine serum albumin (BSA), glucose and tripalmitine equivalents, respectively. The fractions of protein and carbohydrate enzymatically digestible were assessed as described in Danovaro (2010) according to Dell'Anno et al. (2000) and reported as BSA and glucose equivalents, respectively.

Total carbohydrate, protein and lipid contents were converted into carbon equivalents (mg C mg^{-1}) using the conversion factors of 0.40, 0.49 and 0.75, respectively, and their sum defined as the biopolymeric organic carbon (BPC) (Fabiano et al., 1995). Bioavailable organic carbon (BAOC) concentration was calculated as the sum of digestible proteins and carbohydrates converted into carbon equivalents by using the same factors as for their total pools (Danovaro et al. 2001; Pusceddu et al., 2003). The algal contribution to BPC was calculated as the percentage of total phytopigments, once converted into C equivalents, to BPC concentrations.

According to Pusceddu et al. (2010a), we used the algal contribution to BPC as a gross descriptor of freshness of organic particles (Pusceddu et al., 2000; 2009; 2010). The percentage fraction of BAOC over BPC was used as a descriptor of OM food availability for consumers (Pusceddu et al., 2003; Danovaro et al., 2001).

3.2.4. Statistical analyses

To test for temporal variations in the rates of fluxes, biochemical composition and bioavailability of sinking particulate organic matter in the Blanes canyon and the adjacent open slope we used 2-way permutational analyses of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson, 2001). The design included two orthogonal factors: seabed morphology (2 fixed levels: canyon vs. slope) and sampling time (44 fixed levels, each corresponding to about one week of particle collection by the trap). The analyses were carried out for each variable separately

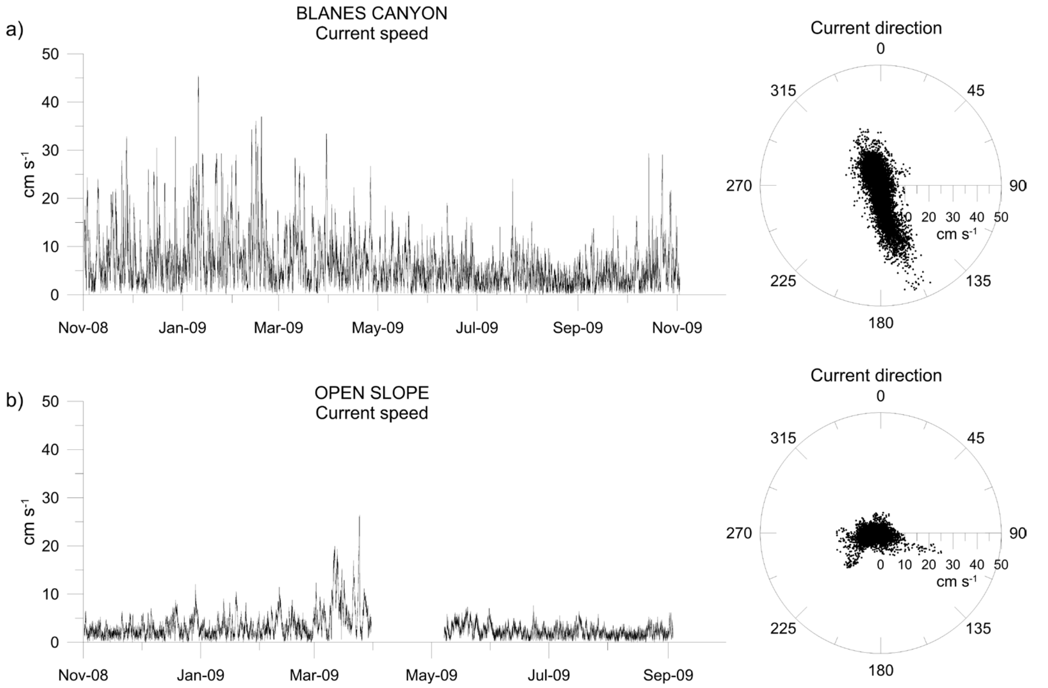

Fig. 3.2. Current speed and direction plots at 21 mab in Blanes canyon (a) station and open slope (b). Radial axes in current direction polar plots are equivalent to the y-axis of current speed plots (cm s^{-1}).

Station		Mass flux [$g\,m^{-2}\,d^{-1}$]	%OC [%]	%Opal [%]	CPE [$\mu g\,g^{-1}$]	Total protein [$mg\,g^{-1}$]	Labile protein [%]	Total carbohydrate [$mg\,g^{-1}$]	Labile carbohydrate [%]	Total lipid [$mg\,g^{-1}$]	Biopolymeric C [$mg\,C\,g^{-1}$]	Bioavailable C [%]
Blanes canyon	Average	22.90	1.1	1.1	49.27	2.43	17.1	2.85	55.1	1.62	3.55	23.5
	Max	101.09	1.4	4.9	157.09	4.93	48.0	5.10	100.0	3.45	6.91	43.2
	Min	0.05	0.7	0.0	18.29	0.66	1.2	1.04	6.9	1.02	1.75	11.6
	S.D.	18.34	0.1	1.3	31.52	1.04	13.0	0.89	24.2	0.49	0.96	6.9
	C.V.	0.80	0.09	1.18	0.63	0.42	0.76	0.31	0.43	0.30	0.27	0.29
	Total	1099.11	1.0	1.0	2217.24	116.56	17.1	136.90	55.1	78.00	170.37	23.5
	N	44	44	44	44	44	44	44	44	44	44	44
Open slope	Average	2.10	1.6	2.0	140.56	2.50	11.9	7.20	23.8	2.77	6.18	13.5
	Max	7.36	3.5	7.2	572.97	7.09	54.5	23.69	64.6	7.58	16.46	50.5
	Min	0.00	1.1	0.1	1.17	0.02	0.5	0.29	1.4	0.01	0.20	6.5
	S.D.	1.94	0.5	1.4	138.64	1.78	11.3	4.52	12.7	1.62	3.35	9.4
	C.V.	0.88	0.30	0.71	0.98	0.71	0.94	0.62	0.53	0.58	0.54	
	Total	98.85	1.6	2.0	6606.14	117.32	11.9	338.26	23.8	130.08	290.35	13.5
	N	44	44	44	44	44	44	44	44	44	44	44

Table 3.1. Statistical parameters of total mass flux and biochemical composition of fluxes (Phytopigment, protein, carbohydrate, lipid, labile protein and carbohydrate, biopolymeric and bioavailable carbon contents) from sediment traps located in the Blanes canyon and the adjacent open slope. S.D. refers to standard deviation. C.V. refers to coefficient of variation.

under unrestricted permutation of raw data (999 permutations), after calculation of Euclidean distances of normalized data. When significant differences were observed, pairwise comparison tests were carried out to assess the direction of differences between the two morphologies at each sampling time/period and among sampling periods/times, separately for each seabed morphology. The same designs and tests were used to assess temporal variations in the composition of sinking organic matter across the canyon and the adjacent open slope. The analysis was conducted including phytopigment, total and hydrolysable protein, total and hydrolysable carbohydrate and total lipid contents and using 999 permutation of residuals under the reduced model. Further, to visualize patterns of variability in the biochemical composition of sinking material bi-plot representations after a canonical analysis of principal coordinates (CAP) were also produced. All statistical tests (PERMANOVA and the associated pairwise comparisons, CAP and the bi-plots) were carried out using the PRIMER6+ software, using the PERMANOVA and CAP routines.

3.3. RESULTS

3.3.1. Environmental conditions

Details on atmospheric assets during the study period are described elsewhere (Lopez-Fernandez et al., submitted). Indeed several sequential storms affected the study area in autumn

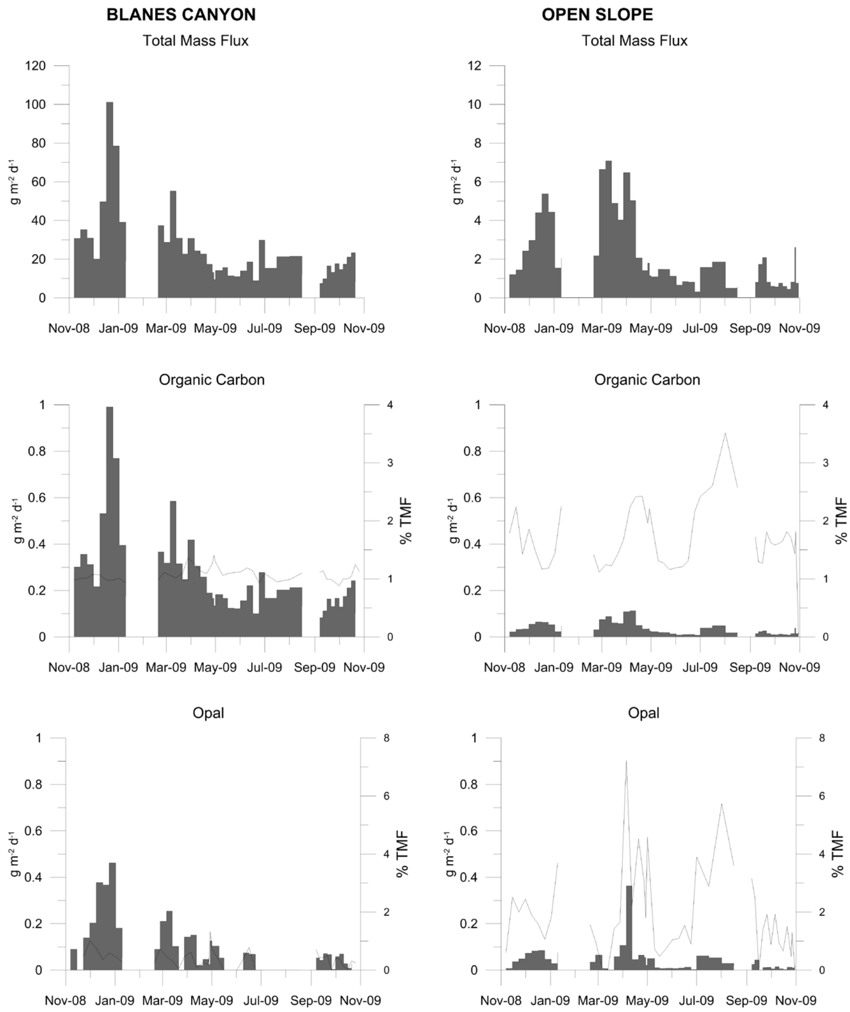

Fig. 3.3. Time series of total mass, organic carbon and opal fluxes (mg m^{-2} d^{-1}) and relative organic carbon and opal contribution (black line represents the % of the compound to TMF) from the sediment traps in the Blanes canyon and the adjacent open slope at 1200m depth.

2008-winter 2009 with the major storm being recorded at the end of December 2008 (Sanchez-Vidal et al., 2012). The storms, with increased wave height and Tordera river discharge, triggered increased current speeds along the Blanes canyon (Sanchez-Vidal et al., 2012; Lopez-Fernandez et al., 2013). In addition between March and May 2009 the current meter, deployed in the open slope recorded the intrusion of Western Mediterranean Deep Waters (WMDW) (data not shown). This water intrusion was originated in the Gulf of Lions and travelled on the slope, following the stream to the north. Such plume was not recorded by the mooring deployed in the canyon.

Overall, inside the Blanes canyon, near-bottom currents were generally strongly constrained by its topography, oriented along the canyon axis in both the up and down directions. Slope currents, in contrast, did not show specific trends (Lopez-Fernandez et al., 2013). Maximum current speed was registered at the canyon mooring (up to 45.5 cm s^{-1} in January 2009). The maximum current speed on the slope (26.4 cm s^{-1}) was observed in March 2009 (Figure 2 a-b).

3.3.2. Total mass, OC and opal flux

Total mass flux, OC and opal percentage contributions to TMF in Blanes canyon and the adjacent open slope are summarized in Table 1 and have been previously discussed by Lopez-Fernandez et al. 2013, which focuses on the physical drivers of total mass and major components fluxes (organic matter, carbonate, biogenic silica and aluminosilicates contents) Throughout the present paper, the Total Mass Flux (TMF) and its elemental composition are provided as a general framework for better interpreting biopolymeric and bioavailable OC fluxes. TMF and the OC and opal percentage contributions to TMF yielded highly contrasting values amongst the canyon and open slope. The mean mass flux in the canyon was consistently up to one order of magnitude higher than that in the adjacent open slope (Figure 3). Despite the differences in the mass flux mean values and in variation ranges, the two stations show similar variation coeffi-

Variable	Contrast	df	MS	F	P
Phytopigment	Canyon vs. Slope (M)	1	54.298	34.17	???
	Sampling Time (T)	43	3.253	1151.90	???
	M × T	43	1.589	562.63	???
	Residuals	176	0.003		
Algal fraction of BPC	Canyon vs. Slope (M)	1	32.796	32.23	???
	Sampling Time (T)	43	4.254	213.11	???
	M × T	43	1.018	50.97	???
	Residuals	176	0.020		
Total protein	Canyon vs. Slope (M)	1	0.775	0.23	ns
	Sampling Time (T)	43	2.239	20.11	???
	M × T	43	3.403	30.56	???
	Residuals	176	0.111		
Labile protein	Canyon vs. Slope (M)	1	5.560	1.73	ns
	Sampling Time (T)	43	2.567	49.19	???
	M × T	43	3.207	61.44	???
	Residuals	176	0.052		
Labile protein fraction	Canyon vs. Slope (M)	1	2.487	0.70	ns
	Sampling Time (T)	43	2.372	74.95	???
	M × T	43	3.557	112.41	???
	Residuals	176	0.032		
Total carbohydrate	Canyon vs. Slope (M)	1	117.630	62.19	???
	Sampling Time (T)	43	1.421	85.57	???
	M × T	43	1.892	113.88	???
	Residuals	176	0.017		
Labile carbohydrate	Canyon vs. Slope (M)	1	8.289	2.70	ns
	Sampling Time (T)	43	2.335	18.25	???
	M × T	43	3.065	23.96	???
	Residuals	176	0.128		
Labile carbohydrate fraction	Canyon vs. Slope (M)	1	104.580	49.01	???
	Sampling Time (T)	43	1.381	33.40	???
	M × T	43	2.134	51.60	???
	Residuals	176	0.041		
Total lipid	Canyon vs. Slope (M)	1	85.979	49.41	???
	Sampling Time (T)	43	2.190	47.95	???
	M × T	43	1.740	38.11	???
	Residuals	176	0.046		
Biopolymeric C	Canyon vs. Slope (M)	1	70.291	35.58	???
	Sampling Time (T)	43	2.223	32.18	???
	M × T	43	1.976	28.60	???
	Residuals	176	0.069		
Bioavailable C	Canyon vs. Slope (M)	1	1.405	0.42	ns
	Sampling Time (T)	43	2.053	13.03	???
	M × T	43	3.386	21.49	???
	Residuals	176	0.158		
Bioavailable fraction of BPC	Canyon vs. Slope (M)	1	102.520	57.99	???
	Sampling Time (T)	43	1.720	28.85	???
	M × T	43	1.768	29.65	???
	Residuals	176	0.060		
Biochemical composition	Canyon vs. Slope (M)	1	515.170	55.70	???
	Sampling Time (T)	43	14.716	80.18	???
	M × T	43	9.249	50.39	???
	Residuals	176	0.184		

Table 3.2. Results of univariate and multivariate analyses of variance testing for habitat and temporal variability in fluxes and biochemical composition of fluxes in the Blanes canyon and the adjacent open slope. =P <0.001; ns=not significant. df refers to degrees of freedom.

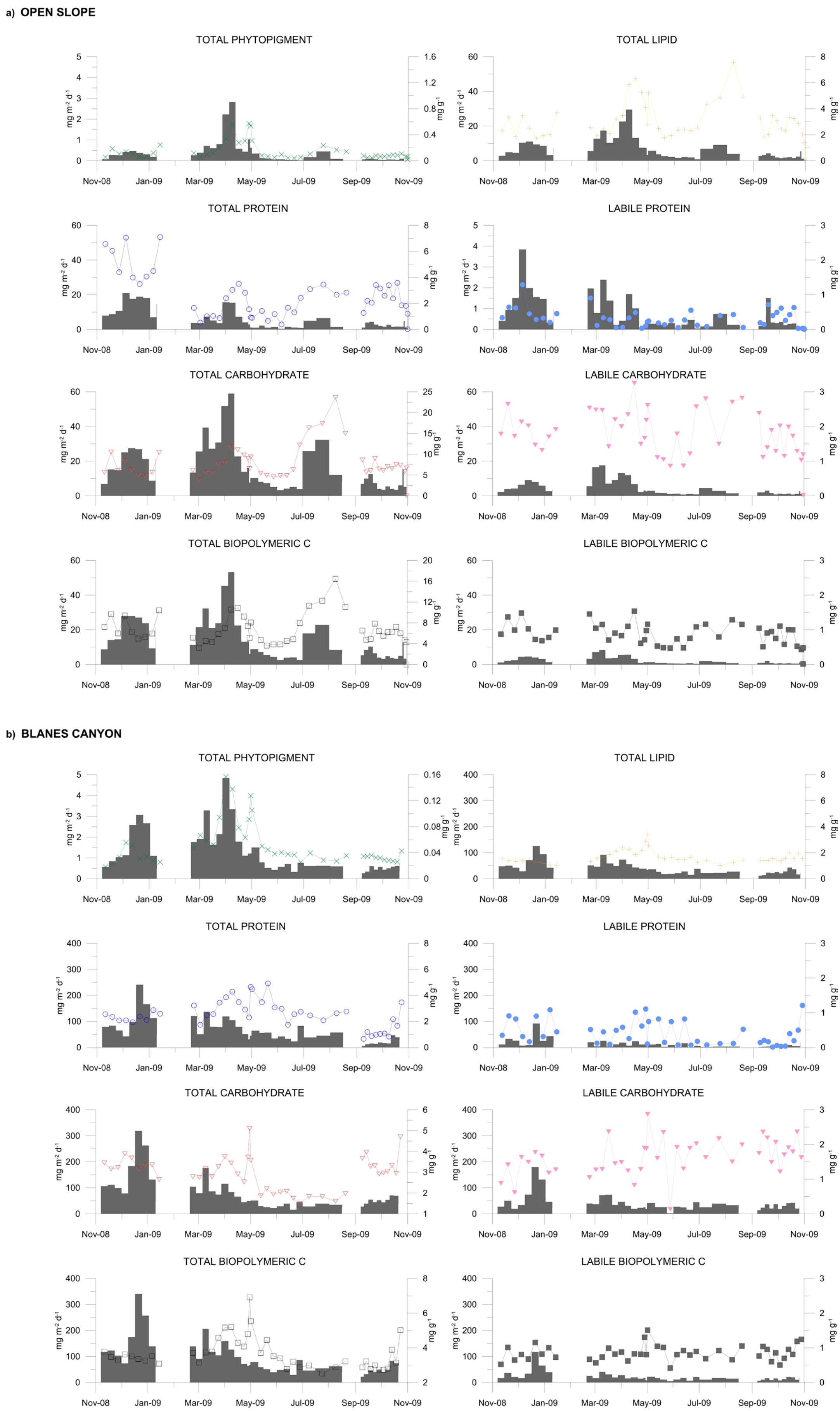

Fig. 3.4. Time series of organic compounds fluxes (mg m^{-2} d^{-1}) and organic compounds contents in the open slope (a) and in the Blanes canyon (b) (line represents the mg g^{-1}) from the sediment traps at 1200m depth.

cients (0.8 and 0.9, respectively) (table.1).

In the open slope TMF shows three maximum peaks in mid-December 2008, mid-January and March 2009 (5.4, 7.4 and 7.1 g m^{-2} d^{-1} respectively) and three minimum values in November 2008, January and end of June 2009 (1.4, 1.5 and 0.3 g m^{-2} d^{-1} respectively).(Figure 3).

In the Blanes canyon the fluxes increased substantially during winter. TMF shows four maximum peaks in December 2008, March, June and October 2009 (101.1, 55.2, 29.8 and 23.3 g m^{-2} d^{-1} respectively) and three minimum peaks in February, mid-May and September 2009 (0.1, 8.8 and 7.5 g m^{-2} d^{-1} respectively) (Figure 3).

OC contribution to TMF in the open slope was consistently higher than in the canyon, with four relevant peaks in November 2008, and January, April and August 2009 (2.2, 2.3, 2.4 and 3.5%, respectively). OC contribution to TMF in the canyon was relatively stable throughout the study period (range 0.7-1.4%) with two apparent peaks at the end of March and end of April (1.4% and 1.3% respectively) (Figure 3).

Opal contribution to TMF in the open slope covaried with the OC contents, showing four relevant peaks in November 2008 (2.5%), January (3.7%), April (7.2%) and August (5.7%) 2009. In the Blanes canyon the opal content of TMF showed three relevant peaks in November 2008 (3.0%), January (4.7%) and October (4.9%) 2009 (Figure 3).

3.3.3. Biochemical composition and bioavailability of OM

Phytopigment, protein, carbohydrate, lipid, BPC and BAOC contents of sinking particles in the study area are reported in Table 1. The 2-way univariate ANOVAs revealed that the contents of all investigated variables in sinking particulate material were significantly affected by the interaction between the two tested factors (Time x spatial) (Table 2).

3.3.3.1. Open slope

In the open slope, the contents of almost all organic compounds show wide and significant temporal variations, characterized by an increase from March to April 2009, a decrease from May to July 2009, and a maximum peak in August 2009 (Figure 4 a). Only total phytopigment and protein contents peaked early (in February 2009 and May 2009, respectively). Total carbohydrate concentrations ranged from 3.8 to 23.7 mg g^{-1} and displayed significant temporal variations with significant peaks in April 2009 (11.7 mg g^{-1}) and August 2009 (23.7 mg g^{-1}). Overall, the digestible fraction of carbohydrates was about 24% of the total carbohydrate pool, with a peak (65%) in February 2009 (corresponding to 2.5 mg labile carbohydrates g^{-1}). Total protein concentrations ranged from 0.02 to 7.1 mg g^{-1}, and displayed three significant peaks at the end of January (7.09 mg g^{-1}), in April (3.5 mg g^{-1}) and at the end of July 2009 (3.5 mg g^{-1}). Labile proteins represent on average about 12% of the total protein pool, with a maximum value of 54% (corresponding to a concentration of 0.9 mg g^{-1}) in December 2008. Total lipid concentrations follow the same temporal pattern as the one observed for total carbohydrates, ranged from 1.4 to 7.6 mg g^{-1} with significant peaks in April 2009 (6.3 mg g^{-1}), and August 2009 (7.6 mg g^{-1}). Overall, total particulate carbohydrates were the dominant class of organic compounds with an average contribution to the BPC around 46%, followed by lipids (33%) and proteins (21%). BPC represents about 35% of the total OC flux in the open slope (range 1-51% with a 36% of variation on an annual basis). A minor fraction (on average 16%, range 6-50%) of BPC reaching the sea bottom in the slope was enzymatically digestible. Total phytopigment concentrations explained only 23% of BPC variance (Type-I regression, n=144, $p<0.05$), with the remaining 67% of BPC reaching the open slope sediments being associated with non-algal sources. BPC and BAOC covary significantly in the open slope, with about 72% of BPC variance being explained by variations in BAOC contents (Type-I regression, n=144, $p<0.001$).

3.3.3.2. Canyon

In the canyon, the contents of almost all organic compounds show wide and significant temporal variations, most of them were characterized by an increase from March to May 2009, with a maximum peak in May 2009, and a decrease from June 2009 (Figure 4 b). Total carbohydrate contents ranged from 1.5 to 5.1 mg g^{-1} and peaked in May 2009 (5.1 mg g^{-1}), when the highest peak in labile carbohydrate content (2.9 mg g^{-1}) was also observed. Overall, enzymatically digestible carbohydrates in the fluxes of the Blanes canyon were about 58% of the total carbohydrate pool. Total protein concentrations do not display any significant peak, though generally higher protein contents were observed in April-May 2009 and ranged from 0.6 to 4.9 mg g^{-1}. Overall, labile protein represented on average about 17% of the total protein pool, with a relative peak in April 2009 (48%), corresponding to 1.1 mg of labile protein g^{-1}. Total lipid ranged from 1.0 to 3.5 mg g^{-1} and followed the same temporal pattern as the one observed for total carbohydrate contents with higher values in March-April 2009 (up to 3.5 mg g^{-1}). In the Blanes canyon, protein, carbohydrate and lipid contributed, on annual average, almost equally (almost 33% each) to the BPC flux. In the canyon, BPC represents, on annual average, about 33% of the total OC flux (range 20-49%, with a 17% of variation on an annual basis). About 24% (range 11-43%) of BPC reaching the sea bottom in the canyon was enzymatically digestible. Total phytopigment concentrations explained about 64% of BPC variance (Type-I regression, n=144, $p<0.05$), with the remaining 36% of BPC reaching the canyon sediments being associated with non-algal sources. BPC and BAOC covary significantly also in the canyon, with about 85% of BPC variance being explained by variations in BAOC contents (Type-I regression, n=144, $p<0.001$).

3.3.3.3. Comparison between fluxes in the open slope and the canyon

Pairwise comparison tests revealed that, for almost the entire study period, fluxes of all investigated variables and the labile fractions of protein and carbohydrate pools were significantly higher in the canyon than in the open slope (Figure 6). The same tests carried out on OM contents (data not shown) reveal different patterns for each investigated variable with contents in the open slope higher than in the canyon being more frequently observed. The PERMANOVA tests (Table 2) revealed that the biochemical composition of sinking particulate matter varied between the canyon and the slope and, in both sites, varied significantly with sampling time. The bi-plot produced after the CAP analysis reveals that, during the study period, the biochemical composition of fluxes in the canyon fluctuated more widely than in the open slope. Two major clusters were identified: one in the canyon in December 2008 concurrently with the major storm and associated with increased fluxes of nutritionally important molecules (i.e., total and labile proteins and labile carbohydrates). Another cluster included samples collected in the canyon and the open slope in March 2009, concurrent with the early phases of the phytoplankton bloom and associated with increased fluxes of total phytopigments (Figure 7).

3.4. DISCUSSION

3.4.1. Mass fluxes in the Blanes canyon and in the adjacent open slope

While several studies on continental margins differentiated between particle fluxes inside and outside of submarine canyons (Puig and Palanques, 1998; Monaco et al., 1999, Martin et al., 2006), there have been only few studies simultaneously assessing both seasonal and spatial changes in the biochemical characteristics of settling organic matter in the canyons of the Mediterranean Sea (Tesi et al., 2008; Sanchez-Vidal et al., 2009, Pasqual et al., 2001). Also, information on the readily degradable fraction of sinking organic particles is practically not existent. Consequently, the present study constitutes the first report considering synoptically seasonal and spatial changes in the characteristics of the settling organic matter, including its enzymatically digestible fraction, in a Mediterranean submarine canyon and its adjacent open slope. This study is based on a biomimetic approach and in spite of its limitations, this technique has provided for heterotrophic consumers, quantitative information on the availability of food for many benthic ecosystems (Mayer et al., 1995; Grémare et al., 1997; Dauwe et al., 1999; Dell'Anno et al., 2000; Danovaro et al., 2001; Grémare et al., 2002; Grémare et al., 2003; Grémare et al., 2005; Vandewiele et al., 2009, Bourgeois et al., 2011).

We report here that during the entire year of the study, the mass fluxes in the axis of the canyon were consistently one order of magnitude higher than those in the adjacent open slope at equal depth. Overall, the presence of canyons drastically alters the regional bathymetry by reducing the distance between terrestrial sediment sources and the shelf break, introducing steep slopes closer to the shoreline and intersecting the along-shelf sediment transport system (Mullenbach et al., 2004). Thus, submarine canyons may capture inputs delivered through the river mouths, littoral drift sediments and sediments from relict shelf bodies (Lastras et al., 2011).

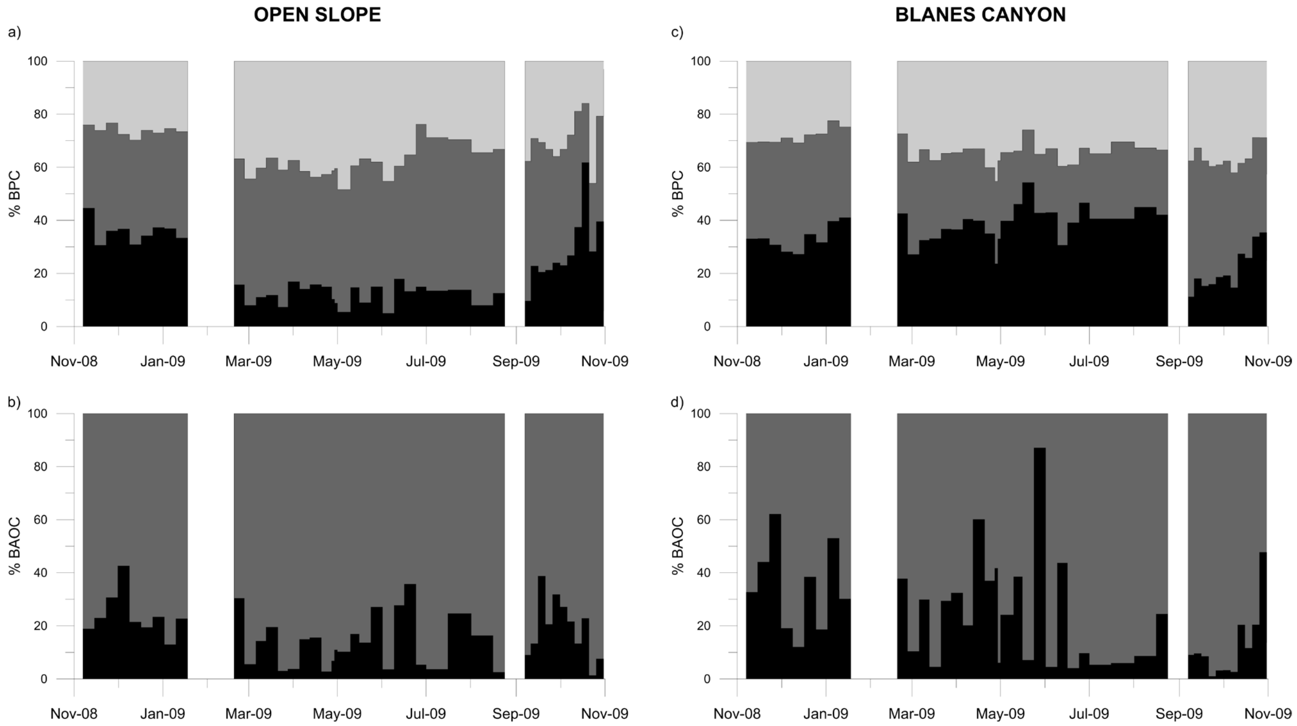

Fig. 3.5. Temporal changes in the biochemical composition of settling particles at 25 mab. Data are presented as percentage contributions of proteins, carbohydrates and lipids to biopolymeric C (% BPC) and as percentage contributions of labile proteins and labile carbohydrates to bioavailable organic carbon (% BAOC) in the two sampling stations open slope (a, b) and Blanes canyon (c, d), respectively.

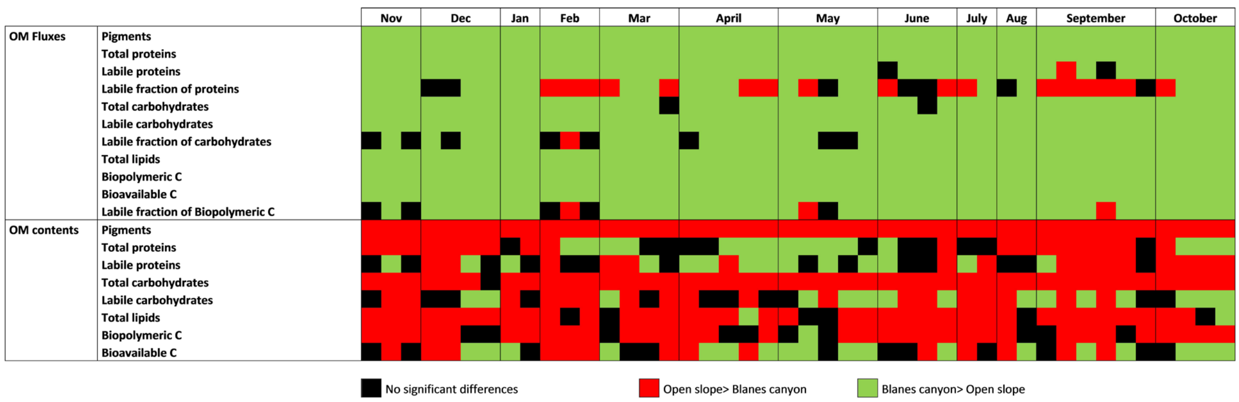

Fig. 3.6. Pairwise test of organic matter fluxes and contents between the two morphologies at each sampling time/period and among sampling periods/ times, separately for each seabed morphology.

Such striking difference has been already described for the Blanes canyon, where the TMF continuously increases from the head of the canyon at 300 m depth until 1500 m depth, unlike in the adjacent open slope where the TMF decrease with the distance to coast (Lopez-Fernandez et al., 2013). Clearly there is a difference between the flows in the two sampling stations due to the location and distance of the "shelf-break." The station OS 1200 situated at approximately 20 km to the 200m isobaths, presents on average a TMF of 2380.9 mg m^{-2} d^{-1} with OC and opal fluxes on average of 40.6 and 49.9 mg m^{-2} d^{-1}, respectively (1.7 and 2.1 % of the TMF, respectively). However, in the station BC1200 situated around 10 km to the 200m isobaths, these fluxes were higher, 22898.2, 240.6 and 269.6 for the TMF, OC and opal fluxes, and the OC and opal contribution to the TMF were lower (1.1 and 1.2% respectively). Nevertheless, it must be considered that the pathway of organic and inorganic matter is not solely driven by vertical settling from the sea surface to the deep ocean, as a large proportion of particulate matter is transported by lateral advection before deposition on the deep seafloor. Therefore, we cannot exclude that a certain fraction of the differences observed in TMF between the canyon and the open slope could be ascribed to the different distance from the coast of the two sampling stations, which could have led traps to intercept particles transported over different horizontal distances. In this regard, how-

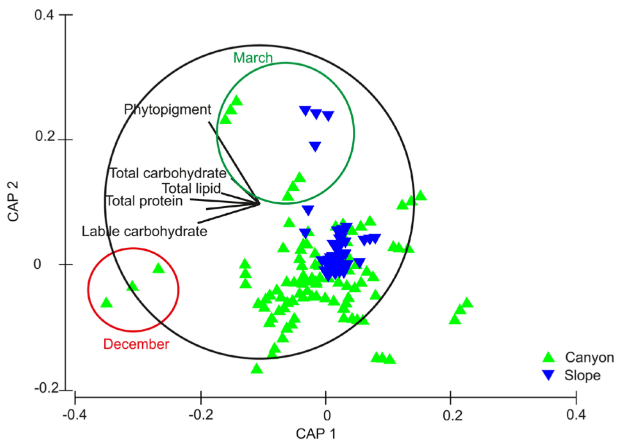

Fig. 3.7. Bi-plot representations after a canonical analysis of principal coordinates (CAP). Samples from the Blanes canyon and the adjacent open slope have been differentiated.

ever, Lopez-Fernandez et al. 2013, showed that the Blanes canyon is mainly influenced by lateral particle inputs, with a strong homogenization process where the load of sediment has been diluted by terrigenous and resuspended material, whereas the slope is more influenced by the vertical transport, tightly connected with biological processes occurring in the upper ocean layers.

The differences in mass flux between the canyon and the adjacent open slope were accentuated during storm periods. The repeated action of high waves increased the shelf water density by resuspension and caused down-canyon currents promoting the transport of the suspended loads through Blanes submarine canyon (Palanques et al., 2006; Sanchez-Vidal et al., 2012).

The total mass flux for all the above mentioned canyons, including the Blanes one, is typically dominated by a lithogenic fraction. As a result, the OC contribution to the TMF in the Blanes canyon and the adjacent open slope is very low (ranging 0.7-1.4% and 1.1-3.5%, respectively), in concordance with studies carried out in other Mediterranean continental margins indented by submarine canyons (Martin et al., 2006, Pasqual et al., 2010). The large dominance of the lithogenic fraction in settling particles from both the canyon and its adjacent open slope is indicative of the presence of a conspicuous input of material entering the trap either from terrigenous inputs or sediment resuspension. This hypothesis is corroborated by the presence of relatively high concentrations of carbohydrates in the trap samples, which represented on average 0.3% and 0.7% of TMF in the canyon and open slope, respectively and 28.7% and 44.5%, respectively of OC. Following the order of overall relative lability for biochemical classes assigned by Wakeham et al., 1997 (pigments> lipids>proteins>carbohydrates) carbohydrates represent the most refractory fraction of organic compounds analyzed in this study.

3.4.2. Bioavailability of sinking organic particles

The biological material was present and evident in both systems during the entire study period and, in some cases, especially in the open slope, contributed significantly to the particle downward fluxes. The OC contribution to the TMF generally decreased with increasing TMF, confirming a preeminent dilution of organic inputs with terrigenous and/or resuspended material, which was even more accentuated inside the canyon. At the same time, during this study, the organic fraction of the TMF is generally higher in the open slope than in the canyon axis. This result would indicate that, despite the large input of inorganic material reaching the sediments, heterotrophic consumers in the open slope sediments may profit from a concentration of food particles consistently larger than that available in the canyon at equal depths. Nevertheless, our results also show that the slope site was mainly characterized by a remarkable seasonal variability in the food quality of sinking particles, with major peaks associated with the seasonal cycle of biological production in the euphotic zone, whereas the canyon site showed a more pronounced temporal variability in the quantity of sinking particles. This striking difference in the quantity/quality of particles sinking in the canyon axis and the adjacent open slope is likely to have conceivable consequences for the nutrition of the deep-sea benthos inhabiting the two different habitats. A certain benthic organism living inside the Blanes canyon would indeed need to ingest more particles to fulfill its food requirements than another one living in the adjacent slope, where the OC fraction of sinking particles is consistently and almost constantly higher than in the canyon. In fact, it can be roughly calculated that an animal in the canyon exposed to a mass unit of sinking material can profit approximately 1% OC, which is about half the amount that an animal in the slope receives. This result indicates that deep-sea benthos in the canyon is generally exposed to a rain of preeminently inorganic material. Nevertheless, our data indicate also that the labile (enzymatically digestible) fraction of organic matter reaching the benthos in the canyon is generally higher than that in the open slope. Thus, the food limitation of the benthos inhabiting deep-sea sediments in the canyon, despite the dilution of OC in a preeminently inorganic matrix, is partly counterbalanced by a higher organic matter bioavailability (8% of OC is enzymatically digestible) than in the open slope (5%).

According to the optimal foraging theory (Shoener, 1971; Pyke et al., 1977), our results suggest that, although a heterotrophic organism living in the canyon should spend more energy in "searching" for OC that OC, once acquired, is more labile than that more easily accessed by an animal living on the open slope. This result indicates that organisms facing particle transport from the canyon are penalized by the mostly inorganic flux, but can counterbalance this, profiting inputs of more labile organic particles.

The results of this study, therefore, provides new insights on the differential modalities that deep-sea benthos inhabiting largely different habitats (e.g., canyon vs. open slope) may experience to survive in a generally food depleted environment. Our results confirm recent studies showing that elevated organic matter inputs in canyons may favor the faunal contribution to carbon processing and create hotspots of faunal biomass and carbon processing along the continental shelf (Van Oevelen et al., 2011). However, whether these inputs have always a positive effect on deep-sea benthos depends also on the rates of sinking and the overall amount of sediment deposited on the deep-sea floor.

By rapidly conveying the organic material produced in the upper water column, submarine canyons are able to often sustain more biomass and biodiversity than the nearby open slope areas (Bianchelli et al., 2008). Moreover, differences in biodiversity between canyons and open slopes are generally larger in terms of faunal community structure (i.e., beta diversity) than in terms of species richness (Danovaro et al., 2009). These differences are mostly explained by the availability of food particles in the sediment (Danovaro et al., 2009), which in turn reflect the nature, origin and food quality of inputs from the upper water column (Danovaro et al., 1999). Thus, our results allow hypothesizing that those faunal differences between soft bottom sediments of canyons and neighboring open slopes could be also the result of community adaptations to different combinations of food quantity and quality in the two different habitats.

3.4.3. Hydrodynamic and climatic controls of bioavailable organic matter inputs to deep sea ecosystems.

Whether the pattern of mass fluxes in the Blanes canyon can be extrapolated to other submarine canyons along Mediterranean margins remains an open question. In fact, several Mediterranean submarine canyons have been defined as major conduits for OC to the deep-sea basin due to local hydrodynamics conditions (Martin et al., 2006; Palanques et al., 2008; Zuñiga et al., 2009). Nevertheless, recent studies have also demonstrated that different (even adjacent) canyons may show large differences in the quantitative and qualitative characteristics of sedimentary organic matter, and that these differences are not only related to the different morphological features of different canyons, but can also depend on the timing of sampling (Pusceddu et al., 2010). In fact, canyons are often episodic event-dominated systems (Palanques et al., 2012), which means that the inputs of particles reaching the interior of canyons are largely (sometimes stochastically) influenced by local climate anomalies, involving river flood events, wind dust inputs and high energy hydrodynamic processes as sea-storms, dense shelf water cascading and deep ocean convection (Canals et al., 2006; Sanchez-Vidal et al., 2012; Palanques et al., 2012), but also by primary production at the surface (Danovaro et al., 2001). In this regard, in fact, it must be considered that the sediment transport through submarine canyons is neither constant nor unidirectional, rather has a pulse-like behavior (Palanques et al., 2012). One of the most dramatic examples of pulsed processes driving the transport of large amounts of sediment and organic matter to the deep sea occurs during severe coastal storms which can be highly efficient in transporting OC from shallow waters on the shelf down to deep waters (Sanchez-Vidal et al., 2012).

Variations in the biochemical composition of sinking particles observed in this study during the storm partially resemble the consequences of dense shelf water cascading and severe coastal storms on the availability of organic C for the deep-sea benthos (Sanchez-Vidal et al., 2012). The biochemical composition presents temporal variations during the sampling period, this highlights the different sources of the organic material arriving to 1200 m deep. During the autumn-winter storms period our data present an increase in total protein and labile contribution to the BPC and low values of lipids, this behavior is not observed during other seasons (Figure 5). In spring and summer, the hydrodynamic conditions are less rough than in storm period, these two seasons are marked by an increase in lipids. Differences in biochemical composition highlight the different structure in the communities on the water column (Figure 5). Lipids are more readily available to consumers than proteins (Taylor et al., 1986), so we could point out that a large amount of labile particles arriving during storms period, against an overwhelming quantity of sediment transported, come by sediment resuspension from the continental shelf and are redistributed towards the deep sea.

The possible advantage of a more labile food for the deep-sea benthos receiving inputs forced by climate anomalies at the sea surface could be however counterbalanced and even canceled by the physical and mechanical disturbance generated by the gravity flow of inorganic particles, possibly suffocating the sea bottom (Pusceddu et al., 2010; Pusceddu et al., 2013), so our results confirm that severe coastal storms can have important and almost immediate consequences on the functioning of the whole system down to the deep seafloor (Sanchez-Vidal et al., 2012).

3.4.4. Synopsis and conclusions

In this study we show that the organic matter collected by sediment traps in spring had a higher nutritional value than in late autumn-winter, and this feature was shared by both the canyon and the adjacent open slope (Figure 4 b, 6). This difference is likely to be due to the typical spring plankton bloom described by several authors in the study area (Estrada et al., 1996; Rossi et al., 2003). During this period the biochemical composition of BPC was characterized by increasing lipid contributions compared with those observed during the storm period, characterized by higher protein contents (Figure 5). Along with proteins, lipids can represent a preferential source of energy for benthic feeders (Medernach et al., 2001; Grémare et al., 1997). In the slope (more influenced by pelagic sedimentation), the increase in the nutritional value of sinking particles is magnified by the effect of the deep-sea convection, that lead the injection of nutrients up into the surface water.

In summer, sediment trap samples showed an increase in the nutritional value of the sediment comparable to the increase during the spring bloom. Lopez-Fernandez et al. (submitted) pointed out during this period an input of Saharan dust in the area. Fertilization process by wind dust and a consequent increase in the sinking flux have been previously described by several authors in the North-western Mediterranean (Zuñiga et al., 2008; Lee et al., 2009; Pasqual et al., 2011). This dust brings new nutrients such as inorganic phosphorous and iron to the surface waters and could increase autotrophic production, and hence the efficiency of the biological C pump in oligotrophic oceans (Pulido-Villena et al., 2008). The entrance of nutrients is more accentuated in the open slope where the pelagic processes are more clearly recorded.

While most of variability in the rates of particle transport can be reliably explained with physical processes like hydrodynamism and climate forcing, we cannot exclude that the differences in the biochemical composition and bioavailability of sinking particles in the Blanes canyon and the adjacent open slope can be also modulated by biological constraints in the water column (e.g. through grazing). Also, we note that our inferences about the biochemical composition of particles should be considered with some caution, as it has been demonstrated elsewhere that the relative proportions of protein, carbohydrate and lipid concentrations and estimates of bioavailability can vary considerably depending on the analytical technique utilized (Hedges et al., 2001). Nevertheless, our results, based on a biomimetic approach, confirm that in both the submarine canyon and the open-slope, the bioavailable organic matter delivery towards deep-sea ecosystems are strongly controlled by hydrodynamic processes (sea-storms, dense-shelf water cascading and offshore convection) and annual bio-climatic controls (winter-spring primary production bloom).

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CAPÍTULO 4

BIOAVAILABLE COMPOUNDS IN SINKING PARTICULATE ORGANIC MATTER, BLANES CANYON, NW MEDITERRANEAN SEA: EFFECTS OF A LARGE STORM AND SEA SURFACE BIOLOGICAL PROCESSES

RESUMEN

El capítulo 4, describe el cañón de Blanes como vía de transporte de materia orgánica lábil desde la plataforma continental hacia los ecosistemas profundos y cómo el suministro de alimentos lábiles está conectado a los procesos que ocurren en la superficie del mar, en particular a la influencia que tienen las tromentas sobre el transporte y la calidad de la materia orgánica.

Para determinar si el cañón submarino de Blanes actúa como un canal de compuestos orgánicos lábiles al fondo del mar, se analizó el contenido de fitopigmentos, proteínas, carbohidratos y lípidos de las partículas que sedimenta durante un período de 6 meses comprendido entre una tormenta grande y la floración primaveral de fitoplancton. Cuatro trampas de sedimentos fueron fondeadas, a 300, 900, 1200, y 1500 m de profundidad a lo largo del eje del cañón desde noviembre 2008 hasta abril de 2009. Los flujos de todas las variables del estudio (carbono orgánico, proteínas, hidratos de carbono y lípidos) alcanzaron su máximo desde mediados a finales de diciembre. Después, los flujos de materia orgánica en el cañón superior disminuyeron hasta valores comparables (BC1200) o mucho más bajos (BC900) que los observados al comienzo del período de seguimiento. La fracción algal biopolimérica C (es decir, el porcentaje de contribución de fitopigmentos al carbono biopolimérico, utilizado aquí como un indicador de frescura partículas), va desde aproximadamente el 14 al 100%, pero fue generalmente baja (valor de la media aproximadamente 32%), y mostró los valores mayores de noviembre a principios de diciembre de 2008 en todas las estaciones, a excepción de la estación a 1.200 m que alcanzó su máximo en abril de 2009. Una fuerte tormenta que se produjo el 26 de diciembre 2008 determinó un fuerte aumento en el transporte de la materia orgánica al fondo a lo largo del cañón de Blanes, aunque asociado a una disminución de su calidad nutricional. Los valores de la relación proteína-carbohidrato (utilizada aquí como un indicador de la calidad nutricional de las partículas) variaron de 0,4 a> 2,0, aumentando a finales de invierno principio de primavera a la profundidad de 900 y 1200 m en asociación con la floración de fitoplancton de primavera en aguas superficiales. El material recogido por las trampas de sedimentos en primavera tenía un valor nutricional más alto que en otoño-invierno en ambas estaciones. De acuerdo con la teoría del aprovechamiento óptimo, los resultados de este estudio sugieren que, después de los eventos episódicos de invierno, los detritívoros de aguas profundas tendría que ingerir más detritus para cumplir con sus requerimientos de alimentos lábil que en primavera, cuando hay más material fresco de las partículas en sedimentación, asociado con las floraciones de fitoplancton. Llegamos a la conclusión que, si bien los cañones submarinos, como el cañón de Blanes actúan como conductos principales para el material exportado fuera de la plataforma continental después de eventos episódicos de alta energía, el suministro de alimento lábil al ecosistema bentónico de aguas profundas está conectado a los procesos biológicos de la superficie del mar.

BIOAVAILABLE COMPOUNDS IN SINKING PARTICULATE ORGANIC MATTER, BLANES CANYON, NW MEDITERRANEAN SEA: EFFECTS OF A LARGE STORM AND SEA SURFACE BIOLOGICAL PROCESSES

Pilar Lopez-Fernandez[1], Silvia Bianchelli[2], Antonio Pusceddu[2], Antoni Calafat[1*], Roberto Danovaro[2], Miquel Canals[1]

1 GRC Geociències Marines, Dept. d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, E-08028 Barcelona, Spain

2 Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Via Brecce Bianche 60131 Ancona, Italy

* Corresponding author: antonicalafat@ub.edu

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ABSTRACT

To ascertain whether the Blanes submarine canyon functions as a conduit of labile organic compounds to the deep margin, we analyzed phytopigment, protein, carbohydrate and lipid contents of sinking particles during a 6-months period comprised between a large storm event and the spring phytoplankton bloom.

Four sediment traps were deployed, at 300, 900, 1200, and 1500 m depth along the axis of the canyon from November 2008 to April 2009. Fluxes of all study variables (organic carbon, proteins, carbohydrates and lipids) peaked from mid to late December. Afterwards, organic matter fluxes in the upper canyon decreased to values comparable (BC1200) or much lower (BC900) than those observed at the beginning of the monitoring period. The algal fraction of biopolymeric C (i.e. the percentage contribution of phytopigments to biopolymeric C utilized here as an indicator of particles' freshness), ranging from 14 to about 100%, was generally low (median value about 32%), and showed the highest values from November to early December 2008 at all stations, except for the station at 1200m which peaks in April 2009.

A severe storm that occurred the 26th of December 2008 determined a strong increase in the downward transport of organic matter along the Blanes Canyon, though associated with a decrease in its nutritional quality. Values of the protein to carbohydrate ratio (utilized here as an indicator of particles' nutritional quality) ranged from 0.4 to >2.0, increasing from late winter to early spring at 900 and 1200 m depth in association with the spring phytoplankton bloom in superficial waters. The material collected by sediment traps in spring had a higher nutritional value than in autumn-winter at both stations. According to the optimal foraging theory, the results of this study suggest that, following winter episodic events, deep-sea detritus feeders would need to ingest more detritus to fulfill their requirements for labile food than in spring, when fresher material is derived from sinking particles associated with phytoplankton blooms.

We conclude that whilst submarine canyons like the Blanes Canyon act as major conduits for material exported from the continental shelf after high-energy episodic events, the supply of labile food to the deep-sea benthic ecosystem is connected to biological processes occurring at the sea surface.

4.1. INTRODUCTION

Over the last years, knowledge on the recent shelf-to-slope export of particulate matter in the Mediterranean Sea essentially derived from measurements of particle fluxes by sediment traps. Several studies have focused on deep-sea food limitation and utilized measurements of organic carbon (OC) and mass fluxes as proxies of the amount of food reaching the deep seafloor (Sanchez-Vidal et al., 2005; Tesi et al., 2008; Zuñiga et al., 2009; Pusceddu et al., 2010b). Previous studies have measured the total organic matter (OM), OC and nitrogen (N) contents of sinking particles, and assumed that these were proxies of food availability for deep-sea benthic consumers (Buscail et al., 1995; Durrieu de Madron et al., 2000; Duineveld et al., 2001; Martin et al., 2006). However, the response of consumers to increased organic matter supply is influenced more by organic matter quality (e.g. bioavailability) rather than by bulk concentration in the ecosystem (Cebrián et al. 1998, Huxel 1999). In fact, recent studies have suggested that the benthos of the deep Mediterranean Sea is not merely controlled by the amount of food resources received as sinking particles, but rather by its actual bioavailability to consumers (Danovaro et al., 2008). The bioavailability of OM for deep-sea biota is related also to the origin (auto- vs. heterotrophic) and lability (i.e. digestibility) of sinking particles (Danovaro et al., 2001; Tesi et al., 2008). However, assessing the OM fraction that can be metabolized by heterotrophic consumption is not an easy task. One approach is to quantify the components that potentially are more readily available to consumers (i.e., semi-labile or labile compounds sensu Pusceddu et al., 2009), such as lipids, proteins and non-structural carbohydrates (Medernach et al., 2001; Grémare et al., 1997; Pusceddu et al., 2005a). In this way, the OM semi-labile fraction can be separated from the refractory fraction (Mayer, 1994; Middelburg, 1999).

The exchange of matter and energy between continental margins and the deep basin has been the subject of several studies in the Mediterranean Sea (Monaco et al., 1999; Durrieu de Madron et al., 2000; Pasqual et al., 2011). Continental margins act both as a sink for particulate matter supplied by rivers and autochthonous biological production, and as a source of material for the adjacent open ocean. However, the extent to which such material actually reaches the ocean interior is not consistent along latitudinal or longitudinal gradients, nor constant in time. In addition, from the topographic viewpoint, continental margins are characterized by complex successions of open slopes, submarine canyons and landslide-affected areas (Weaver et al., 2004). Among these, submarine canyons deeply cut the continental slope and may extend to the continental rise downwards and to the continental shelf upwards. Submarine canyons dissect most of Europe's continental margins, with some of them opening their heads at relatively short distances from the shoreline (Canals et al., 2004; Amblas et al., 2006; Tyler et al., 2009; Lastras et al., 2011). The physiographical location of some submarine canyons makes them sites of intense exchanges in between the shoreline, the continental shelf and the deep continental margin. Canyons also affect local hydrodynamic conditions and enhance productivity (Durrieu de Madron, 1994; Monaco et al., 1999; Mullenbach and Nittrouer, 2000; Puig et al., 2000, 2003; Rogers et al., 2003; Bosley et al., 2004; Weaver et al., 2004; Canals et al., 2006; Allen and Durrieu de Madron, 2009; De Leo et al., 2010).

Deep-sea biota, for their energetic requirements, depend to a large extent on allochthonous OM inputs mainly represented by phytodetritus sinking from the upper water column (Pfannkuche, 1993; Lampitt and Antia, 1997; Fabiano et al., 2001). However, a large fraction of sinking matter is lost during particle descent by heterotrophic consumption, dilution and dissolution. As a result, it has been assumed for decades that deep-sea fauna is generally food-limited (Gage and Tyler, 1991). In the last decade, this paradigmatic assumption has been progressively constrained. Some deep-sea sites act as hot-spots of OM enrichment because of local hydrodynamic, topographic or climatic conditions (Danovaro et al., 2001, 2003; Pusceddu et al., 2010). In particular, some submarine canyons have been identified as major conduits of material flushed from the shelf and accumulated in the deep adjacent basin (Monaco et al., 1999; Durrieu de Madron et al., 2000; Schmidt et al., 2001; Epping et al., 2002; Van Weering et al., 2002; Canals et al., 2006; Zuñiga et al., 2009). However, such a distinctive feature is not consistent in all submarine canyons (Pusceddu et al., 2010). Therefore, assessing how continental margins concentrate and export particulate OM to the open ocean is a necessary step to estimate their influence on deep-sea ecosystems (Smith et al., 2008).

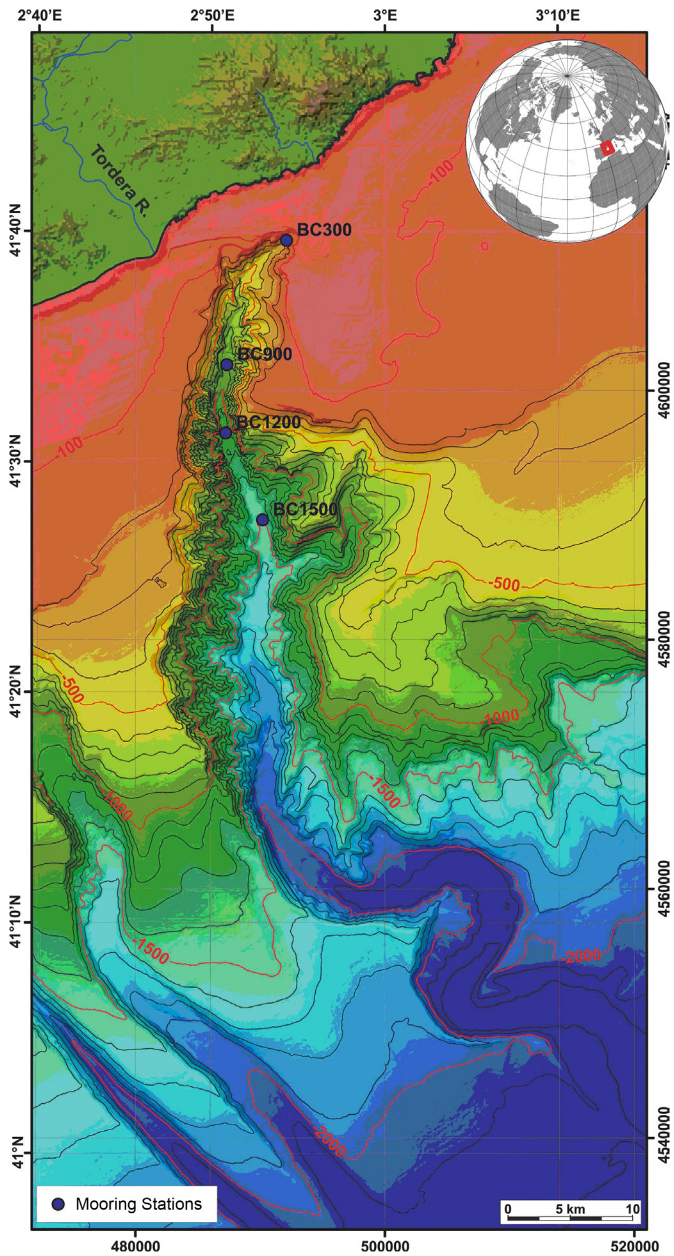

Fig. 4.1. Bathymetric map of Blanes Canyon showing the location of mooring station BC300 to BC1500 along the canyon axis. The location of Tordera River is also shown. Depthin meters. Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits).

Submarine canyons in the Western Mediterranean have been identified as hot spots of biodiversity where many biological processes are altered or intensified (Hickey, 1995; Gili et al., 1999). These canyons are also considered biodiversity refuges (Gili et al., 1999) and key areas for the recruitment and maintenance of living resources (Cartes, 1994; Sardà et al., 1994; Stefanescu et al., 1994; Sardà and Cartes, 1997). In the last years, some large scale systematic investigations of vulnerable deep-sea habitats in continental margins have been conducted. We investigated the quantity and biochemical composition of OM of sinking particles in the Blanes submarine canyon (BC) to verify whether it may function as a preferential conduit of labile organic compounds to the deep margin and adjacent basin.

4.2. THE STUDY AREA

The N-S oriented BC is located in the North Catalan margin (NW Mediterranean Sea) where it deeply incises the continental shelf (Lastras et al., 2011). The head of the canyon is less than 4 km from the coastline, with the canyon rim at only 60 m depth. Tordera River opens in the coastline landward of the canyon head. It is a typical Mediterranean torrential stream whose main discharge corresponds to short-lived episodic floods (Rovira and Batalla, 2006; Sanchez-Vidal et al, 2013). BC has a rather complex topography, a V-shaped cross section in its upper course, and a U-shaped cross section along its middle and lower course, where it markedly meanders

(Fig. 1) (Lastras et al., 2011). The topography of its walls plays a significant role in the variability of currents within the canyon, with a highly variable flow in the smoother eastern wall and a unidirectional offshore flow over the western wall (Zuñiga et al., 2009).

4.3. MATERIAL AND METHODS

4.3.1. Sampling of sinking particles

Four mooring lines were deployed for six months from November 2008 to April 2009 along a transect following the axis of BC. The lines were deployed at four stations in the canyon head (BC300), the upper canyon (BC900 and BC1200) and the middle canyon (BC1500), with numbers to the right of each station code corresponding to water depth. Each line was equipped with sediment trap-currentmeter pairs. The sequential-sampling sediment traps have a cylindrical–conical shape with a height/diameter ratio of 2.5 and a collecting area of 0.125 m^2. All sediment traps were placed 25 m above the bottom and equipped with 12 receiving cups. Traps deployed at stations BC300, BC900 and BC1500 m were scheduled for a sampling interval of 15 days, thus yielding 12 samples each during the 6-months long monitoring period. The sediment trap deployed at station BC1200 m was programmed with a sampling interval of 7-8 days, thus yielding 24 samples in total during the same 6-months monitoring period. Trap BC 300 has a bit delayed sampling period due to the fact that it was accidentally caught by fishermen and then replaced. Afterwards, the higher resolution data of BC1200 were averaged over 15 day's intervals to get a resolution for the whole monitoring period similar to that of the three other traps. A total of 5 samples from BC300 and BC1500, and 10 samples from BC900 and BC1200 have been analyzed, a larger number of analyses having been prevented either by too small sample volumes or occasional failure of sediment traps. Prior to deployment, the rotator collector was cleaned with detergent and rinsed several times with distilled water in the lab. Receiving cups were filled with a sodium borate buffered 5% formaldehyde solution in 0.45 μm pre-filtered seawater to avoid degradation of the collected particles. After recovery, samples were stored in the dark at 2-4 °C until they were processed in the lab. Once there, samples were visually checked and the supernatant removed. Swimmers were separated by wet sieving on a 1-mm nylon mesh and handpicked under a dissecting microscope. A high precision peristaltic pump was then used to obtain subsamples through repeated splitting of the cleaned raw samples. After that, formaldehyde and salt in the samples was cleaned through centrifugation with cold Milli-Q water to avoid particles' explosion, and then freeze-dried and stored at 4°C in the dark until further analysis. Total mass fluxes (TMF) were normalized to mg $m^{-2}d^{-1}$.

4.3.2. Biochemical composition and nutritional quality of settling particles

In sediment traps remaining for long periods into the water, the use of preservative in the collecting cups is required to minimize microbial influence (Gardner et al., 1983). Though this may cause problems with the determination of some classes of organic compounds, previous comparative works with untreated samples demonstrated that the determination of protein, carbohydrate and lipid contents is not affected if the preservative is formaldehyde (Wakeham et al., 1993; Dell'Anno et al., 2002). The only possible problem is the lethal effect of the preservative on zooplankton, which can lead to collections that do not represent particle fluxes. For this reason larger swimmers were removed before analysis.

OC and N contents in the settled particles were measured using an elemental analyzer (EA Flash series 1112 and NA2100) according to Fabres et al. (2002)

Chlorophyll-a and phaeopigments analyses were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted after 12 h at 4°C in the dark from about 10 mg of freeze dried triplicate sub-aliquots of the trap material using 3-5 ml of 90% acetone as extractant. Extracts were analyzed fluorometrically as such to estimate chlorophyll-a and phaeopigments, the later after acidification with 200 μl 0.1N HCl. Different methods for assessing chlorophyll-a concentrations in marine sediments can provide under- or over- estimates (Pinckney et al., 1994), also because of the relative importance of chlorophyll degradation products (Szymczak-Zyla and Kowalewska, 2007). For this reason, we summed up chlorophyll-a and phaeopigment concentrations (i.e. total phytopigments) (Pusceddu et al., 2010). Total phytopigment concentrations were converted into C equivalents using 40 as a conversion factor. Although the C content of phytopigments can vary between 30 to 100 (Pusceddu et al., 2009), this factor was used for comparison with previous deep-sea data (Pusceddu et al., 2010b).

Protein, carbohydrate and lipid particle contents were analyzed spectrophotometrically according to Pusceddu et al. (2009) and concentrations expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. All analyses were performed on about 0.2 mg 2-5 sub-aliquots of trap material. More details on the analytical procedures are reported in Danovaro (2010). Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents (mg C mg-1) using the conversion factors of 0.40, 0.49 and 0.75 respectively, and their sum defined as the biopolymeric organic carbon (BPC) (Fabiano et al., 1995). Although only a fraction of biopolymeric C is rapidly reactive to heterotrophic digestion (Pusceddu et al., 2003; Pusceddu et al., 2009), there are several evidences from a variety of pristine and impacted marine environments that benthic fauna variations are tightly linked with changes in the quantity and composition of biopolymeric C in the sediment as well as in sinking particles (Albertelli et al., 1999; Pusceddu et al., 2007; Bianchelli et al., 2008; Pusceddu et al., 2009; Cerrano et al., 2010; Duros et al., 2011; Mirto et al., 2011). Phytopigment, protein, carbohydrate, lipid and BPC fluxes were normalized to mg m^{-2} d^{-1}.

According to Pusceddu et al. (2010), we utilized the contributions of phytopigment to BPC and the values of the protein to carbohydrate ratio as descriptors of freshness and nutritional quality of organic particles, respectively (Pusceddu et al., 2000; Pusceddu et al., 2009; Pusceddu et al., 2010b). The ratio of total phytopigments (once converted into C equivalents) to BPC is an estimate of the freshness of the organic material deposited in the sediment: since photosynthetic pigments and their degradation products are assumed to be labile compounds in a trophodynamic perspective, the lower their contribution to OC in the sediment the older the organic material is. Moreover, since the percentage fraction of OC associated with phytopigments is also typically associated with a higher fraction of enzymatically digestible compounds (i.e. promptly available for heterotrophs) (Pusceddu et al., 2003), higher values of this ratio will also be indicative of a comparatively higher nutritional quality (Dell'Anno et al., 2002). Since N is the most limiting factor for heterotrophic nutrition and proteins (which degrade faster than carbohydrates) are N-rich products, the protein to carbohydrate ratio is indicative of ageing and nutritional value of the OM (Danovaro et al., 1993; Dell'Anno et al., 2002; Tselepides et al., 2000; Pusceddu et al. 2009).

4.3.3. Statistical analyses

First, we analyzed the temporal variability in the fluxes of all investigated variables in the four locations, separately, using a one-way analysis of variance (ANOVA), using the time factor with 5-10 fixed levels as the unique source of variation. Each level refers to a sampling period equal to 15 days of particles' collection from November 2008 to April 2009. Sampling periods 1 to 3 correspond to late fall, 4 to 5 to early winter, 6 to 7 to late winter and 8 to 10 to early spring.

Then, the cross effects of sampling time and space were assessed using samples collected during the whole set of 10 sampling periods (November 2008 to April 2009) only from the traps at BC900 and BC1200 using a two-way analysis of variance (ANOVA). The design included two factors: Station (St), treated as a fixed factor with two levels (at 900 and 1200 m depth) and Time (Ti), treated as a fixed factor orthogonal to stations, with ten consecutive levels. In this case, when significant differences were encountered among sampling times in each trap and between sampling depths at each sampling period, Student-Newman-Keuls (SNK) post-hoc comparison tests (at $\alpha = 0.05$) were carried out. Before the analyses, the homogeneity of variances was checked whenever necessary using the Cochran's test on appropriately transformed data. Analysis of variance (ANOVA) is sufficiently robust to the departures from the assumption of data normality, particularly with balanced designs and many independent estimates of sample variance. Therefore, for those data for which the transformation did not allow to obtain homogeneous variances, these were not transformed and a more conservative level of significance was considered (Underwood, 1997).

The same designs were utilized to assess temporal vs. spatial variability in the biochemical composition of fluxes using distance-based permutational (non-parametric) multivariate analyses of variance (PERMANOVA) (Anderson, 2001;

McArdle and Anderson, 2001). The PERMANOVA test is an analogous of the multivariate analysis of variance (MANOVA), which is too stringent in its assumptions for most ecological multivariate data sets (Anderson, 2001). Non-parametric methods based on permutation tests such as the one performed by the PERMANOVA tool are preferable since they allow to partition the variability in the data according to a complex design or model and to base the analysis on a multivariate distance measure that is reasonable for ecological data sets (McArdle and Anderson, 2001). The analysis was based on Euclidean distances of previously normalized data, using 4999 random permutations of the appropriate units under the reduced model (Anderson and ter Braak, 2003).

Univariate analyses of variance (ANOVA) and SNK tests were conducted using the GMAV 5.0

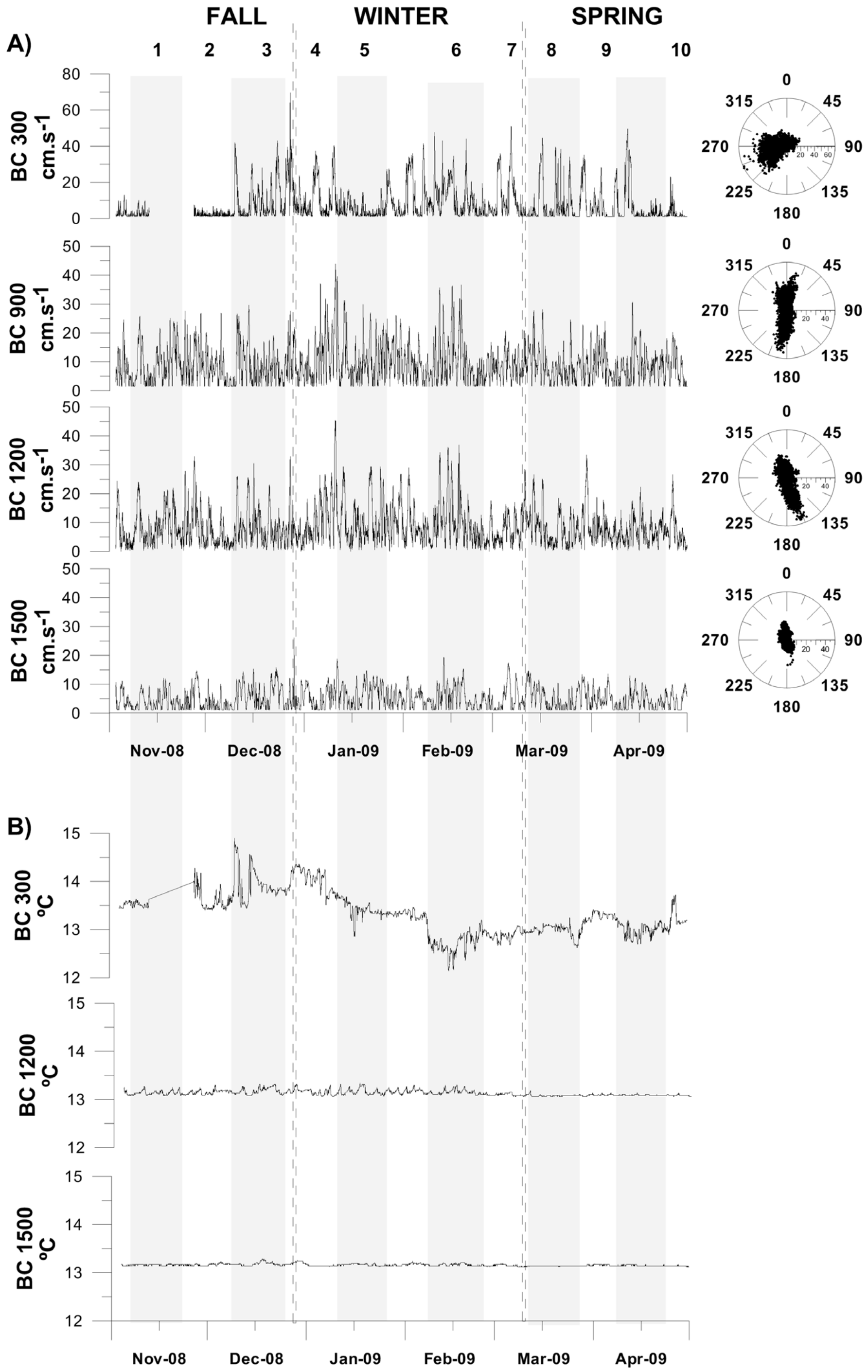

Fig. 4.2. Current speed and direction (A) and temperature (B) plots at 23 mab in the four mooring stations of Blanes Canyon BC300 to BC1500. Note that the vertical scale forcurrent speed in BC 300 differs from the other stations. Radial axes in current direction polar plots are equivalent to the y-axis of current speed plots. Mooring station codesare as follows: Blanes Canyon (BC) and water depth (three to four digits). Sampling periods are represented by the grey bars and the number of each period above the figure.fig2B.jpg

Station	Sampling period (15 days)	Start sampling period	OCF ($mg\ m^{-2}\ d^{-1}$)	Proteins ($mg\ m^{-2}\ d^{-1}$)	Carbohydrates ($mg\ m^{-2}\ d^{-1}$)	Lipids ($mg\ m^{-2}\ d^{-1}$)	Phytopigments ($mg\ m^{-2}\ d^{-1}$)	Biopolymeric C ($mg\ m^{-2}\ d^{-1}$)
BC300	1	28/11/2008	95,11	28,46	56,54	17,79	0,76	52,43
	2	09/12/2008	125,31	29,88	62,78	20,81	1,04	58,32
	3	25/12/2008	520,81	108,60	266,83	59,57	1,26	218,86
	4	10/01/2009	235,37	87,99	117,63	30,87	0,50	115,99
	5	26/01/2009	5,05	1,71	2,57	0,78	0,01	2,53
BC900	1	07/11/2008	274,42	63,24	140,99	29,78	0,64	116,72
	2	23/11/2008	283,20	58,47	109,09	30,14	1,10	99,45
	3	09/12/2008	345,90	94,37	136,07	32,98	1,22	129,16
	4	25/12/2008	269,54	65,33	105,97	29,82	1,04	100,42
	5	10/01/2009	280,09	72,28	97,77	26,66	0,93	96,81
	6	11/02/2009	30,78	10,17	8,21	2,82	0,08	10,21
	7	26/02/2009	8,18	3,04	1,89	0,92	0,02	2,83
	8	13/03/2009	7,39	2,76	2,11	0,96	0,02	2,86
	9	28/03/2009	5,08	1,56	1,16	1,13	0,01	2,04
	10	27/04/2009	31,85	9,99	8,67	4,42	0,10	11,56
BC1200	1	07/11/2008	328,40	80,58	108,55	48,56	0,70	121,84
	2	23/11/2008	264,26	53,09	88,59	34,90	1,07	90,82
	3	09/12/2008	761,12	168,61	250,89	98,51	2,82	264,26
	4	25/12/2008	581,86	138,90	196,68	67,68	1,88	202,70
	5	10/01/2009	87,57	48,66	49,74	19,32	0,49	58,32
	6	11/02/2009	340,51	82,80	98,52	65,51	2,36	130,53
	7	26/02/2009	440,82	105,87	153,02	99,02	6,32	191,60
	8	13/03/2009	338,18	99,52	72,26	55,77	1,87	117,04
	9	28/03/2009	280,07	90,57	103,64	74,47	2,58	142,86
	10	27/04/2009	149,82	50,55	23,10	17,47	0,46	44,65
BC1500	1	07/11/2008	75,32	27,17	22,55	8,41	0,26	28,23
	2	23/11/2008	124,76	26,64	36,63	12,48	0,62	37,97
	3	09/12/2008	160,02	37,88	45,26	18,75	0,81	51,39
	4	25/12/2008	495,31	94,36	107,62	39,87	1,29	120,38
	5	10/01/2009	300,49	56,82	69,79	24,72	0,98	75,46

Table 4.1. Total organic carbon (OCF) and main biochemical constituents fluxes (mean values) measured from November 2008 to April 2009 in sediment trap samples from Blanes Canyon. Sampling periods (numbers 1 to 10) and the date of the beginning of the period (15 days-long). Mooring station codes are as follows: Blanes Canyon (BC), water depth (three to four digits).

software (University of Sidney, Australia). The PERMANOVA analyses were carried out using the sub-routine included in the PRIMER6+ software.

4.4. **RESULTS**

4.4.1. Hydrology

During the monitoring period unstable weather conditions were observed with low pressures and easterly winds accompanied by intense rainfall and rough sea conditions. In November and December 2008 several big storms affected the North Catalan margin. One of them, occurring the 26th and 27th of December, was the most severe storm recorded over the last 25 years in the area. A buoy close to the BC head recorded significant wave heights up to 5 m. Since rainfall was intense the discharge of Tordera River reached 50 $m^3\ s^{-1}$ (Lopez-Fernandez et al., 2013; Sanchez-Vidal et al., 2012). Particle and OM fluxes associated to November and December 2008 storms and floods were captured in all mooring stations.

The highest mean current speeds during the reported monitoring period, 9.2 and 8.6 cm s^{-1}, were recorded at stations BC900 and BC1200, respectively, even though the maximum current speeds by far were measured at the canyon head (BC300) in December 2008, with values up to 70 cm s^{-1}. The lowest mean speed of all stations (5 cm s^{-1}) was registered at the middle canyon (BC1500), but the minimum current speeds correspond to BC1200 m situated at the upper canyon, with only 0.8 cm s^{-1}. Current direction was parallel to the canyon axis, with mean current direction in the various stations towards the S-SE (201º-230º), thus suggesting a strong bathymetric control (Fig. 2), in line with numerous observations in other submarine canyons (Shepard et al., 1979). Current direction at station BC300 in the canyon head was more variable.

The time series analysis of near-bottom current intensities showed several days-long pulses occurring during the entire monitoring period. Generally, current velocity variations at the different depths showed a similar pattern. However, on occasions intensifications registered at 300 m depth were decoupled from records at 1500 m depth. This was, for instance, the case at the end of December 2008 and from 26th of January to 11th of February 2009 (Fig. 2A). In other cases, maximum current speeds close to 70 cm s-1 were recorded at the canyon head at 300 m depth while only about 45 cm s^{-1} were measured at both 900 and 1200 m depth.

During the monitoring period, the temperatu-

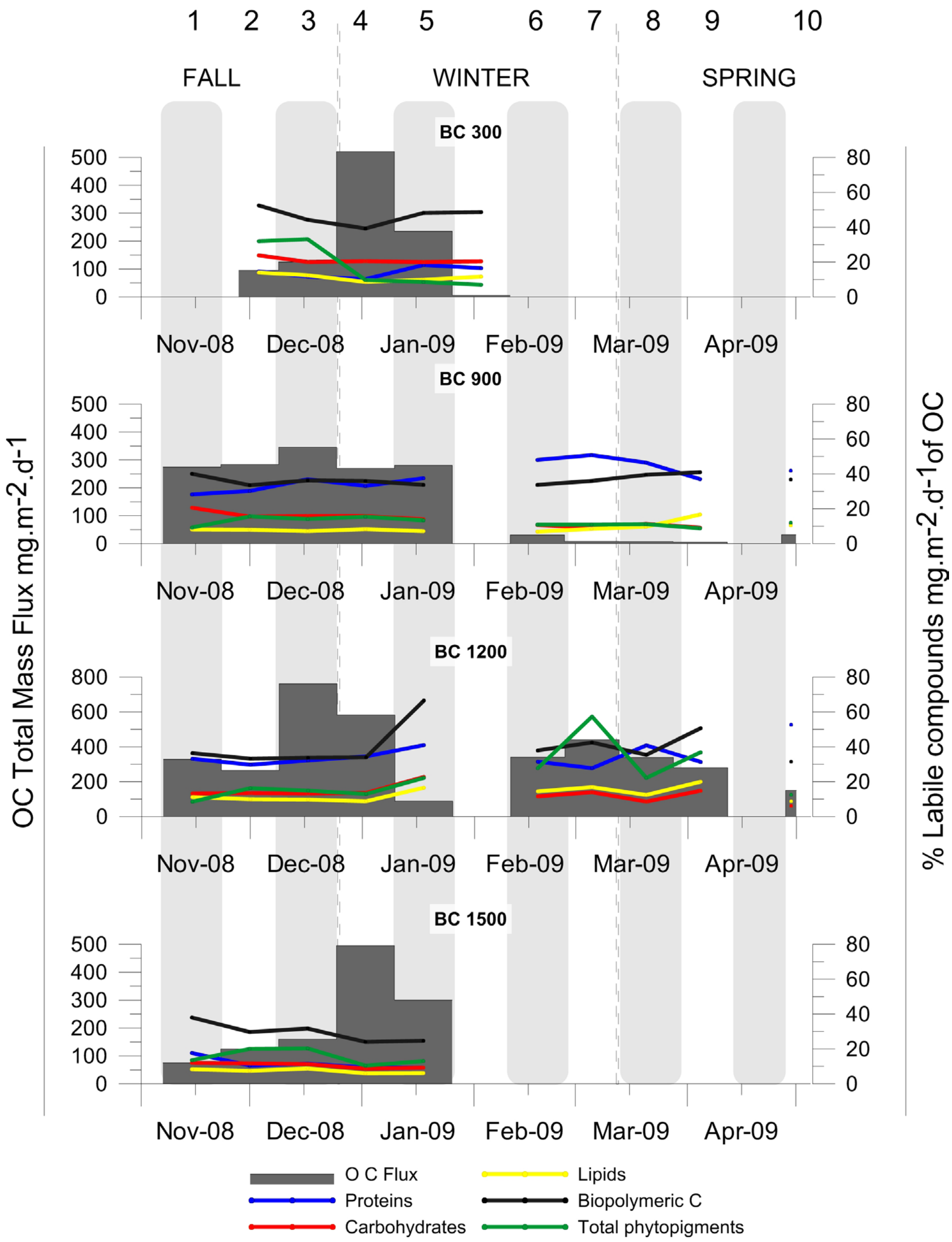

Fig. 4.3. Total OC flux and contribution of phytopigments, proteins, carbohydrates, lipids and biopolymeric C to the total OC (all expressed as%) at 25 mab in the four sampling stations BC300, BC900, BC1200 and BC1500 in Blanes Canyon. Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits). Sampling periods are represented by the grey bars and the number of each period above the figure.

re in the head of the canyon (BC300) fluctuated between 13.3 and 14.9ºC. Temperature remained more or less steady with only very narrow variations (<0.5°C) at stations BC1200 and BC1500 in the upper and middle canyon (Figure 2B). No temperature record is available for BC900.

4.4.2. Depth and time variability of organic carbon flux

OC flux from November 2008 to April 2009 ranged from 5.05 to 761.12 mg m^{-2} day^{-1}, values that represent between 1 and 2 % of the TMF (Table 1). The lowest OC flux was recorded in February 2009 at BC300, while the highest was registered by the mid-late of December 2008 in the upper canyon at BC1200, also time coinciding with high values BC900. At the head of the canyon (BC300) and in the deepest station BC1500 the top value was delayed to late December-beginning of January (Figure 3). In all sampling stations, total OC flux fluctuated among sampling periods, though with narrower temporal variations observed at the upper canyon (BC900).

4.4.3. Depth and time variability in the biochemical composition of fluxes

Estimates of the total fluxes of biochemical compounds including phytopigments, proteins, carbohydrates, lipids and BPC in the four stations along the BC axis are reported in Table 1.

Variable	Station	Source	df	MS	F	P	SNK
Phytopigments	BC300	Period	4	0.7126	66.3	***	3 > 2 > 1 > 4 > 5
		Residual	10	0.0108			
		Total	14				
	BC900	Period	4	0.8056	330.6	***	3 > 2, 4 > 5 > 1 > 6, 10, 7, 8, 9
		Residual	10	0.0024			
		Total	14				
	BC1200	Period	4	2.1336	1323.4	***	7 > 3 > 6 > 9 > 4, 8 > 2 > 1 > 5, 10
		Residual	10	0.0016			
		Total	14				
	BC1500	Period	4	0.4482	517.2	***	4 > 5 > 3 > 2 > 1
		Residual	10	0.0009			
		Total	14				
Proteins	BC300	Period	4	6051.9	19.2	***	3, 4 > 2, 1, 5
		Residual	10	315.94			
		Total	14				
	BC900	Period	4	31.648	225.3	***	3 > 5, 4, 1, 2 > 10, 6 > 8, 7, 9
		Residual	10	0.1405			
		Total	14				
	BC1200	Period	4	4548.7	20.2	***	3 > 4 > 7, 1 > 6, 2 > 9, 8 > 5, 10
		Residual	10	225.6			
		Total	14				
	BC1500	Period	4	10.6146	32.4	***	4 > 5 > 3, 2, 1
		Residual	10	0.3275			
		Total	14				
Carbohydrates	BC300	Period	4	30674.9	33.38	***	3 > 4, 2, 1, 5
		Residual	10	918.9			
		Total	14				
	BC900	Period	4	11262.5	106.9	***	1, 3 > 2, 4, 5 > 6, 10, 7, 8, 9
		Residual	10	105.4			
		Total	14				
	BC1200	Period	4	30.6789	57.2	***	3 > 4 > 7 > 6 > 9, 1, 2, 8 > 5 > 10
		Residual	10	0.5363			
		Total	14				
	BC1500	Period	4	13.9271	568.6	***	4 > 5 > 3 > 2 > 1
		Residual	10	0.0245			
		Total	14				
Lipids	BC300	Period	4	1410.7	101.8		3 > 4 > 2,1 > 5
		Residual	10	13.9			
		Total	14				
	BC900	Period	4	7.6934	341.5	***	3, 1, 2, 4, 5 > 10 > 6 > 9, 8, 7
		Residual	10	0.0225			
		Total	14				
	BC1200	Period	4	2503.9	54.0	***	3, 7 > 9, 4, 6, 8, 1 > 2 > 5, 10
		Residual	10	46.4			
		Total	14				
	BC1500	Period	4	454.281	44.13	***	4 > 5 > 3 > 2, 1
		Residual	10	10.2937			
		Total	14				
Biopolymeric C	BC300	Period	4	4.0000	88.8	***	3 > 4 > 2, 1 > 5
		Residual	10	0.7173			
		Total	14				
	BC900	Period	4	8312.9	127.1	***	3 > 1, 2, 4, 5 > 6, 10, 7, 8, 9
		Residual	10	65.4			
		Total	14				
	BC1200	Period	4	24.05	46.0	***	3 > 4, 7 > 6, 1, 9 > 8 > 2 > 5, 10
		Residual	10	0.5223			
		Total	14				
	BC1500	Period	4	14.3851	77.6	***	4 > 5 > 3 > 2, 1
		Residual	10	0.1853			
		Total	14				

Table 4.2. Results of the one-way ANOVA testing for differences in the quantity of organic matter in sediment trap samples from Blanes Canyon. df = degree of freedom. MS = mean square. F = F value; P = probability level. <?><?><?>P < 0.001. <?><?>P < 0.01. <?>P < 0.05. Results of the SNK tests ascertaining differences between sampling periods are also reported (n = 5 for BC300 and BC1500; n = 10 for BC900 and BC1200). Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits).

The one-way ANOVA revealed that fluxes of labile compounds changed significantly among sampling periods in all stations (Table 2), with clear and significant peaks observed in mid December at the head and upper canyon stations (BC300, BC900 and BC1200) and a delayed peak in late December at BC1500. After December, fluxes in the traps at 900 and 1200 m depth decreased down to values comparable or even lower than those observed at the beginning of the monitoring period.

The two-way ANOVA carried out on samples collected over the entire monitoring period at the stations in the upper canyon (BC900 and BC1200) revealed that the Space × Time interaction had significant effects on the fluxes of all labile compounds (Table 3). The a posteriori SNK tests revealed relatively consistent temporal changes at these two depths for all investigated variables, but also significant differences between fluxes at the two depths for most sampling periods from November 2008 to April 2009.

The protein fraction of the OC flux represented on average about 12% of the OC flux and ranged from 9.3 % to 27.2% of the OC flux, at BC1500 m and BC1200, respectively, both values registe-

ng the ten 15 days-long sampling periods from November 2008 to April 2009.
***P < 0.001. Results of SNK tests are also reported.

Variable	Source	df	MS	F	P	SNK tests: Temporal variations 900 m	1200 m	Spatial variations at each sampling period: 1	2	3	4	5	6	7	8	9	10
Phytopigments	St	1.0	36	4294	***												
	Ti	9.0	4	484	***												
	St x Ti	9.0	6	701	***	2,3 > 4 > 5 > 1 > 6, 7, 8, 9, 10	7 > 3 > 6 > 9 > 4, 8 > 2 > 1 > 5, 10	ns	ns	1200 > 900	1200 > 900	900 > 1200	1200 > 900	1200 > 900	1200 > 900	1200 > 900	1200 > 900
	Res	40.0	0.0														
	Total	59.0															
Proteins	St	1.0	241	801	***												
	Ti	9.0	24	81	***												
	St x Ti	9.0	19	63	***	3 > 1, 4, 5 > 2 > 6, 10 > 7, 8 > 9	3 > 4 > 7, 8 > 1, 6, 9 > 2, 5, 10	1200 > 900	ns	1200 > 900	1200 > 900	900 > 1200	1200 > 900	1200 > 900	1200 > 900	1200 > 900	1200 > 900
	Res	40.0	0.3														
	Total	59.0															
Carbohydrates	St	1.0	38	2432.4	***												
	Ti	9.0	8	478.5	***												
	St x Ti	9.0	6	371.6	***	1, 3 > 2 > 4, 5 > 6, 10 > 7, 8 > 9	3 > 4 > 7 > 1, 2, 6, 9 > 8 > 5 > 10	900 > 1200	ns	1200 > 900	1200 > 900	900 > 1200	1200 > 900	1200 > 900	1200 > 900	1200 > 900	1200 > 900
	Res	40.0	0.0														
	Total	59.0															
Lipids	St	1.0	26657	1054	***												
	Ti	9.0	1411	56	***												
	St x Ti	9.0	1749	69	***	1, 2, 3, 4, 5 > 6, 7, 8, 9, 10	3, 7 > 9 > 4, 6 > 8 > 1 > 2 > 5, 10	1200 > 900	ns	1200 > 900	1200 > 900	ns	1200 > 900	1200 > 900	1200 > 900	1200 > 900	1200 > 900
	Res	40.0	25														
	Total	59.0															
Biopolymeric C	St	1.0	36	4294	***												
	Ti	9.0	4.0	484	***												
	St x Ti	9.0	6	701	***	3 > 2, 4, 5 > 1 > 6, 10 > 6 > 7, 8	7 > 3 > 9 > 6 > 4, 8 > 1 > 5, 10	ns	ns	1200 > 900	1200 > 900	900 > 1200	1200 > 900	1200 > 900	1200 > 900	1200 > 900	1200 > 900
	Res	40.0	0.0														
	Total	59.0															

Table 4.3. Results of the 2-way analysis of variance ANOVA testing for differences in organic matter quantity in sediment trap samples from BC900 and BC1200during the ten 15 days-long sampling periods from November 2008 to April 2009. St = station. Ti = time. Res = residuals. df = degree of freedom. MS = mean square. F = F value. P = probability level. **P < 0.001. Results of SNK tests are also reported.

Trap	Source	df	MS	F	P
BC300	Time	4	56164.8	32.6	***
	Residual	10	1720.5		
	Total	14			
BC900	Time	4	2266.1	5.3	**
	Residual	10	428.8	2.0	
	Total	14			
BC1200	Time	4	51908.1	31.8	***
	Residual	10	1633.2		
	Total	14			
BC1500	Time	4	10177.5	53.6	***
	Residual	10	189.7		
	Total	14			

Table 4.4. Results of the PERMANOVA testing for differences in the biochemical composition of organic matter in sediment trap samples from Blanes Canyon. df = degree of freedom. MS = mean square F = F value. P = probability level. ***P < 0.001. **P < 0.01. *P < 0.05. Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits).

red in January 2009 (Figure 3).

On average, carbohydrates were the dominat biopolymeric compound of the OC flux at all sampling stations. The carbohydrate fraction represented on average about 14% of the OC flux, varying from 6.2% to 23.8 % at the upper canyon and the canyon head (BC1200 and BC300), in April 2009 and November 2008, respectively. At the head of the canyon (BC300), carbohydrates were about 20% on average for all the monitoring period (Figure 3).

Lipid contribution to OC flux did not vary significantly from one station to the other from November 2008 to January 2009 (i.e., in the first 5 sampling periods) in contrast with the increase observed in the upper canyon (BC900 and BC1200) from February to April 2009 (i.e., in the last 5 sampling periods). The lipid fraction of OC flux represents on average 10% of the OC flux and ranged from 6.0% to 19.9% at BC1500 m in January 2009 and BC1200 in March 2009, respectively (Figure 3).

Phytopigments represented a fraction arround 16% of the OC flux on average for all traps and

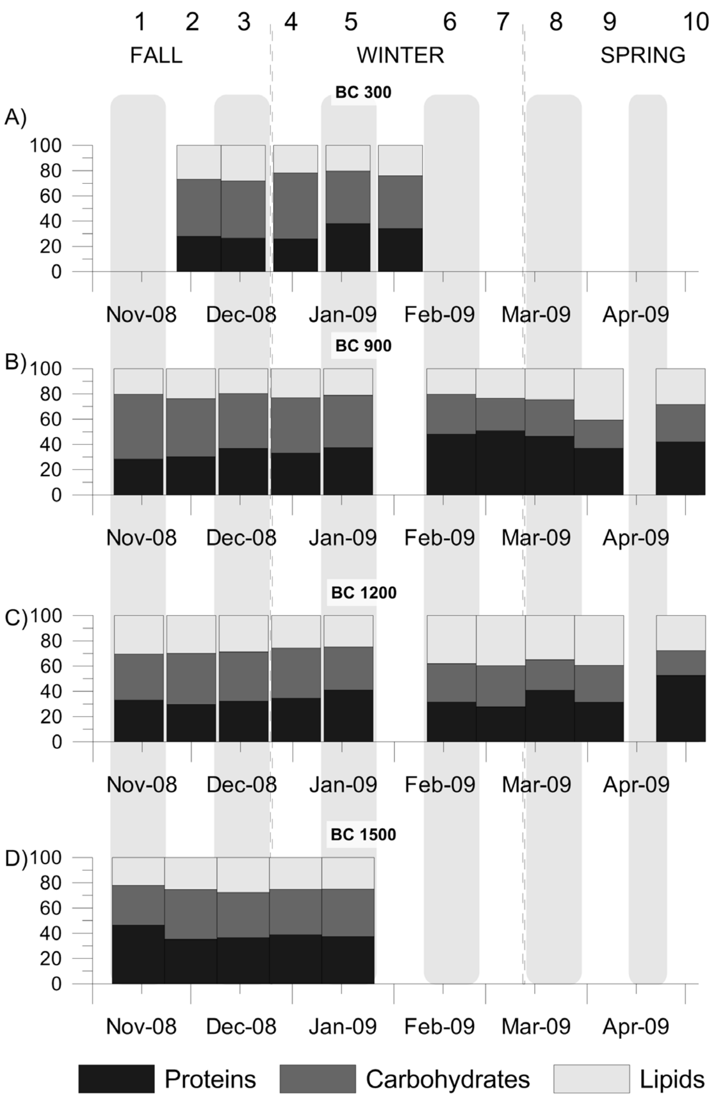

Fig. 4.4. Temporal changes in the biochemical composition of settling particles at 25 mab in the four sampling stations BC300 (A), BC900 (B), BC1200 (C) and BC1500 m (D) in Blanes Canyon. Data are presented as percentage contributions of proteins, carbohydrates and lipids to biopolymeric C. Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits).

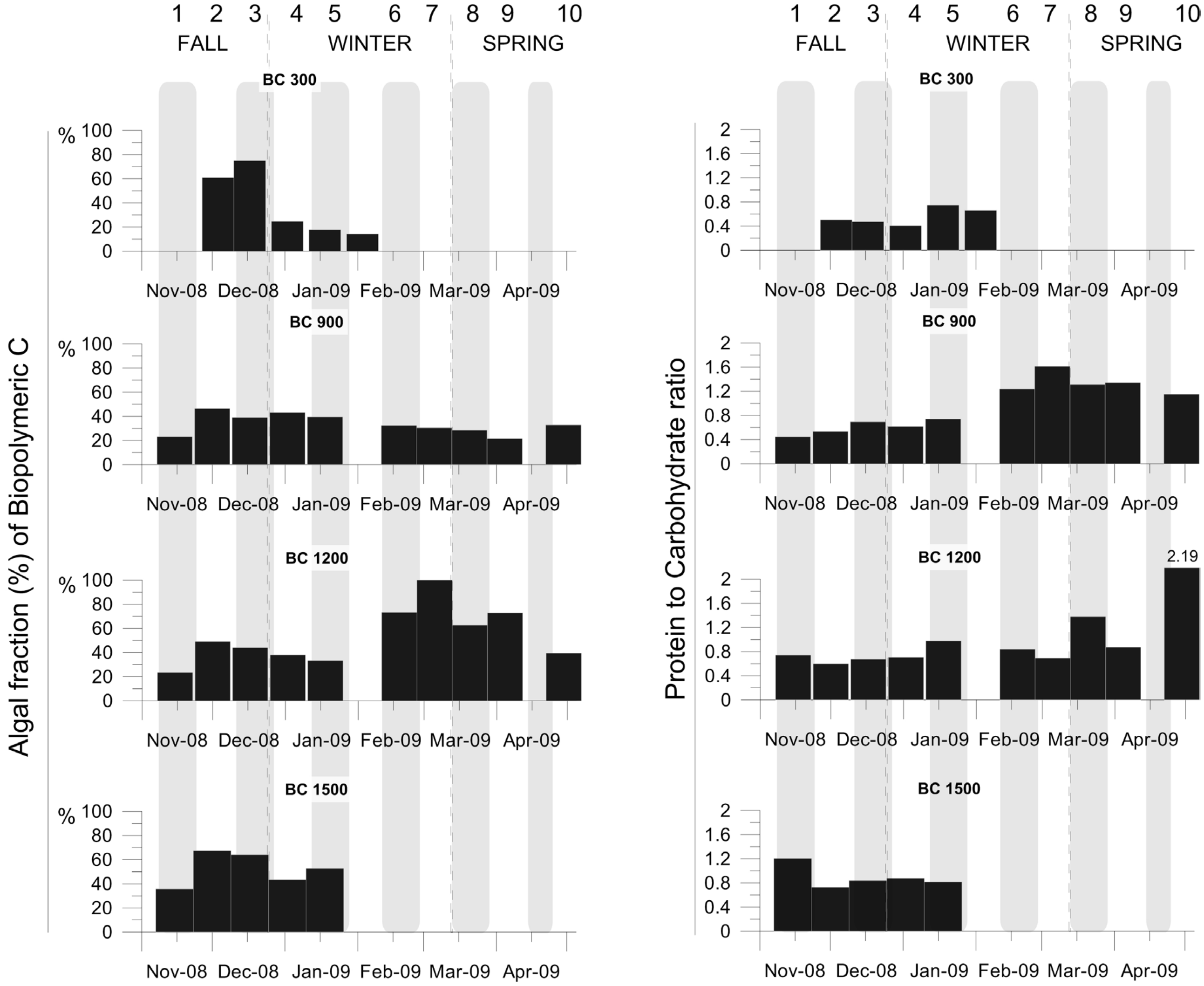

Fig. 4.5. Temporal changes in algal contribution to biopolymeric C (in percentage) and the protein to carbohydrate ratio in settling particles within Blanes Canyon. Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits).

sampling periods. The algal fraction of biopolymeric particles collected by the traps ranged from 15% at BC300 in late December 2008 to about 100% at BC1200 in March 2009 (Figure 3).

On average, biopolymeric C represented from 47 to 30% of the OC flux at the head and middle canyon (BC300 and BC1500), respectively. At BC300 m and BC1500 the biopolymeric fraction of the OC flux was highest during November 2008 (sampling period 1) with a contribution to the OC flux of 52.5 and 38.0%, respectively, and then fluctuated during the following sampling periods until January 2009. The BPC fraction remained almost constant at BC900 (36.6 ± 0.9 % on average) and showed two marked peaks at BC1200 (66.5% and 50.6%) in January 2008 and end of March 2009 (sampling periods 5 and 9) (Figure 3).

Overall, fluxes of phytopigments and BPC decreased throughout the entire monitoring period. In particular, fluxes measured from November 2008 to January 2009 (in the first 5 sampling periods) were significantly higher than those observed from February 2009 to April 2009 (the last 5 sampling periods). For all investigated variables at the middle canyon, fluxes in BC1200 were significantly higher than those observed at BC900 with some exceptions (i.e., phytopigments and proteins in January 2009 -sampling period 5-; carbohydrates in November 2008 and January 2009 -sampling periods 1 and 5-). Both phytopigment and BPC fluxes were not statistically different between the two traps at BC900 and BC1200 in November 2008 during sampling period 1

Overall, the PERMANOVA revealed that the biochemical composition of settling particles varied significantly with time at all sampling stations (Table 4). In particular, from November 2008 to January 2009 (first 5 sampling periods), settling particles at the head of the canyon (BC300) were characterized by a slight increase with time in the protein contribution to BPC (from 28 to 38 % of BPC), accompanied by a decrease of the lipid fraction (from 27 to 20% of BP) and fairly constant values of the carbohydrate contribution (around 45 %) (Figure 4A). At the upper canyon (BC900) the increase with time of the protein contribution to BPC from November 2008 to January 2009 (first 5 sampling periods) (From 28 to 37 % of BPC) was accompanied by a slight increase of the lipid fraction (from 20 to 24 % of BPC) and a concurrent decrease of the carbohydrate fraction (Figure 4B) (from 51 to 41 % of BPC). At BC1200, the proteins contribution increased considerably from November 2008 (sampling period 1) to January 2009 (sampling period 5) (from 30 to 41% of BPC) to increase considerably in April 2009 (last sampling period) (Figure 4C) (values up to 53% of BPC), carbohydrate decreased (from 40 to 34 %of BPC) from December 2008 to January 2009 (sampling periods 3 to 5), whereas lipid contribution fluctuated around the mean value observed from November 2008 to January 2009 (first 5 sampling periods) (28% of BPC) and peaked in March and April 2009 with a contribution of 40% of BPC in periods 7 and 9. In the trap located at the deepest station at 1500 m depth, from November to January (first 5 sampling periods), protein contribution to BPC decreased in November 2008 to remain stable during December 2008 and January 2009, accompanied by an slight increase in the lipid fraction (from 22 to 28% of BPC) and by an invariant carbohydrate contribution (Figure 4D).

The algal fraction of BPC settled in the sediment traps was arround 50% However, at all sampling stations the algal fraction of BPC varied significantly with time, with generally higher values observed in November 2008 and December 2008 (first 2 or 3 sampling periods) at stations BC300, BC900 and BC1500 and in early March 2009 (sampling period 7) at BC1200 (Figure 5). Values of the protein to carbohydrate ratio in the trap material ranged from 0.4 to >2.0 and exhibited significant temporal variability in all investigated stations. In winter months (sampling periods 4 to 7) this ratio increased at the head of the canyon (BC300) and decreased at the middle canyon (BC1500), while from late winter to early spring (sampling periods 8 to 10) it increased in upper canyon stations BC900 and BC1200, so that a consistent tendency was not observed (Figure 5).

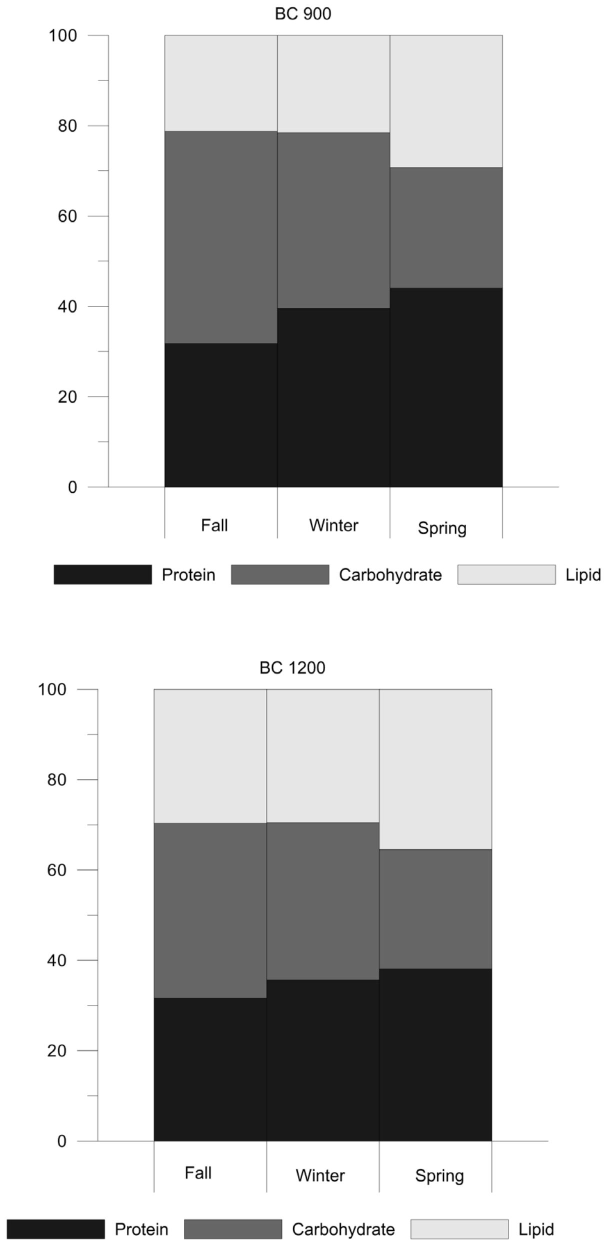

Fig. 4.6. Temporal changes in the biochemical composition of settling particles in stations BC900 and BC1200 of Blanes Canyon. Reported are percentage contributions of protein, carbohydrate and lipid to biopolymeric C. Fall (November 2008–December 2008, sampling periods 1 to 4); Winter (January–March 2009, sampling periods 5 to 8); Spring (March–April 2009, sampling periods 9 to 10). Mooring station codes are as follows: Blanes Canyon (BC) and water depth (three to four digits). Not to scale.

4.5. DISCUSSION AND CONCLUSIONS

Information about total mass and OC fluxes and their biochemical composition has progressively accumulated since the 70s (McCave 1975; Honjo et al., 1982; Danovaro et al., 1999; Gooday, 2002). In this study, we show for a six months period comprised between a large storm event in winter and the phytoplantkton bloom in spring that OC fluxes in the Blanes canyon are of intermittent nature, with relatively short-lived winter peaks (López-Fernández et al., 2013). The main input of OC to the benthic compartment occurred from December to January at all investigated sites in the canyon head, upper course and middle course. Our results also indicate a shift of peak fluxes from the canyon head and upper canyon to the middle canyon and, probably, beyond as indicated by the top fluxes recorded in January and February 2009 at the deepest station BC1500 (Figure 3). These observations are in good agreement with mass flux seasonal patterns noticed in other submarine canyons of the NW Mediterranean Sea, such as the Cap de Creus, Lacaze-Duthiers, Aude, Herault and Petit Rhone canyons (Fabres et al., 2008).

In contrast, much less information is available on the biochemical composition of OM fluxes in submarine canyons. Previous studies, such as those by Tesi et al. (2010) and Pasqual et al. (2011), have in general highlighted clear changes in the biochemical composition and nutritional quality of settling OM, which have been typically attributed to: i) pulses and timing of biological production in the upper ocean (e.g. Danovaro et al., 1999); and ii) local climate forcing modifying the relative importance of terrigenous vs. marine OM contents (Tesi et al., 2008; Sanchez-Vidal et al., 2009; Sanchez Vidal et al., 2012). In this regard, it has been generally observed that coastal storms mediated pulses of materials entering also by lateral advection after escaping from the continental shelf and being subsequently injected into the canyons' interior, usually involving a strong dilution of the organic fraction within the total mass flux (Zúñiga et al., 2009, Sanchez-Vidal et al., 2012).

In this study, downward fluxes of phytopigments and the whole spectrum of biopolymeric compounds (proteins, carbohydrates and lipids; Table 2, 3 and 4) vary significantly among sampling periods. In particular, fluxes of all biochemical compounds increased since the beginning of the study, in November 2008, showed synchronous or close peaks in winter at all stations, and decreased consistently afterwards. Variations in the biochemical composition of sinking particles point out that the severe storm that occurred the 26th of December 2008 in the study area led to a strong increase in the downward transport of OM in Blanes canyon (Sanchez-Vidal et al., 2012). The associated inputs of total OM entering the canyon's interior were thus accompanied by increased fluxes of all labile compounds. Nevertheless, we also found that peaks in OC fluxes during such winter storm involved a decrease in the percentages of biopolymeric and algal fractions within these fluxes (Figure 3).

These results indicate that in the Blanes canyon inputs of bioavailable food (sensu Danovaro et al., 2001) to the bathyal ecosystem are considerably diluted both by the storm-triggered large increase in OC flux and, mainly, in total mass flux, itself composed mostly of lithogenic particles (Lopez-Fernandez et al., 2013). Heterotrophic organisms forage in such a way to find, capture and consume food containing the most available calories while expending the least amount of energy possible. The optimal foraging behavior (sensu McArthur and Pianka, 1966), has been invoked several times to explain how organisms living in food limited environments – like the deep sea – can gain the needed energy from very low organic C inputs (Jumars et al., 1990). According to the optimal foraging theory and from the point of view of benthic detritus feeders, in spite of a larger amount of material reaching the seafloor during storm events, the search for suitable food source (optimal quantity of labile food) might be more complicated (McArthur and Pianka 1966). It might also be that such large injections of diluted labile compounds are available and consumed during rather long periods of time, thus compensating to some extent the "complications" for detritus feeders during the first stages after such massive injection occurred.

In spring only stations in the upper canyon (BC900 and BC1200) can be compared (Fig. 3). A common feature to both stations in spring is that the OM collected by sediment traps had a higher nutritional value than in late autumn-winter (Figure 5). This difference may be attributed to the spring planktonic bloom described by several authors in the study area (Estrada et al., 1996; Rossi et al., 2003). This hypothesis is supported by the analysis of the biochemical composition of biopolymeric C data combined at the seasonal scale (Figure 6). From this picture, it clearly emerges that during spring biopolymeric C was characterized by increasing lipid contributions when compared with the two previous seasons. Along with proteins, lipids can represent a preferential source of energy for benthic feeders (Medernach et al., 2001; Grémare et al., 1997). These results confirm that in Blanes canyon the spring injection of organic matter derived from sinking phytoplankton provides the benthos with highly nutritive food particles. Therefore, again following to the optimal foraging theory, we can infer that deep-sea detritus feeders would need to ingest less material in spring than in autumn-winter to get the optimal quantity of labile food. Recently, Pasqual et al. (2011) illustrated the importance of seasonal vs. episodic pelagic settling and continental shelf advection events in controlling the exchange of OM across the continental margin in the nearby Gulf of Lion. Using pigments, lignin phenols and amino acids as markers of marine and terrigenous fluxes of OM, these authors observed a progressive increase in OM degradation during along-canyon particle transport. They also noticed a strong decrease in the organic fraction of TMF during a dense shelf water cascading event that occurred in spring 2006. Our results from BC strongly support the hypothesis that submarine canyons act as principal conduits of material entering the shallow continental shelf after river floods and coastal storms, which involves an episodic supply of OM with high nutritional value to the deep-sea benthic ecosystem. The nutritional value of such food supply is, at the same time, tightly connected with biological processes occurring in the upper ocean layers above the continental shelf and slope.

Studies carried out mainly in the last two decades have evidenced that continental margins all over the world ocean play a key role in biogeochemical cycling and in supporting the metabolism of deep-sea organisms (Bauer and Druffel, 1998; Dell'Anno and Danovaro, 2005). Sediment and OM transport through canyons and adjacent open slopes is, nevertheless, neither constant nor unidirectional. Sediments along submarine canyons are in fact typically characterized by fluctuating – even pulsing - inputs of material from the upper continental shelf: these can lead to sudden though temporary events of accumulation of organic matter on the canyon's seafloor (Canals et al., 2006; Company et al., 2008; Pusceddu et al., 2010a). Such a "pulsing like" injection of material is confirmed also in the Blanes canyon. The Catalan margin is indented by a high number of submarine canyons deeply influenced by the local climate forcing. Our results, therefore, allow inferring that processes taking place in submarine canyons along the Catalan margin may control or, at least, have a strong influence on benthic metabolism at the whole basin scale in the NW Mediterranean Sea. Moreover, we could also infer that the spatial heterogeneity associated to submarine canyons likely shapes their own biodiversity, including that of the deep-sea basin facing the canyons. In this regard, for instance, recent investigations have proven that canyons' biodiversity along the Mediterranean Sea margins contribute significantly to maintain high levels of regional biodiversity, by hosting high numbers of exclusive species (Bianchelli et al., 2008; Danovaro et al., 2009; Bianchelli et al., 2010).

It comes out from our data that submarine canyons driven by intermittent pulses controlled by meteorological forcings have a preeminent role in transferring material from the highly productive continental shelf to the nutritionally depleted deep-sea, which is in agreement with previous investigations (Tesi et al., 2010; Pusceddu et al., 2010a; Sanchez-Vidal et al., 2012). Such transport, as for BC, is crucial and its significance could be compared to that of vertical fluxes in the open sea. Nevertheless, during high-energy events such as those described, the quality of particulate food made available to the deep benthic ecosystem decreases considerably, mainly by dilution by high loads of lithogenic material, thus involving a potential limitation for feeding the deep-sea benthos.

Coastal storms have thus important effects on the whole system from the ocean surface and shallow continental shelf to the deep seafloor (Sanchez-Vidal et al., 2012). Like for other high-energy events (e.g. dense shelf water cascading or wind-induced sediment resuspension; Pusceddu et al., 2010a; Pusceddu et al., 2005a), changes in food availability related to large coastal storms can have major consequences on biodiversity and ecosystem functioning in the deep-sea. So that further targeted long-term investigations on biosphere-geosphere interactions along continental margins and, more specifically, within submarine canyons are needed to better understand the impact of atmosphere-driven high-energy events over deep-water ecosystems as a whole.

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5

CAPÍTULO 5

RESUMEN DE RESULTADOS Y DISCUSIÓN

A continuación se presenta el resumen de los datos (véase descripción completa en los capítulos 2, 3 y 4) y la discusión sobre de la variabilidad temporal de la magnitud y composición de los flujos de partículas dentro del sistema del cañón submarino de Blanes, poniendo especial atención a la biodisponibilidad de la materia orgánica para los consumidores del bentos.

5.1. FLUJO DE MASA Y COMPOSICION DEL MATERIAL PARTICULADO

Los datos obtenidos en el cañón submarino de Blanes y en el talud adyacente presentan grandes variaciones tanto en composición como en cantidad de partículas que llegan al fondo. Dentro del cañón de Blanes, aunque la evolución general del flujo de masa presenta patrones similares en todas las profundidades (Fig. 5.1), se observa, por ejemplo, un máximo del flujo de masa entre diciembre de 2008 y enero de 2009 [83 g m^{-2} d^{-1} a BC300, 35 g m^{-2} d^{-1} a BC900, 75 g m^{-2} d^{-1} en el BC1200, 50 g m^{-2} d^{-1} a BC1500], aunque los datos de las trampas de 300 y 1200 posiblemente se subestimaron debido a la obstrucción de las trampas por un exceso de flujo. A partir de febrero hasta abril de 2009 hubo una disminución en los valores de los flujos registrados [0.4 g m^{-2} d-1 en BC300, 0.2 g m^{-2} d^{-1} en BC900 y 0.1 g m^{-2} d-1 en BC1200]. De mayo a noviembre de 2009 se muestran dos máximos relativos, que tuvieron lugar a principio de julio [25 g m^{-2} d^{-1} en BC900 y 21 g m^{-2} d^{-1} en BC1200] y finales de septiembre [18 g m^{-2} d^{-1} en BC900 y 19 g m^{-2} d^{-1} en BC1200]. Las muestras de las trampas BC300 y BC 1500 se perdieron después de abril y febrero de 2009, por lo que no es posible realizar una descripción de un cuadro más completo (Fig. 5.2).

El flujo de masa en el talud, muestra los valores más altos desde noviembre 2008 hasta abril 2009 con dos máximos, uno en diciembre de 2008-enero de 2009 [9 g m^{-2} d^{-1} en OS900, 5 g m^{-2} d^{-1} en OS1200 y 2 g m^{-2} d^{-1} en OS1800] y uno en marzo-abril de 2009 [7 g m^{-2} d^{-1} en OS900, 6 g m^{-2} d^{-1} en OS1200 y 2 g m^{-2} d^{-1} en OS1800]. A partir de abril de 2009 existe una disminución general hasta noviembre de 2009 con los valores mínimos en OS900 [0.5 g m^{-2} d^{-1}] y OS1800 [0.02 g m^{-2} d^{-1}], y flujos más estables en OS1200 [2 g m^{-2} d^{-1}] y OS1500 [0.36 g m^{-2} d^{-1}].

En cuanto a la composición de los flujos de masa (Fig. 2.5 y 5.2), la fracción litogénica fue el componente dominante de las partículas en todos los ambientes estudiados BC y OS, con un promedio de contribución al flujo de masa de 60-70% y 66-72% respectivamente. En todas las estaciones la fracción litogénica disminuyó en primavera y verano (es decir, de mayo a agosto de 2009), tendencia que está más acentuada en el ambiente de talud.

El carbonato cálcico ($CaCO_3$) fue el segundo constituyente dominante del flujo de masa en los dos ambientes, con valores alrededor del 25% excepto en la estación más superficial, BC300 con 37%. El contenido de $CaCO_3$ fue ligeramente mayor en las estaciones de cañón que en las del talud. En el cañón la contribución de $CaCO_3$ al flujo de masa total fue máxima en la estación BC300 (43%) en diciembre de 2008 y el valor mínimo se registro en la estación de BC1200 (14%) en febrero de 2009. En el talud los valores extremos (28% y 19%) se midieron en otoño (octubre de 2009) y en verano (julio de 2009) ambos en la estación OS1500.

Los porcentajes de los flujos de materia orgánica fueron bastante estables desde la cabecera del cañón hasta las estaciones más profundas, a lo largo de todo el período de seguimiento, presentando los valores máximos y mínimos de 3.84% y 1.26% en noviembre de 2008 y diciembre de 2008 respectivamente, registrados ambos en la misma estación, BC300. En el talud la contribución de materia orgánica al flujo de masa fue mayor y más variable que en el interior del cañón, con valores que van desde 2.07% a 10.66% en las estaciones de OS900 y OS1800 respectivamente, ambos valores registrados en junio de 2009.

La contribución de ópalo al flujo total de masa dentro del cañón presenta dos picos máximos de 4.64 y 7.24% en las estaciones de BC1200 y BC1500 respectivamente, ambos en invierno (enero de 2009 y diciembre de 2008 respectivamente). Mientras que en el talud el valor máximo se registro en junio de 2009 con un porcentaje de 9.67% en la estación de OS1800.

Los resultados de las trampas de sedimento ponen de manifiesto las diferencias entre las muestras obtenidas dentro del cañón submarino y las obtenidas del talud adyacente. Estos dos dominios fisiográficos se diferencian en términos de flujos de partículas tanto en magnitud como en composición de los mismos. Al igual que en otros cañones submarinos cercanos como es el caso de La Fonera (Martin et al., 2006) y Cap de Creus (Pasqual et al., 2010), los flujos de masa dentro del cañón submarino de Blanes, fueron siempre mayores (casi un orden de magnitud) que los flujos de masa registrados en el talud a las mismas profundidades. Esta diferencia se hace más evidente durante e inmediatamente después de las tormentas, como las que tuvieron lugar entre noviembre de 2008 y enero de 2009 (véase capitulo 2). Los flujos de masa dentro del cañón de Blanes muestran como tendencia general entre el otoño de 2008 y el invierno de 2009, un aumento con la profundidad del agua (Fig. 2.5) confirmando el modelo de que los cañones submarinos actúan como canales preferenciales de los flujos de partículas, debido a su topografía (Gardner et al., 1989; Durrieu de Madron, 1994) sobre todo durante los periodos de alta actividad hidrodinámica (reforzamiento de corrientes geostróficas, procesos de descenso de agua densa de plataforma y grandes tormentas) (Martin et al., 2006; Palanques et al, 2006; Sánchez-Vidal et al., 2012).

Sobre una media anual, el flujo de masa dentro del cañón, aumenta con la profundidad hasta 1500 m. Sin embargo, la obstrucción de las botellas receptoras en BC300 después de la tormenta a finales de diciembre de 2008 puede haber sesgado la información sobre el flujo de masa en esta estación, lo que implica que el aumento observado en el cañón de debe interpretarse con cautela. Esto aparentemente contradice el trabajo previo de Zúñiga et al. (2009), donde encontraron una disminución del flujo de masa hacia el fondo. Nuestros datos en 2008-09, muestran valores de flujo de masa significativamente más altos que los encontrados por Zúñiga et al. (2009) para el periodo 2003-04. Nuestros resultados muestran valores de flujo medio anual de masa desde 12,68 g m^{-2} d^{-1} a 300 m de profundidad, en la estación más somera, hasta 26,56 g m^{-2} d^{-1} a 1500 m, en la estación más profunda, dentro del periodo de muestreo 2008-09 en contraste con los de Zúñiga et al. (2009) durante el periodo de muestreo 2003-04, con valores que van desde 13,98 g m^{-2} d^{-1} a 600 m de profundidad hasta 3,82 g m^{-2} d^{-1} a 1700 m. En invierno 2003-04 solo tuvo lugar una tormenta, en contraste con el número y la magnitud de las tormentas de el invierno de 2008-2009. Estas tormentas alimentaron al cañón con altas cantidades de partículas sedimentarias de la plataforma. Esta diferencia, pone de manifiesto la alta variabilidad interanual de los flujos de partículas en el área de estudio, en su mayoría relacionada con diferentes escenarios meteorológicos que implican la presencia de olas de alta energía y la duración de los mismos (ver capitulo 2 sección 5.2)

Procesos similares en la relación entre el flujo de masa y la profundidad dentro de un cañón submarino, ha sido también descrito en el cañón de La Fonera, cercano a nuestra zona de estudio. En el cañón de La Fonera, Martin et al., (2006) y Palanques et al., (2006) sugieren que estos aumentos en el flujo de masa son provocados por las entradas laterales de partículas a través de las cárcavas del flanco septentrional del cañón, como resultado de la actividad de la pesca de arrastre y el efecto de las tormentas en la plataforma adyacente.

En el talud adyacente, el flujo de masa total muestra una disminución con el aumento de la distancia a costa. En consecuencia los valores de flujo de masa van desde 3.53 g m^{-2} d^{-1} en la estación más somera OS900 a 0.77 g m^{-2} d^{-1} en la estación de OS1800. Esto sugiere una disminución de la influencia hidrodinámica y por tanto en los aportes desde la plataforma, en la sedimentación de partículas a favor de una mayor influencia hemipelágica.

La estabilidad en la composición del flujo de masa, con una fracción predominantemente litogénica (alrededor del 70%), en general, es más visible en el cañón, donde la contribución de materia orgánica al flujo de masa no varió significativamente con la variación del flujo total de masa (alrededor del 2%). Esto señala que la materia particulada transportada dentro del cañón, experimenta una fuerte homogenización durante la resuspensión y el transporte de

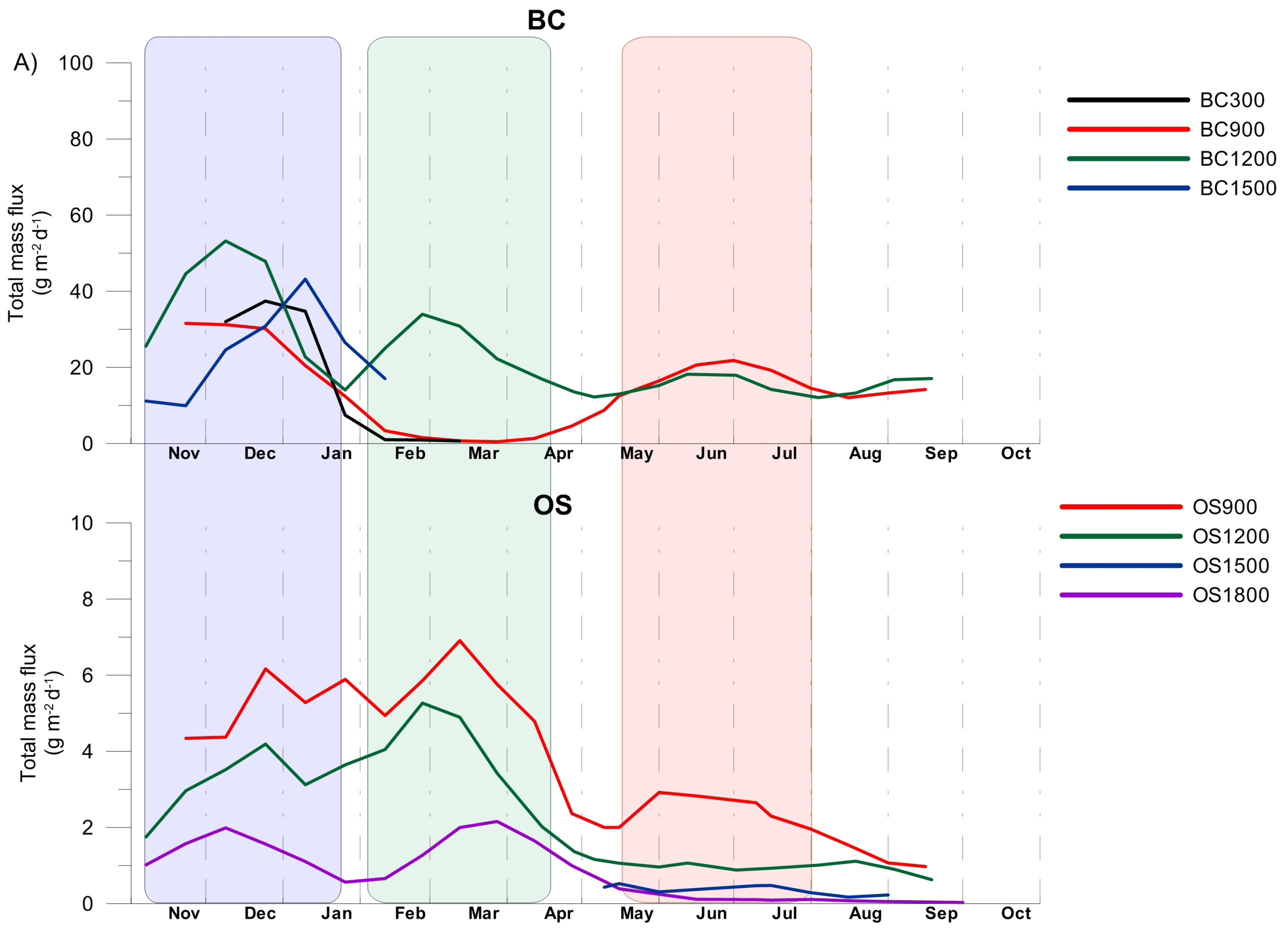

Fig. 5.1. Flujo total de masa (g.m-2.d-1) en el canon de Blanes (BC) y en el talud adyacente (OS)en todas las estaciones de muestreo.

sedimento. Por otro lado, las concentraciones de materia orgánica y ópalo en las estaciones del talud adyacente, presentan mayor variabilidad estacional y una disminución de las mismas al aumentar el flujo de masa. Lo que constata la mayor influencia de los procesos hemipelágicos y su variabilidad temporal.

5.1.1. Procesos hidrodinámicos y atmosféricos que afectan los flujos de partículas

Para una mejor visualización de la tendencia temporal de los flujos de masa, hemos hecho una representación de los flujos totales de masa para cada trampa de sedimento (Fig. 5.1). La variabilidad temporal de los flujos de masa en todas las estaciones durante el período de seguimiento muestra la existencia de tres períodos, donde el flujo total de masa aumentó por diferentes procesos (Fig. 5.1). Entre los diferentes procesos a los que podemos atribuir la variabilidad temporal se incluyen: la presencia de tormentas, los procesos de formación de agua densa, la convección de mar abierto, el florecimiento fitoplanctónico, las entradas de polvo del Sahara y la pesca de arrastre de fondo.

Impacto de las tormentas en los flujos de partículas

Desde noviembre de 2008 hasta finales de enero de 2009 la zona de estudio se caracterizó por un clima inestable con el paso de tormentas secas y húmedas (véase descripción en capitulo 2 sección 3.3) asociadas a fuertes vientos, oleaje alto y ocasionalmente lluvias fuertes (Fig. 2.2). El paso de una tormenta afecta a todos los aspectos de la removilización, el transporte y la deposición de las partículas (Liu y Lin, 2004). Cada una de las tormentas, estuvo asociada a persistentes vientos y olas altas que probablemente generaron fuertes corrientes en la plataforma, con la suficiente fuerza para movilizar y suspender gran cantidad sedimentos (Pedrosa-Pàmies et al., 2013), originando un flujo de partículas hacia el fondo del mar por dentro del cañón. Debido a los fuertes vientos, se produjo una acumulación de la masa de agua a lo largo de la costa, este efecto provocó un flujo intenso de turbidez que entró por la cabecera del cañón de Blanes (Sánchez-Vidal et al., 2012). Además, la tensión en cizallas producida por las olas en superficie dio lugar a la resuspensión de los sedimentos de plataforma aumentando así la densidad del flujo y facilitando el transporte de las partículas en y por el cañón. Dentro del cañón la velocidad de corriente registrada en el eje del cañón alcanzó 70 cm s^{-1} en BC300 y hasta 32 cm s^{-1} en BC1200. Esto se puede interpretar como que el cañón actuó de conducto principal para el transporte de sedimentos de plataforma, como también se deduce por las altas concentraciones de sedimentos suspendidos registradas por los transmisómetros cerca del fondo. Este aumento, se notó especialmente durante la tormenta que tuvo lugar el 26 de diciembre de 2008 (Sánchez-Vidal et al., 2012), y probablemente también, aunque en menor medida, en las tormentas que ocurrieron en noviembre de 2008 y enero de 2009 (Figs. 2.2 y 2.4). El transporte de sedimentos re-suspendidos hacia el fondo continuó hasta que la turbulencia fue incapaz de mantener la carga de partículas en suspensión y estas comienzan su sedimentación (Puig et al, 2003; Pedrosa-Pàmies et al, 2013). Prueba de ello es la gran cantidad de partículas de sedimento recolectadas durante los tres meses tormentosos entre noviembre de 2008 y enero de 2009. En las estaciones del talud también se notó un aumento del flujo de masa, aunque de menor magnitud, lo que sugiere que las partículas fueron transportados hacia el fondo de la cuenca, no sólo a través del cañón, sino posiblemente también a lo largo del talud adyacente (Fig. 2.5).

En el interior del cañón, la estación BC1200 recibió un flujo total de masa mayor que en la estación BC900 más somera, esto nos sugiere una probable transferencia lateral de las partículas respecto al eje del cañón por medio de las cárcavas que recortan el flanco este del cañón. En la estación más profunda del cañón, BC1500, se observa un aumento notable del flujo de masa, como resultado de la última tormenta de enero de 2009, en comparación con las estaciones más someras donde los flujos eran más altos después de las dos tormentas anteriores, este resultado se podría explicar en primer lugar, por un agotamiento de los sedimentos susceptibles de ser resuspendidos en las estaciones menos profundas, debido al paso de las tormentas anteriores y, en segundo lugar, por la movilización de los sedimentos acumulados temporalmente a profundidades inferiores a 1500 m de profundidad, en la parte baja del cañón. Esta explicación es de alguna manera similar a la dada para el transporte de sedimentos en suspensión en los ríos torrenciales, que experimentan una reducción progresiva de la carga de partículas en suspensión después de una sucesión de procesos (Alexandrov et al., 2003, Hudson et al., 2003 y, Rovira y Batalla, 2006). Esta conclusión se refuerza al comparar los de flujos de masa a finales de enero y principios de febrero de 2009 en todas las estaciones del eje del cañón, donde como hemos mencionado anteriormente, las estaciones más someras muestran los flujos de masa más bajos o incluso nulos durante la tormenta de enero de 2009, mientras que la estación más profunda (BC1500) muestra flujos de sedimento notablemente más altos (Fig. 2.5). Que las partículas tengan una fuente inicial común y el transporte “paso a paso” a lo largo del cañón, que implica la resuspensión de las partículas previamente acumuladas en zonas menos profundas, ayuda a la comprensión de la falta de diferencias significativas en la composición entre los flujos asociados a las diversas tormentas. Durante este período de tormentas los flujos de partículas se compone principalmente de material litogénico con pequeñas contribuciones de ópalo en las estaciones de cañón (Fig.2.5). La baja variabilidad de la materia orgánica y su falta de relación con las concentraciones de ópalo en las estaciones de cañón (Fig. 2.6) sugieren que el ópalo llegó probablemente a partir de fragmentos del esqueleto de sílice resuspendido de la plataforma.

En general, los valores registrados durante los tres meses del periodo de tormentas representan el 60% de los flujos de masa registrados en el cañón de Blanes y el 44% de los flujos de masa en las estaciones del talud.

Impacto de la formación de agua densa y el florecimiento fitoplanctonico en los flujos de partículas

En febrero de 2009 una disminución repentina de la temperatura hasta 12.14 º C y un aumento en la velocidad de la corriente de hasta 50 cm s-1 en la estación BC300 indican la llegada de agua intermedia occidental (WIW), es decir, agua densa de plataforma, probablemente desde el Golfo de León que se propaga hasta el cañón de Blanes como WIW. No es la primera vez que aguas WIW se describen en el cañón submarino de Blanes, tanto mediante modelos físicos de circulación (Ulses et al. 2008), como mediante la

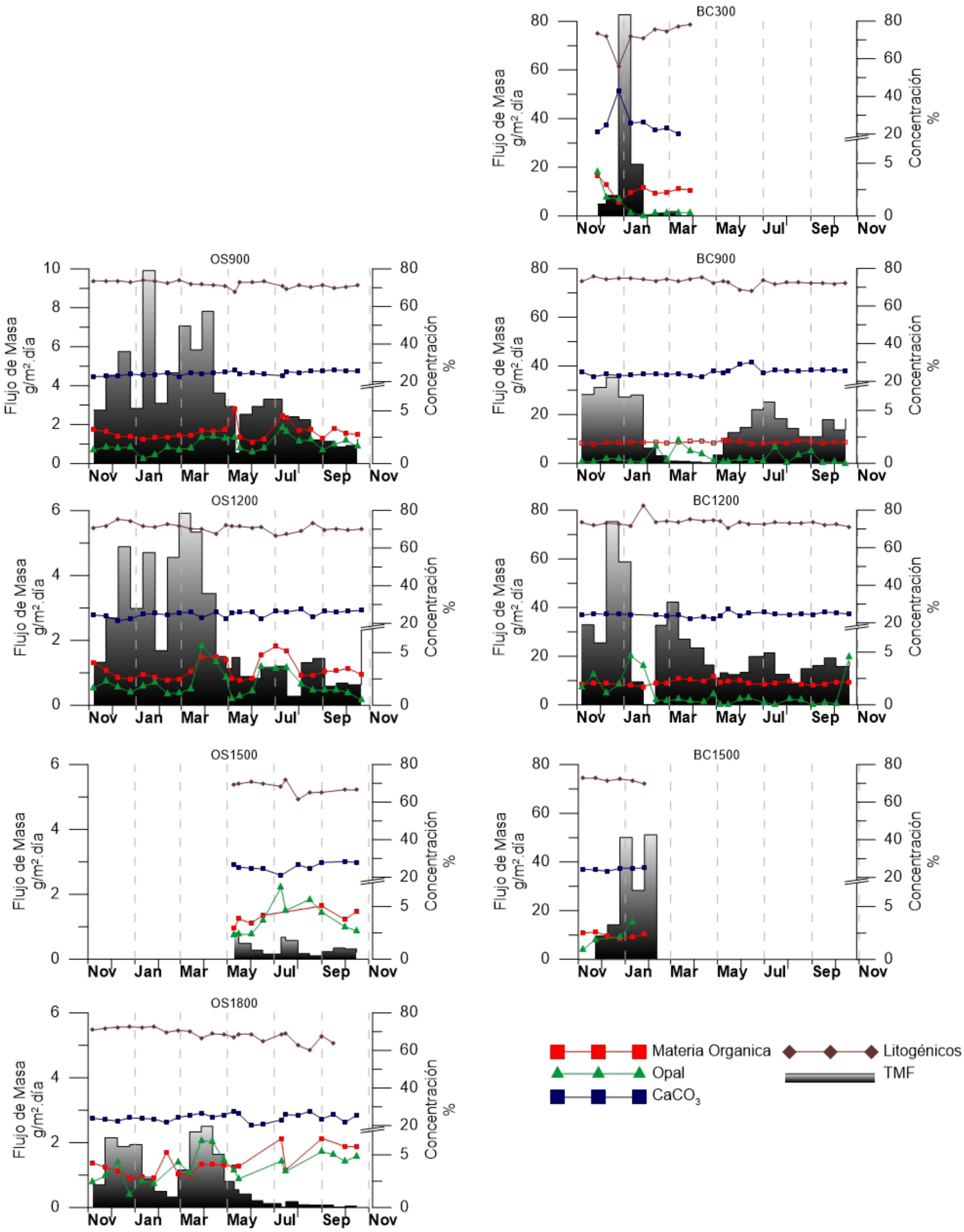

Fig. 5.2. Series temporales del flujo total de masa (g.m-2.d-1) (barras grises) y los componentes mayoritarios (% en peso, material organic en rojo, opal en verde, CaCO3 en azul y litogénicoas en marron)

medida de variables físicas, temperatura y salinidad (Zúñiga et al., 2009).

En el invierno de 2009, la cascada de aguas densas de plataforma en el Golfo de León no fueron particularmente intensa (Puig et al., 2013), esto también se refleja en el cañón de Blanes, ya que el acontecimiento registrado de WIW fue de corta duración y no llegó a las estaciones más profundas (no se registró en las estaciones BC1200 y BC1500). Las trampas de sedimentos no presentaron ningún aumento en los flujos de masa, aunque no podemos descartar la obstrucción de los recipientes recolectores.

En marzo 2009, el registro de aguas frías y más saladas en las estaciones del talud (OS), se interpreta como el resultado de la llegada de la masa de agua denominada Agua Profunda del Mediterráneo occidental (WMDW). La entrada de esta masa de agua se registra en el talud desde marzo hasta principios de mayo de 2009, junto con un aumento de la velocidad de corriente de hasta 26 cm s-1 y un descenso de la temperatura del agua desde 13.1ºC hasta 12.95ºC (Fig. 2.3).

Esta masa de agua se forma bajo condiciones invernales extremas en el Golfo de León y en el Mar de Liguria. En invierno cuando el aire es muy frio y sopla sobre el mar, enfría y evapora el agua. En el Mediterráneo, la evaporación es tan grande que la salinidad del agua le permite alcanzar una densidad tal que se hunde hasta el fondo. Este proceso da lugar a lo que se denomina convección profunda (López-Jurado et al., 2005).

En las estaciones más alejadas de costa OS1200 y OS1800 los flujos máximos de todo el período de estudio se registraron en marzo de 2009 (Fig. 2.5). Nuestra hipótesis es que esto fue causado por el transporte o la resuspensión de sedimentos marinos finos por dichas aguas. Estudios recientes han demostrado que, independientemente de la resuspensión y transporte por una cascada de agua densa de la plataforma en aguas profundas, las altas velocidades de las corrientes asociadas con la convección profunda en alta mar, también tienen la capacidad de volver a resuspender las partículas en el margen profundo y la cuenca (Martin et al, 2010;. Stabholz et al., 2012). A nivel geoquímico, esta situación se traduce en una disminución de los componentes biogénicos (OC y ópalo) de los flujos de masa al inicio del proceso.

Después de la mezcla vertical de la columna de agua y la re-estabilización de la capa superficial, tuvo lugar la floración de fitoplancton ("bloom" de fitoplancton). Este "bloom" ocurre por lo general, a finales de invierno-primavera en el área de estudio (Estrada et al, 1996; Rossi et al, 2003), los nutrientes alcanzan aguas poco profundas debido a la mezcla invernal y son el desencadenante de la floración de fitoplancton (Margalef, 1985). La floración de fitoplancton causó un aumento en las concentraciones de Clorofila-a (Fig. 2.2) y un aumento de la sedimentación de las partículas biogenicas. En consecuencia, la composición de los flujos de masa que recogieron las trampas de sedimento, era más rica en materia orgánica y ópalo (Fig. 2.5). Durante los periodos del bloom fitoplanctónico, las aguas superficiales se empiezan a calentar y se desarrolla la picnoclina. Una vez que el fitoplancton ha agotado los nutrientes disponibles, los organismos empiezan a morir y hundirse. La influencia de la sedimentación pelágica es más patente en el talud adyacente que en el interior del cañón, ya que en el cañón al transportar mayor cantidad de partículas, la materia orgánica queda diluida. En el talud las concentraciones de ópalo explican la mayor parte de la varianza del OC, mientras que no existe correlación entre estas dos variables dentro del cañón (Fig. 2.6). Esto es debido a la casi constante mezcla y homogeneización de las partículas en el interior del cañón a causa de las fuertes corrientes, que impiden que la señal asociada a la sedimentación pelágica sea evidente. (Fig. 2.6.B).

En términos generales, la convección en mar abierto de 2009 junto con la producción primaria asociada significo el 13% del flujo OC en el cañón de Blanes y el 34% en el talud

Impacto de las entradas de polvo atmosférico sobre los flujos de partículas

Entre junio y septiembre de 2009 las trampas situadas en el talud registraron un aumento en compuestos orgánicos (OC y ópalo biogénico) (Fig.2.5) sin ningún aumento evidente en la concentración de clorofila-a superficial observada en las imágenes de satélite (Fig. 2.2). El origen de las entradas de materiales frescos bajo esta situación en los meses de verano podría ser explicado por el desarrollo de un máximo de clorofila profunda estrechamente asociado a la nutriclina (Estrada, 1996). Además en el noroeste del Mediterráneo se han descrito procesos causados por la llegada de viento cargado de polvo que pueden, hasta cierto punto, compen-

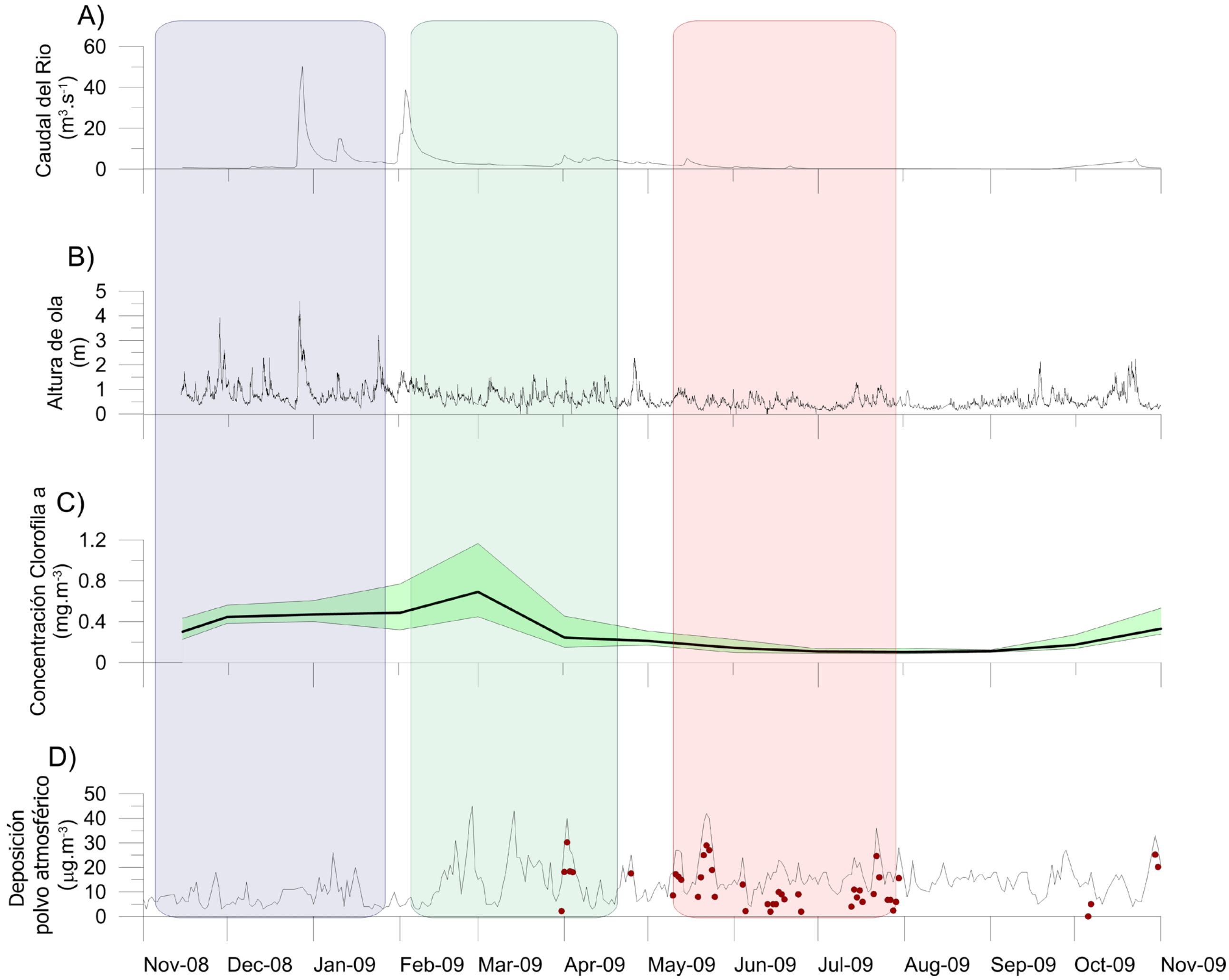

Fig. 5.3. Condiciones ambientales en la zona del studio durante el period de muestreo, desde noviembre 2008 hasta noviembre del 2009. (A) Descarga diaria del rio Tordera (m3.s-1); (B) altura de ola significante (m); (C) media mensual, máximo y minimo de la concentración de clorofila obtenida a través del satélite SeaWIFS (mg.m-2); y (D) deposición de polvo (linea) y deposición de polvo del Sahara (puntos rojos).

sar el agotamiento de los nutrientes debido a la estratificación del agua y producir floraciones de fitoplancton secundarias (Goutx et al., 2000; Zuñiga et al., 2008; Pasqual et al., 2011).

Debido a la proximidad de la región mediterránea al norte de África y al desierto del Sahara en concreto, esta zona es afectada, recurrentemente, por este fenómeno de intrusiones de polvo provenientes del Sahara. Grandes cantidades de polvo mineral se movilizan desde las regiones áridas del norte de África y se inyecta en la atmósfera en condiciones climáticas favorables, lo cual lleva a su deposición en el Mediterráneo occidental (Guerzoni et al, 1997; Guerzoni et al, 1999; Ridame y Guieu, 2002). Dichos aportes traen nuevos nutrientes, como hierro y fósforo inorgánico que se disuelve en las aguas superficiales del Mediterráneo, y estimulan la producción primaria durante los períodos de verano, a pesar de que la columna de agua este estratificada (es decir, no hay entradas de nutrientes de aguas profundas al no haber mezcla vertical).

Al final de la primavera y principios del verano de 2009, hubo una llegada elevada de polvo del Sahara (Fig. 2.2) a la zona del Mediterráneo noroccidental y en paralelo, se registro un aumento de las componentes biogénicos visible en las muestras recogidas por las trampas de sedimento en el talud. La llegada de nuevos nutrientes pudo haber causado un bloom de fitoplancton a principios de verano. En el capítulo 3 vemos como las muestras de las de trampa de sedimentos del verano de 2009 muestran un aumento en la concentración fitopigmentos y a su vez un aumento en el valor nutritivo de los flujos de partículas comparable a las muestras correspondientes a la del bloom de fitoplancton de primavera. El hecho de que la imagen vía satélite no registre un aumento de la clorofila-a para este periodo, inducida por las entradas de polvo del Sahara (Fig. 2.2), no debe interpretarse como una falta de respuesta biológica marina, sino como consecuencia de la falta de sensibilidad de los sensores del satélite en la detección de variaciones muy pequeñas de clorofila-a (Volpe et al., 2009), o simplemente por el desarrollo de un máximo subsuperficial de clorofila profundo, como señala Estrada et al., (1993).

El aumento de flujo de partículas biogénicas fue más evidente en las estaciones del talud, debido a que la influencia pelágica es mayor y la advección lateral de sedimentos resuspendidos en esta zona tiene menor importancia. Además, en la correlación OC vs. ópalo asociada a la llegada de polvo del Sahara, la línea de regresión nos da una pendiente mayor que durante el periodo del bloom fitoplanctónico de primavera (fig. 2.6) lo que sugiere un cambio en la comunidad pelágica entre el periodo de floración y la fertilización por aportes eólicos, con menos contribución de ópalo, indicando un cambio de organismos productores de silíce (diatomeas) por otros organismos productores de carbonato. Esta idea es apoyada por la alta concentración de $CaCO_3$ en los flujos de partículas en el Cañón de Blanes, que apunta a la sedimentación de los organismos con conchas carbonatadas, secundadada por la inspección visual de las muestras con abundantes pterópodos (Fig.2. 4). Este hecho provoca una combinación de la producción secundaria y el ajuste de fitoplancton calcáreo.

Impacto de la pesca de arrastre de fondo en los flujos de partículas

No obstante la entrada de polvo del Sahara, no justifica el aumento relativo en el flujo de masa que se observó entre mayo y julio de 2009, en las trampas situadas a 900 m de profundidad en ambos dominios, cañón y talud y, en menor medida, a 1200 m de profundidad Este flujo de masa contenía poco material biogénico. La influencia de la pesca de arrastre se ha planteado como hipótesis de ser la causa de tales inesperados flujos de partículas que se producen en los meses de verano, caracterizado por condiciones de mar en calma, con olas pequeñas y baja escorrentía superficial (Puig y Palanques, 1998;. Palanques et al, 2005; Puig et al,. 2012). De hecho, el cañón de Blanes y los taludes adyacentes contienen caladeros donde el arrastre de fondo es comúnmente practicado.

La flota de arrastre local pesca hasta 800 m de profundidad (Ramirez-Llodra et al., 2010, su Fig. 1), con el esfuerzo de pesca principal concentrado a lo largo del talud oriental desde finales de invierno hasta principios del verano y sobre la pared oriental y el eje del cañón desde finales de verano a mediados del invierno (Company et al, 2008; Sarda et al, 2009). El flanco occidental del cañón se usa poco para la pesca, debido a su topografía escarpada y rugosa (Ramirez-Llodra et al., 2010).

Nuestra hipótesis es que el aumento de los flujos de partículas registradas a 900 m y 1200 m en el verano de 2009 podrían haber sido causados por la pesca de arrastre que conduce a la formación de nubes de resuspensión (Puig et al., 2012), seguido por la posterior sedimentación de las partículas, en su mayoría material litogénico, directamente sobre los propios caladeros o a corta distancia debido a la calma en dichas profundidades durante esa época del año. En condiciones más dinámicas, como las de invierno, tal resuspensión, inducida por el hombre, y su sedimentación son menos evidentes o imperceptibles, probablemente debido a una dilución más grande de los flujos en el medio o por el transporte de las corrientes más rápido y más lejos.

En general, el peso relativo en el flujo total anual de OC de la producción primaria vinculada a las entradas de polvo y de resuspensión debido a la pesca de arrastre de fondo, que ocurre en su mayoría al mismo tiempo, es del 17% en el cañón de Blanes y el 18% en el talud. Obviamente, el carácter sincrónico de estos dos factores, entradas de polvo y la pesca de arrastre de fondo, hace muy difícil separar con fiabilidad la contribución de cada uno de ellos con el total de los flujos de OC.

5.2. COMPOSICIÓN BIOQUÍMICA Y BIODISPONIBILIDAD DE LA MATERIA ORGANICA.

Existen pocos estudios que evalúan simultáneamente los cambios espacio-temporales de las características bioquímicas de la materia orgánica en los cañones submarinos del Mar Mediterráneo (Tesi et al., 2008; Sanchez-Vidal et al., 2009, Pasqual et al., 2011). Además, la información sobre la fracción de la materia orgánica fácilmente digerible (materia orgánica lábil) en muestras de trampas de sedimento es prácticamente inexistente. El presente estudio constituye el primer trabajo que considera sinópticamente los cambios estacionales y espaciales en las características de la materia orgánica, incluyendo la fracción lábil, en un cañón submarino del Mediterráneo y su talud adyacente. Este estudio se basa en un enfoque biomimético (abstracción de un buen diseño de la naturaleza) y a pesar de sus limitaciones, esta técnica ha proporcionado información cuantitativa sobre los consumidores heterótrofos y la disponibilidad de alimento para muchos ecosistemas bentónicos (Mayer et al., 1994; Grémare et al., 1997; Dell'Anno et al., 2000; Danovaro et al., 2001; Grémare et al., 2002; Grémare et al., 2003; Grémare et al., 2005; Vandewiele et al., 2009, Bourgeois et al., 2011). En este estudio se utilizaron las trampas de sedimento situadas a 1200 m de profundidad, tanto en el cañón de Blanes como en el talud, con una resolución de 7/8 días. Además se analizaron y caracterizaron los componentes biopoliméricos (semilábiles: proteínas, carbohidratos y lípidos) la fracción fácilmente digerible de la materia orgánica (proteínas lábiles y carbohidratos lábiles) y los pigmentos totales.

Para estudiar las variaciones temporales con los datos anteriores se realizó un análisis de varianza multivariado con base en permutaciones (PERMANOVA; Anderson, 2001; McArdle y Anderson, 2001). El diseño incluyó dos factores ortogonales: espacio-morfología del lecho marino (2 niveles fijos: cañón vs talud) y el tiempo de muestreo (44 niveles fijos, cada uno correspondiente a una semana de recolección de partículas de la trampa) (véase capitulo 3 sección 2.4).

Los resultados estadísticos revelaron que el contenido de todas las variables investigadas en las muestras (fitopigmentos, proteínas, carbohidratos, lípidos, BPC y BAOC), fueron significativamente afectados por la interacción entre los dos factores analizados (Tiempo x espacio) (Tabla 3.2).

Como resumen de dichos análisis estadísticos

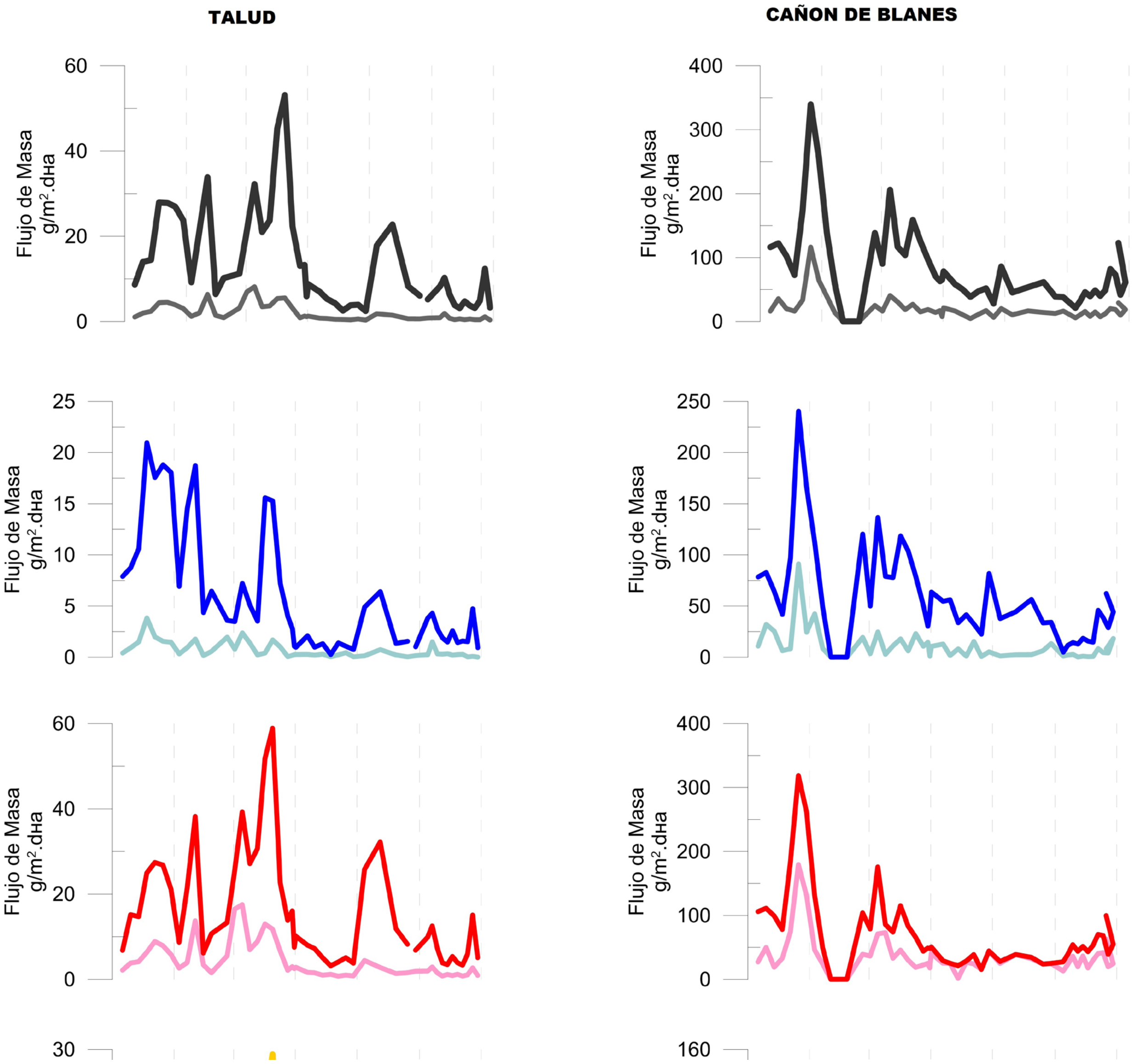

Fig. 5.4. Serie temporal del contenido flujo de los compuesto organicos biodisponibles (mg g-1) de las trampas de sedimento a 1200 metros de profundidad

podemos decir que en el cañón de Blanes, las proteínas, los carbohidratos y los lípidos contribuyeron, en promedio anual, casi por igual (casi el 33% cada uno) en el flujo de BPC. El BPC representó, en promedio anual, aproximadamente el 33% del total del flujo de OC (del 20-49%, con un 17% de variación sobre una base anual). Alrededor del 24% (del 11-43%) del BPC que llegó al fondo del mar en el cañón era lábil. La concentración total de fitopigmentos explica aproximadamente el 64% de la varianza del BPC, con el 36% restante del BPC asociado a fuentes no-algales. El BPC y el BAOC covarían significativamente también en el cañón, con cerca del 85% de la varianza del BPC explicada por las variaciones en el contenido de BAOC

En el cañón, el contenido de casi todos los compuestos orgánicos muestran variaciones temporales amplias y significativas, la mayoría de ellos se caracterizan por un aumento de marzo a mayo de 2009 (Fig. 5.4). Por ejemplo los lípidos presentan un máximo en abril de 2009 (hasta 3,45 mg g^{-1}) y lo carbohidratos totales en mayo de 2009 (5,1 mg g^{-1}). El máximo de carbohidratos lábiles (2,87 mg g^{-1}) también tuvo lugar en mayo de 2009, representando alrededor del 58% del total de carbohidratos Las concentraciones de proteínas totales no muestran ningún máximo significativo, aunque se observó un mayor contenido de proteína durante el periodo de abril-mayo de 2009 (alrededor de 4,9 mg g^{-1}). En general, las proteínas lábiles representaron en promedio alrededor del 17% del total de proteínas, con un máximo relativo en abril de 2009 (48%), lo que corresponde a 1,11 mg g-1de proteína lábil.

En el talud, los carbohidratos totales fueron, en general, la clase dominante de los compuestos biopoliméricos, con un aporte medio al BPC en torno a un 46%, seguido de los lípidos (33%) y proteínas (21%). El BPC representa aproximadamente el 35% del total de flujo de OC en el talud (del 1-51% con un 36% de variación sobre una base anual). Dentro del BPC que llegó al fondo en el talud, solo un promedio del 16% era lábil (del 6-50%). La concentración total de fitopigmentos explica sólo 23% de la varianza de BPC, con el 67% restante del BPC asociado a fuentes no-algales. El BPC y el BAOC varían significativamente en el talud, aproximadamente el 85% de la varianza del BPC se puede explicar por variaciones en el contenido de BAOC.

En el talud, el contenido de casi todos los compuestos orgánicos también muestra variaciones temporales amplias y significativas, que se caracterizan en general, para los carbohidratos y lípidos, por un aumento de marzo a abril de 2009 con máximos significativos en abril de 2009 (11,7 mg g^{-1} y 6.34 mg g^{-1} respectivamente), una disminución de mayo a julio de 2009, y un máximo en agosto de 2009, con valores de carbohidratos de 23,7 mg g^{-1} y de 7.58 mg g^{-1} de lípidos (Figura 3.4).

Las proteínas y los fitopigmentos, presentan sus máximos en enero de 2009 (7.09 mg g^{-1}), y mayo de 2009 (0.57 mg g^{-1}), respectivamente.

La fracción digerible de carbohidratos fue alrededor del 24% del total de carbohidratos, con un máximo (65%) en febrero de 2009 (correspondiente a 2,48 mg g^{-1} de carbohidratos lábiles). Las proteínas lábiles representan en promedio cerca de 12% del total de proteínas, con un valor máximo de 54% (correspondiente a una concentración de 0,9 mg g^{-1}) en diciembre de 2008.

Con objeto de analizar el efecto que tuvo el periodo de tormentas en la calidad y el valor nutricional dentro del cañón submarino de Blanes, se ha estudiado la composición bioquímica de la materia orgánica, (fitopigmentos, proteínas, carbohidratos, lípidos y BPC) de las muestras recogidas por las trampas de sedimento dentro del cañón submarino de Blanes (estaciones BC300, BC900, BC1200 y BC1500) desde noviembre de 2008 hasta abril de 2009.

Los flujos de fitopigmentos y todo el espectro de compuestos biopoliméricos (proteínas, carbohidratos y lípidos, Tabla 4.3) varían significativamente durante el periodo de tormentas. En particular, los flujos de todos los compuestos bioquímicos aumentaron desde el comienzo del estudio, en noviembre de 2008, mostrando máximos sincrónicos o cercanos en invierno en todas las estaciones (carbohidratos, lípidos, proteínas y pigmentos), y después disminuyeron consistentemente. Las variaciones en la composición bioquímica de las partículas sedimentadas señalan que la fuerte tormenta que se produjo el 26 de diciembre de 2008 en el área de estudio produjo un fuerte aumento en la cantidad de materia orgánica transportada por el cañón de Blanes.

La fracción algal-BPC, indicador de la frescura de la MO, calculada en las trampas de sedimento durante el periodo de tormentas, fue generalmente muy baja, no superior a 0,15%. Sin embargo, en todas las estaciones de muestreo, la fracción algal-BPC varió significativamente con el tiempo, con valores generalmente más altos en noviembre de 2008 y diciembre de 2008 en las estaciones BC300 BC900, y BC1500 y a principios de marzo de 2009 en BC1200 (Fig. 4.3). Los valores de la relación proteína-carbohidrato, indicador de la calidad de nutricional, en las muestras variaron de 0,4 a > 2,0 y mostraron una variabilidad temporal significativa en todas las estaciones investigadas. En los meses de invierno (finales de diciembre hasta mitad de marzo) esta proporción aumentó en la cabecera del cañón (BC300) y disminuyó en la trampa más profunda del cañón medio (BC1500), mientras que a partir de finales de invierno a comienzos de primavera (mitad de marzo hasta final de abril) se incrementó en las estaciones de BC900 y BC1200, de modo que no se observó una tendencia consistente (Fig. 4.5). Esto puede estar influenciado por el agotamiento pronunciado del sedimento transportado paso a paso explicado en el punto 5.1.

En general, las entradas correspondientes de materia orgánica total en el interior del cañón, fueron acompañadas, con un aumento de los flujos de todos los compuestos biopoliméricos. Sin embargo, también se encontró que los picos en los flujos de OC durante la tormenta de invierno implicó una disminución en los porcentajes de las fracciones biopoliméricas y algal dentro de estos flujos (Fig. 4.5)

5.2.1. Importancia trófica de los flujos de masa en el Cañón de Blanes vs. el talud adyacente: biodisponibilidad de las partículas en sedimentación

Es evidente que hay una diferencia entre los flujos en las dos estaciones de muestreo debido a su ubicación. La estación OS 1200 situado a unos 20 km de la isóbata de 200 m, presenta en promedio un TMF de 2380.98 mg m^{-2} d^{-1} y valores de flujo de OC y ópalo de 40.57 y 49.87 mg m^{-2} d^{-1} en promedio, respectivamente (1,70 y 2,09% de la TMF, respectivamente). Por otro lado los flujos en la estación BC1200 situada a unos 10 km de la isóbata de 200 m, presenta con valores de 22.898,17 mg m^{-2} d^{-1} para los flujos de masa y 240,57 y 269,63 para los flujos de OC y ópalo, con una contribución del OC y el ópalo al TMF menor (1,05 y 1,18% respectivamente). Debemos considerar que el camino que sigue la materia orgánica e inorgánica desde la superficie del mar hasta el fondo de la cuenca no es sólo debido a la sedimentación vertical, ya que una gran proporción de las partículas es transportado por advección lateral antes de la deposición en el lecho marino. Por lo tanto, no podemos excluir que parte de las diferencias observadas en el TMF entre el cañón y el talud adyacente pueda atribuirse a la distancia a costa de las dos zonas de muestreo, esta variable podría haber llevado a las trampas a interceptar partículas transportadas sobre diferentes distancias horizontales.

La entrada de sedimentos en la trampa de origen terrígeno o bien de material resuspendido, es corroborada por la presencia de concentraciones relativamente altas de carbohidratos en las muestras, que representaron en promedio 0,3% y 0,7% del flujo total de masa en el talud y el cañón, respectivamente, y 28,7% y 44,5%, respectivamente, del OC total. Siguiendo el orden de la biodisponibilidad para los componente bioquímicos según Wakeham et al. (1997) (pig mentos>lípidos>proteínas>carbohidratos), los carbohidratos constituyen la fracción más refractaria de compuestos orgánicos analizados en este estudio.

La presencia de una mayor fracción orgánica en el flujo total de masa del talud que en el eje del cañón, parece indicar que, los consumidores heterótrofos de los sedimentos del talud se benefician de una concentración de partículas de comida consistentemente mayor, que la disponible en el cañón a igual profundidad. Sin embargo, nuestros resultados también muestran que el talud se caracteriza principalmente por una notable variabilidad estacional en la calidad de los alimentos de las partículas descendentes, con máximos de concentración asociados con el ciclo estacional de la producción biológica en la zona eufótica, mientras que el cañón muestra una más pronunciada variabilidad temporal en la cantidad de partículas que sedimentan. Esta notable diferencia en la cantidad / calidad de las partículas que entran en el eje del cañón y el talud adyacente, probablemente tiene consecuencias en la nutrición del bentos de aguas profundas que habitan en estos dos hábitats. Es decir, un organismo bentónico que viva en el interior del cañón de Blanes tendría que ingerir más partículas para cumplir con sus necesidades alimentarias que otro que viviera en el talud adyacente, donde el porcentaje de partículas de OC que sedimenta es casi siempre superior a la del cañón. No obstante, nuestros datos indican también que la fracción lábil de la materia orgánica que llega al bentos en el cañón es generalmente más alto que en el talud. Por lo que el bentos que habita en sedimentos de aguas profundas en el cañón, a pesar de recibir una menor concentración de partículas alimentarias, tienen una mayor disponibilidad de materia orgánica lábil. De forma aproximada podemos calcular que un animal dentro del cañón y expuesto a una unidad de masa de material puede beneficiarse de alrededor del 1% de partículas alimentarias, mientras que un animal en el talud recibe aproximadamente el doble de esta cantidad (1,7%). En el cañón, la dilución de estas partículas alimentarias en una matriz principalmente inorgánica está parcialmente compensada por una mayor biodisponibilidad de la materia orgánica. El 8% de las partículas alimentarias dentro del cañón son lábiles, mientras que en el talud adyacente solo el 5% es lábil.

La forma de alimentación de los organismos heterótrofos se basa en encontrar, capturar y consumir alimentos con la mayor cantidad de calorías disponibles gastando la menor cantidad de energía posible (Shoener, 1971; Pyke et al, 1977). La teoría del "aprovisionamiento óptimo" (McArthur y Pianka, 1966), se ha utilizado para explicar cómo los organismos que viven en ambientes limitados de alimentos - como el mar profundo pueden obtener la energía necesaria a partir de un consumo muy bajo de materia orgánica (Jumars et al, 1990). Por lo que a pesar de que un organismo heterótrofo que viven en el cañón debe gastar más energía en "buscar" partículas alimentarias, una vez adquiridas estas partículas, son más lábiles que las partículas alimentarias que recibe un animal que vive en el talud adyacente, aunque tenga más fácil acceso a ellas. Este resultado se traduce en que aunque los organismos dentro del cañón sean penalizados por un flujo de partículas en su mayoría inorgánico, pueden contrarrestarlo aprovechando aportes de más partículas lábiles.

Este estudio, proporciona nuevos conocimientos sobre las diferentes modalidades que los organismos bentónicos que habitan en diferentes hábitats profundos, pueden experimentar para sobrevivir en un entorno con pocas partículas alimentarias. Nuestros resultados confirman recientes estudios que demuestran, que aportes elevados de materia orgánica en los cañones pueden favorecer la contribución faunística y crear "hot spots" de biomasa y de procesamiento de carbón a lo largo del margen continental (Van Oevelen et al., 2011). Sin embargo, que las entradas de materia orgánica tenga un efecto positivo en el bentos, depende también de las tasas de sedimentación y de la cantidad global de sedimento depositado en el fondo del mar.

Debido a que los cañones submarinos actúan como canal preferencial en el transporte de partículas, y con ello de materia orgánica, estos por norma general albergan mayor biomasa y biodiversidad que los taludes adyacentes. (Bianchelli et al., 2008). Por otra parte, las diferencias en la biodiversidad entre los cañones y el talud son generalmente más grandes en términos de estructura de la comunidad faunística (es decir, la diversidad beta) que en términos de riqueza de especies (diversidad alfa) (Danovaro et al., 2009).

Estas diferencias se explican principalmente por la disponibilidad de las partículas alimentarias en el sedimento (Danovaro et al., 2009), que son consecuencia de la naturaleza, el origen y la calidad alimentaria de las partículas provenientes de la columna de agua superior (Danovaro et al., 1999). Por lo tanto, nuestros resultados nos permiten plantear la hipótesis de que las diferencias en la fauna sésil entre los sedimentos del fondo de los cañones y el talud adyacente son el resultado de las adaptaciones de las comunidades bentónicas a las diferentes combinaciones de cantidad y calidad de alimentos en los dos hábitats.

5.2.2. Control hidrodinámico y climático de las entradas de materia orgánica biodisponible para los ecosistemas profundos

Si el comportamiento de los flujos de masa en el cañón de Blanes se puede extrapolar a otros cañones submarinos a lo largo de los márgenes del Mediterráneo sigue siendo una pregunta abierta. Varios cañones submarinos del Mediterráneo han sido definidos como canales principales para el transporte de OC hacia la cuenca profunda debido a las condiciones hidrodinámicas locales (Martin et al, 2006, Palanques et al, 2008; Zuñiga et al, 2009). Sin embargo, otros estudios recientes han demostrado que diferentes cañones (incluso próximos) pueden mostrar grandes diferencias en las características cuantitativas y cualitativas de la materia orgánica sedimentaria, y que estas diferencias no sólo están relacionados con las diferentes características morfológicas de los cañones sino que también, pueden depender del momento del muestreo (Pusceddu et al., 2010). De hecho, los cañones submarinos son a menudo sistemas dominados por procesos episódicos (Palanques et al., 2012), lo que significa que las entradas de partículas al interior de los cañones son en gran parte influenciadas por las anomalías climáticas locales, incluyendo: crecidas fluviales, entradas de polvo eólico y procesos hidrodinámicos marinos de alta energía, como las tormentas, cascada agua densa de la plataforma y convección oceánica profunda (Canals et al, 2006; Sánchez-Vidal et al, 2012; Palanques et al, 2012), además de la producción primaria en la superficie (Danovaro et al., 2001). En este sentido, se debe considerar que el transporte de sedimentos a través de cañones submarinos no es constante ni unidireccional, sino que más bien tiene un comportamiento alternante intermitente (Palanques et al., 2012).

Uno de los ejemplos de los procesos que impulsan el transporte de grandes cantidades de sedimentos y materia orgánica a las profundidades del mar se produce durante fuertes tormentas costeras (Sanchez-Vidal et al 2012).

Nuestros resultados indicarían que en el cañón Blanes las entradas de partículas alimentarias (sensu Danovaro et al., 2001) para el ecosistema batial se diluyen considerablemente con la ocurrencia de tormentas, ya que el aumento de flujo OC es consecuencia de un aumento en el flujo de masa total, principalmente compuesto de partículas litogénicas.

Desde el punto de vista de un detritívoro bentónico, a pesar de que existe una mayor cantidad de material orgánico al alcance en el fondo del mar durante las tormentas, la búsqueda de una alimentación adecuada (cantidad óptima de nutrientes) puede ser más complicada. Por otro lado, podría ser que las grandes inyecciones de partículas alimentarias diluidas, están disponibles y se consuman durante períodos de tiempo más largos, compensando de este modo las "complicaciones" para los consumidores de detritus que sufrirían durante las entradas masivas de partículas tras el paso de una tormenta.

Nuestros resultados indican que al igual que para otros procesos de alta energía (por ejemplo, durante cascadas de agua densa de la plataforma (Pusceddu et al, 2005; Pusceddu et al, 2010a), los cambios en la disponibilidad de alimentos en relación a las grandes tormentas costeras pueden tener importantes consecuencias en la biodiversidad y funcionamiento de los ecosistemas en las profundidades del mar.

Durante el período de las tormentas de otoño-invierno 2008-09 los datos muestran un aumento de las proteínas totales y lábiles y por tanto de su contribución al BPC y a su vez bajos valores de lípidos, este comportamiento no se observa en otras épocas del año. En periodo de primavera y verano 2009, las condiciones hidrodinámicas son menos energéticas que en el periodo anterior, estos dos periodos están marcados por un aumento de los lípidos. Los lípidos son más biodisponibles para los consumidores que las proteínas (Taylor, Karl y Pace, 1986). Podríamos decir que las diferencias en la composición bioquímica resaltan la diferente estructura de las comunidades bentónicas.

La posible ventaja de un alimento más lábil para el bentos de aguas profundas que recibe las entradas forzadas por las anomalías climáticas de la superficie del mar, podría ser contrarrestada e incluso cancelada por la perturbación física y mecánica generada por el flujo por gravedad de las partículas inorgánicas (Pusceddu et al. 2010; Pusceddu et al. 2013), por lo que nuestros resultados confirman que las fuertes tormentas costeras pueden tener consecuencias importantes y casi inmediata sobre el funcionamiento de todo el sistema hasta el fondo marino profundo.

En el talud continental adyacente, a materia orgánica recogida mediante trampas de sedimentos durante la primavera tiene un valor nutricional más alto que a finales de otoño-invierno, esta característica es compartida tanto en el cañón como en el talud continental adyacente (Figura 3.4.b; 3.6). Esta diferencia es probable que sea debido a la floración de plancton descrita anteriormente para el área de estudio (Estrada et al, 1996; Rossi et al, 2003). Durante este período la composición bioquímica de BPC se caracteriza por el aumento de las contribuciones de lípidos en comparación con los observados durante el período de tormenta, que se caracteriza por altos contenidos de proteína (Figura 3.5). Junto con las proteínas, los lípidos pueden representar una fuente de energía preferencial para los consumidores bentónicos (Medernach et al, 2001; Grémare et al, 1997). En el talud, más influenciado por la sedimentación pelágica, el aumento en el valor nutricional de las partículas que sedimentan se magnifica, bien por el efecto de la convección de aguas profundas y la menor llegada de material litogénico.

En verano, nuestros datos mostraron un aumento en el valor nutricional de los sedimentos comparable al aumento durante la floración de primavera que podría ser el resultado de la fertilización tras la entrada de polvo sahariano en la zona (fig 2.2) Estas entradas de polvo sahariano coinciden con aumentos de la producción autótrofa, y por lo tanto, la eficacia de la bomba de carbono biológico en océanos oligotróficos (Pulido-Villena et al., 2008).

Aunque la mayor parte de la variabilidad en las tasas de transporte de partículas se puede explicar sin problemas con los procesos físicos como hidrodinamismo y el forzamiento climático, no podemos excluir el cambio que la composición química de las partículas orgánicas sufre durante el hundimiento debido al consumo de plancton heterótrofos (incluyendo procariotas) (Hedges et. al, 2001), por lo que las diferencias en la composición bioquímica y la biodisponibilidad de las partículas en sedimentación en el cañón de Blanes y el talud adyacente pueden ser también moduladas por las limitaciones biológicas de la columna de agua.

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CAPÍTULO 6
CONCLUSIONES

El presente trabajo sobre los flujos de partículas en el sistema del cañón submarino de Blanes y en el talud adyacente, nos ha permitido caracterizar dichos habitas marinos en función de la distribución espacio-temporal de flujos de masa, su composición y el valor nutricional de la materia orgánica que se deposita.

> Se ha observado que tanto los flujos de masa, cómo su composición, están estrechamente relacionados con distintos procesos atmosféricos e hidrodinámicos (como las tormentas, la convección profunda, las entradas de polvo del desierto…etc.).
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> Se ha especificado para cada proceso las afectaciones en la calidad y cantidad de materia orgánica biodisponible para los organismos de la cuenca profunda. Nuestros datos mostraron que la materia orgánica recogida en las trampas de sedimentos durante la primavera tenía un valor nutricional más alto que durante el periodo de tormentas. Además la entrada de polvo sahariano en la zona podría ser la causa del aumento del valor nutricional de los sedimentos, en verano, comparable al aumento durante la floración de primavera. Por lo que podemos identificar los factores ambientales que potencialmente controlan la diversidad y distribución de los ecosistemas profundos en el Mediterráneo noroccidental.
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> Nuestros resultados apoyan el modelo de que los cañones submarinos actúan como conductos principales del material desde la plataforma continental hasta el fondo de la cuenca, siendo los flujos de masa dentro del cañón submarino de Blanes, siempre mayores (casi un orden de magnitud) que los flujos de masa registrados en el talud a las mismas profundidades. Las crecidas fluviales y las tormentas costeras suponen una fuente, episódica pero, de gran magnitud de materia orgánica con alto valor nutricional para el ecosistema bentónico de aguas profundas, como fue el caso del periodo del invierno del 2008 que contribuyó con el 60% del flujo de OC en el Cañón de Blanes y el 40% en el talud.
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> La transferencia de partículas en la zona del cañón más profundo puede ser favorecida por las entradas laterales de sedimento debido a la densa red de cárcavas en los flancos del cañón, incluyendo material resuspendido por la pesca de arrastre. Como se ve en la figura 2.7, el flujo anual de partículas recuperadas en el cañón submarino de Blanes a 1200 m de profundidad es superior al resto de los flujos anuales recuperados en las demás estaciones de muestreo.

El transporte de materia orgánica dentro del cañón de Blanes es crucial, y su importancia en la cadena trófica puede ser comparada con la de los flujos verticales en el mar abierto. Estos aportes episódicos de materia se traducen en importantes cambios a corto plazo en la biodisponibilidad de la materia orgánica en el fondo marino del cañón de Blanes.

> Durante los procesos de alta energía (cómo representa la tormenta estudiada del 26 de Diciembre de 2008) la calidad de los alimentos disponibles para el ecosistema bentónico profundo disminuye considerablemente, principalmente debido a la dilución por el alto contenido de material litogénico, lo que implica una potencial limitación para la alimentación de las comunidades bentonicas de aguas profundas.
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> La zona del talud adyacente está más influenciado por otros tipos de forzamiento hidrodinámico, tales como la llegada de aguas profundas asociadas a la convección de mar abierto, que puede resuspender sedimentos del talud, y a la aparición del bloom fitoplanctónico y posiblemente eventos de polvo subsahariano.
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> En la zona de talud continental, la cantidad y composición de las partículas en sedimen-

tación estan determinadas por las variaciones estacionales y presenta una influencia pelágica clara.

Los consumidores heterótrofos en los sedimentos del talud pueden beneficiarse de una concentración de partículas de comida consistentemente mayor que la disponible en el cañón a profundidades iguales.

Cabe destacar, que la fracción lábil de materia orgánica que alcanza el bentos en el interior del cañón es mayor que en el talud adyacente. Las diferencias en la biodisponibilidad del OC, pueden ser debidas a la diferencia en la tasa de transporte de partículas que llegan a la parte inferior entre el cañón (más rápido) y el talud adyacente (más lento).

Podemos resumir diciendo que la transferencia de materia en la zona del cañón submarino de Blanes (y en especial de materia orgánica biodisponible) desde la plataforma continental, altamente productiva, hacia la cuenca profunda, está fuertemente controlada por los procesos hidrodinámicos (tormentas, cascadas de aguas densas y convección profunda) y los controles de bioclimáticos anuales ("bloom" de producción primaria de invierno-primavera). Esto provoca diferentes combinaciones de cantidad y calidad de alimentos entre el cañón y el talud adyacente, causando una diferencia faunística entre los sedimentos de los dos hábitats tras las adaptaciones tróficas de las comunidades del fondo.

Estos datos, ponen de manifiesto la "conexión" entre los procesos climáticos de superficie y las aguas profundas, contribuyendo a cambiar nuestra visión paradigmática del interior de los océanos como el último ecosistema de gran estabilidad.

NECESITO del mar porque me enseña
no sé si aprendo música o conciencia.
Pablo Neruda

ANEXO