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Dynamics of benthopelagic food webs of the Catalan slope (NW Mediterranean Sea): environmental drivers and influence on reproductive cycles.

Tesi doctoral

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Sólo sé que no sé nada.

Sócrates

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ABSTRACT / RESUM

ABSTRACT

Food is considered the main limiting factor in the Deep Sea, although few studies have tested this hypothesis. At the same way, seasonality observed in diverse aspects of the fauna in this ecosystem has been attributed to seasonal changes in food availability. These relationships have been analysed to date for fauna of low trophic levels, but such links regarding megafaunal predators remain rather untested.

The present thesis deals with the analysis of the seasonal dynamics of the bathyal benthic and benthopelagic megafauna communities over a year period, and their relationship with inputs and availability of food. For this purpose, the thesis is based on data collected in the four seasons of a natural year in the Catalan Slope (NW Mediterranean Sea). The Catalan Slope is an oligotrophic system where both vertical and advective fluxes contribute to organic matter arrival to bathyal depths, both fluxes presenting marked mesoscale temporal fluctuations. We determined the seasonal patterns in the structure and functioning of the deep megafaunal assemblages, mainly fish and decapod crustaceans, by means of the analysis of their composition, food web organisation and feeding ecology of the dominant species. Understanding the relationship between seasonality in food inputs and the different seasonal patterns taking place among megafauna requires comprehensive studies encompassing the several food sources and faunal trophic levels of food webs. For this reason, besides data on megafauna, the present thesis includes data concerning the main processes providing food to bathyal depths (surface primary production and river discharge) as well as data simultaneously sampled regarding the abiotic characteristics of the environment (e.g. temperature, salinity) and about the food available there, from indicators of different organic sources (e.g. total lipids and total organic carbon in sediments, fluorescence 5 m above the seabed) to densities of potential prey for megafauna (i.e. zooplankton, suprabenthos and infauna). The relationships between the food sources and the faunal trends were explored by multivariate statistical methodologies. In addition, we studied the influence of food on reproductive cycles of fish and decapod crustaceans.

Data used for this thesis was collected on the continental middle slope of the Catalan Sea, between 423 and 1175 m, in five oceanographic cruises between February 2007 and February 2008. Samples were obtained from three depth strata.

In Chapter 2, we examined the spatial and temporal (seasonal) patterns of abundance and biomass of benthopelagic megafauna assemblages. Bathymetric and topographic (canyon) changes occurred, related to patterns in prey biomass. Megafauna assemblages also changed seasonally related to the stratification *versus* homogeneity of the water column, basically defined by changes in salinity and temperature. Greater densities of species with low trophic levels (e.g. *Cymbulia peroni*, *Gennadas elegans*) were observed under homogenous water column. Both peaks of surface production in February and of river discharge in April and the related patterns in near-bottom turbidity favoured greater densities of megafauna. The same peaks of surface primary production and of river discharge corresponded to a maximum in megafaunal biomass in summer after *ca.* 3–5 months. Peaks of macrofaunal key prey taxa (zooplankton, micronekton and benthic infauna) were observed after peaks of primary production and *ca.* 2 months before peaks in abundance and biomass of megafauna, suggesting macrofauna channelled the organic matter inputs to higher trophic levels.

In chapters 3 and 4, we studied the seasonal patterns in the structure of the benthic and the benthopelagic food webs by analysing the carbon and nitrogen stable isotopes of macro- and megafauna and of sinking and sedimented particulate organic matter. We observed a continuum of values in the isotope ratios of benthic fauna, which indicated a wide spectrum of feeding strategies (from active suspension feeders [ASF] to top predators) and complex food webs consisting of at least 3 trophic levels. ASF (e.g. the bivalve *Abra longicallus*) and surface deposit feeders (e.g. the thalassiniid shrimp *Calocaris macandreae*) had similar trophic level, which was the lowest of the benthic community. Both likely fed upon sinking particles, but ASF responded earlier to the late-winter surface bloom of production. Enriched ^{15}N of sub-surface deposit feeders pointed to the existence of a new branch in the food web based on the consumption of refractory material, bacteria and matter from biodeposition processes. The benthic community was sustained by multiple carbon sources throughout the whole year, with a widest array of carbon sources under water column stratification. Environmental analysis revealed that materials derived from the late-winter peak of surface primary production were the main food source for the benthic community under water column homogeneity. Besides, terrestrial inputs channelled through maximal river discharges in April were an additional food source for benthos in summer, after *ca.* 2 months, in periods of low water turbidity.

The analyses of stable isotopes of benthopelagic fish and decapod crustaceans revealed a trophic segregation between these two groups: fish had higher trophic levels and ingested less amounts of benthic prey than decapod crustaceans. Within each taxon, the community was structured as a function both of the benthic-pelagic gradient in the water-sediment interface where megafauna species found their prey and of the own predator and prey size, the latter factor being especially important among fish. The study of diets of dominant fish and decapod crustacean species developed in the next two chapters led to similar conclusions. By stable isotopes we identified two food webs based on pelagic (macroplankton) *versus* benthic production. Benthopelagic megafauna relied on marine snow after peaks in surface production. Conversely, a larger array of food sources, probably from advection, sustained the community in periods of water column stratification. Seasonal changes in food web structure agreed with the patterns of macrofauna production, ultimately linked to inputs of primary food sources. The ^{13}C depletion after winter among migratory macroplankton feeders is consistent with greater consumption of pelagic prey, which depend on phytodetritus inputs from surface production as food source. The ^{15}N enrichment in summer among benthos feeders suggests greater consumption of enriched hyperbenthic macrofauna, which feed upon sedimented organic matter or matter near the seabed. Consistently, seasonal changes in the prey used by macroplankton feeders were determined by changes in the amount of lipids and of chlorophyll pigments in sediments, both proxies of phytodetritus inputs. In contrast, changes in the prey used by benthos feeders were explained by variations in total organic carbon (TOC) on sediments and in food in the adjacent water layer (determined by measuring fluorescence 5 m above the seabed), proxies of sedimented or (re)suspended organic matter respectively.

In chapters 5 and 6, we studied the trophic dynamics and the reproductive cycles of dominant fish and decapod crustacean species, and we observed some common patterns in both taxa. Fish and decapods were segregated into feeding guilds based on the consumption of benthic or mesopelagic prey. Additionally small fish species were segregated from the rest and mainly consumed hyperbenthos and small macroplankton. Changes in food availability were critical drivers of seasonal changes in the trophic dynamics of both fish and decapods, and different feeding guilds coupled distinctively with food inputs. Benthos feeder fishes increased feeding activity upon hyperbenthic and deposit feeding macrofauna (*Calocaris macandreae*) in summer, two months after the peak of surface production when more TOC was available in the sediments. Macroplankton feeders and small-sized fish increased feeding activity towards mesopelagic crustaceans or highly natatory hyperbenthos after spring, in association with greater inputs of phytodetritus (i.e. lipids in sediments) derived from surface production blooms. Besides, greater feeding intensity enhanced quick storage of lipids in the muscle of small-sized fish. Macroplankton feeder decapods responded earlier to the late-winter surface bloom, increasing feeding intensity towards greater variety of zooplankton prey in spring (April). Differently, feeding intensity of the benthos feeder decapod *Aristeus antennatus* was enhanced by the availability of both benthic and mesopelagic prey. Consistently, its diet varied between all consecutive seasons related with the exploitation of hyperbenthic and planktonic macrofauna in addition to benthos. Besides, the phase of the reproductive cycle also seems to influence feeding patterns, and increased food consumption and ingestion of more energetic prey, mainly mesopelagic (e.g. euphausiids, Pasiphaeidae, fish) but also hyperbenthic (*Natatolana borealis*), took place in pre-reproductive periods for most species in spite of their trophic guild.

Gonad maturation (i.e. gonadosomatic index - GSI) was associated with abundances of primary trophic resources and of specific prey, suggesting trophic availability regulates the reproductive cycles, at least partially. GSI was controlled by surface production processes and associated phytodetrital inputs in all feeding groups, with a delay of *ca.* 2-3 months. Temporal trends in GSI differed among species from the same trophic guild both for fish and for decapods, indicating that seasonal availability and use of food do not affect all species reproductive processes equally.

RESUM

En general, es considera que la disponibilitat d'aliment és el principal factor limitant en l'ecologia del Mar Profund, tot i que pocs estudis han provat aquesta afirmació. De la mateixa manera, l'existència d'estacionalitat en diversos aspectes de la fauna batial ha estat atribuïda als canvis estacionals en la disponibilitat d'aliment. La relació entre aquests dos fenòmens ha estat analitzada a dia d'avui en fauna de nivell tròfic baix. No obstant, existeix molt poca informació respecte aquesta connexió en megafauna situada en els nivells tròfics més alts de la xarxa tròfica.

La present tesi doctoral consisteix en l'anàlisi de les dinàmiques estacionals de les comunitats de megafauna bentònica i bentopelàgica batial durant el període d'un any i en l'estudi de la relació entre aquestes dinàmiques i els fluxos i la disponibilitat d'aliment. Per assolir aquest propòsit, la tesi es basa en dades recollides en les quatre estacions d'un any natural en el talús continental de la Mar Catalana (Mediterrani NO). El talús continental de la Mar Catalana és un sistema oligotròfic on ambdós fluxos vertical i advectiu contribueixen a l'aportació de matèria orgànica a profunditats batials. Aquests dos fluxos presenten canvis estacionals marcats. Hem determinat els patrons estacionals en l'estructura i el funcionament de les comunitats profundes de megafauna, essencialment peixos i crustacis decàpodes, a través de les anàlisis de la seva composició, l'organització de la xarxa tròfica i l'ecologia alimentària de les espècies dominants. La comprensió de la relació entre l'estacionalitat en l'arribada d'aliment i els patrons estacionals que s'observen en la megafauna requereix d'estudis que integrin les diferents fonts d'aliment i els diversos nivells tròfics que componen les xarxes tròfiques. Per aquesta raó, a part de informació sobre la megafauna, la present tesi inclou dades sobre els principals processos que proporcionen aliment a profunditats batials (producció primària superficial i descàrrega de rius) i també dades sobre les característiques abiòtiques del medi (p. ex. temperatura, salinitat) i sobre l'aliment disponible en el mateix lloc, des de indicadors de diferents fonts orgàniques (ex. lípids i carboni orgànic en sediments, fluorescència 5 m per sobre del fons) fins a densitat de preses potencials de la megafauna (és a dir zooplàncton, suprabentos i infauna). Hem explorat les relacions entre les fonts d'aliment i els patrons faunístics mitjançant metodologies estadístiques multivariants. A més, hem estudiat la influència de l'aliment en els cicles reproductius de peixos i crustacis decàpodes.

Les dades emprades en aquesta tesi van ser recollides en el talús continental de la Mar Catalana, entre 423 i 1175 m, en cinc campanyes oceanogràfiques realitzades entre febrer de 2007 i febrer de 2008. Les mostres van ser recollides en 3 estrats batimètrics.

En el capítol 2 de la present tesi, hem examinat els patrons espacials i temporals (estacionals) d’abundància i biomassa de les comunitats de megafauna bentopelàgica. Hem detectat canvis batimètrics i topogràfics (canó submarí), relacionats amb els patrons de biomassa de determinades preses. Les comunitats de megafauna també van canviar estacionalment en relació a l’estratificació *versus* l’homogeneïtat de la columna d’aigua, bàsicament definides per canvis en la salinitat i la temperatura. En èpoques d’homogeneïtat de la columna d’aigua s’observaren majors densitats d’espècies de nivells tròfics baixos (ex. *Cymbulia peroni*, *Gennadas elegans*). Els pics de producció primària superficial al febrer i de descàrrega dels rius a l’abril afavoriren majors densitats de megafauna. Els mateixos pics de producció primària i descàrrega dels rius correspongueren a un màxim de biomassa de la megafauna a l’estiu després d’aproximadament 3-5 mesos. Els pics de preses clau (zooplàncton, micronecton i infauna bentònica) observats en períodes intermedis probablement actuen canalitzant les aportacions de matèria orgànica cap a nivells tròfics més alts.

En els capítols 3 i 4, hem estudiat els patrons estacionals en l’estructura de les xarxes tròfiques bentònica i bentopelàgica mitjançant l’anàlisi de les proporcions (ratios) dels isòtops estables de carboni i nitrogen en la macro- i la megafauna i en la matèria orgànica particulada (POM) sedimentada i en suspensió. La fauna bentònica presentava un contínuum en els valors de les proporcions dels isòtops estables indicatiu d’un ampli espectre d’estratègies alimentàries (des de suspensívors actius [ASF] fins a predadors de nivells més alts) i d’una xarxa tròfica complexa en què s’han pogut identificar almenys tres nivells tròfics. Els ASF (p. ex. el bivalve *Abra longicallus*) i els detritívors superficials (p. ex. el decàpode talassínid *Calocaris macandreae*) tenien un nivell tròfic similar, que era el més baix de tota la comunitat bentònica. Probablement ambdós consumien partícules en suspensió, però els ASF respongueren abans al pic de producció superficial que té lloc a finals d’hivern. El ^{15}N altament enriquit dels detritívors sub-superficials apunta a l’existència d’una nova ramificació en la xarxa tròfica basada en material refractori, bactèries i matèria derivada de biodeposició. La comunitat bentònica se sostenia en múltiples fonts de carboni durant tot l’any, amb un espectre més ampli de fonts de carboni en èpoques d’aigua estratificada. L’anàlisi ambiental ha revelat que la principal font d’aliment per a la comunitat bentònica en èpoques d'homogeneïtat de la columna d'aigua consistia en materials derivats del pic de producció primària superficial que té lloc a finals d'hivern. Les aportacions terrígenes canalitzades a través de la màxima descàrrega dels rius a l'abril constituïen una font d'aliment addicional pel bentos a l'estiu, després d'aproximadament 2 mesos, en períodes de baixa terbolesa de l'aigua.

Les anàlisis d'isòtops estables de peixos i crustacis decàpodes bentopelàgics han revelat una segregació tròfica entre aquests dos grups: els peixos tenien nivells tròfics més alts i consumien menys preses bentòniques que els decàpodes. Dins de cada tàxon, la comunitat estava estructurada, per una banda, en funció del gradient bèntic-pelàgic en la interfície aigua-sediment on les espècies de megafauna troben les seves preses i, per l'altra, en funció de la grandària dels propis predadors i de les seves preses, aquest darrer factor essent especialment important per als peixos. Els estudis dietaris desenvolupats en els 2 següents capítols han conduit a conclusions similars. A través dels isòtops estables, hem identificat dues xarxes tròfiques basades en la producció bentònica o pelàgica. La megafauna bentopelàgica se sostenia en la "neu marina" (*marine snow*) després dels pics de producció en superfície. Per contra, un espectre més ampli de fonts d'aliment, probablement provinents de fluxos advectius, sostenia la comunitat en períodes en què la columna d'aigua estava estratificada. Els canvis estacionals en l'estructura tròfica de la comunitat concordaven amb els patrons de producció de macrofauna, relacionats per últim amb les aportacions de fonts d'aliment primàries. L'empobriment del ^{13}C després de l'hivern en els macroplanctòfags migradors és consistent amb un major consum de preses pelàgiques, que s'alimenten de fitodetrits derivats de la producció en superfície. L'enriquiment del ^{15}N a l'estiu en els bentòfags suggereix un major consum de macrofauna hiperbentònica enriquida, que s'alimenta de matèria orgànica sedimentada i de matèria en suspensió a prop del fons. De forma coherent, els canvis estacionals en les preses consumides per la megafauna macroplanctòfaga estaven determinats per canvis en la quantitat de lípids i pigments clorofíl·lics en els sediments, ambdós paràmetres essent aproximacions de a l'arribada de fitodetrit. En canvi, els de la fauna bentívora s'explicaven per canvis en el carboni orgànic total en sediments i en l'aliment present a prop del fons (determinat a través de la mesura de la fluorescència 5 m per sobre del fons), ambdós paràmetres essent aproximacions de la quantitat d'aliment en el sediment i en suspensió a prop del fons.

En els capítols 5 i 6, hem estudiat les dinàmiques tròfiques i els cicles reproductius de les espècies dominants de peixos i crustacis decàpodes i hem trobat alguns patrons comuns per als dos tàxons. Els peixos i els decàpodes es van segregar en grups tròfics basats en el consum de preses bentòniques o mesopelàgiques. A més, les espècies de peixos petites es van segregar de la resta, consumint principalment suprabentos i macroplàncton petit. Els canvis en la disponibilitat d'aliment van ser determinants en els canvis estacionals observats en les dinàmiques tròfiques d'ambdós peixos i decàpodes. Els diversos grups tròfics s'acoblaven amb les aportacions d'aliment de forma diferent. Els peixos bentòfags van augmentar l'activitat alimentària envers macrofauna suprabentònica i detritívora (*Calocaris macandreae*) a l'estiu, dos mesos després del pic de producció primària en superfície quan hi havia més carboni orgànic total en els sediments. Els peixos planctòfags i les espècies de peixos petites van incrementar l'activitat alimentària envers crustacis mesopelàgics i suprabentos amb elevada capacitat natatòria després de la primavera, coincidint amb increments en les aportacions de fitodetrits (és a dir, lípids en el sediment) derivats dels pics de producció en superfície. A més, l'elevada activitat alimentària va afavorir el ràpid emmagatzematge d'energia en el múscul en les espècies petites. Els decàpodes macroplanctòfags van respondre abans que els peixos al *bloom* de producció superficial de finals d'hivern, augmentant l'activitat alimentària envers una major varietat de preses del zooplàncton a l'abril. En canvi, l'activitat alimentària de la gamba bentòfaga *Aristeus antennatus* es va veure afavorida per la disponibilitat de preses tant bentòniques com planctòniques. D'acord amb això, la seva dieta va canviar entre totes les estacions consecutives, en relació amb l'explotació de macrofauna suprabentònica i planctònica a més de la bentònica. A més a més, la fase del cicle reproductiu aparentment també influeix en els patrons alimentaris, i l'activitat alimentària i la ingestió de preses més energètiques, sobretot mesopelàgiques (p. ex. eufausiacis, Pasiphaeidae, peixos) però també suprabentòniques (*Natatolana borealis*), van augmentar en períodes pre-reproductius en la majoria d'espècies, independenment del grup tròfic al que pertanyen.

La maduració de les gònades (índex gonadosomatic – GSI) es va veure associada a les abundàncies de recursos tròfics primaris i de preses específiques, suggerint que la disponibilitat d'aliment regula els cicles reproductius, almenys parcialment. El GSI estava controlat en tots els grups tròfics per processos de producció en superfície i per les aportacions de fitodetrits associades, amb un retard d'entre 2 i 3 mesos. Els patrons temporals de GSI diferien entre espècies del mateix grup tròfic tant en peixos com en crustacis decàpodes, cosa que indicava que l'estacionalitat en la disponibilitat i en l'ús de l'aliment no afecta els processos reproductius de les diferents espècies de la mateixa manera.

CHAPTER 1 - INTRODUCTION

INTRODUCTION

1. State of the art

1.1. The Benthic Boundary Layer

The Deep Sea is usually defined as beginning at the shelf break, where the continental shelf ends, usually at a depth of *ca.* 200 m (e.g. Gage and Tyler, 1991; Thistle., 2003). In this environment, the water column is generally characterised by an exponential decline of pelagic biomass with depth (Vinogradov and Tseitlin, 1983). Instead, biomass of living organisms increases near the Deep Sea floor, in a region called the *Benthic Boundary Layer* (Wishner, 1980; Angel, 1990). The Benthic Boundary Layer (BBL) is the near-bottom region that extends from the top of the benthic nepheloid layer (*ca.* 50-100 m above the bottom) to about half a metre within the sediment (McCave, 1976). It is a complex physical structure (Gage and Tyler, 1991) in which an increase in the suspended matter is recorded. This matter brings nutrients and energy to organisms living within the BBL.

1.2. Fauna of the Benthic Boundary Layer

Swimming capacity, size, and feeding habits are common criteria for classifying BBL fauna. This is comprised of those animals living either on the ocean floor, the *benthos*, or those associated with the immediately overlying water, the *benthopelagic* fauna (Gage and Tyler, 1991). The benthos can be subdivided into those usually active, crawling or attached organisms living on the surface of the ocean bed, the epifauna, and those living buried in the sediment, the infauna. The benthopelagic fauna either inhabit the BBL most of their lives or only temporarily, the latter with an average distribution principally linked to the water column in which they swim (nekton) or drift (plankton) (Vereshchaka, 1995; Mees and Jones, 1997; Cartes, 1998a; Cartes et al., 2010).

At high taxonomic levels (i.e., phylum, class, and order), the soft-bottom deep-sea BBL fauna essentially consists of: the megafauna (fauna collected with bottom trawls, or distinguishable by means of bottom photographs taken at more than about one meter off the bottom: Rowe, 1982; Thistle, 2003), comprising primarily fishes, decapod crustaceans and echinoderms; the macrofauna (fauna retained by sieves with meshes of about 62 microns or smaller: Mare, 1942; McIntyre, 1969), mainly including polychaetes, bivalve molluscs, isopods and amphipods (Thistle, 2003); and the meiofauna (those animales retained by the finest screens down to a mesh opening of 62 microns or smaller), consisting mostly of foraminifers nematodes and harpacticoid copepods (Gooday, 1986). The benthopelagic macrofauna that constitutes a permanent part of the BBL is called the suprabenthos or hyperbenthos, which is mainly composed of peracarid crustaceans (e.g. mysids), and that spending only some time of their lives in the sediment-water interface is known as the near-bottom zooplankton, which consists of several taxa (e.g. euphausiids, natantian decapods) (Sainte-Marie and Brunel, 1985; Mees and Jones, 1997). Both macro- and meiofauna have both benthic and hyperbenthic (swimming) species. In addition to the category to which organisms belong, they are also classified in terms of their feeding mode. These include the usual categories of suspension feeders, deposit feeders, carnivores and scavengers (Gage and Tyler, 1991).

1.3. Food inputs to the Deep Sea

The relative importance of the diverse taxa and feeding modes varies through the worlds' oceans both at the macro- and the mesoscale. In addition to the geological history of each area (e.g. Mediterranean Sea *versus* Atlantic Ocean: Barrier, 1989; Bouchet and Taviani, 1992; Salas, 1996), its trophic characteristics have been described as a key factor defining the faunal composition and abundance (Sokolova, 1997). In fact, food availability is considered as the most important limiting factor in deep sea ecology (Gage and Tyler, 1991). The arrival of particulate organic matter (POM), as main food source, to the BBL is through two main pathways: the vertical and the advective fluxes of material (Fig. 1). The vertical flux of material constitutes the main input of OM to the deep-sea (e.g. Rowe and Staresinic, 1979; Miquel et al., 1994; Gooday, 2002). Downward flux of matter derives from primary production in the euphotic zone and it mainly consists of what is loosely referred to as marine snow (Sumich, 1999), which is a combination of phytodetritus (i.e. aggregated detrital material mainly containing exopolymers, mucous, phytoplankton, plankton exoskeletons, faecal pellets and bacteria) and zooplankton (e.g. Miquel et al., 1994; Beaulieu, 2002). Additionally, active transport through vertical migrations of mesopelagic organisms takes place (Sardou et al., 1996; Gardner, 1997). The vertical flux from the epipelagic zone provides a potential link between surface and the deep sea communities (Rowe, 1983; Watts et al., 1992). Advective fluxes comprise suspended sediments supplied by rivers or resuspended on the shelf that are

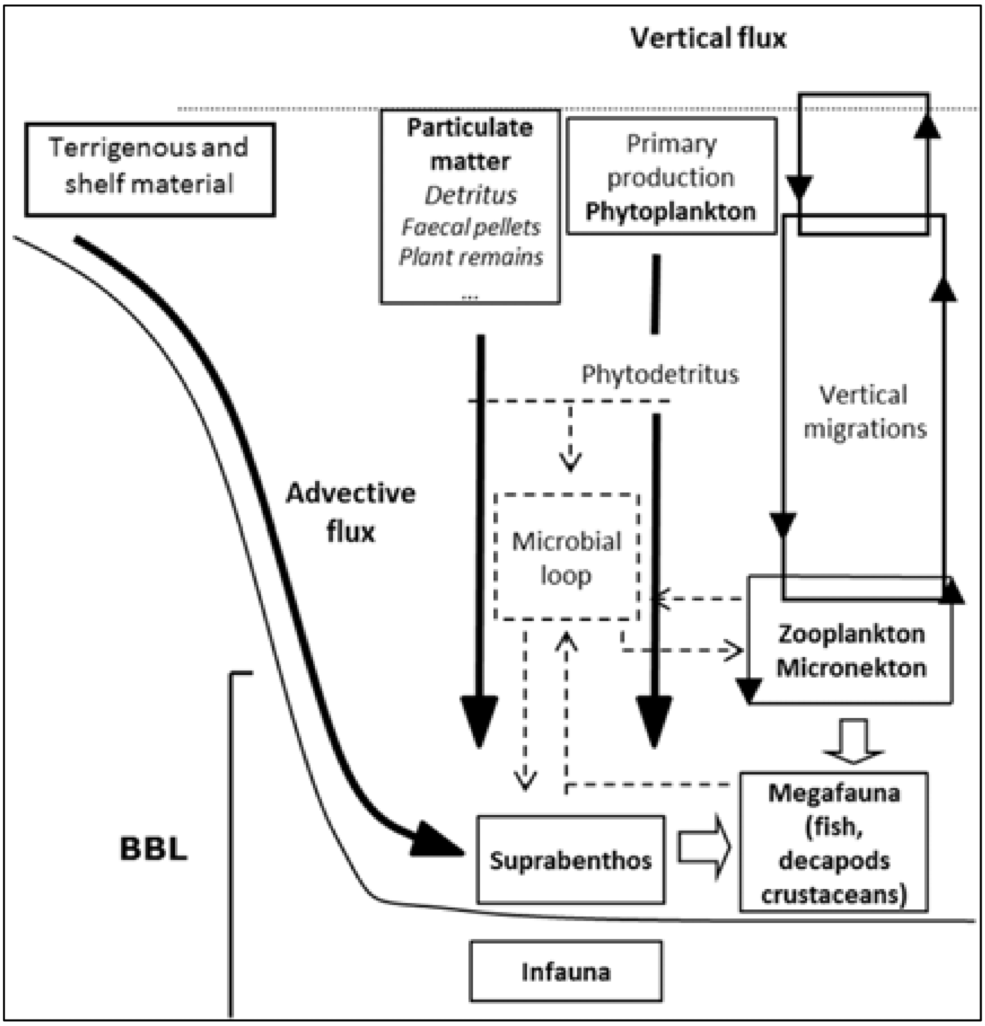


Fig. 1. Scheme of energy fluxes in the Benthic Boundary Layer (BBL). Adapted from Cartes et al. (2004).

transferred down the slope mainly through near-bottom nepheloid layers (Gartner, 1989), especially within submarine canyons (Durrieu de Madron, 1994; Puig and Palanques, 1998; Palanques et al., 2006). In addition, advective fluxes sort upper sediment layers causing resuspension of organic matter from the bottom.

1.4. Spatial trends in fauna and food availability

The spatial differences in productivity regimes and the associated food inputs enhance the proliferation of different meiofauna and macrofaunal groups, resulting in food webs where top predators prey on pelagic or benthic organisms (e.g. Maynou and Cartes, 2000; Cartes et al., 2002a; Carrassón and Cartes, 2002; Serrano et al., 2011; Fanelli et al., 2011a,b) (Fig. 1). For example, the oligotrophic deep Mediterranean (Minas et al., 1988; Miquel et al., 1994) is dominated by decapod crustaceans (Cartes and Sardá, 1993; Politou et al., 2008), characterised by low levels of food consumption

(Cartes and Maynou, 1998) and mainly feeding on macrofauna (e.g. Cartes, 1993a-c; 1994; Kapiris, 2004; Fanelli and Cartes, 2008). Instead, the megafaunal invertebrate community of the more productive deep Atlantic (Laborde et al., 1999; Heussner et al., 1999) is dominated by suspension and deposit feeding echinoderms (Iken et al., 2001) (e.g. Haedrich et al., 1975; Lampitt, 1986; Billett et al., 2001). Also at the macroscale, differences have been recorded within the Mediterranean Sea. Deep water fish assemblages of the Eastern Mediterranean present a particularly low number of species and low abundances (Stefanescu et al., 1992; Labropoulou and Papaconstantinou, 2000; Kallianotis et al., 2000; Madurell et al., 2004), and deep meiofaunal and macrobenthic communities (Tselepides and Eleftheriou, 1992; Danovaro et al., 1999) are impoverished compared to the Western. In connection with this, food webs in the Eastern Mediterranean are, in general, more sustained by mesopelagic food resources, notably Myctophidae (e.g. Blaber and Bulman, 1987; Merrett and Haedrich, 1997; Madurell et al., 2004). Instead, in the Western Basin, we find trophic webs in which benthic resources are more important (Cartes and Maynou, 1998; Cartes et al., 2004), especially near submarine canyons. These differences have generally been attributed to the greater oligotrophy of the Eastern Mediterranean waters, which owes to low surface primary production and low continental influence (Danovaro et al., 1999). A similar situation is observed at the mesoscale level, when comparing continental and insular slopes within the western Mediterranean basin. Greater benthos densities (Cartes and Maynou, 1998; Cartes et al., 2009a) and the consequent greater contribution of benthos to the food supply for megafauna (crustaceans and fish) in the continental slopes have been linked to the presence of several submarine canyons in the continental margin of the NW Mediterranean (i.e. Catalan Sea) (Buscail et al., 1990; Cartes et al., 2002b; Palanques et al., 2006). In contrast, communities living around insular slopes are more based on pelagic production due to the lack of continental advective fluxes (Madurell and Cartes, 2005; Cartes et al., 2009a).

Mesoscale spatial changes in faunal communities and in food availability also take place through the bathymetric gradient. As a matter of fact, such faunal changes have repeatedly been associated to the generalized decrease in the flux of labile organic material with depth (Alldredge, 1992; Miquel et al., 1994) due to the consumption and to the biodegradation of organic matter in the microbial loop (Pomeroy and Wiebe, 1988; Legendre, 1990; Legendre and Le Fèvre, 1995) (Fig. 1). Of the several aspects of assemblages that change with depth, the most well-known are enumerated next. As a general rule, the densities of meiofauna (Pfannkuche, 1985; DeBovée et al., 1990; Danovaro et al., 1995), macrofauna (Flach and Heip, 1996; Cartes et al., 2002a; Brandt et al., 2007) and megafauna (e.g. fish: Stefanescu et al., 1993,1994; Bergstad et al., 1999; decapods: Haedrich et al., 1980; Cartes and Sardà, 1992; benthic invertebrates: Lampitt et al., 1986; Cartes et al., 2009a) decrease with depth. Changes in the composition of assemblages take place through a more or less continuous substitution of dominant and subdominant species (e.g. Hecker, 1990; Merrett and Haedrich, 1997; Wei et al., 2010) along the bathymetric gradient, and size-spectra of the different taxa change (e.g. Rex and Etter, 1998; Morales-Nin et al., 2003). A generalized bigger-deeper trend is observed among fish up to *ca.* 1200 m (e.g. Macpherson and Duarte, 1991; Fujita et al., 1995; Moranta et al., 1998) but no such clear pattern is found among decapods or echinoderms (Polloni et al., 1979; Sardà and Cartes, 1993; Morales-Nin et al., 2003; Follesa et al., 2009). The relative contribution of the different feeding guilds also varies with depth (Gage and Tyler, 1991; Cartes, 1998b; Cartes et al., 2009a). Additionally, there is a decline in the feeding activity of megafaunal fish and decapods with depth (Cartes, 1998b; Carrassón and Cartes, 2002).

The general pattern of decreasing flux of particles with increasing depth is not always valid, and advective phenomena usually cause increases in the flux of particles in deep areas. Lateral inputs often take place through submarine canyons, being especially important where they indent sedimentary slopes (Macquart Moulin and Patriti, 1996; Vetter and Dayton, 1999). Particulate organic matter (POM) accumulates within canyons (Vetter and Dayton, 1998; Buscail and Germain, 1997) and also on the adjacent slopes, such as the depositional areas (e.g. Duineveld et al., 2001; Epping et al., 2002; Cartes et al., 2002b). Such accumulation provides more labile sediments enriched in organic carbon and with high C/N ratios (Epping et al., 2002; Cartes et al., 2002b; Cartes et al., b). Concurring with the relative eutrophy found within submarine canyons, the general pattern of faunal decrease with depth is interrupted and greater densities and biomasses of fauna within canyons are usual (Macquart Moulin and Patriti, 1996; Vetter and Dayton, 1998; 1999; Cartes et al., 2010b; De Leo et al., 2010). These structures are also recruitment areas for species of quite different trophic levels from suprabenthos (Cartes and Sorbe, 1999; Cartes et al., 2010b) to fishes (Stefanescu et al., 1994), and may also become local “hotspots” of production (Vetter, 1994; Vetter et al., 2010) and diversity (*sensu lato* after Myers et al., 2000), more strictly habitats with on average greater diversity than surrounding areas (Rowe et al., 1982; Vetter, 1994; Vetter et al., 2010).

Faunal changes with depth or geomorphological discontinuities may not only be a consequence of changes in food availability, but marine organisms may actually respond to a combination of different factors (e.g. salinity, temperature, pressure, turbidity) that often change along these spatial gradients. Because of this, it is difficult to specify which factors are primarily responsible for the spatial biotic changes observed. Many authors have discussed the role of the possible factors structuring bathyal communities with depth (e.g. Fariña et al., 1997; Colloca et al., 2003; Fock et al., 2004; Menezes et al., 2006; Fanelli et al., 2007; Politou et al., 2008), but such studies have been usually based in comparisons with biotic and abiotic data available from previous descriptions. Studies encompassing simultaneous samplings of fauna and environmental and/or trophic factors in order to relate them are limited. In addition, most of them concern meio- or macrofauna or fauna feeding at low trophic levels (Danovaro et al., 1995; Witte, 2000; Riaux-Gobin et al., 2004; Escobar-Briones et al., 2008; Wei et al., 2010; Cartes et al., 2010a), but such studies in predator megafauna are very scarce (Vetter and Dayton, 1999; Cartes et al., 2008a; 2009b; Serrano et al., 2011; Fanelli et al., 2012).

1.5. Mesoscale temporal trends in fauna and food availability

The main seasonal variations in the Deep Sea are associated to (i) changes in the hydrographic conditions and to (ii) fluctuations in the quantity and quality of available organic material. Hydrographic conditions vary in relation to seasonal circulation of water masses, which can originate changes in the physical parameters (e.g. Font, 1987; Steele et al., 2004; Ivanov et al., 2009) that in turn affect the distribution of organisms (Cartes et al., 1994; Williams et al., 2001; Colloca et al., 2003; Fock et al., 2004; Riaux-Gobin et al., 2004; Menezes et al., 2006; Capezzuto et al., 2010; Cartes et al., 2010a). In general, transfer of material from the surface layers varies mainly according to seasonal variations in primary production in the photic zone (e.g. Estrada, 1991; Karl et al., 1996; Gong et al., 2003), which often take the form of highly seasonal pulses of particles (e.g. Miquel et al., 1994; Rice et al., 1994; Smith et al., 1996; Beaulieu et al., 2002; Cartes et al., 2002b). Changes in advective fluxes vary mainly in relation to discharges of continental run-off (Monaco et al., 1990; Buscail et al., 1990), to storms (Puig et al., 2004) and to cascading events, such as those in the Gulf of Lions (Canals et al., 2006; Palanques et al., 2006). In addition, physical gradients such as the thermocline (e.g. Arthur et al., 1983) and shelf-slope density fronts (Font, 1988; Palanques and Biscaye, 1992), and main flows like geostrophic currents (Baker and

Hickey, 1986; Durrieu de Madron et al., 1990), can act as barriers for the flux of matter to the sea both by vertical and advective fluxes, thus also exerting some control in the transfer of particulate matter to the open sea. Besides altering food inputs to bathyal depths, these phenomena also entail variations in physical properties of the environment.

Seasonality observed in several aspects of deep sea fauna suggests some ecological response to the mesoscale environmental changes. Community and population responses within *small benthic organisms* (i.e. from bacteria to meiofauna: Soltwedel, 1997; Pfannkuche and Soltwedel, 1998) are relatively well known so far (see Gooday, 2002 for a review). These organisms feature the strongest and more rapid responses to seasonal organic matter inputs, presenting generalized positive relationships between their density, biomass, growth and reproduction and food availability (Gooday and Turley, 1990; deBovée et al., 1990; Guidi-Guilvard et al., 2000; Danovaro et al., 2000; Riaux-Gobin et al., 2004).

Regarding larger fauna (i.e. macro- and megafauna), some studies have identified seasonal changes at the community level (e.g. macrofauna: Sardou et al., 1996; Cartes et al., 2008b; megafauna: Cartes et al., 1994; Sardà et al., 1994; Kallianotis et al., 2000; Moranta et al., 2008). Short-term temporal variations in megafaunal communities are mainly due to both the replacement and the variation in size structure of some dominant and subdominant species (e.g. Moranta et al., 2008), related to the periodicity in reproduction and recruitment (Gage, 1994). Besides, seasonal shifts in the composition of the community of benthopelagic megafaunal predators take place (Cartes et al., 1994; Sousa et al., 2005; Sánchez et al., 2008). Also, intrannual changes in abundance and biomass at the community level have been detected, although results are not consistent across studies (e.g. Kallianotis et al., 2000; Maynou and Cartes, 2000; Labrapoulou and Papaconstantinou, 2000; Colloca et al., 2003).

Because of the large size, longer life-histories and higher trophic levels of macro-and megafauna compared to small benthic organisms, their responses to food inputs are more lagged (Galéron et al., 2001) and thus more difficult to establish. The associations between BBL macrofaunal densities or biological cycles and fluxes of food to bathyal depths have been discussed (Drazen et al., 1998; Sorbe, 1999; Cartes, 1998a; Vallet and Dauvin, 1999), and only more recently delayed responses of macrofauna communities to food inputs have been established (Cartes et al., 2002b; Fanelli et al., 2009a; Cartes et al., 2008b; 2010a; Mamouridis et al., 2011). For megafauna, changes in communities have been attributed to seasonal fluctuations in the availability of their prey (i.e. BBL macrofauna) (Cartes, 1998a; Cartes et al., 2002b). With respect to this, oscillations in the relative abundances of the different macrofauna compartments (i.e. infauna, suprabenthos and zooplankton) favour greater densities of organisms from different trophic guilds in different seasons (Madurell et al., 2004; Sánchez et al., 2008). Yet, the relationship between megafauna community responses and fluctuations in organic matter inputs to bathyal depths has seldom been established (Madurell et al., 2004; Cartes et al., 2007; 2008b; 2010b; Moranta et al., 2008; Sánchez et al.,2008). Identification of such relationships requires comprehensive studies encompassing the several food sources and faunal trophic levels of food webs. Also, as considered for depth, inclusion of the main environmental variables associated to hydrographic conditions in such studies would allow the discrimination between the influence of hydrographic and trophic factors on the temporal patterns taking place.

1.6. Food web structure

The recurrent findings on the strong influence of food availability on many aspects of deep-sea communities highlight the limiting role of food in deep-sea processes that was summarized by Gage and Tyler in 1991. This may be especially important in oligotrophic systems such as the deep Mediterranean Sea. Under such condition, organisms develop strategies that contribute to partition their food resources, thus reducing feeding overlap (competition for food). Depth, food size (Carrassón and Cartes, 2002; Gage, 2003; Colloca et al., 2010), and the vertical distribution of food in the sediment or in the water column are the main factors contributing to food partitioning among both macro- and megafauna within the BBL.

Among BBL macrofauna, vertical partitioning (Cartes et al., 1994) results in a gradual decrease in the dependence on suspended matter and an increase in the exploitation of sedimented material from zooplankton to benthos, with hyperbenthos exploiting both resources (Fanelli et al., 2009a). In agreement, temporal dynamics of zooplankton depend primarily on variations in the vertical inputs (Cartes et al., 2003; 2008b; 2010a), and seasonal pattern of the benthic and hyperbenthic fauna are more affected by variations in the amount and quality of food in the sediment (Cartes et al., 2002b; Fanelli et al., 2009a; Mamouridis et al., 2011).

The consumption of suspended material in the water-sediment interface by benthopelagic macrofauna and by bacteria leads to lower organic content on sedimented compared to suspended matter (Buscail et al., 1990). This implies an additional food restriction for benthic species that may be overcome by efficient foraging strategies and an activity targeted to where maximum return on effort is obtained. Although some knowledge of the overall structure of deep-sea benthic food webs exists (Iken et al., 2001), it still remains to be fully investigated. In general, it is known that suspension feeders depend either on sinking POM or on resuspended material (Lampitt, 1985). On the sea floor, fresh POM inputs that become mixed with the superficial sediment layer by benthic storms, tidal movement and bioturbation (e.g. Lampitt, 1985; Smith, 1992), are the principal food source for all surface deposit feeders. Besides, meiofauna constitute an additional food source (Iken et al., 2001). Depending on the amount of sedimented matter, sediment reworked by bioturbation and the feeding activity of larger animals incorporates only a relatively small fraction of this material into deeper sediments, making it available to sub-surface deposit feeders (Lisitsyn and Vinogradov, 1982; Gooday and Turley, 1990). Considering all these processes by which organic matter becomes available to the different trophic levels found on benthos, different temporal responses to food inputs are expected. However, it is still poorly understood how the different trophic niches among the bathyal benthic macrofauna community are sustained by the energy inputs throughout the year. This issue presents an additional complexity in areas where not only the vertical component is implied in the food inputs but also advective fluxes have an important effect on the dynamics in food availability (e.g. NW Mediterranean Sea: Cartes et al., 2009a).

Regarding benthopelagic megafauna, partitioning of food resources has been well defined and it has been described as the main driver of niche segregation (Macpherson, 1981; Jumars and Gallagher, 1982; Ross, 1986). Megafaunal predators partition the vertical space for feeding and they tend to exhibit some preference towards benthic, hyperbenthic or planktonic prey. This has led to a major classification of organisms in trophic guilds (e.g. Cartes et al., 2002a). Within each main guild, prey and predator size is an important driver of food partitioning. Besides, most species with similar trophic preferences segregate along the depth dimension (Cartes, 1993b). Despite the preference of megafaunal predators for some prey taxa, their dietary composition varies seasonally and predators can even change trophic guild transitorily in order to use a specific resource (Macpherson, 1977). These changes entail variations in the feeding relationships among organisms and in the trophic structure of the community. For example, some studies have revealed seasonal variations in dietary overlap among species in response to changes in prey consumption (Macpherson, 1977; Cartes, 1998b). Although still poorly understood, these variations have been attributed to seasonal fluctuations in abundances of the potential prey of megafauna (i.e. BBL macrofauna) (Cartes, 1998a; Cartes et al., 2008a; Fanelli and Cartes, 2008; 2010), especially pelagic prey. However, the role of the different source materials reaching bathyal depths in sustaining the megafaunal community and the corresponding seasonal patterns in food webs remains little known. Dependence of deep-sea predator megafauna on surface production has been already reported both at bathyal (Polunin et al., 2001) and abyssal (Drazen, 2008; Stowasser et al., 2009) environments, but such information in areas subjected to both vertical and horizontal fluxes is not available. As observed for benthic macrofauna, how the different food inputs contribute to sustaining the BBL benthopelagic megafauna from the different trophic guilds throughout the year is rather unknown (Stowasser et al., 2009) and would be important for understanding the functioning of deep-sea ecosystems.

1.7. Trophic ecology

Traditionally, studies of food web dynamics and on their seasonal changes have used gut content analyses to explain aspects of community structure (e.g. Carrassón and Cartes, 2002; Jennings et al., 2002; Madurell and Cartes, 2005; Cartes et al., 2007). Gut contents reflect food consumed at particular points in time and space, and they provide a great deal of information on gut fullness variation, on specification of prey and of trophic effects of the density and distribution of both food sources and consumers. Nevertheless, this approach has limitations. During analyses of gut contents certain types of dietary materials that may be rapidly digested (e.g. gelatinous plankton, detritus) but may yet be important in sustaining marine food webs (Fanelli and Cartes, 2008; Fry, 2006) can be underestimated. Also, voiding of gut contents upon capture and the crushing or grinding of food makes identification of prey difficult (Fanelli and Cartes, 2008), particularly when refractory or amorphous foods are ingested (Pinnegar and Polunin, 2000). This becomes especially important when analysing suspension and deposit-feeding fauna, since the impossibility to identify the composition of detritus ingested (Tyler et al., 1992a, b). This has often led to poor characterization of those organisms (Hall and Raffaelli, 1993) that often results in excessive lumping together of species that may greatly affect the apparent properties of food webs (Goldwasser and Roughgarden, 1997). Additionally, while gut content analysis of secondary consumers is useful for assessing prey consumption and selectivity, it does not reveal the end members sustaining megafauna communities, specifically not the origin (terrestrial *versus* marine) of organic matter. Gut contents therefore offer a partial basis for elucidating the detailed interactions which must exist (Paine, 1988). Limitations of gut contents can be especially important in the study of food webs in the deep ocean, because of the constraints associated with sampling at great depths (e.g. everted stomachs in fish, low feeding intensity among deep sea fauna). In this respect, there are additional tools available (analyses of pigments, of lipid biomarkers and of stable carbon and nitrogen isotopes) that help overcoming the shortcomings of gut content analyses, and that may be especially useful in the study of deep-sea food webs.

Analysis of pigments by means of high-performance liquid chromatography (HPLC) has allowed determining the composition of phytoplankton both in sea water samples (e.g. Bustillos-Guzmán, 1995; Vidussi et al., 2000; Uitz et al., 2006) and in detrital material, either deposited in the sediments (Rice et al., 1986; Freiberg et al., 2011) or contained in guts of suspension and deposit feeders (Wigham et al., 2003; Howell et al., 2004; Cartes et al., 2007). HPLC allows the identification of a suite of phytoplankton pigments (chlorophylls and carotenoids): chlorophyll a (and divinyl-chlorophyll a), that is the universal proxy for phytoplankton biomass, and some accessory pigments, which can be used as taxonomic biomarkers (Jeffrey et al., 1997). Through analysis of the pigments within the stomach content of an organism ingesting phytodetritus it is possible to determine the algal components of its diet. The question as to if, and how, phytodetritus is partitioned is key to understanding the functioning within the benthic ecosystem. Selective or non-selective feeding in deep-sea benthic species has been identified by comparing pigmentary composition of gut content and surrounding sediment, and partitioning of the phytodetrital matter among species has been studied by comparing pigmentary composition of gut contents in coexisting species (Duineveld et al., 1997; Wigham et al., 2003; Howell et al., 2004).

In contrast to gut contents and HPLC methods, other techniques applied to the study of food webs provide information of food assimilated instead of that ingested. Lipid biomarkers (Graeve et al. 1994a) and stable isotope analyses are increasingly common in the last decades in marine studies. Fatty acid markers are specific to a particular individual organism or groups of organisms (Cook et al., 2010), and retain a signature of the food sources through the trophic web (Sargent et al. 1987; Dalsgaard et al. 2003). By the lipid biomarker approach certain fatty acids, or ratios between “marker lipids”, can provide precise indication of the diet of marine animals and of their trophic position, without however precise quantitative (e.g. relative proportion of each prey) information on their diet. As HPLC, these methods are particularly useful when gut content analyses are difficult to perform, which is especially true in small species and in detritus feeders. The use of stable nitrogen (N) and carbon (C) isotopes has become popular for gaining extra insights into the functioning of marine and estuarine food webs (e.g. Cabana and Rasmussen 1996; Pinnegar and Polunin 2000; Fisher et al. 2001) and for providing time-integrated information about feeding relationships and food pathways through food webs within complex systems (Peterson and Fry, 1987; Kharlamenko et al., 2001; Persic et al., 2004). Stable isotopes have been used to estimate the trophic levels of organisms (Owens 1988) and to identify the relative trophic position of various organisms within the food web (Vander Zanden et al. 1996), integrating the assimilation of energy or mass flow through all the different trophic pathways leading to an organism. Given that stable isotopes analysis is based on the preferential release of lighter isotopes during respiration and excretion, it can be used to differentiate assimilated food from that initially ingested (Guiguer et al., 2002; Persic et al., 2004). Analyses of stable isotopes can provide an indication of the prey assimilated over a considerable period of time (Hesslein et al., 1993), thus, are less subject to temporal bias. In addition, they have the potential to simultaneously capture complex interaction, including trophic omnivory, and to track energy or mass flow through ecological communities (Peterson and Fry., 1987; Cabana and Rasmussen, 1996). The ratio of stable isotopes of nitrogen ($\delta^{15}N$) can be used to estimate the trophic position of an organism because consumers are usually enriched by 1–5‰ (average 3.4‰) compared with their diet (Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987). In contrast, carbon isotope ratios ($\delta^{13}C$) are widely used as indicators of sources of primary production in the ecosystem and the flow of carbon from primary producers to consumers (Gu et al., 1997). Consumers have an isotopic carbon composition similar to their diets and typically they are enriched by only 1.1‰ or less within oceanic systems (e.g., DeNiro and Epstein 1978; Fry and Sherr 1984; France and Peters 1997). In a marine or coastal ecosystem, different potential sources of carbon have different $\delta^{13}C$ signatures; e.g., macroalgae (–27‰ to –8‰), seagrasses (–15‰ to –3‰), marine phytoplankton (–24‰ to –18‰), and terrestrial outflow (–30‰ to –10‰) (Fry and Sherr, 1984). The relationship between $\delta^{13}C$ *versus* $\delta^{15}N$ can be a useful indicator if there is one or more source material supporting biological communities (Polunin et al., 2001): weak correlations between $\delta^{13}C$ and $\delta^{15}N$ are indicative of an array of possible sources of production. Conversely, strong correlations are indicative of a single type of primary source as the case of deep-sea communities (Polunin et al., 2001). Given the constraints and paucity of gut-content data, stable isotopes can clearly help to elucidate some aspects of the structure of deep-sea food webs. Like gut-content data, though, stable isotopes have several limitations. Among these, there is the resolution of only broad categories of prey organisms by $\delta^{15}N$ or $\delta^{13}C$ values (Polunin and Pinnegar, 2000). This is particularly true for deep-sea communities, where primary food sources arrive from the photic zone after being remineralised, enriched and degraded by microbial activity, which potentially reduces the chances of correctly identifying types of source material (Pinnegar and Polunin, 1999).

Studies on food web structure and seasonal changes using stable isotopes are relatively common in shallow waters (e.g. Pinnegar and Polunin, 2000; Daveport and Bax, 2002; Carlier et al., 2007), but knowledge on this issue at bathyal depths is scarce. At the deep sea, studies considering macrofauna are limited (e.g. suprabenthos: Madurell et al., 2008, Fanelli et al., 2009a; benthos: Iken et al., 2001; zooplankton: Fanelli et al., 2011b), and no knowledge has been yet developed regarding the benthic compartment in areas with strong continental influence. With respect to megafauna, some studies on temporal dynamics of food web structure using stable isotopes have focused on specific taxa (e.g. pandalid shrimps: Fanelli and Cartes, 2008; fishes: Fanelli and Cartes, 2010; cephalopods: Fanelli et al., 2012), but studies on megafaunal communities have been barely addressed and are usually restricted to areas with low or none continental impact (Polunin et al., 2001; Cartes et al., 2007; Mincks et al., 2008; Jeffreys et al., 2009; Stowasser et al., 2009).

1.8. Biological cycles and food availability

Considering that natural fluctuations in the environment are the trigger of seasonal reproductive processes (Gage and Tyler, 1991), it is likely that intrannual changes in food inputs are the main drivers of seasonal biological cycles in a physically stable environment such as the deep sea. Accordingly, both continuous and seasonal reproductive cycles and recruitment patterns have been found in deep sea fauna, from macrofauna (Saltzman, 1996; Cartes and Sorbe, 1998; Cartes et al., 2001; Albessard and Mayzaud, 2003) to megafauna (e.g. benthic invertebrates: see Gage and Tyler

(1991) and references therein; cephalopods: Barratt et al., 2007; Hoving and Lipinski, 2009; decapods: Maiorano et al., 2002; Company et al., 2003; Vinuesa, 2007; fish: Martino et al., 2001; Rotllant et al., 2002; Drazen et al., 2002; Tsikliras et al., 2010). To date, the study of the coupling between reproduction and seasonality in food inputs has been mainly limited to the organisms situated at the lowest levels of the trophic chains. Phytodetritus deposition stands out as a key environmental factor favouring the reproduction of some groups of deep-sea macrofaunal (Bishop and Shalla, 1994; Tyler et al., 1994; Cartes and Sorbe, 1996) and detritivorous megafaunal (Wingham et al., 2003; Hudson et al., 2004; Howell et al., 2004) species. In areas subjected to advective flow, associated inputs of organic carbon also enhanced recruitment of hyperbenthic and benthic macrofauna species (Cartes and Sorbe, 1998; Cartes, 1998a; 2001). However, the influence that such changes in food availability may have on the biological cycle of high trophic level megafauna remains largely unknown. Biological cycles of benthopelagic shrimps have been associated to vertical fluxes of organic matter reaching bathyal depths (Puig et al., 2001), and delayed responses to blooms in surface production have been observed (Cartes et al., 2008a; Fanelli and Cartes, 2008; Briones-Fourzán et al., 2010). The time lag between the physiological response of secondary consumers and the organic matter inputs is attributable to the additional trophic step between them. Consistently, the biological cycles of some bathyal benthopelagic shrimp species were related to changes in prey consumption (Cartes et al., 2008a; Fanelli and Cartes, 2008). In this respect, greater feeding intensities and greater consumption of energetic prey preceded gonad growth. However, studies linking feeding dynamics and reproductive patterns in deep-sea benthopelagic decapods are few and the relationship between food availability and reproduction remains still more largely unexplored (Drazen, 2002).

Studies on the biological cycles of both fish and decapod crustaceans have usually focused on single or congeneric species that are bathymetrically segregated (the case of macrourids in Deep Sea: e.g. Massutí et al., 1995; Fanelli and Cartes, 2004), but such work considering coexisting species belonging to different families has barely been addressed. For decapods, a pattern of successive reproductive cycles among middle-slope species has been described (Company et al., 2003). For fish, instead, no consistent pattern in reproductive timing has been found, and distinctive species-specific timing of biological cycles of coexisting slope fish is usual (e.g. Massutí et al., 1995; Rotllant et al., 2002). On one hand, this suggests that seasonal availability of energy does not affect all species' reproductive processes equally. Although some biological aspects related to energy allocation and use could be responsible for these differences, the diverse responses to seasonality in relation to the feeding guild of each species could have some effect on their timings of reproduction. On the other hand, different timings of reproduction suggest segregation of spawning in time, which should be useful for reducing competition among offspring and thus increasing reproductive success. This is consistent with the spatial partitioning in recruitment grounds according to season and/or depth of closely related species that has been observed in some areas (e.g. Moranta et al., 2008). Therefore, not only could trophic resource partitioning among adults be important in the biological cycles of megafauna, but also avoidance of the simultaneous use of the same food source among offspring could contribute to regulation of timing of their reproduction. Understanding the coupling of specific aspects of megafaunal life-histories with the availability of different trophic resources that are directly used by other taxa requires more detailed studies, involving the joint dynamics of the deep macrofauna.

2. Study area

2.1. Environmental features

The continental slope is the area located seaward of the continental shelf edge, constituting the boundary between oceanic and continental crust. The slope is characterised by a marked steepness (Marshall, 1954). The Catalan Sea slope is located in the continental side of the north western Mediterranean Sea (Fig. 2) and is characterised by muddy bottoms with fine, mostly silty sediment particles dominating along the entire slope (Emelyanov, 1972). This slope has a narrow continental shelf cut by submarine canyons that transfer organic matter from the continent to the deep sea (Puig and Palanques 1998, Sanchez-Vidal et al. 2009, Cartes et al. 2010a,b). At depths of *ca.* over 500 m there is a permanent nepheloid layer located at 350-450 m, the position and intensity of which is related with water masses and the position of the shelf-slope front (Puig and Palanques, 1998). We sampled the continental slope off Barcelona, in a fishing ground known as *Serola* (Fig. 2). Additionally, samples were obtained inside the Besòs submarine canyon, in the southern wall locally called *El Buscarró* and on a neighbouring area 20 km south of Serola, called *Abissinia*.

The Mediterranean Sea is characterised by annual thermal stability of the water mass (~12.8º C) below ~200 m (Hopkins, 1985). However, important temporal fluctuations

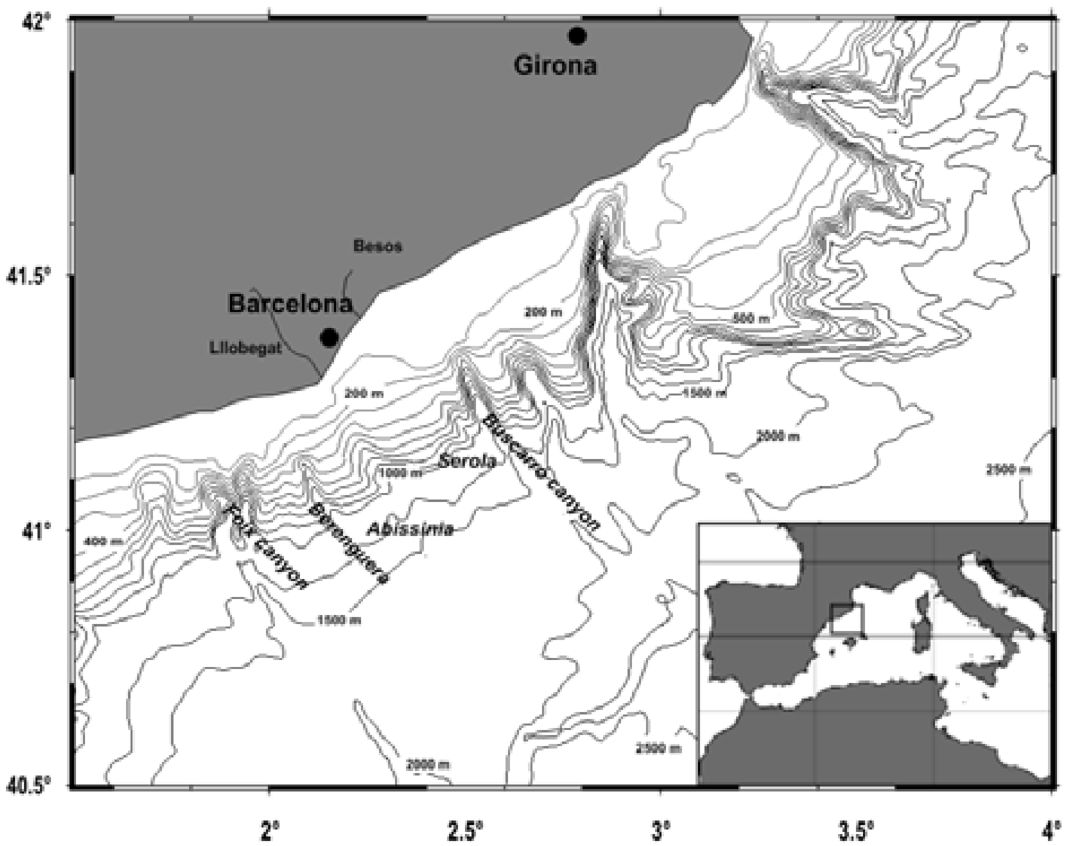
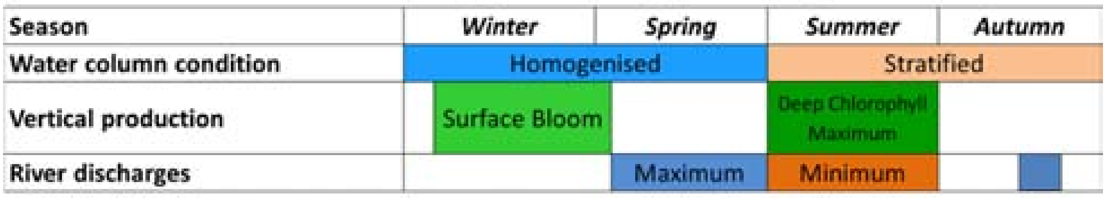


Fig. 2. Map of the study area

associated with pulses of food to bathyal depths take place. These changes derive on one hand from seasonal changes of primary production (Estrada, 1991) and the variable vertical flux of particles (Miquel et al., 1994; Cartes et al., 2002a). In the Catalan Sea, primary production peaks during a late winter surface bloom (Margalef and Catsellví, 1967; Bosc et al., 2004), whereas there is a deep chlorophyll maximum (DCM) in open waters during the stratified period (Estrada, 1991) (Fig. 3). A homogenised water column is present in winter and early spring, with most downward flux occurring in those mixed waters. Stratification of the water column is usual from April to November, and is associated with much lower vertical particle fluxes (Miquel et al., 1994) (Fig. 3). On the other hand, changes in advective fluxes may also play an important role in variations of organic matter input in the deep sea. The advective flux of OM and the physical conditions in the canyons vary in relation to discharges of continental run-off (Monaco et al., 1990; Buscail et al., 1990), to cascading events in the Gulf of Lions and to water column conditions along the NW Spanish coast (Canals et al., 2006; Palanques et al., 2006). They are usually greatest in spring and least in summer.

The distribution of water masses also varies seasonally at bathyal depths in our study area. The Levantine Intermediate Water (LIW), characterised by a maximum of salinity (S ~ 38.5 pss) and temperature (T ~ 13.5º C) (Font, 1987; Brankart and Pinardi, 2001), is present throughout the year between 300 and 800 m, presenting its maximum flow before or close to the period of stratification (Font et al., 1987; Brankart and Pinardi, 2001; Salat et al., 2002; López-Jurado et al., 2008).



Season	*Winter*	*Spring*	*Summer*	*Autumn*
Water column condition	Homogenised		Stratified	
Vertical production	Surface Bloom		Deep Chlorophyll Maximum	
River discharges		Maximum	Minimum	🟦

Fig. 3. Scheme of the seasonal pattern in main features controlling food inputs to bathyal depths.

2.2. Faunal characteristics

The continental slope of the Catalan Sea presents the generalised decline in biomass with depth except for a characteristic biomass peak of demersal fish, specifically Alepocephalidae, at depths of *ca.* 1200-1400 m which was also found in the N Atlantic (north-western Mediterranean: Stefanescu et al. 1993, North Atlantic: Gordon 1986). This peak has been linked to increases of their main prey (i.e. near-bottom jellyfish: Hargreaves et al., 1984; Cartes et al., 2013) by different authors (Cartes and Carrassón, 2004; Lebrato et al., 2012; Cartes et al., 2013). In addition, submarine canyons indenting the slope present generalised greater megafaunal abundance and biomass than the adjacent slope, although species composition is similar (Cartes et al., 1994; Stefanescu et al., 1994).

In the Catalan slope depth boundaries based on faunal changes comparable to those described in other parts of the world's oceans have been reported (e.g. Mediterranean Sea: Massutí and Moranta, 2003; Cartes et al., 2004; Atlantic Ocean: Koslow, 1993; Menezes et al., 2006; Indian Ocean: Koslow et al., 1994; Pacific Ocean: McClatchie et al., 1997; Antarctic Ocean: Pakhomov et al., 2006). Consequently, three depth zones have generally been identified: the upper, the middle and the lower slopes (Abelló et al., 1988; Abelló and Valladares, 1988; Cartes and Sardà, 1992; Cartes, 1993d).

The middle slope is a distributional zone between ~ 600 m and ~ 1200 m that has been consistently identified in studies of crustacean and fish assemblages along the

Catalonian coasts (Abelló et al., 1988; Cartes and Sardà, 1993; Stefanescu et al., 1993; 1994). It is situated below the shelf-slope break and the upper slope, and is characterised by homogeneous communities (Cartes et al., 2009a) and maximum diversities, e.g. among decapods (Cartes et al., 1994). The composition, distribution and dynamics of megafaunal communities in this area have been studied extensively (e.g. Stefanescu et al., 1992; 1994; Cartes and Sardà, 1993; Cartes et al., 1994; 2009a;). In the Mediterranean Sea, studies have been usually carried out on the distributions of fish (Stefanescu et al., 1994; Madurell et al., 2004; Menezes et al., 2006; Moranta et al., 2008) and of decapods (Cartes et al., 1994; Fariña et al., 1997; Fanelli et al., 2007), but fewer studies have considered jointly the whole community (fish, decapods and other invertebrates: Morales-Nin et al., 2003; Colloca et al., 2003; Cartes et al., 2004).

Megafauna communities of the bathyal domain of the Catalan Sea are dominated by benthopelagic fish and decapod crustaceans. Fishes represent the largest biomass among all megafauna, and decapod crustaceans dominate the middle slope of the NW Mediterranean Sea in terms of numerical abundance (Cartes and Sardà, 1992; Stefanescu et al., 1994). Over the middle slope, fish communities are dominated by relatively small species, such as macrourids (i.e. *Trachyrhynchus scabrus* and *Nezumia aequalis*) and *Phycis blennoides* (Stefanescu et al., 1994). Decapod communities are characterised by high diversities of benthic and nektobenthic decapod species and some typical bathypelagic species that coexist (Cartes and Sardà, 1993). This assemblage is dominated by the nektobenthic shrimp *Aristeus antennatus* and the benthic shrimp *Calocaris macandreae*, but assemblage composition varies seasonally and high densities of mesopelagic shrimps (e.g. *Pasiphaea multidentata*) are observed in spring over the upper and the middle slopes (Cartes et al., 1994). *Calocaris macandreae* is also a basic component of the diets of the majority of the megafaunal groups, such as *A. antennatus* (Cartes, 1994), crabs (Cartes, 1994), macrourids (Macpherson, 1981), and other fishes (Macpherson, 1979). Megafaunal benthic invertebrates are poorly diversified (Alvà, 1987) and not generally dominant in terms of biomass (Cartes and Sardà, 1992). Most characteristic species at mid-slope depths are the echinoid *Brissopsis lyrifera* and the holothurian *Molpadia musculus*, which attain their highest densities in areas of high local production (Cartes et al., 2009a). In contrast, benthic macrofauna are relatively abundant compared to other areas of the Mediterranean Sea (Mamouridis et al., 2011), related to the continental influence in this area. The macroinfaunal compartment is dominated by surface and subsurface deposit feeding polychaetes and crustaceans (Mamouridis et al., 2011) and it is especially important for being a dominant trophic resource for fish and large crustaceans inside Catalonian canyons (e.g. Macpherson, 1981; Cartes, 1994; Cartes and Maynou, 1998; Carrassón and Cartes, 2002).

Despite this difference in abundance between fish and decapods, these two taxa consume similar amounts of food annually over the middle slope around Catalan canyons, and play leading roles in the consumption of virtually all macrobenthic and macroplanktonic production (Cartes and Maynou, 1998). Thus it seems that food constitutes a limited resource.

High levels of food resource partitioning in the area have been well established both for decapods and fish (Cartes, 1998; Carrassón and Cartes, 2002). Dominant species have mixed diets based on benthopelagic and mesopelagic prey (e.g. Mauchline and Gordon 1986; 1991; Cartes, 1993a-c; 1994; Fanelli and Cartes, 2010), but usually have distinct preference towards one of these categories. In addition, fishes and decapods generally employ different trophic strategies (Haedrich et al., 1980; Cartes and Sardà, 1993) in respect to prey selection (mainly affected by prey size). Fish and decapod species inhabiting the middle slope of the Catalan Sea are secondary consumers mainly feeding on macrofauna, and only large specimens *of P. blennoides* and some sharks also prey on larger fauna (decapods, cephalopods and other fishes) (fish: Macpherson, 1978; 1979; Fanelli et al., 2009b; Fanelli and Cartes, 2010; decapods: Cartes, 1993a-c; 1994; Fanelli and Cartes, 2008). The macrobenthos (including hyperbenthos) is their main source of prey, and pelagic resources are secondary although seasonally important. Bathymetric zonation among species with similar trophic preferences is also patent, and especially intense among species situated at high trophic levels (e.g. sharks among fish: Cartes and Carrassón, 2004).

Seasonal changes in dietary composition of deep-sea megafauna species from this area have been reported repeatedly (Cartes, 1994; Madurell and Cartes, 2005; Cartes et al., 2008a; Fanelli and Cartes, 2008; 2010), for example to at least 1200 m in *Aristeus antennatus* (Cartes, 1994), and have been linked to seasonality of prey (e.g. Cartes et al., 2002a). Related to dietary variations, resource partitioning is weaker during some periods, usually autumn, following peaks in abundance of specific prey, essentially the euphausiid *Meganyctiphanes norvegica* (Macpherson, 1981; Cartes, 1998b). Regarding the knowledge of the slope species' life histories, temporality in reproductive cycles and recruitment patterns of both fish and decapods of the Catalan Sea is relatively well documented to *ca.* 1000 m (e.g. Massutí et al., 1995; 1996; Rotllant et al., 2002;

Company et al., 2003), with increasing gaps in species biology information deeper. To the current knowledge, different patterns in the reproductive cycle of slope species have been identified, so the life strategy of species seems rather species-specific.

In summary, despite the temporal changes in both the structure and dynamics (including different temporal scales) of deep-water communties and in the trophic relationships among dominant species inhabiting the Catalan slope have been relatively well described and analysed, we are still far from a good knowledge about which environmental variables control such changes. This is due to the scarcity of multidisciplinary studies, like this one, that attempted to relate the biological responses of species and communities with abiotic and biotic variables controlling them.

3. Hypothesis

Deep Sea ecosystems are no longer considered as stable environments in the small/mid temporal scales, and knowledge of the existence of seasonal processes in deep-sea ecosystems is steadily increasing. More and more, studies point to seasonality in food inputs as the main regulator of short-term temporality, although such connections are still scarcely known when considering fauna belonging to high trophic levels. We hypothesize that, as observed in fauna at low trophic levels, seasonal changes found in diverse aspects of communities and populations of megafauna respond to seasonality in food inputs. Both the vertical and the advective fluxes of food may exert some influence on the patterns observed in the megafaunal communities.

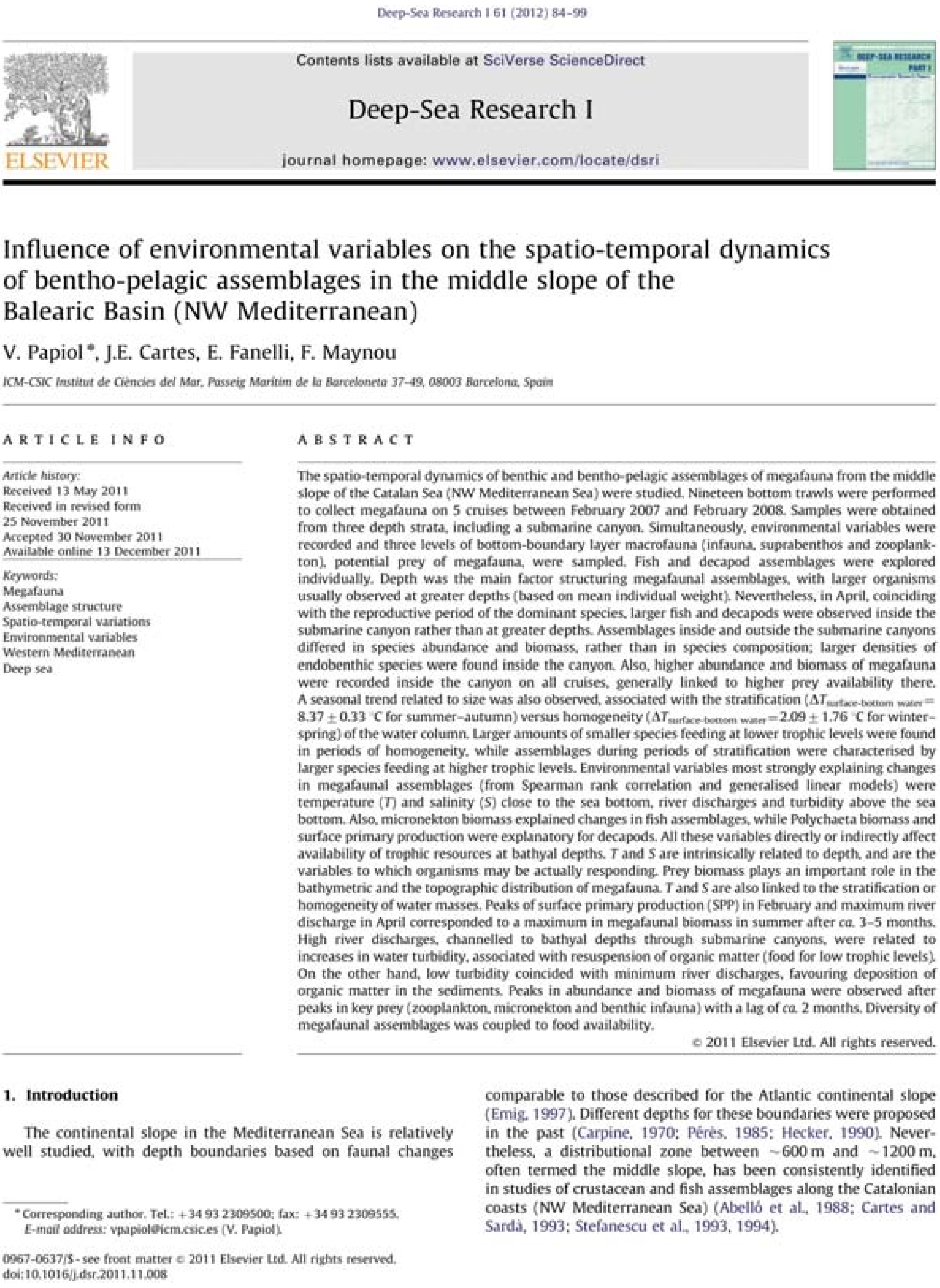
4. Aims

The global aim of the present thesis is to assess the seasonal changes occurring in bathyal benthopelagic communities (the Benthic Boundary Layer), both in their structure and trophic dynamics, and to identify which (and whenever possible how) environmental variables, including food availability, exert a control on these changes.

More specifically we aimed:

1- to describe the main spatial and, especially, temporal (seasonal) patterns of distribution of the middle slope megafaunal community.
2- to identify those environmental variables/factors having the greatest influence on the structure and dynamics of megafaunal assemblages on the Catalan (Balearic Basin).
3- to describe the trophic web structure and seasonal changes of the benthic and the benthopelagic communities in the middle slope.
4- to assess the food sources sustaining the benthic and the benthopelagic megafaunal communities together with the main environmental variables controlling them.
5- to define the trophic and reproductive seasonal patterns of the whole assemblage of fish and decapods.
6- to determine the relationship between the reproductive and feeding strategies, and their coupling with primary food sources and environmental variability, both for fish and for decapods.

CHAPTER 2 - INFLUENCE OF ENVIRONMENTAL VARIABLES ON THE SPATIO-TEMPORAL DYNAMICS OF BENTHO-PELAGIC ASSEMBLAGES IN THE MIDDLE SLOPE OF THE BALEARIC BASIN (NW MEDITERRANEAN)



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Influence of environmental variables on the spatio-temporal dynamics of bentho-pelagic assemblages in the middle slope of the Balearic Basin (NW Mediterranean)

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Deep sea

A B S T R A C T

The spatio-temporal dynamics of benthic and bentho-pelagic assemblages of megafauna from the middle slope of the Catalan Sea (NW Mediterranean Sea) were studied. Nineteen bottom trawls were performed to collect megafauna on 5 cruises between February 2007 and February 2008. Samples were obtained from three depth strata, including a submarine canyon. Simultaneously, environmental variables were recorded and three levels of bottom-boundary layer macrofauna (infauna, suprabenthos and zooplankton), potential prey of megafauna, were sampled. Fish and decapod assemblages were explored individually. Depth was the main factor structuring megafaunal assemblages, with larger organisms usually observed at greater depths (based on mean individual weight). Nevertheless, in April, coinciding with the reproductive period of the dominant species, larger fish and decapods were observed inside the submarine canyon rather than at greater depths. Assemblages inside and outside the submarine canyons differed in species abundance and biomass, rather than in species composition; larger densities of endobenthic species were found inside the canyon. Also, higher abundance and biomass of megafauna were recorded inside the canyon on all cruises, generally linked to higher prey availability there. A seasonal trend related to size was also observed, associated with the stratification ($\Delta T_{\text{surface-bottom water}} = 8.37 \pm 0.33$ °C for summer–autumn) versus homogeneity ($\Delta T_{\text{surface-bottom water}} = 2.09 \pm 1.76$ °C for winter–spring) of the water column. Larger amounts of smaller species feeding at lower trophic levels were found in periods of homogeneity, while assemblages during periods of stratification were characterised by larger species feeding at higher trophic levels. Environmental variables most strongly explaining changes in megafaunal assemblages (from Spearman rank correlation and generalised linear models) were temperature (T) and salinity (S) close to the sea bottom, river discharges and turbidity above the sea bottom. Also, micronekton biomass explained changes in fish assemblages, while Polychaeta biomass and surface primary production were explanatory for decapods. All these variables directly or indirectly affect availability of trophic resources at bathyal depths. T and S are intrinsically related to depth, and are the variables to which organisms may be actually responding. Prey biomass plays an important role in the bathymetric and the topographic distribution of megafauna. T and S are also linked to the stratification or homogeneity of water masses. Peaks of surface primary production (SPP) in February and maximum river discharge in April corresponded to a maximum in megafaunal biomass in summer after *ca.* 3–5 months. High river discharges, channelled to bathyal depths through submarine canyons, were related to increases in water turbidity, associated with resuspension of organic matter (food for low trophic levels). On the other hand, low turbidity coincided with minimum river discharges, favouring deposition of organic matter in the sediments. Peaks in abundance and biomass of megafauna were observed after peaks in key prey (zooplankton, micronekton and benthic infauna) with a lag of *ca.* 2 months. Diversity of megafaunal assemblages was coupled to food availability.

1. Introduction

The continental slope in the Mediterranean Sea is relatively well studied, with depth boundaries based on faunal changes comparable to those described for the Atlantic continental slope (Emig, 1997). Different depths for these boundaries were proposed in the past (Carpine, 1970; Pérès, 1985; Hecker, 1990). Nevertheless, a distributional zone between ~600 m and ~1200 m, often termed the middle slope, has been consistently identified in studies of crustacean and fish assemblages along the Catalonian coasts (NW Mediterranean Sea) (Abelló et al., 1988; Cartes and Sardà, 1993; Stefanescu et al., 1993, 1994).

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The middle slope is situated below the shelf-slope break and the upper slope, and in the western Mediterranean Sea it is characterised by homogeneous biocenoses/communities (Cartes et al., 2009a) and maximum diversities, e.g. among decapods (Cartes et al., 1994). Species composition along the middle slope undergoes some changes at regional or larger scales; in particular, it changes eastwards in the Mediterranean Sea (Labropoulou and Papaconstantinou, 2000; Kallianiotis et al., 2000; Madurell et al., 2004).

Continental slopes in the western Mediterranean, especially off Catalonia and the Balearic Islands, have been studied extensively regarding the composition, distribution and dynamics of megafaunal communities (Off Catalonia: Cartes and Sardà, 1993; Cartes et al., 1994, 2009a; adjacent to the Balearic Islands: Maynou and Cartes, 2000; Moranta et al., 2008). In the Mediterranean Sea as a whole, several separate studies have been carried out on the distributions of fish (Stefanescu et al., 1994; Madurell et al., 2004; Menezes et al., 2006; Moranta et al., 2008) and of decapods (Cartes et al., 1994; Fariña et al., 1997; Fanelli et al., 2007), but fewer studies have considered jointly the megafaunal fish, decapods and other invertebrates (Sardà et al., 1994; Morales-Nin et al., 2003; Colloca et al., 2003; Cartes et al., 2004). Moreover, the ecological factors controlling distributions of megafaunal assemblages at bathyal depths remain poorly known, largely because simultaneous information on environmental variables and faunas remains scarce.

Regarding the main natural gradients structuring assemblages of megafauna, several studies have revealed depth to be the dominant factor (Cartes and Sardà, 1992; Stefanescu et al., 1993; Gaertner et al., 1999; Labropoulou and Papaconstantinou, 2000; Colloca et al., 2003). Also, in recent years temporal changes in bathyal assemblage composition have been studied, and season has been found to affect significantly the structure of megafaunal assemblages (Cartes, 1994; Maynou and Cartes, 2000; Madurell et al., 2004; Moranta et al., 2008). Both spatial and temporal gradients may act as proxies for many other environmental factors, e.g. temperature, salinity and food availability (Francis et al., 2002; Colloca et al., 2003; Cartes et al., 2004; Fock et al., 2004; Menezes et al., 2006), to which organisms may actually be responding. While factors structuring bathyal communities and assemblages have been discussed previously (Labropoulou and Papaconstantinou, 2000; Carrassón and Cartes, 2002; Moranta et al., 2008; Cartes et al., 2009a), and while the biotic and abiotic characteristics of the study area have been described, the relationships among bathymetric and/or seasonal changes in community structure and the environmental variables driving them have received little attention.

The Mediterranean Sea is characterised by annual thermal stability of the water mass (~12.8 °C) below ~200 m (Hopkins, 1985). However, important temporal fluctuations are associated with pulses of food to bathyal depths. These changes derive on one hand from seasonal changes of primary production (Estrada, 1991) and the variable vertical flux of particles (Miquel et al., 1994; Cartes et al., 2002a). In the Catalan Sea, primary production peaks during a late winter surface bloom, whereas there is a deep chlorophyll maximum (DCM) in open waters during the stratified period (Estrada, 1991). A homogenised water column is present in winter and early spring, with most downward flux occurring in those mixed waters. Stratification of the water column is usual from April to November, and is associated with much lower vertical particle fluxes (Miquel et al., 1994). On the other hand, changes in advective fluxes, such as those that generate nepheloid layers in submarine canyons, also seem to play an important role in variations of organic matter input in the deep sea. The submarine canyons are contact zones between the circalittoral and bathyal communities (Reyss, 1971), and in the study area they channel significant amounts of sediment and associated organic matter (OM) across the slope (Buscail et al., 1990; Palanques et al., 2006) enhancing the food supply (Vetter and Dayton, 1998) in depocenters. Those become local hotspots of secondary production. Additionally, advective fluxes sort upper sediment layers causing resuspension of OM from the bottom. The advective flux of OM and the physical conditions in the canyons vary in relation to discharges of continental run-off (Monaco et al., 1990; Buscail et al., 1990), to cascading events in the Gulf of Lions and to water column conditions along the NW Spanish coast (Canals et al., 2006; Palanques et al., 2006).

Organic matter reaching bathyal depths is channelled to megafauna by zooplankton in the near-bottom waters and by suprabenthos and infauna that constitute the diet of bathyal demersal fish (Cartes and Maynou, 1998). Thus, OM inputs and macrofaunal communities (potential prey of megafauna) both have significant influences on the biology and density of large benthopelagic fish and invertebrates. For this reason, comprehensive studies of trophic web dynamics are necessary to identify the factors structuring megafaunal assemblages.

The characteristics of water masses also affect the distribution of assemblages at bathyal depths (Colloca et al., 2003; Menezes et al., 2006; Pakhomov et al., 2006). In our study area, the Levantine Intermediate Water, characterised by a maximum of salinity (~38.5 pss) and temperature (~13.5 °C) (Font, 1987; Brankart and Pinardi, 2001), is present throughout the year between 300 and 800 m, presenting its maximum flow before or close to the period of stratification (Font, 1987; Brankart and Pinardi, 2001; Salat et al., 2002; López-Jurado et al., 2008).

We have sought to identify those environmental factors having the greatest influence on the structure and dynamics of megafaunal assemblages on the slope of the Balearic Basin. Specifically, we aim to

i) describe the main spatial and temporal patterns of distribution of the middle slope megafaunal community and
ii) identify the physical, chemical and biological environmental drivers of those patterns.

2. Materials and methods

2.1. Sampling of megafauna

The study was carried out in the bathyal Catalan Sea (Balearic Basin, NW Mediterranean: Fig. 1) at depths ranging from 423 to 1175 m. Within the project BIOMARE, a total of 5 multidisciplinary (including trawl) surveys (BIOMARE B1, B2, B3, B4 and B08) were carried out between February 2007 and February 2008 on a seasonal basis (February, April, June/July and October) (Table 1), thus covering an entire year.

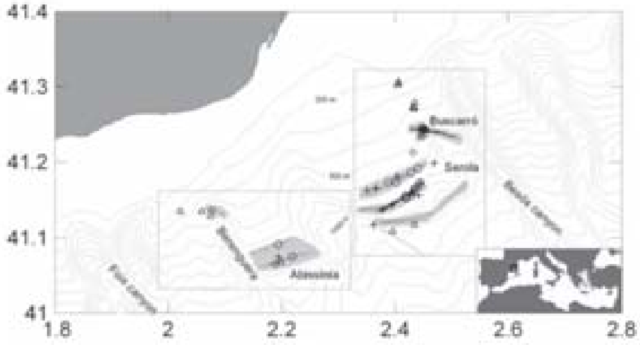

Fig. 1. Study area and sampling points with gear used specified: OTSB-14 (–); suprabenthic sledge and WP2 (○); Box-Corer (+); Multi-Corers (◇); CTD (△).

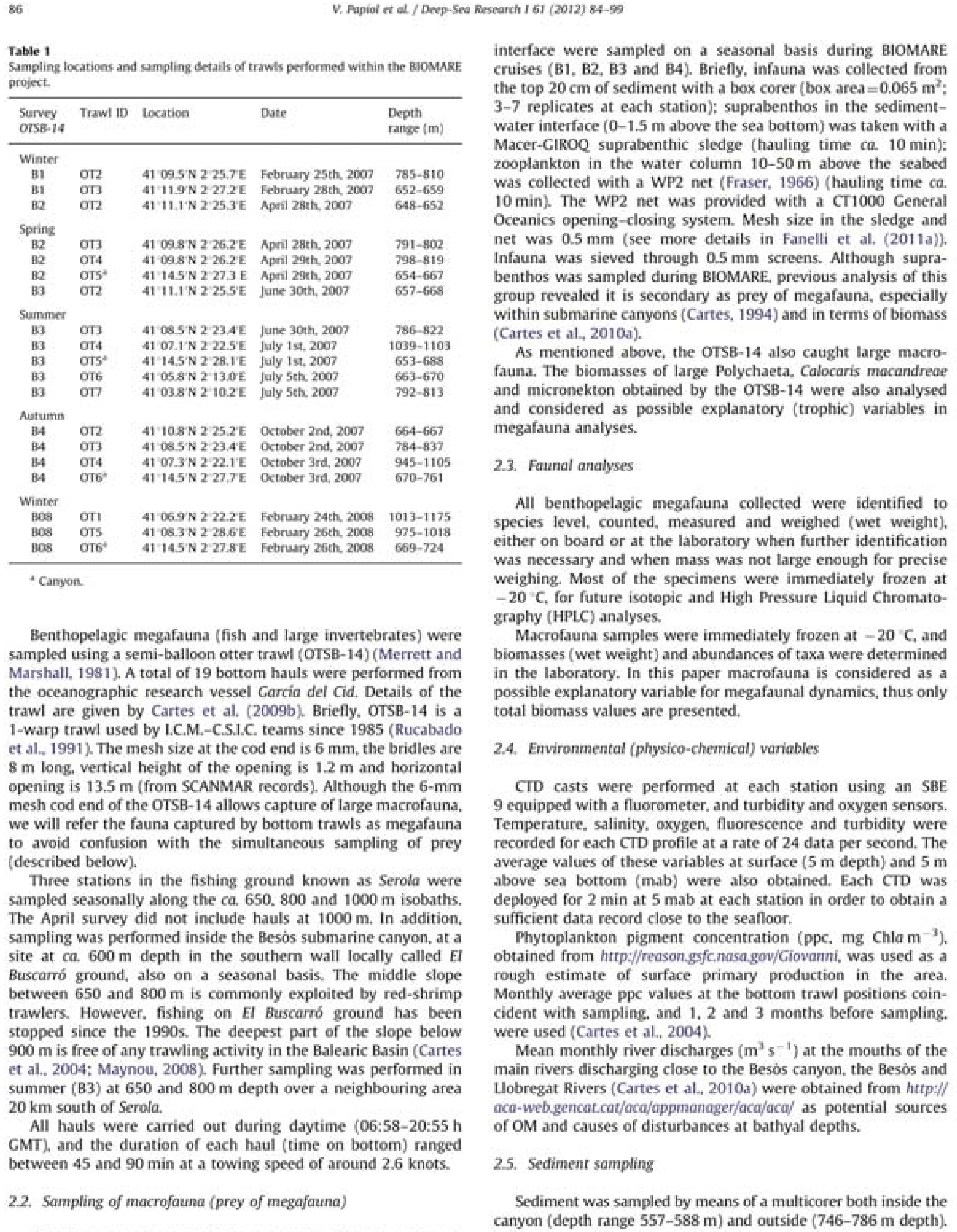

Table 1
Sampling locations and sampling details of trawls performed within the BIOMARE project.

Survey *OTSB-14*	Trawl ID	Location	Date	Depth range (m)
Winter				
B1	OT2	41°09.5′N 2°25.7′E	February 25th, 2007	785–810
B1	OT3	41°11.9′N 2°27.2′E	February 28th, 2007	652–659
B2	OT2	41°11.1′N 2°25.3′E	April 28th, 2007	648–652
Spring				
B2	OT3	41°09.8′N 2°26.2′E	April 28th, 2007	791–802
B2	OT4	41°09.8′N 2°26.2′E	April 29th, 2007	798–819
B2	OT5[a]	41°14.5′N 2°27.3 E	April 29th, 2007	654–667
B3	OT2	41°11.1′N 2°25.5′E	June 30th, 2007	657–668
Summer				
B3	OT3	41°08.5′N 2°23.4′E	June 30th, 2007	786–822
B3	OT4	41°07.1′N 2°22.5′E	July 1st, 2007	1039–1103
B3	OT5[a]	41°14.5′N 2°28.1′E	July 1st, 2007	653–688
B3	OT6	41°05.8′N 2°13.0′E	July 5th, 2007	663–670
B3	OT7	41°03.8′N 2°10.2′E	July 5th, 2007	792–813
Autumn				
B4	OT2	41°10.8′N 2°25.2′E	October 2nd, 2007	664–667
B4	OT3	41°08.5′N 2°23.4′E	October 2nd, 2007	784–837
B4	OT4	41°07.3′N 2°22.1′E	October 3rd, 2007	945–1105
B4	OT6[a]	41°14.5′N 2°27.7′E	October 3rd, 2007	670–761
Winter				
B08	OT1	41°06.9′N 2°22.2′E	February 24th, 2008	1013–1175
B08	OT5	41°08.3′N 2°28.6′E	February 26th, 2008	975–1018
B08	OT6[a]	41°14.5′N 2°27.8′E	February 26th, 2008	669–724

[a] Canyon.

Benthopelagic megafauna (fish and large invertebrates) were sampled using a semi-balloon otter trawl (OTSB-14) (Merrett and Marshall, 1981). A total of 19 bottom hauls were performed from the oceanographic research vessel *García del Cid*. Details of the trawl are given by Cartes et al. (2009b). Briefly, OTSB-14 is a 1-warp trawl used by I.C.M.–C.S.I.C. teams since 1985 (Rucabado et al., 1991). The mesh size at the cod end is 6 mm, the bridles are 8 m long, vertical height of the opening is 1.2 m and horizontal opening is 13.5 m (from SCANMAR records). Although the 6-mm mesh cod end of the OTSB-14 allows capture of large macrofauna, we will refer the fauna captured by bottom trawls as megafauna to avoid confusion with the simultaneous sampling of prey (described below).

Three stations in the fishing ground known as *Serola* were sampled seasonally along the *ca.* 650, 800 and 1000 m isobaths. The April survey did not include hauls at 1000 m. In addition, sampling was performed inside the Besòs submarine canyon, at a site at *ca.* 600 m depth in the southern wall locally called *El Buscarró* ground, also on a seasonal basis. The middle slope between 650 and 800 m is commonly exploited by red-shrimp trawlers. However, fishing on *El Buscarró* ground has been stopped since the 1990s. The deepest part of the slope below 900 m is free of any trawling activity in the Balearic Basin (Cartes et al., 2004; Maynou, 2008). Further sampling was performed in summer (B3) at 650 and 800 m depth over a neighbouring area 20 km south of *Serola*.

All hauls were carried out during daytime (06:58–20:55 h GMT), and the duration of each haul (time on bottom) ranged between 45 and 90 min at a towing speed of around 2.6 knots.

2.2. *Sampling of macrofauna (prey of megafauna)*

Macrofauna was sampled to assess the trophic resources available for megafauna. Three levels of the macrofauna occupying different positions with respect to the sediment/water interface were sampled on a seasonal basis during BIOMARE cruises (B1, B2, B3 and B4). Briefly, infauna was collected from the top 20 cm of sediment with a box corer (box area = 0.065 m^2; 3–7 replicates at each station); suprabenthos in the sediment–water interface (0–1.5 m above the sea bottom) was taken with a Macer-GIROQ suprabenthic sledge (hauling time *ca.* 10 min); zooplankton in the water column 10–50 m above the seabed was collected with a WP2 net (Fraser, 1966) (hauling time *ca.* 10 min). The WP2 net was provided with a CT1000 General Oceanics opening–closing system. Mesh size in the sledge and net was 0.5 mm (see more details in Fanelli et al. (2011a)). Infauna was sieved through 0.5 mm screens. Although suprabenthos was sampled during BIOMARE, previous analysis of this group revealed it is secondary as prey of megafauna, especially within submarine canyons (Cartes, 1994) and in terms of biomass (Cartes et al., 2010a).

As mentioned above, the OTSB-14 also caught large macrofauna. The biomasses of large Polychaeta, *Calocaris macandreae* and micronekton obtained by the OTSB-14 were also analysed and considered as possible explanatory (trophic) variables in megafauna analyses.

2.3. *Faunal analyses*

All benthopelagic megafauna collected were identified to species level, counted, measured and weighed (wet weight), either on board or at the laboratory when further identification was necessary and when mass was not large enough for precise weighing. Most of the specimens were immediately frozen at −20 °C, for future isotopic and High Pressure Liquid Chromatography (HPLC) analyses.

Macrofauna samples were immediately frozen at −20 °C, and biomasses (wet weight) and abundances of taxa were determined in the laboratory. In this paper macrofauna is considered as a possible explanatory variable for megafaunal dynamics, thus only total biomass values are presented.

2.4. *Environmental (physico-chemical) variables*

CTD casts were performed at each station using an SBE 9 equipped with a fluorometer, and turbidity and oxygen sensors. Temperature, salinity, oxygen, fluorescence and turbidity were recorded for each CTD profile at a rate of 24 data per second. The average values of these variables at surface (5 m depth) and 5 m above sea bottom (mab) were also obtained. Each CTD was deployed for 2 min at 5 mab at each station in order to obtain a sufficient data record close to the seafloor.

Phytoplankton pigment concentration (ppc, mg Chl*a* m^{-3}), obtained from *http://reason.gsfc.nasa.gov/Giovanni*, was used as a rough estimate of surface primary production in the area. Monthly average ppc values at the bottom trawl positions coincident with sampling, and 1, 2 and 3 months before sampling, were used (Cartes et al., 2004).

Mean monthly river discharges (m^3 s^{-1}) at the mouths of the main rivers discharging close to the Besòs canyon, the Besòs and Llobregat Rivers (Cartes et al., 2010a) were obtained from *http://aca-web.gencat.cat/aca/appmanager/aca/aca/* as potential sources of OM and causes of disturbances at bathyal depths.

2.5. *Sediment sampling*

Sediment was sampled by means of a multicorer both inside the canyon (depth range 557–588 m) and outside (746–786 m depth). Since infauna is the macrofaunal group most affected from a trophic point of view by sediment quality, sediment sampling was performed inside the canyon in parallel with infauna collection.

Sediment was immediately frozen at −20 °C for later analyses. Total organic carbon (TOC) and total nitrogen (TN) were determined from the CO_2 and N_2 produced by combustion using a Thermo Electron Flash EA 1112 elemental analyzer. REDOX potential (mV) was obtained from sediments using a ThermoOrion 250A sensor. Voltage was read at the sediment surface, at 6 cm and 10 cm depths.

The percentage of sediment organic matter was quantified as loss on ignition (LOI) by ashing 2–3.5 g of sediment (dry weight after 60 °C during 24 h or until reaching constant weight) for 2 h at 550 °C.

2.6. *Data analysis*

Megafaunal species recorded in less than 5% of the samples were omitted from the data set to prevent an undue influence on the results (Gauch, 1982). Abundance and biomass were standardized to a common swept area of 1 ha (ind ha^{-1} and g ha^{-1}, respectively), according to the values proposed by Cartes et al. (2009b) for an OTSB-14 bottom trawl.

First, in order to evaluate megafaunal species groupings, cluster analysis was applied to the abundance data matrix, using the non-parametric Spearman rank correlation as a distance index. Second, to explain observed similarities or dissimilarities (distances) between the groups resulting from the cluster analyses, multidimensional scaling (MDS) analyses were carried out on abundance data. ANOSIM (ANalysis Of SIMilarities) was employed to test the significance of differences among the groups resulting from the cluster analyses, and SIMPER was used to identify those species that most typify each of the groups. For this latter routine, a square root transformation was applied to adapt the data to the Bray–Curtis distance (Clarke and Warwick, 1995). Since fishes and decapods are the two dominant taxa in the deep Mediterranean (Cartes et al., 2004), analyses were also performed separately for these megafaunal groups.

Trends in abundance and biomass of megafauna were analysed also on a seasonal basis, as was macrofaunal biomass (wet weight of infauna as g m^{-2} of sediment and of suprabenthos and zooplankton as mg m^{-3} of filtered water). Temporal trends of biomass of large Polychaeta, *Calocaris macandreae* and micronekton obtained by the OTSB-14 were also analysed, because of the substantial role they play in the diet of megafauna. Diversity of each assemblage identified was calculated using the Shannon–Wiener (H') and the species richness (S) indices. Spatial and temporal trends in diversity were also obtained. In addition, fish and decapod mean individual weights were calculated for each sampling period and depth.

Environmental and trophic (i.e. macrofaunal biomass) variables were normalised and standardized before analyses. A draftsman plot (i.e. scatter plots of all pairwise combinations of variables) (Clarke and Warwick, 1995) was applied to environmental variables to identify whether any of them were strongly correlated, thus providing redundant information. Redundant variables ($\rho > 0.70$) could be discarded, simplifying the matrix. Water column homogeneity or stratification was calculated as the difference between water temperature at surface and 5 m above the seabed.

To identify which environmental variables explained differences in the distributions of the distinct assemblages, non-parametric Spearman rank correlation coefficients were calculated between the set of environmental variables and (1) the two dimensions of the MDS and (2) standardised values of abundance. The relationships between abundance of species (the dependent variable) and environmental variables were also analysed by two multivariate approaches: (1) Generalised Linear Models (GLM) and (2) Canonical Correspondence Analysis (CCA) (Ter Braak, 1986). GLMs were carried out considering (a) the abundance and (b) the diversity (H') of all taxa, as well as the abundance and diversity of fishes and decapods separately. The independent variables explored were temperature 5 mab ($T_{5\ mab}$), salinity 5 mab ($S_{5\ mab}$), water turbidity 5 mab ($Turb_{5\ mab}$), river flow at the time of sampling as well as river flow 1, 2 and 3 months before the sampling, and SPP simultaneous and 1 month before the sampling. Also, the trophic variables considered were the biomass of suprabenthos, infauna, zooplankton, micronekton, Polychaeta and *C. macandreae*, the last three from OTSB-14 hauls. For the GLMs and CCAs biomass of suprabenthos, infauna and zooplankton were excluded, given the lack of data for some hauls.

The generalised linear model (GLM) is a flexible generalisation of ordinary least squares regression. The GLM generalises linear regression by allowing the linear model to be related to the response variable via a link function and by allowing the magnitude of the variance of each measurement to be a function of its predicted value. The distribution family used was Gaussian with logarithmic link. Model selection was based on minimising Akaike's Information Criterion (AIC).

CCA analyses were performed on abundance data for dominant megafaunal species and the set of environmental variables previously mentioned. Ordination axes generated by CCA are linear combinations of environmental variables; arrows in the plots representing environmental explanatory variables are proportional in length to their importance (Ter Braak, 1986). Therefore, community variation can be directly related to environmental variation. Abundance data were log-transformed prior to CCA calculations and a permutation test (based on 1000 permutations) was performed to evaluate whether the set of environmental variables could significantly explain the observed species composition in terms of abundance.

All the univariate and multivariate analyses were carried out using the software packages PRIMER 6 & PERMANOVA+ (Clarke and Warwick, 1995), STATISTICA 6.0 and XLSTAT (Addinsoft).

3. Results

A total of 7859 specimens belonging to 160 species (47 fish, 40 decapod crustaceans and 73 other invertebrates) was collected.

3.1. *Megafaunal assemblages*

The MDS analyses performed on OTSB-14 data showed that depth was the main assemblage structuring factor (Fig. 2). Combining the

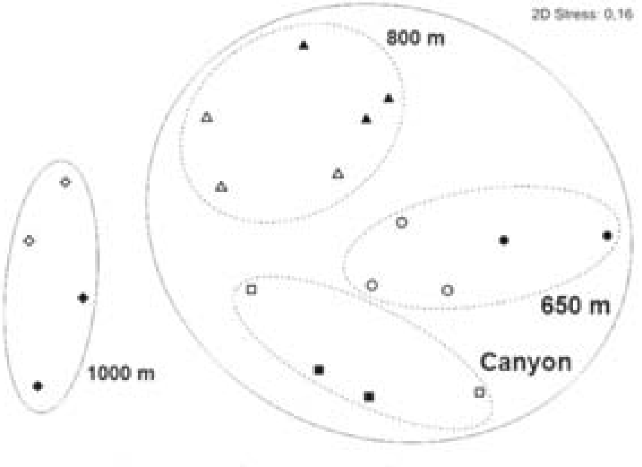

Fig. 2. MDS ordination plot of abundance data from OTSB-14 catches based on Spearman rank correlation. Data points are identified by depth: squares = 600 m (inside canyon); circles = 650 m (outside canyon); triangles = 800 m; diamonds = 1000 m. Filled symbols indicate a homogenous water column, unfilled symbols indicate a stratified water column.

results of cluster analysis with the MDS ordination, it is possible to distinguish two main groups: samples from the 1000 m station were segregated from those from shallower depths (600, 650 and 800 m). ANOSIM demonstrated that assemblages at all depths were distinct (all ANOSIM comparisons gave $p < 0.05$), particularly for hauls taken at 1000 m.

SIMPER analysis revealed which species were typical for each depth group (Table 2). The assemblage at 1000 m was more homogeneous than the rest, having the greatest within station similarity among the four depths (62.59%). At 1000 m cumulative abundance of 43% was reached by including only four species: *Aristeus antennatus*, *Pontophilus norvegicus*, *Lepidion lepidion* and *Munida tenuimana*. At 800 m, *M. tenuimana*, *P. norvegicus* and *A. antennatus* were again dominant, but 7 species were required to account for 41% of the abundance. At 650 m, *M. tenuimana*, *Monodaeus couchii*, *Processa canaliculata and Sergestes arcticus* were dominant, accumulating 26% of the abundance, while 9 species were required to reach 43% of the abundance. Finally, inside the submarine canyon (600 m) *Calocaris macandreae* dominated, together with *M. tenuimana*, *Plesionika martia* and *A. antennatus*, altogether accumulating 29% of the abundance.

The MDS ordination revealed a grouping related to the homogeneity vs. stratification of the water column (Fig. 2). ANOSIM confirmed a significant segregation between samples belonging to the period of water column homogeneity (B1, B2 and B08) and those from the period of stratification (B3 and B4) ($R=0.162$; $p < 0.05$). Seasonally, ANOSIM indicated significant segregation between assemblages present in spring (April) and in summer (June/July) ($R=0.528$; $p < 0.01$), but not among other seasons.

SIMPER performed on samples collected under different conditions of the water column (homogenous vs stratified) revealed a greater contribution of smaller species (e.g. *Cymbulia peroni*, *Calocaris macandreae*, *Gennadas elegans*) when the water column was homogenous (winter and spring) (Table 3). Larger species were more important in periods of stratification. In the same sense, SIMPER performed on seasonal data revealed that smaller species, such as those mentioned above, characterised the assemblage in spring, while larger species (e.g. *Aristeus antennatus*, *Lampanyctus crocodilus*, *Phycis blennoides*) were found in summer.

3.2. *Fish and decapods assemblages*

Since fishes and decapods are the two dominant taxa in the deep Mediterranean and occupy, on average, a different trophic level (Cartes et al., 2004, 2009c), analyses of these megafaunal groups were performed separately.

3.2.1. *Fish assemblages*

Fish assemblages at 600 m inside the canyon differed significantly from those at 650, 800 and 1000 m outside the canyon (ANOSIM all $p < 0.05$). Outside the canyon fish assemblages changed progressively down the slope: the difference between the 650 m and 1000 m assemblages was statistically significant (ANOSIM $R=0.744$, $p < 0.05$), but the intermediate comparisons (650–800 m, 800–1000 m) did not reveal shifts in faunal composition of the same magnitude.

Regarding temporality, fish assemblages did not change significantly according to the condition of the water column, although significant changes were found between assemblages present in spring and in summer. Water column stratification was a significant segregation factor only for the stations at 650 and 800 m outside the submarine canyon.

Table 2
Percentage contribution of typifying species (SIMPER analysis) to within-group similarity by depth, based on abundance data for samples obtained by the OTSB-14. Cut-off for low contribution: 60%.

Species	Av. abundance	Contribution %	Cum. %	Species	Av. abundance	Contribution %	Cum. %
650 m assemblage				***800 m assemblage***			
Average similarity: 57.93				**Average similarity: 56.92**			
Munida tenuimana	3.80	11.12	11.12	*Munida tenuimana*	3.76	9.26	9.26
Monodaeus couchii	2.66	5.89	17.01	*Pontophilus norvegicus*	3.28	8.20	17.46
Processa canaliculata	2.38	4.66	21.67	*Aristeus antennatus*	2.77	7.54	24.99
Sergestes arcticus	1.38	4.01	25.67	*Pagurus alatus*	1.78	4.69	29.68
Boreomysis arctica	1.45	3.82	29.49	*Abra longicallus*	1.85	4.41	34.09
Phycis blennoides	1.62	3.73	33.22	*Calocaris macandreae*	1.92	4.27	38.37
Pontocaris lacazei	1.63	3.55	36.77	*Anapagurus laevis*	1.43	3.34	41.71
Plesionika martia	1.69	3.46	40.23	*Gennadas elegans*	1.93	3.20	44.91
Calocaris macandreae	1.57	3.38	43.61	*Pontocaris lacazei*	1.07	3.13	48.03
Symphurus ligulatus	1.32	3.33	46.94	*Cirolana borealis*	1.39	2.84	50.88
Pasiphaea multidentata	1.17	3.30	50.24	*Lampanyctus crocodilus*	1.47	2.66	53.54
Lampanyctus crocodilus	1.52	3.23	53.47	*Polycheles typhlops*	0.94	2.19	55.72
Gennadas elegans	1.46	3.12	56.59	*Notacanthus bonapartei*	0.84	2.11	57.83
Aristeus antennatus	1.69	2.99	59.57	*Acanthephyra eximia*	0.71	2.07	59.90
Cymbulia peroni	1.29	2.85	62.43	*Nezumia aequalis*	0.78	1.97	61.88
600 m (Canyon) assemblage				***1000 m assemblage***			
Average similarity: 58.20				**Average similarity: 62.59**			
Calocaris macandreae	5.19	9.86	9.86	*Aristeus antennatus*	3.47	13.48	13.48
Munida tenuimana	3.05	6.82	16.67	*Pontophilus norvegicus*	3.38	13.21	26.70
Plesionika martia	2.70	6.02	22.69	*Lepidion lepidion*	2.92	10.84	37.53
Aristeus antennatus	3.16	5.92	28.61	*Munida tenuimana*	1.40	5.14	42.67
Lampanyctus crocodilus	2.46	5.77	34.38	*Nezumia aequalis*	1.45	4.95	47.62
Polycheles typhlops	2.15	5.07	39.45	*Lampanyctus crocodilus*	1.14	4.39	52.01
Nezumia aequalis	1.73	3.87	43.31	*Gennadas elegans*	1.04	3.38	55.39
Cymbulia peroni	1.83	3.67	46.98	*Notacanthus bonapartei*	1.23	3.36	58.75
Sergestes arcticus	1.59	3.53	50.51	*Alepocephalus rostratus*	1.15	3.33	62.08
Hymenocephalus italicus	1.75	3.36	53.87				
Monodaeus couchii	2.33	3.30	57.17				
Pontocaris lacazei	1.61	3.25	60.42				

Table 3
Percentage contribution of typifying species (SIMPER analysis) to within-group (water column stratification) similarity, based on abundance data from samples obtained by the OTSB-14. Cut-off for low contribution: 60%.

Species	Av. abundance	Contribution %	Cum. %
Homogenous water column assemblage			
Average similarity: 46.35			
Munida tenuimana	3.39	9.17	9.17
Aristeus antennatus	2.53	6.70	15.87
Pontophilus norvegicus	2.47	5.71	21.58
Cymbulia peroni	1.73	5.68	27.26
Calocaris macandreae	2.66	4.58	31.84
Gennadas elegans	1.77	3.79	35.63
Polycheles typhlops	1.29	3.49	39.12
Boreomysis arctica	1.80	3.09	42.21
Lampanyctus crocodilus	1.22	2.82	45.02
Nezumia aequalis	1.05	2.75	47.78
Pontocaris lacazei	1.05	2.62	50.40
Phycis blennoides	1.01	2.44	52.84
Galeus melastomus	0.82	2.32	55.16
Lepidion lepidion	1.25	2.25	57.41
Pasiphaea multidentata	0.92	2.21	59.62
Cyclothone braueri	1.38	2.20	61.82
Stratified water column assemblage			
Average similarity: 51.40			
Aristeus antennatus	2.88	9.03	9.03
Munida tenuimana	2.89	8.57	17.60
Lampanyctus crocodilus	1.98	5.81	23.41
Pontophilus norvegicus	1.93	4.72	28.13
Sergestes arcticus	1.40	4.44	32.57
Phycis blennoides	1.47	3.98	36.55
Monodaeus couchii	1.6	3.55	40.10
Argyropelecus hemigymnus	1.08	3.33	43.43
Polycheles typhlops	1.22	3.10	46.53
Calocaris macandreae	1.72	2.93	49.47
Gennadas elegans	1.15	2.89	52.35
Boreomysis arctica	1.00	2.73	55.08
Pontocaris lacazei	1.21	2.38	57.46
Nezumia aequalis	0.99	2.10	59.57
Galeus melastomus	0.84	2.01	61.58

3.2.2. *Decapod assemblages*

Decapod assemblages differed among all depths (Global $R = 0.743$; $p < 0.001$) and were homogenous throughout the whole year in all depth strata.

3.3. *Trends in abundance and biomass*

3.3.1. *Fish*

Fish abundance was consistently higher in June/July (inside canyon) and October (650 and 800 m) than in February–April (Fig. 3a) at depths shallower than 1000 m, increasing in most cases from February to June/July and reaching a maximum in October (except inside canyon). At 1000 m we found an opposite trend with abundance decreasing from February to October. By stations (depths), the most common tendency was for fish abundance to be higher inside than outside canyons.

At the two shallowest stations (inside canyon and 650 m) we found a similar seasonal pattern for fish biomass: increase from February to June/July, dropping in October (Fig. 3a). At 600 m, for instance, fish biomass increased from February (1220 g ha^{-1}) to June/July (1984 g ha^{-1}) and then decreased to 811 g ha^{-1} in October. An exception was at 800 m, where biomass was higher in February than in April. At 1000 m biomass was very similar all year round. Regarding trends of biomass vs. depth, biomass consistently reached the highest values at two stations: inside the canyon and at 1000 m. Biomass outside the canyon was higher at greater depths all the year (>1.6 kg ha^{-1} at 1000 m).

3.3.2. *Decapods*

At <1000 m we regularly found the highest decapod abundance in April and October, the lowest abundance in June/July (Fig. 3b). Deeper than 1000 m we did not find this pattern and abundance showed small oscillations with the highest value in June/July. Decapod abundance decreased with depth (Fig. 3b) with the highest values inside the canyon (at 600 m), and with some exceptions at 800 m in April and June/July Decapod biomass showed more irregular patterns than abundance (Fig. 3b), especially at the two shallowest stations (inside the canyon and at 650 m outside). At greater depths (800 and 1000 m) biomass peaked in June/July (502–762 g ha^{-1}).

3.3.3. *All megafauna*

Since decapod crustaceans were the numerically dominant taxon, total abundance of megafauna showed the same decreasing tendency in abundance with depth (Fig. 3c). Because fish always dominated megafaunal biomass, patterns in fish and total megafaunal biomass were similar (Fig. 3a–c).

3.4. *Trends in mean individual weight*

Mean fish weight (W: Biomass/Abundance) increased with depth in February and increased further in October, when the highest W recorded was found at 1000 m. In contrast, a strong drop in W was observed from 600–650 m to 800 m in April with a similar, though less clear, tendency in June/July (Fig. 4a). The W of decapods increased with depth in June/July and October (Fig. 4b), but W decreased from 600–650 m to 800 m in February and April.

3.5. *Trends in diversity*

Fish diversity was generally higher inside the canyon than at the stations located outside. H' for fish showed a different temporal pattern at the two shallowest stations from that at the two deepest (Fig. 5a). At 600 and 650 m H' was highest in February, decreasing to the lowest values in June/July and increasing again in October. At both 800 and 1000 m the highest H' values were found in June/July. H' values for decapod crustaceans peaked in June/July (Fig. 5b), with an increase from February and April. The only exception was at 650 m, where H' was highest in April.

A peak of diversity (H', total megafauna) was regularly found in June/July all across the slope (Fig. 5c), with only the exception of the station at 650 m, as described for decapod crustaceans. At 1000 m H' showed greater stability (smaller oscillations) all year compared to the shallower stations. In terms of species richness (S, not presented) trends were similar to those described for H'.

In general, diversity was lowest at the deepest station (*ca.* 1000 m) in all cases.

3.6. *Macrofauna*

Infaunal biomass at 600 m (inside the canyon) was much higher than at 800 m (outside the canyon), except for February 2007 (Fig. 6a). At 600 m, minimum infaunal biomass was observed in February of both 2007 and 2008 (around 3 g m^{-2}). There was a big increase from February to June/July, when maximum biomass was reached (6.293 g m^{-2}). In October, this biomass started decreasing and reached a minimum again in February. The trend at 800 m was opposite, with maximal values of biomass in February (3.753 g m^{-2}), and minimal ones in June/July (1.173 g m^{-2}).

Large Polychaeta (Fig. 6b) and the burrowing decapod *Calocaris macandreae* (Fig. 6c) caught by the OTSB-14 trawl were considerably more abundant inside the canyon than outside it, as was found for infauna collected in box cores. Inside the canyon, temporal trends

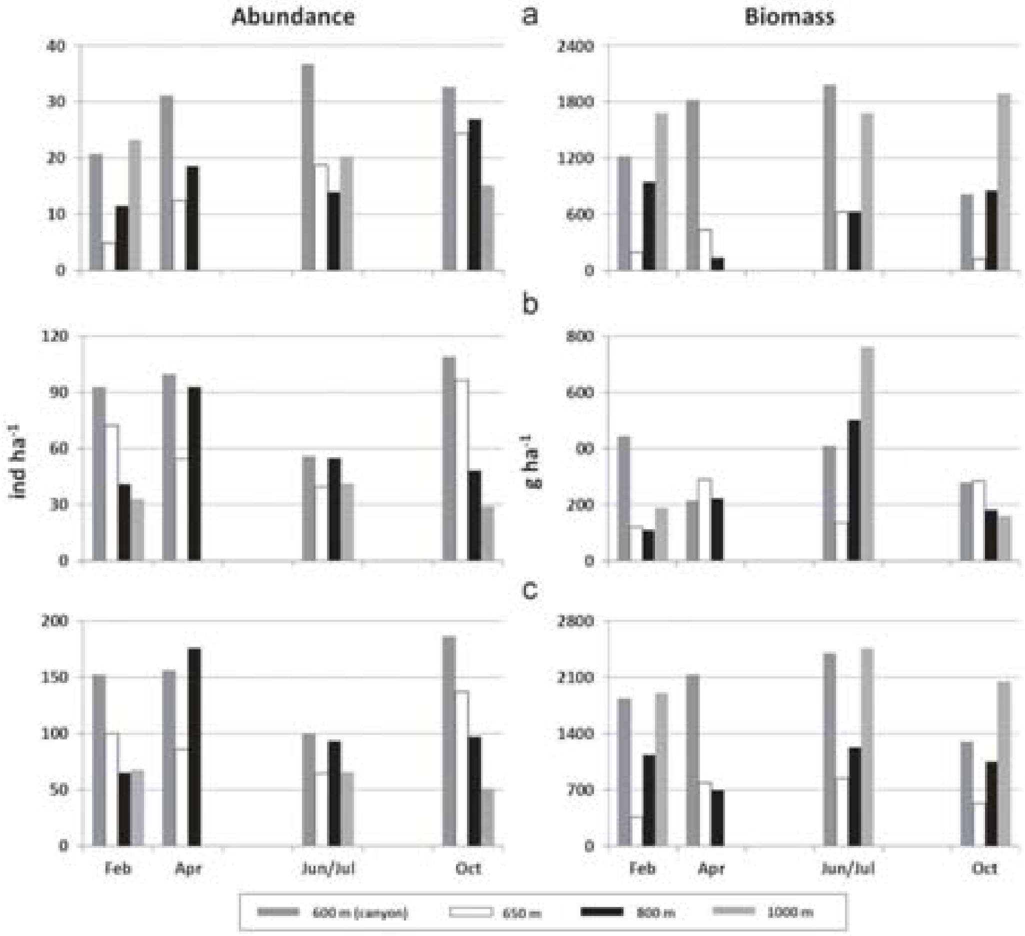

Fig. 3. Temporal trends in (a) fish, (b) decapod crustaceans and (c) total abundances and biomasses, at the four depth strata sampled.

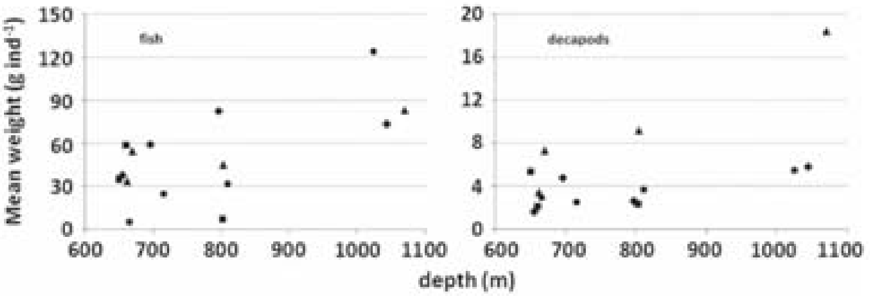

Fig. 4. Bathymetric distribution of mean individual weight of fish and decapods sampled by the OTSB-14 in the different sampling periods (February: ▲; April: ■; June/July: ▲; October: ●).

in biomass of Polychaeta and *C. macandreae* from the trawl were similar to those of infauna from the box corer, except for a remarkable decrease in June/July. Outside the canyon, biomass values remained low throughout the whole year and maximum values were found in April for both taxa. No large Polychaeta were collected at 1000 m.

Zooplankton biomass increased sharply from February to April at all depths (Fig. 6d), decreased considerably by June/July and then increased slightly again by October. The April peak in biomass attained 26 mg m^{-3} at 650 m and 21 mg m^{-3} at 800 m, because of a population burst of the thecosomatous pteropod *Cavolinia inflexa*. A general increase of micronekton biomass was observed from February to June/July (Fig. 6e), when micronekton biomass was greatest at all depths, except for a single peak observed in October at 800 m.

3.7. Environmental variables

Temperature at 5 mab was between 13.1 and 13.4 °C (Fig. 7a) at 650, 800 and 1000 m throughout the year, with the lower values in deeper water. At 600 m, temperature increased in June/July and showed maximum values in October. A temperature peak was observed at 800 m only in April. Comparison of temperature (T) at the surface and at 5 mab ($T_{5\ \mathrm{mab}}$) allowed us to identify when the

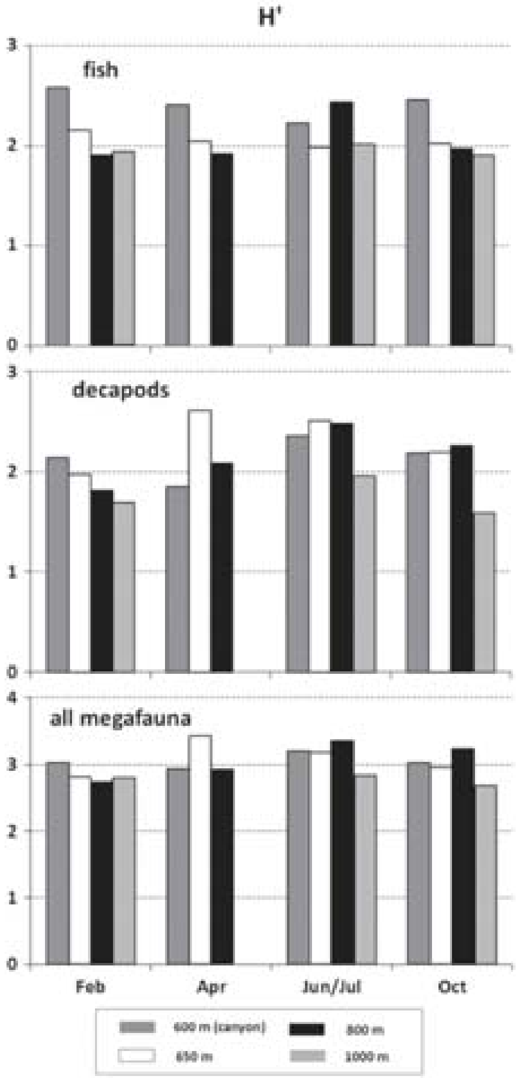

Fig. 5. Temporal trends in fish, decapod crustaceans and all taxa diversity, calculated as Shannon–Wiener function (H') for all the depth strata sampled.

water column was stratified or homogenous. It was homogenous in February and April (ΔT from 0.50 to 3.94 °C), and stratified in June and October (ΔT from 7.90 to 8.93 °C).

Salinity at 5 mab ($S_{5\ \mathrm{mab}}$) was 38.43–38.56 pss (Fig. 7b). Near-bottom salinity was greater at 600 and 650 m and greater in June/July and October than the rest of the year. A peak of $S_{5\ \mathrm{mab}}$ occurred in April at 800 m, parallel to a peak of T.

Water turbidity at 5 mab ($\mathrm{Turb}_{5\ \mathrm{mab}}$) was highest in February at all stations outside the canyon (Fig. 7c). Inside the canyon at 600 m, turbidity was lower in February than in April. In all observations outside the canyon turbidity decreased from February to June/July and increased afterwards.

Surface Primary Production followed the same temporal sequence at all sites: minimum values in June/July (0.143 mg Chl*a* m^{-3}), and maximum values in January and April (0.332 and 0.383 mg Chl*a* m^{-3}, respectively) (data not shown as a figure).

Runoffs of Llobregat and Besòs Rivers presented similar variations, Llobregat discharge peaks being considerably higher than those of Besòs (Cartes et al., 2010a). Flow of both rivers was maximal in April (15 m^3 s^{-1} and 6 m^3 s^{-1} for the Llobregat and the Besòs, respectively), and secondary peaks in river flow were observed in August and October. Minimum flow in both rivers was in March and July. Inside the canyon at 600 m, TOC% was highest in February and lowest in June, increasing afterwards. An inverse cycle was found at 800 m (Fig. 7d).

3.8. *Correlations with explanatory environmental variables*

The non-parametric Spearman's rank correlations established that the main axis of the MDS (dimension 1), defining the distribution of distinct assemblages, were significantly correlated mainly with $T_{5\ \mathrm{mab}}$ and $S_{5\ \mathrm{mab}}$ ($p < 0.001$), but also with $\mathrm{Turb}_{5\ \mathrm{mab}}$, zooplankton biomass ($p < 0.01$), river discharge at the time of sampling and Polychaeta and *C. macandreae* biomass ($p < 0.05$) (Table 4). Dimension 2 of the MDS was not correlated with any variable, although hauls were separated according to whether they were conducted inside or outside the canyons.

Total megafauna and decapods were correlated (Spearman ρ) with $T_{5\ \mathrm{mab}}$, $S_{5\ \mathrm{mab}}$, zooplankton biomass, river flow at the time of sampling and *C. macandreae* and Polychaeta biomass (Table 5). Fish abundances were correlated to micronekton biomass.

3.9. *Multivariate analyses*

3.9.1. *GLM*

GLM performed on abundance of all taxa explained 77.9% of the deviance with 4 variables that were $T_{5\ \mathrm{mab}}$, $S_{5\ \mathrm{mab}}$, SPP 1 month before the sampling and river $\mathrm{flow}_{\mathrm{sim}}$ (Table 6). For fish abundance, $S_{5\ \mathrm{mab}}$ was once again a significant variable in the model, together with $\mathrm{Turb}_{5\ \mathrm{mab}}$; the fish model explained 41.9% of the total deviance. In the case of decapods, 82.3% of the total deviance was explained by the same 4 variables explaining all taxa abundance, reflecting the fact that decapods were the most abundant taxon.

GLM carried out on diversity (H') of the whole assemblage explained 32.5% of the total deviance (results not included), including only one variable, which was micronekton biomass. In the case of fish diversity, $T_{5\ \mathrm{mab}}$ and *C. macandreae* biomass were the model explanatory variables, explaining 44.5% of the total deviance. The GLM for decapod diversity also consisted of two variables ($T_{5\ \mathrm{mab}}$ and $\mathrm{SPP}_{3\ \mathrm{months}}$) and covered 41.4% of the total deviance.

3.9.2. *CCAs*

A total of 58.92% of the variance in our CCA ordination was explained by factors correlated with the first two axes (Fig. 8), results parallel to those for the MDS ordination based on the OTSB-14 hauls (Fig. 2). In this sense, the hauls grouped according to depth and the location of hauls inside/outside the canyon. Hauls from 1000 m were found on the upper right side of the plot. A gradation towards the left and centre was found with decreasing depth, with hauls inside the canyon being on the upper left part of the plot.

Regarding abundances of the dominant species, *C. macandreae*, the brachyuran crab *Monodaeus couchi* and the shrimp *Plesionika martia* were linked with the biomasses of large Polychaeta and *C. macandreae*. In contrast, two macrourids, *Trachyrhynchus scabrus* and *Nezumia aequalis*, the gadid *Phycis blennoides* and the myctophid *Lampanyctus crocodilus* had positive relationships with micronekton biomass, as well as with river $\mathrm{flow}_{3\ \mathrm{months}}$, and inverse relationships with $\mathrm{SPP}_{\mathrm{sim}}$ and $\mathrm{SPP}_{1\ \mathrm{month}}$, $\mathrm{Turb}_{5\ \mathrm{mab}}$ and river $\mathrm{flow}_{\mathrm{sim}}$. The opposite situation was found for *Munida tenuimana* and *Symphurus ligulatus*. Abundances of the red shrimp *Aristeus antennatus* and the morid fish *Lepidion lepidion*, had negative relationships with $T_{5\ \mathrm{mab}}$ and $S_{5\ \mathrm{mab}}$, implying a positive relationship with depth (these two species were most abundant in samples at 800 m and at 1000 m, respectively). On the contrary, an inverse relationship was found between

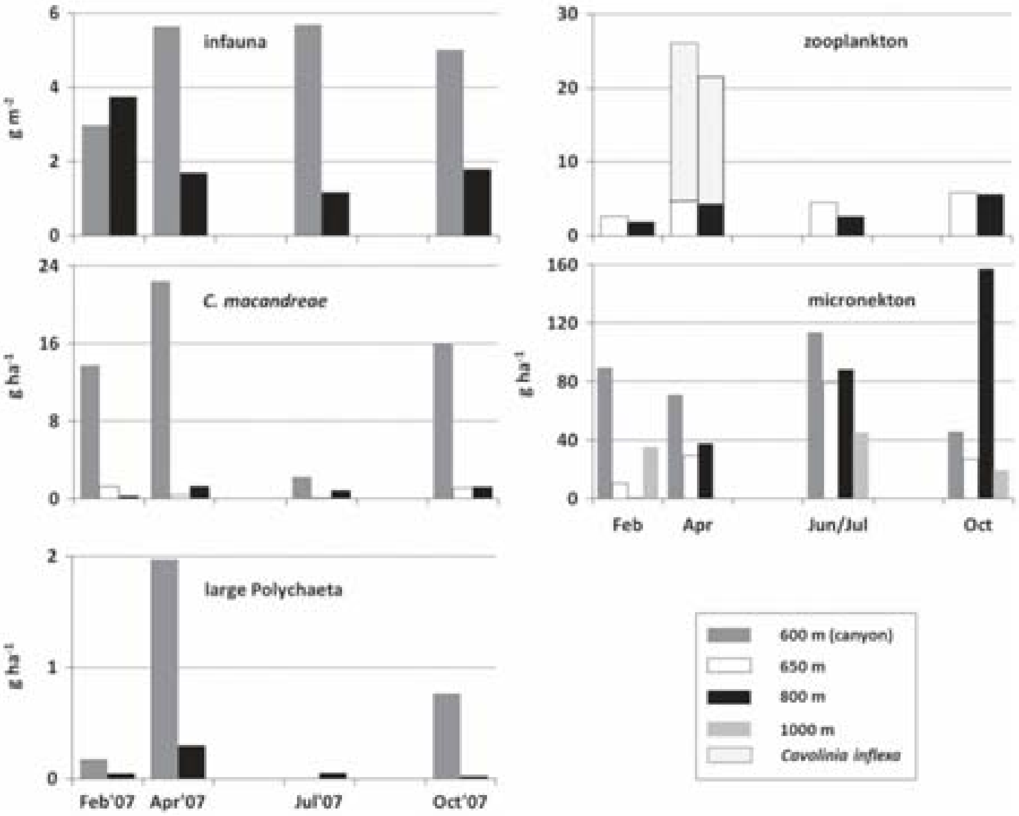

Fig. 6. Temporal trends of total biomass of potential prey of megafauna at the different depth strata sampled.

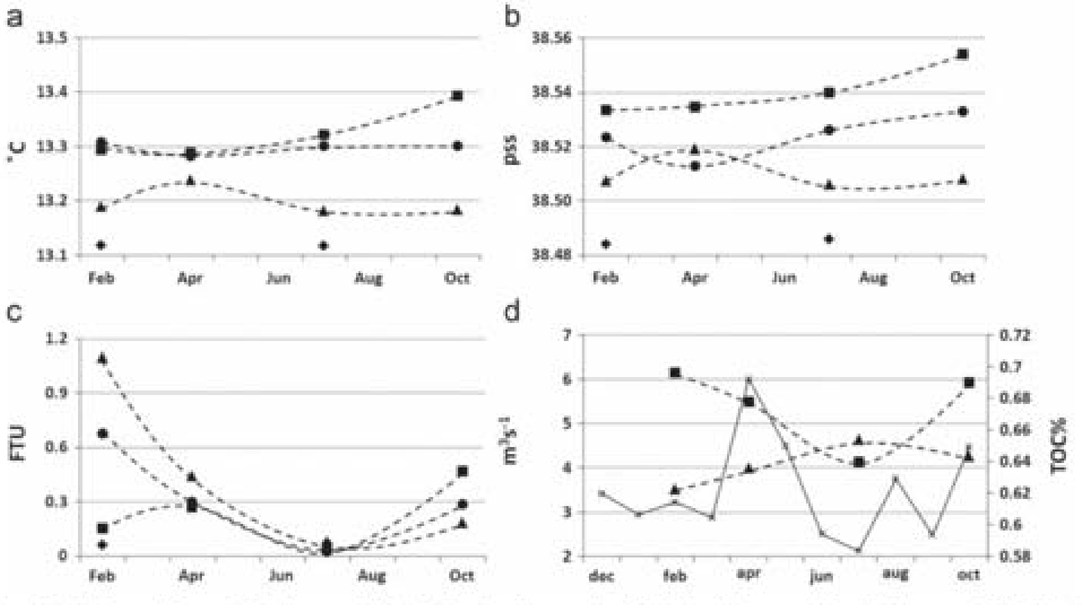

Fig. 7. Seasonal trends in (a) $T_{5\ \mathrm{mab}}$ (b) $S_{5\ \mathrm{mab}}$ (c) Turb$_{5\ \mathrm{mab}}$ and (d) river flow (month means) and TOC% in sediment, at 600 m (inside canyons) (■), 650 m (●), 800 m (▲) and 1000 m (◆).

Brissopsis lyrifera and depth. The thaliacean *Salpa fusiformis*, and to a lesser extend the mesopelagic shrimp *Gennadas elegans*, were strongly related to SPP$_{\mathrm{sim}}$. River flow$_{1\ \mathrm{month}}$ and river flow$_{2\ \mathrm{months}}$ before sampling were excluded from CCA due to their overlap with other explanatory variables.

4. Discussion

Several authors have examined the changes with depth or season in deep-sea megafaunal assemblages, including the causal roles of a number of environmental variables (Tyler, 1988; Cartes et al., 1994, 2007; Moranta et al., 2008). However, there are still few studies analysing the influence of *in situ* environmental variables on the spatio-temporal distribution of deep-sea fauna (Cartes et al., 2007, 2008a; Moranta et al., 2008; Sánchez et al., 2008). We designed our multidisciplinary approach to achieve such an analysis for bathyal depths at a multispecies level, analysing the spatial and temporal variations in the distribution and diversity of megafaunal assemblages in relation to environmental variables measured simultaneously. The analysis is based on samples taken with a single trawl type, the OTSB-14, to remove the effects of varying trawls on the composition and biomass of megafaunal samples (Cartes et al., 2009b). A parallel sampling performed with a commercial trawl (at the same stations and on the same dates) gave similar trends in the spatial and temporal patterns described here (e.g. there was a significant change in assemblages as a function of the stratification/homogeneity of the water column), although the composition of assemblages was different (authors' unp. data), as expected from previous comparisons (Cartes et al., 2009b).

Table 4

Significant Spearman correlations ($p < 0.05$) between environmental variables and the two dimensions of the MDS performed on OTSB-14 abundance catches.

Dimension 1	Valid N	Spearman R	$t(N-2)$	p-Level
$T_{5\ \mathrm{mab}}$	18	0.812	5.565	4×10^{-5}
$S_{5\ \mathrm{mab}}$	18	0.748	4.507	4×10^{-4}
$\mathrm{Turb}_{5\ \mathrm{mab}}$	18	0.659	3.506	0.003
Zooplankton biomass	14	0.678	3.199	0.008
Polychaeta biomass	19	0.551	2.721	0.015
River $\mathrm{flow}_{\mathrm{sim}}$	19	0.516	2.484	0.024
C. macandreae biomass	19	0.512	2.455	0.025

$T_{5\ \mathrm{mab}}$: temperature 5 m above bottom; $S_{5\ \mathrm{mab}}$: salinity 5 m above bottom; $\mathrm{Turb}_{5\ \mathrm{mab}}$: turbidity 5 m above bottom; River $\mathrm{flow}_{\mathrm{sim}}$: river flow simultaneous to sampling.

Table 5

Significant Spearman correlations ($p < 0.05$) between environmental variables and total assemblage, fish and decapod abundances obtained by OTSB-14 catches.

Total abundance	Valid N	Spearman R	$t(N-2)$	p-Level
C. macandreae biomass	19	0.844	6.494	5×10^{-6}
Polychaeta biomass	19	0.684	3.870	0.001
$S_{5\ \mathrm{mab}}$	18	0.680	3.707	0.002
$T_{5\ \mathrm{mab}}$	18	0.562	2.718	0.015
River $\mathrm{flow}_{\mathrm{sim}}$	19	0.515	2.479	0.024
Zooplankton biomass	14	0.579	2.462	0.030
Fishes abundance				
Micronekton biomass	19	0.514	2.471	0.024
Decapods abundance				
C. macandreae biomass	19	0.885	7.821	5×10^{-7}
$S_{5\ \mathrm{mab}}$	18	0.801	5.345	6×10^{-5}
Polychaeta biomass	19	0.649	3.519	0.003
$T_{5\ \mathrm{mab}}$	18	0.658	3.496	0.003
Zooplankton biomass	14	0.634	2.843	0.015
River $\mathrm{flow}_{\mathrm{sim}}$	19	0.492	2.330	0.032

$T_{5\ \mathrm{mab}}$: temperature 5 m above bottom; $S_{5\ \mathrm{mab}}$: salinity 5 m above bottom; $\mathrm{Turb}_{5\ \mathrm{mab}}$: turbidity 5 m above bottom; River $\mathrm{flow}_{\mathrm{sim}}$: river flow simultaneous to sampling.

4.1. Spatial and temporal changes in megafauna

It is well established that depth is the main gradient structuring the abundance, diversity and size spectra of deep-sea megafaunal communities (Macpherson and Duarte, 1991; Cartes and Sardà, 1992; Stefanescu et al., 1993; Sardà et al., 1994; Fujita et al., 1995; Merrett and Haedrich, 1997; Rex and Etter, 1998; Gaertner et al., 1999; Clain and Rex, 2000; Colloca et al., 2003; Moranta et al., 2004). We sampled the middle slope fauna, the distribution of which off Catalonia is well defined at depths between *ca.* 600 and 1200 m (Abelló et al., 1988; Cartes and Sardà, 1993; Stefanescu et al., 1993; Sardà et al., 1994). Although we analysed the same faunal assemblage, previously characterised by homogeneous communities (Cartes et al., 2009a), we still found some influence of depth in our sampling. This is partly because changes in faunistic composition between megafaunal assemblages consist of a more or less continuous substitution of dominant and subdominant species with depth (Hecker, 1990; Merrett and Haedrich, 1997). In this way, we found some species at 1000 m that have their main distribution centre deeper, on the lower slope (e.g. *Alepocephalus rostratus* and *Lepidion lepidion*: Stefanescu et al., 1993). Also, a regular pattern of larger individuals at greater depths was observed at 1000 m. Depth-size related trends (discussed among Mediterranean fish by Macpherson and Duarte (1991) and Stefanescu et al. (1992)) can be explained by various factors e.g. the depth range occupied by each species, by ontogenic migratory movements, both by larger animals migrating deeper (bigger-deeper) (e.g. Polloni et al., 1979)

Table 6

Generalised Linear Models performed on abundance of all taxa, fishes and decapods off the Catalonian slope.

Total abundance						**Degrees of freedom = 17**	
	Explained dev.	Residual dev.	% Explained	AIC	F	p-Value	Estimate
NULL		36094.74					
$\mathbf{T_{5\ mab}}$	11982.71	24112.02	33.20		19.52	7e-04	−2.648
$\mathbf{S_{5\ mab}}$	6907.32	17204.71	19.14		11.25	0.005	23.951
$\mathbf{Chla_{1month}}$	4670.43	12534.28	12.94		7.61	0.016	0.108
River $\mathbf{flow_{sim}}$	4552.66	7981.62	12.61		7.42	0.017	0.030
Total model			**77.89**	172.78			
Fishes abundance							
NULL		1265.79					
$\mathbf{S_{5\ mab}}$	277.68	988.11	21.94		5.661	0.031	12.862
$\mathbf{Turb_{5\ mab}}$	188.5	553.7	19.94		5.147	0.038	−0.808
Total model			**41.88**	125.87			
Decapods abundance							
NULL		12587.71					
$\mathbf{T_{5\ mab}}$	5640.85	6946.86	44.81		33.004	7e-05	−1.411
$\mathbf{S_{5\ mab}}$	2013.98	4932.88	16.00		11.784	0.004	20.527
$\mathbf{Chla_{1\ month}}$	1066.51	3866.37	8.47		6.240	0.027	−0.134
River $\mathbf{flow_{sim}}$	1644.53	2221.85	13.06		9.622	0.008	0.030
Total model			**82.35**	149.76			

(Gardner, 1989) by bottom currents, slumps and river discharges (Rowe et al., 1982; Houston and Haedrich, 1984; Gardner, 1989). The decrease of TOC in sediments inside the canyon at 650 m (from February to June–July), parallel to the increase at 800 m (maximum in June–July) outside canyons and deeper, suggest new food inputs are mainly channelled through submarine canyons over the slope offshore from Barcelona, as already reported by Puig and Palanques (1998), Nittrouer et al. (2006) and Fabrès et al. (2008).

Assemblages also changed seasonally at slope depths, with variations in megafauna mainly reflecting the replacement of species throughout the year and changes in population size structures, as already reported by Moranta et al. (2008). Our analysis further revealed that these seasonal changes in megafaunal assemblages were related to the condition of homogeneity (February and April) or stratification (June/July and October) of the water column, basically defined by changes in salinity and temperature of water masses. Larger densities of species more dependent on fresh inputs of OM and that feed at lower trophic levels (Fanelli and Cartes, 2010; Fanelli et al., 2011b), such as *Calocaris macandreae*, *Cymbulia peroni* or *Boreomysis arctica*, were observed in periods of water column homogeneity. On the other hand, species that feed at higher trophic levels (e.g. *Aristeus antennatus*, *Phycis blennoides*) (Polunin et al., 2001) were more abundant in periods of water column stratification.

4.2. *Explanatory environmental variables*

Near-bottom salinity ($S_{5\ \mathrm{mab}}$, 5 m above the bottom) and temperature ($T_{5\ \mathrm{mab}}$), turbidity ($\mathrm{Turb}_{5\ \mathrm{mab}}$) and river discharge were the variables more frequently entering models explaining changes in assemblage composition and biomass/diversity trends. Zooplankton/micronekton biomass explained fishes distrubutions, and benthic macrofauna biomass and SPP 1 month prior to the sampling explained decapods distributions. Some of these variables, specifically $T_{5\ \mathrm{mab}}$, $S_{5\ \mathrm{mab}}$ and micronekton biomass, are correlated with depth. All of them directly (e.g. micronekton) or indirectly (*T*, *S* and river discharge) affect availability of trophic resources for megafauna at bathyal depths; for example, zooplankton (Cartes et al., 2008a) and river discharge (Cartes et al., 2010a). Food is probably the main factor causing spatio-temporal changes of deep-sea fauna, and it has repeatedly been indicated as the most plausible explanation for patterns found in species distribution and zonation (Cartes and Sardà, 1993; Cartes and Carrassón, 2004), especially in an almost thermally stable environment such as the deep Mediterranean.

4.2.1. *Environmental variables and spatial changes*

Depth was the main factor structuring megafaunal assemblages in the present study. However, depth is in fact a proxy for a combination of several environmental variables affecting deep-sea organisms. For example, temperature and salinity are correlated with depth and they may have a more direct influence on species distribution (e.g. in the case of the shrimp *Aristaeomorpha foliacea*: Cartes et al. (2011)) than depth *per se*.

Also, spatial distribution of prey has been suggested to structure megafaunal assemblages (Stefanescu et al., 1993; Bergstad et al., 1999; Colloca et al., 2003; Menezes et al., 2006). Zooplankton/micronekton and benthic infauna are the main food source for megafaunal fish (BIOMARE unp. data) and decapods (Cartes et al., 2010a, b) over the Catalonian slope. The significant relationships between potential prey and megabenthos biomass must, at least partially, be attributable to a gradual decrease with depth of key prey for fish and decapods, especially mesopelagic lantern fish and euphausiids (Cartes, 1998b; Cartes et al., 2002b). Mesopelagic macroplankton has some influence on bathyal communities at 1200 m (Cartes and Sardà, 1993; Stefanescu et al., 1993), though the maximum biomass of macroplankton occurs at shallower depths. Macroplankton even tends to aggregate at night *ca.* 200–400 m over the shelf-break (Sardou et al., 1996; Genin, 2004; Cartes et al., 2009d) and in canyon heads (Macquart-Moulin and Patriti, 1996), where it is consumed by shelf-slope dwelling species such as *M. merluccius* (Cartes et al., 2009d). Put more simply, there is less food available for megafauna at greater depths (Mauchline and Gordon, 1991). The general bigger–deeper trend we observed between 600 and 1000 m is probably linked to decreasing food resources. The dominance of larger animals at greater depths results from their lesser energetic requirements. Within species, relative food consumption or energy requirements decrease with increasing size, i.e. per unit of biomass (e.g. among fish: Koslow, 1996).

As trophic resources have important seasonal variations (see Fig. 6), size trends with depth can also vary as a function of season. At mid-slope depths, we observed in April (both for fish and decapods) a strong increase in mean weight from 800 m to 650 m and into the submarine canyon, contrary to the general bigger–deeper trend. This may be explained by seasonal migratory movements of slope fauna into canyons in search of prey (e.g. micronekton and infauna; Fig. 6). Temporal migrations into or out of canyons have been reported previously, e.g. for fish (Stefanescu et al., 1994) and for the decapod *Aristeus antennatus* (Tobar and Sardà, 1987; Sardà et al., 1994). Over the middle slope a number of dominant species reach gonad maturity from spring to early summer, immediately before their spawning periods (e.g. *Aristeus antennatus* from July to September Cartes et al. (2008b); *Plesionika martia* from June to August Fanelli and Cartes (2008); *Phycis blennoides* from June to August Gallardo-Cabello and Gual-Frau (1984)). The size (and abundance) increases inside the canyon in April may be attributable to the synchronisation of high energy requirements of individuals for gonad development in spring before reproduction and the high availability of key prey (e.g. infauna in general, large polychaetes and the burrowing decapod *Calocaris macandreae*) inside canyons in April. This will lead to the aggregation of predators inside canyons for feeding (e.g. Fanelli and Cartes, 2008; Cartes et al., 2008b). Indeed, higher macrofauna biomass can be found close to the canyon heads (as reported inside La Jolla Canyon to 500 m: Vetter and Dayton (1998)).

In contrast to our results, a drop in mean fish weight was observed by Stefanescu et al. (1994) inside La Berenguera canyon, which they attributed to a recruitment event. This was probably because they worked in more productive areas located closer to the canyon head.

4.2.2. *Environmental variables and temporal changes*

Changes in $T_{5\ \mathrm{mab}}$ and $S_{5\ \mathrm{mab}}$ also reflect changes in the water masses, which affect distributions of megafaunal assemblages (Williams et al., 2001; Colloca et al., 2003; Fock et al., 2004; Menezes et al., 2006). The Levantine Intermediate Water (LIW) was present all year in the water column during BIOMARE cruises, with the LIW core at *ca.* 350–550 m. Nevertheless, starting in June/July 2007 just above 650 m on the middle slope of the Catalan Sea, we found increases of *T* from ~13.3 °C to ~13.4 °C and *S* from ~38.52 pss to ~38.55 pss that match the characteristics of the LIW (Font, 1987) (Fig. 7). Although present all year round, LIW moves more rapidly (speeds of 5 cm/s) over Catalonian slopes in winter (Font, 1987), and its *T* and *S* maxima were clearly differentiated from overlying waters during July and October in 2007; thus, the increases of $S_{5\ \mathrm{mab}}$ and $T_{5\ \mathrm{mab}}$ in summer and thereafter appeared to be related to LIW influx, coinciding with the period of water column stratification. Assemblages of megafauna and deep-macroplankton (Cartes et al., 2010b) had important seasonal variations that should, in turn, be mainly coupled to homogeneity/stratification of the water column.

Water column condition seems to be an important parameter regulating OM inputs to bathyal depths. The condition of the water column affects the vertical fluxes of OM; there is greater bulk particle flux from surface primary production (SPP), with maximum values of mass, total organic carbon and nitrogen fluxes during vertical mixing events. The flux of particles from the surface is less in stratified periods (Miquel et al., 1994), in which the thermocline produces a strong density gradient that retains particles (Puskaric et al., 1992). Advective fluxes are also subject to temporal variability of physical conditions related to the condition of the water column (Puig and Palanques, 1998; Palanques et al., 2006), as well as to river discharges (Monaco et al., 1990; Buscail et al., 1990; de Bovée et al., 1990; Cartes et al., 2009a, 2010a). The thermocline, present in periods of stratification, constitutes an interface that also retains sediment particles discharged by the rivers (Puig and Palanques, 1998; Palanques et al., 2006). Apart from the OM matter they channel to bathyal depths, advective currents have an important influence on food availability at bathyal depths by affecting the dynamics of resuspension/deposition of particles in the sea bottom (Nittrouer et al., 2006) and the quality of the deposited particles. Peaks in river discharge in the area were strongly related to the high values of water turbidity found near the bottom in April and October (Fig. 7), which may indicate resuspension of POM and formation of bottom nepheloid layers. Zooplankton, feeding on suspended POM in near-bottom waters as well as on material from surface production (Fanelli et al., 2011a), had maximum biomass in April after the peaks in SPP, river discharge (Fig. 7) and turbidity. Thiel (1983) and de Bovée et al. (1990) pointed out the relationship of meiofaunal and macrofaunal biomass to production processes in the surface layers of the water column, which is reflected in the existence of seasonality among different habitats. Larger densities of macroplankton/micronekton (mostly preying on mesozooplankton, Fanelli et al., 2011a) were found close to the bottom over the Catalonian slope afterwards (Fig. 6e; Cartes et al., 2010b), enhanced by the formation of the thermocline and by the reinforcement of the permanent front at the shelf-slope break (at *ca.* 400 m) during summer (Font et al., 1988). Micronekton was preyed upon by megafaunal fish and decapods (Cartes, 1998a, b; Fanelli et al., 2009). We consistently observed peaks of megafaunal biomass, specially of fish, in June–July and October after peaks in (meso)zooplankton (April) and micronekton (June–July), and *ca.* 3–5 months after the peaks of surface production (in February) and the maximum of river discharge (in April).

By contrast, minimal river discharge in June/July was related to lowest turbidity at all depths, suggesting a decrease of both near-bottom fluxes. These relatively tranquil conditions near the seafloor, enhanced by the presence of a thermocline in periods of water column stratification (from June/July to October) (Puig and Palanques, 1998), favour POM deposition in the sediments, as supported by TOC% results (Fig. 7d) at 800 m (out of canyon). Higher TOC in the sediments implies higher food availability for benthos (macroinfauna), which directly influences the abundance and biomass of meiofauna and macrofauna (de Bovée et al., 1990; Buscail et al., 1990 and references therein). In fact, the temporal trends found in infaunal biomass in the area follow those of TOC% with a delay of *ca.* 2 months (Mamouridis et al., 2011). The biomass of megafauna also increased from February to April and June–July, suggesting the development of feeding aggregations at the same time and after *ca.* 2 months to the same periods of infauna peaks. Thus, as already described by Moranta et al. (2008) and Cartes et al. (2009a) for the Balearic Basin, the temporal variations in megafauna might ultimately relate to seasonal production in the surface layers and transfer of this organic matter to greater depths.

Processes other than local river (e.g. Besòs) inflow, however, can have important effects on the dynamics of deep waters in the area, such as the peak of turbidity found in February outside of the canyon. Isotopic analyses of POM in the near-bottom water column (5_{mab}) have pointed to an important advective influx of terrigenous organic matter ($\delta^{13}C = -26.40‰$) (Fanelli et al., 2011b). Cascading events taking place in the Gulf of Lions in winter and affecting the northern Spanish Mediterranean coast (Font et al., 2007) could enhance advective fluxes. These events could be triggered by higher runoff from the Rhone River, situated to the northeast of the study area, in the December to February period (data from Global Runoff Data Centre).

4.3. *Influence on diversity*

We did not find the inverse bell shaped tendency defined by Gage and Tyler (1991) for faunal assemblages over the slope. Instead, we observed slightly lower diversity at the deepest station, in accordance to the depth-pattern described by Rex and Etter (2010) for the Mediterranean Sea. Due to the relatively narrow (423–1175 m) depth range we explored, our sampling put more emphasis on temporality.

Diversity (H') of megafauna was related to temperature/salinity and to prey availability. As H' is based on species abundance, it is logical that the same variables (T and S) discussed for abundance are also related to diversity. More strikingly, we found diversity relationships with biomass of some micronekton (midwater decapods, myctophids or euphausiids) and of *Calocaris macandreae*. Both are key prey for a wide number of top predators, including shrimps (*A. antennatus*, Cartes, 1994), rattails such as *Nezumia aequalis*, *T. trachyrhynchus* and gadids like *Phycis blennoides* (Cartes and Carrassón, 2004; authors unp. data), in the slope systems of the Balearic Basin. So, prey availability may affect the abundance of a substantial number of megafaunal predators (e.g. by aggregation) on the Balearic slope, thus affecting H'. Related to this, the decrease of mesopelagic micronekton biomass with depth (as signalled by Cartes (1994)) may cause a decrease in diversity at 1000 m, by the decreasing predator abundance. This fits with the general idea that decreases in diversity (with depth) have usually been associated to productivity and food supply (Rex et al., 2005; Mittelbach et al., 2001; Waide et al., 1999) and may be related to the regularly reported decline of diversity from regions of moderate productivity to regions of low productivity (Levin et al., 2001). Seasonally, peaks of H' were regularly found in June–July, well after the highest peaks of food biomass (zooplankton and benthic infauna) and the highest values of SPP in April. These results are clearer for decapods than for fish, the latter on average feeding in a higher trophic level than the former. In any case, diversity patterns vary from taxon to taxon being group-specific, with no single environmental driver apparent for the patterns observed (Snelgrove and Smith, 2002; Haedrich et al., 2008). Therefore, a more extensive study delimited to concrete functional groups may reveal environmental drivers that could be masked by the broad resolution of the taxa considered in the present study.

In conclusion, changes in the composition, biomass and diversity of benthopelagic fish and decapods (megafauna) were closely related over Catalonian slopes with water mass conditions (stratified, homogenised), basically defined by changes in salinity and temperature, that are generally linked to food inputs for megafaunal prey. River discharges may also play an important role in these dynamics, contributing to changes observed in near-bottom turbidity. At the level of broad taxa analysed here, megafaunal diversity was mainly driven by food availability.

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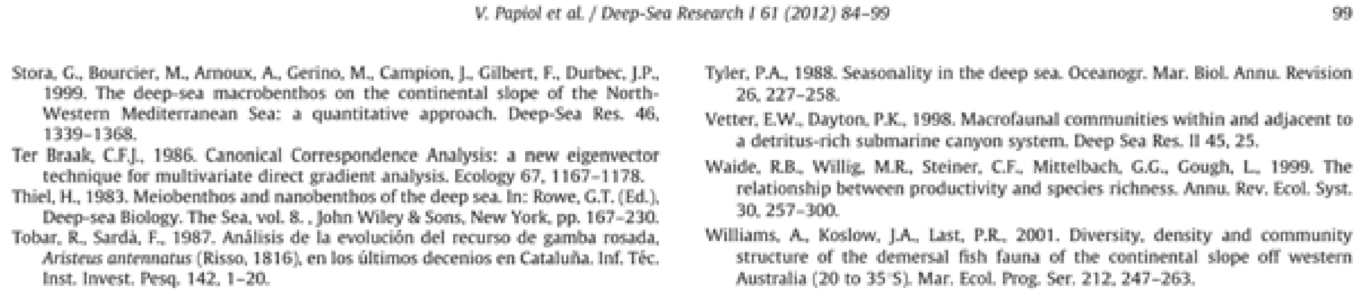

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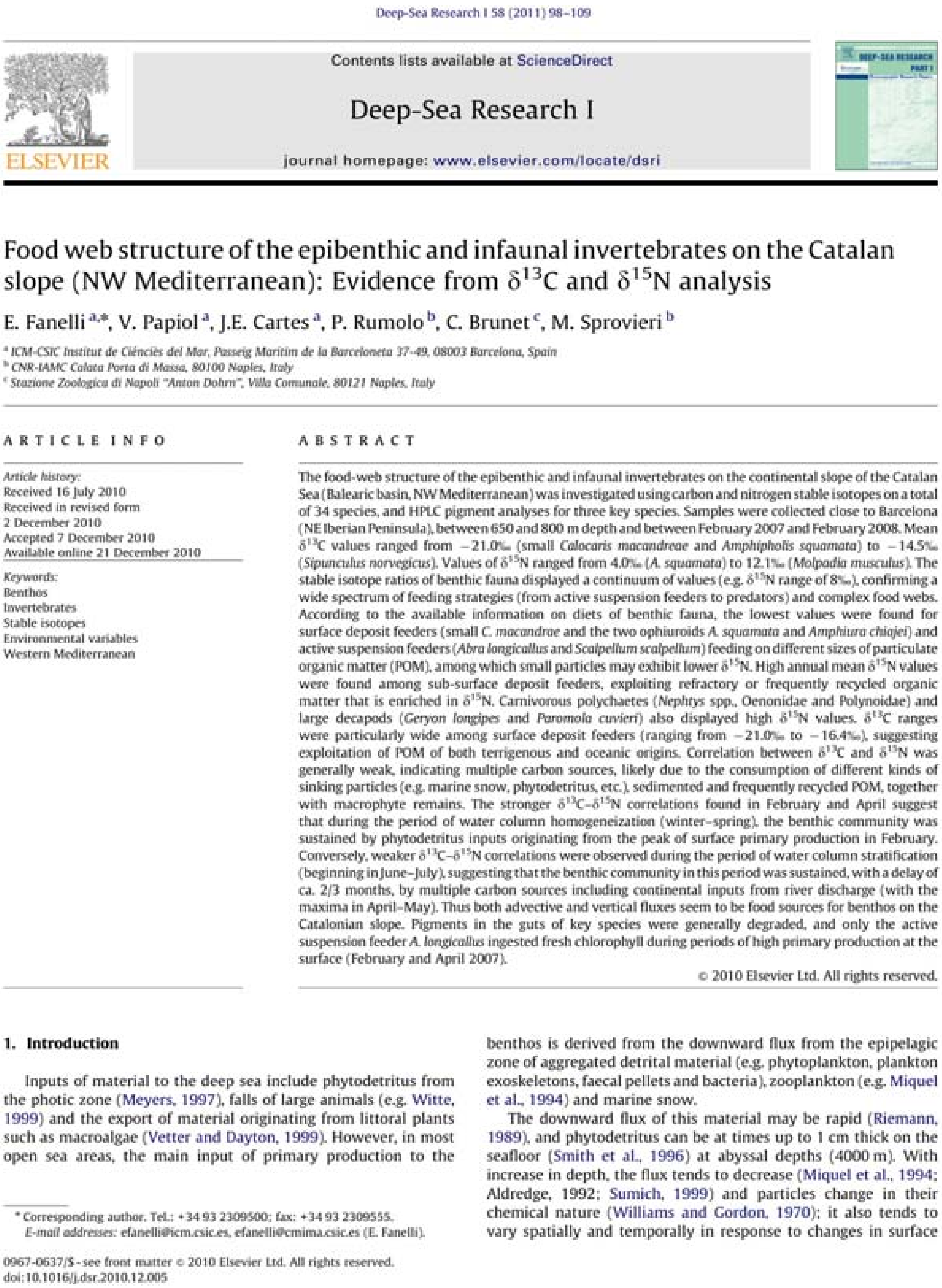
CHAPTER 3 - FOOD WEB STRUCTURE OF THE EPIBENTHIC AND INFAUNAL INVERTEBRATES ON THE CATALAN SLOPE (NW MEDITERRANEAN): EVIDENCE FROM δ^{13}C AND δ^{15}N ANALYSIS



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Food web structure of the epibenthic and infaunal invertebrates on the Catalan slope (NW Mediterranean): Evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis

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ABSTRACT

The food-web structure of the epibenthic and infaunal invertebrates on the continental slope of the Catalan Sea (Balearic basin, NW Mediterranean) was investigated using carbon and nitrogen stable isotopes on a total of 34 species, and HPLC pigment analyses for three key species. Samples were collected close to Barcelona (NE Iberian Peninsula), between 650 and 800 m depth and between February 2007 and February 2008. Mean $\delta^{13}C$ values ranged from −21.0‰ (small *Calocaris macandreae* and *Amphipholis squamata*) to −14.5‰ (*Sipunculus norvegicus*). Values of $\delta^{15}N$ ranged from 4.0‰ (*A. squamata*) to 12.1‰ (*Molpadia musculus*). The stable isotope ratios of benthic fauna displayed a continuum of values (e.g. $\delta^{15}N$ range of 8‰), confirming a wide spectrum of feeding strategies (from active suspension feeders to predators) and complex food webs. According to the available information on diets of benthic fauna, the lowest values were found for surface deposit feeders (small *C. macandrae* and the two ophiuroids *A. squamata* and *Amphiura chiajei*) and active suspension feeders (*Abra longicallus* and *Scalpellum scalpellum*) feeding on different sizes of particulate organic matter (POM), among which small particles may exhibit lower $\delta^{15}N$. High annual mean $\delta^{15}N$ values were found among sub-surface deposit feeders, exploiting refractory or frequently recycled organic matter that is enriched in $\delta^{15}N$. Carnivorous polychaetes (*Nephtys* spp., Oenonidae and Polynoidae) and large decapods (*Geryon longipes* and *Paromola cuvieri*) also displayed high $\delta^{15}N$ values. $\delta^{13}C$ ranges were particularly wide among surface deposit feeders (ranging from −21.0‰ to −16.4‰), suggesting exploitation of POM of both terrigenous and oceanic origins. Correlation between $\delta^{13}C$ and $\delta^{15}N$ was generally weak, indicating multiple carbon sources, likely due to the consumption of different kinds of sinking particles (e.g. marine snow, phytodetritus, etc.), sedimented and frequently recycled POM, together with macrophyte remains. The stronger $\delta^{13}C$–$\delta^{15}N$ correlations found in February and April suggest that during the period of water column homogeneization (winter–spring), the benthic community was sustained by phytodetritus inputs originating from the peak of surface primary production in February. Conversely, weaker $\delta^{13}C$–$\delta^{15}N$ correlations were observed during the period of water column stratification (beginning in June–July), suggesting that the benthic community in this period was sustained, with a delay of ca. 2/3 months, by multiple carbon sources including continental inputs from river discharge (with the maxima in April–May). Thus both advective and vertical fluxes seem to be food sources for benthos on the Catalonian slope. Pigments in the guts of key species were generally degraded, and only the active suspension feeder *A. longicallus* ingested fresh chlorophyll during periods of high primary production at the surface (February and April 2007).

1. Introduction

Inputs of material to the deep sea include phytodetritus from the photic zone (Meyers, 1997), falls of large animals (e.g. Witte, 1999) and the export of material originating from littoral plants such as macroalgae (Vetter and Dayton, 1999). However, in most open sea areas, the main input of primary production to the benthos is derived from the downward flux from the epipelagic zone of aggregated detrital material (e.g. phytoplankton, plankton exoskeletons, faecal pellets and bacteria), zooplankton (e.g. Miquel et al., 1994) and marine snow.

The downward flux of this material may be rapid (Riemann, 1989), and phytodetritus can be at times up to 1 cm thick on the seafloor (Smith et al., 1996) at abyssal depths (4000 m). With increase in depth, the flux tends to decrease (Miquel et al., 1994; Aldredge, 1992; Sumich, 1999) and particles change in their chemical nature (Williams and Gordon, 1970); it also tends to vary spatially and temporally in response to changes in surface

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production (Riemann, 1989; Miquel et al., 1994). Food supply is generally considered the main limiting factor in deep-sea communities (Gage and Tyler, 1991), and consequently marine snow constitutes a valuable food resource for deep-sea microbes, metazoans and bathyal detritivores (Smith et al., 1996). Bacteria may have important ecological roles in the highly oligotrophic deep environments of the Mediterranean, for example through decomposition of particulate matter derived from the upper layers (Danovaro et al., 1993). In spite of the evident role of marine snow in food supply, there has been little attempt to assess the diversity of source materials consumed by organisms in deep-sea ecosystems. Communities in proximity to canyon systems, where strong advective fluxes channelling terrestrial material or marine macrophyte remains to the deep-seafloor are frequent, may derive food from different sources (Vetter and Dayton, 1998, 1999).

Benthic deep-sea communities are species-rich, abundant and productive (reviewed by Rowe (1983)), and it has been suggested that their diversity is close to that of rain forests and other tropical systems (e.g. Grassle et al., 1990). Although meiobenthos, especially foraminiferans, account for a large proportion of this high species diversity (Gooday, 1986), macro and megabenthic species, especially polychaetes, contribute significantly to the richness of benthic communities (Cosson et al., 1997). Although knowledge of the ecology of single deep-sea species is steadily increasing, the overall structure of deep-sea food webs remains to be fully investigated. The majority of species are reported to be deposit feeders, ingesting and reworking vast amounts of sediments. Consequently, competition for food is expected to be extremely high. On the other hand, in a severely food-limited system, one would expect the development of feeding strategies serving either to reduce or to avoid competition (Jumars et al., 1990).

On the floor of the Balearic Basin the bivalve *Abra longicallus* and the holothurians *Molpadia musculus* and *Mesothuria intestinalis* attain their highest densities on the mainland slope in production hotspots (Cartes et al., 2009). However, how the bathyal community is sustained, despite the restricted energy input from the water column, is still poorly understood (Smith, 1987). Clearly, the advective flux of organic matter (OM) via submarine canyons is an important factor (Cartes et al., 2009).

Traditional approaches to food web analysis include gut content analysis, together with field and laboratory observations. Those approaches are difficult when studying the deep sea because of restricted accessibility, low temporal and spatial resolution of sampling, as well as technical problems. These problems include the fact that live organisms for experimental studies are difficult to obtain and gut content analyses are hampered by damage to specimens during sampling and from pressure effects. In the last decades, stable isotope analysis has been established as an alternative approach to investigate the relative trophic positions of organisms and their sources of carbon (e.g. Fry and Sherr, 1988). Carbon isotope composition in living animals usually provides clues to the origin of the ingested organic matter through an increase in $\delta^{13}C$ of ca. 1‰ per trophic level (De Niro and Epstein, 1978; Wada et al., 1991) and is useful to discriminate between the pelagic vs. benthic origin of food (France, 1995) or between terrestrial vs. marine sources (Hobson, 1987). Nitrogen isotope signature can be used to define the trophic level of organisms as $\delta^{15}N$ usually increases of ca. 2.5–3.4‰ from food to consumer (Minagawa and Wada, 1984; Post, 2002). Experimental and field studies demonstrate that naturally occurring stable isotopes of carbon and nitrogen show a stepwise enrichment between prey and consumer tissue during the assimilation processes (De Niro and Epstein, 1978; Minagawa and Wada, 1984). Selective metabolic fractionation leads to a preferential loss of lighter isotopes during respiration (carbon) and excretion (nitrogen) (De Niro and Epstein, 1978; Tieszen et al., 1983).

As part of a Spanish-funded project (BIOMARE), in the present study, information on stable isotope signatures is integrated with our own data on gut contents and pigment analyses (available for some detritivore species) and data from the literature to (1) identify the trophic web structure and the potential food sources of the epibenthic and infaunal invertebrates community on the Catalan slope; (2) elucidate temporal patterns in isotopic signatures; and (3) explore and identify which environmental variables best explain the observed patterns.

2. Materials and methods

2.1. Sampling and study area

Benthic invertebrates were collected from the Catalan Sea slope area (Balearic Basin, NW Mediterranean: Fig. 1) within the BIOMARE project by trawling the seafloor with a semi-balloon otter trawl (OTSB-14). The OTSB-14 is a 1-warp trawl with 6 mm mesh at the codend, a horizontal opening between wings of ca. 7 m and vertical mouth height of ca. 1.2 m. Horizontal and vertical mouth dimensions were recorded by SCANMAR sensors mounted in the mouth of the trawl. A total of 23 hauls were performed off Barcelona, between February 2007 and February 2008 at depths between 651 and 1105 m; two in February 2007 (BIOMARE 1 or B1), four in April 2007 (BIOMARE 2 or B2), six in June–July 2007 (BIOMARE 3 or B3), five in October 2007 (BIOMARE 4 or B4) and three in February 2008 (BIOMARE08 or B08).

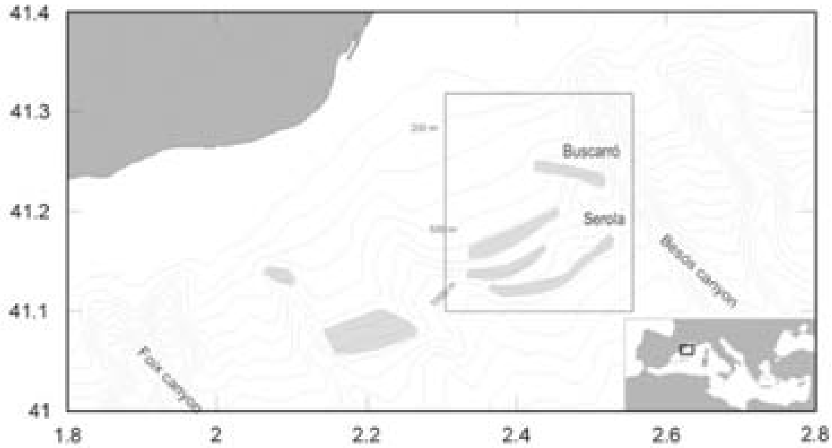
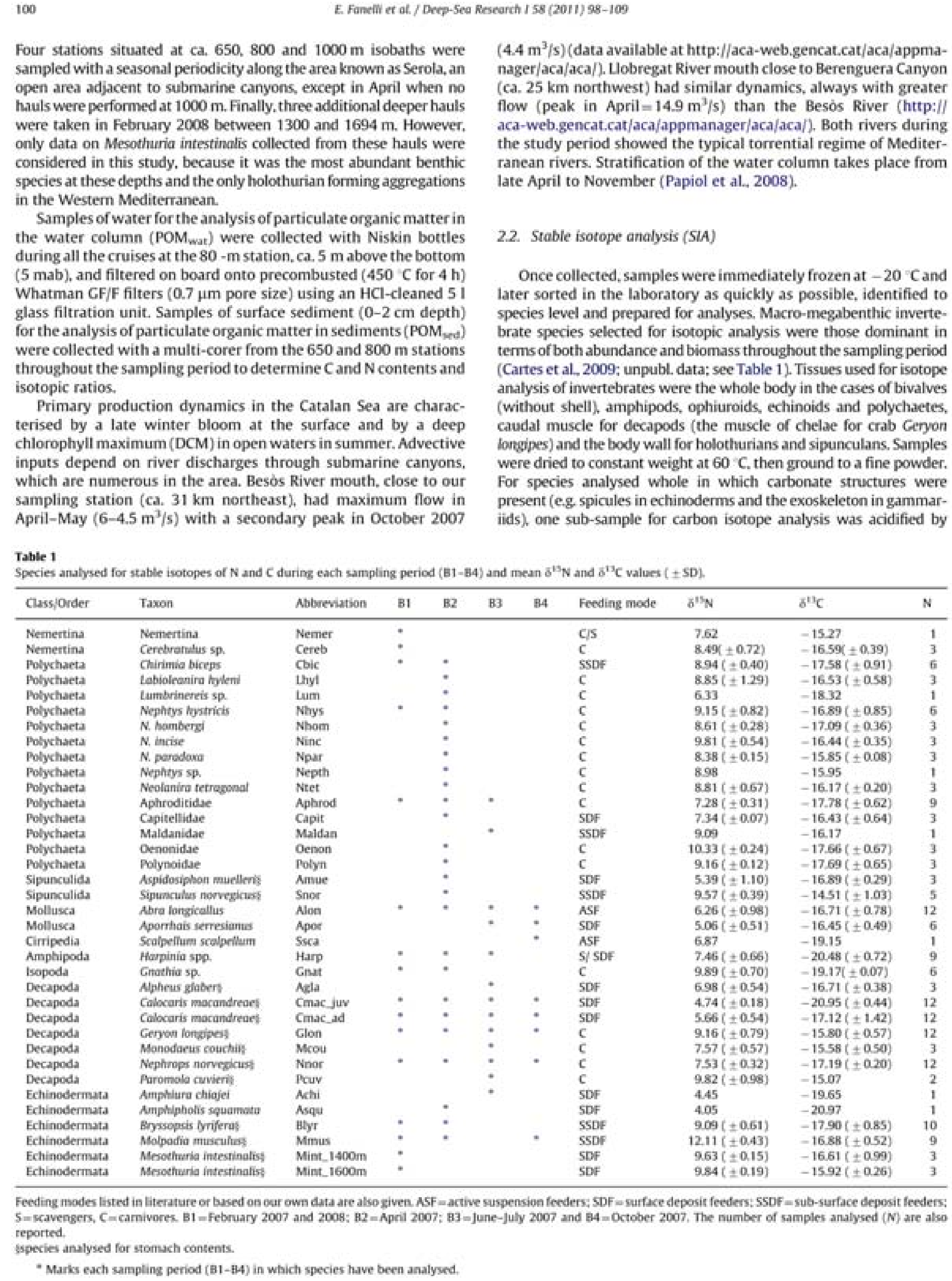


Fig. 1. Map of the whole BIOMARE study area. The quadrate indicates the area where samples used in this study were collected and in grey the sites where trawl hauls, box-corers and CTDs were carried out.



Four stations situated at ca. 650, 800 and 1000 m isobaths were sampled with a seasonal periodicity along the area known as Serola, an open area adjacent to submarine canyons, except in April when no hauls were performed at 1000 m. Finally, three additional deeper hauls were taken in February 2008 between 1300 and 1694 m. However, only data on *Mesothuria intestinalis* collected from these hauls were considered in this study, because it was the most abundant benthic species at these depths and the only holothurian forming aggregations in the Western Mediterranean.

Samples of water for the analysis of particulate organic matter in the water column (POM_{wat}) were collected with Niskin bottles during all the cruises at the 80 -m station, ca. 5 m above the bottom (5 mab), and filtered on board onto precombusted (450 °C for 4 h) Whatman GF/F filters (0.7 μm pore size) using an HCl-cleaned 5 l glass filtration unit. Samples of surface sediment (0–2 cm depth) for the analysis of particulate organic matter in sediments (POM_{sed}) were collected with a multi-corer from the 650 and 800 m stations throughout the sampling period to determine C and N contents and isotopic ratios.

Primary production dynamics in the Catalan Sea are characterised by a late winter bloom at the surface and by a deep chlorophyll maximum (DCM) in open waters in summer. Advective inputs depend on river discharges through submarine canyons, which are numerous in the area. Besòs River mouth, close to our sampling station (ca. 31 km northeast), had maximum flow in April–May (6–4.5 m^3/s) with a secondary peak in October 2007 (4.4 m^3/s) (data available at http://aca-web.gencat.cat/aca/appmanager/aca/aca/). Llobregat River mouth close to Berenguera Canyon (ca. 25 km northwest) had similar dynamics, always with greater flow (peak in April = 14.9 m^3/s) than the Besòs River (http://aca-web.gencat.cat/aca/appmanager/aca/aca/). Both rivers during the study period showed the typical torrential regime of Mediterranean rivers. Stratification of the water column takes place from late April to November (Papiol et al., 2008).

2.2. Stable isotope analysis (SIA)

Once collected, samples were immediately frozen at −20 °C and later sorted in the laboratory as quickly as possible, identified to species level and prepared for analyses. Macro-megabenthic invertebrate species selected for isotopic analysis were those dominant in terms of both abundance and biomass throughout the sampling period (Cartes et al., 2009; unpubl. data; see Table 1). Tissues used for isotope analysis of invertebrates were the whole body in the cases of bivalves (without shell), amphipods, ophiuroids, echinoids and polychaetes, caudal muscle for decapods (the muscle of chelae for crab *Geryon longipes*) and the body wall for holothurians and sipunculans. Samples were dried to constant weight at 60 °C, then ground to a fine powder. For species analysed whole in which carbonate structures were present (e.g. spicules in echinoderms and the exoskeleton in gammariids), one sub-sample for carbon isotope analysis was acidified by

Table 1
Species analysed for stable isotopes of N and C during each sampling period (B1–B4) and mean $\delta^{15}N$ and $\delta^{13}C$ values (±SD).

Class/Order	Taxon	Abbreviation	B1	B2	B3	B4	Feeding mode	$\delta^{15}N$	$\delta^{13}C$	N
Nemertina	Nemertina	Nemer	*				C/S	7.62	−15.27	1
Nemertina	*Cerebratulus* sp.	Cereb	*				C	8.49(±0.72)	−16.59(±0.39)	3
Polychaeta	*Chirimia biceps*	Cbic	*	*			SSDF	8.94 (±0.40)	−17.58 (±0.91)	6
Polychaeta	*Labioleanira hyleni*	Lhyl		*			C	8.85 (±1.29)	−16.53 (±0.58)	3
Polychaeta	*Lumbrinereis* sp.	Lum		*			C	6.33	−18.32	1
Polychaeta	*Nephtys hystricis*	Nhys	*	*			C	9.15 (±0.82)	−16.89 (±0.85)	6
Polychaeta	*N. hombergi*	Nhom		*			C	8.61 (±0.28)	−17.09 (±0.36)	3
Polychaeta	*N. incise*	Ninc		*			C	9.81 (±0.54)	−16.44 (±0.35)	3
Polychaeta	*N. paradoxa*	Npar		*			C	8.38 (±0.15)	−15.85 (±0.08)	3
Polychaeta	*Nephtys* sp.	Nepth		*			C	8.98	−15.95	1
Polychaeta	*Neolanira tetragonal*	Ntet		*			C	8.81 (±0.67)	−16.17 (±0.20)	3
Polychaeta	Aphroditidae	Aphrod	*	*	*		C	7.28 (±0.31)	−17.78 (±0.62)	9
Polychaeta	Capitellidae	Capit		*			SDF	7.34 (±0.07)	−16.43 (±0.64)	3
Polychaeta	Maldanidae	Maldan			*		SSDF	9.09	−16.17	1
Polychaeta	Oenonidae	Oenon		*			C	10.33 (±0.24)	−17.66 (±0.67)	3
Polychaeta	Polynoidae	Polyn		*			C	9.16 (±0.12)	−17.69 (±0.65)	3
Sipunculida	*Aspidosiphon muelleri*§	Amue		*			SDF	5.39 (±1.10)	−16.89 (±0.29)	3
Sipunculida	*Sipunculus norvegicus*§	Snor		*			SSDF	9.57 (±0.39)	−14.51 (±1.03)	5
Mollusca	*Abra longicallus*	Alon	*	*	*	*	ASF	6.26 (±0.98)	−16.71 (±0.78)	12
Mollusca	*Aporrhais serresianus*	Apor			*	*	SDF	5.06 (±0.51)	−16.45 (±0.49)	6
Cirripedia	*Scalpellum scalpellum*	Ssca				*	ASF	6.87	−19.15	1
Amphipoda	*Harpinia* spp.	Harp	*	*	*		S/ SDF	7.46 (±0.66)	−20.48 (±0.72)	9
Isopoda	*Gnathia* sp.	Gnat	*	*			C	9.89 (±0.70)	−19.17(±0.07)	6
Decapoda	*Alpheus glaber*§	Agla			*		SDF	6.98 (±0.54)	−16.71 (±0.38)	3
Decapoda	*Calocaris macandreae*§	Cmac_juv	*	*	*	*	SDF	4.74 (±0.18)	−20.95 (±0.44)	12
Decapoda	*Calocaris macandreae*§	Cmac_ad	*	*	*	*	SDF	5.66 (±0.54)	−17.12 (±1.42)	12
Decapoda	*Geryon longipes*§	Glon	*	*	*	*	C	9.16 (±0.79)	−15.80 (±0.57)	12
Decapoda	*Monodaeus couchii*§	Mcou			*		C	7.57 (±0.57)	−15.58 (±0.50)	3
Decapoda	*Nephrops norvegicus*§	Nnor	*	*	*	*	C	7.53 (±0.32)	−17.19 (±0.20)	12
Decapoda	*Paromola cuvieri*§	Pcuv			*		C	9.82 (±0.98)	−15.07	2
Echinodermata	*Amphiura chiajei*	Achi			*		SDF	4.45	−19.65	1
Echinodermata	*Amphipholis squamata*	Asqu		*			SDF	4.05	−20.97	1
Echinodermata	*Bryssopsis lyrifera*§	Blyr	*	*			SSDF	9.09 (±0.61)	−17.90 (±0.85)	10
Echinodermata	*Molpadia musculus*§	Mmus	*	*		*	SSDF	12.11 (±0.43)	−16.88 (±0.52)	9
Echinodermata	*Mesothuria intestinalis*§	Mint_1400m	*				SDF	9.63 (±0.15)	−16.61 (±0.99)	3
Echinodermata	*Mesothuria intestinalis*§	Mint_1600m	*				SDF	9.84 (±0.19)	−15.92 (±0.26)	3

Feeding modes listed in literature or based on our own data are also given. ASF = active suspension feeders; SDF = surface deposit feeders; SSDF = sub-surface deposit feeders; S = scavengers, C = carnivores. B1 = February 2007 and 2008; B2 = April 2007; B3 = June–July 2007 and B4 = October 2007. The number of samples analysed (*N*) are also reported.
§species analysed for stomach contents.

* Marks each sampling period (B1–B4) in which species have been analysed.

adding 1 M HCl drop-by-drop to remove inorganic carbonates (the cessation of bubbling was used as a criterion to determine the amount of acid to add; Jacob et al., 2005), and then samples were dried again at 60 °C for 24 h. Acidification is required because carbonates have a less negative $\delta^{13}C$ than organic carbon (De Niro and Epstein, 1978).

Although some authors suggest extracting lipids in samples prior to stable isotope analysis, a defatting approach is unusual for invertebrates (Iken et al., 2001; Nyssen et al., 2002, 2005; Carlier et al., 2007), and the few published works on deep-sea invertebrates all present isotope data from non-defatted analyses (e.g. Iken et al., 2001; Polunin et al., 2001; Fanelli et al., 2009). Furthermore, defatting removes possible seasonal signals of phytodetritus inputs, considering the lipid nature of chlorophyll *a* and derivates (Fabiano et al., 1993). Since one of our objectives is to analyse seasonal trends in isotopic signals, we preferred to use untreated samples for direct comparison with the available literature and for investigation of natural signals of fresh food inputs. Nevertheless, in order to have an indication of lipid content in our samples, the relationship between C/N ratios and the $\delta^{13}C$ signatures was used (sensu France, 1996). C/N ratios are a relatively good surrogate for tissue lipid content (i.e. samples containing more lipids have higher C/N ratios; Tieszen et al., 1983). C/N ratios were measured simultaneously during stable isotope analysis from the elemental percentages and $\delta^{13}C$ values were normalised for lipid concentration according to the equation of Post et al. (2007): $\delta^{13}C$ values of untreated samples (not defatted) were converted to $\delta^{13}C_{normalized}$ ($\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99\ C/N_{sample}$). Thus the relationship between C/N ratios and the $\delta^{13}C$ values was explored by means of ANCOVA analysis, with season as the covariate.

Biological samples were weighed (ca. 1 mg of dry weight) in tin cups. Analyses of filters for POM_{wat} were run on dried subsamples (at 60 °C for 24 h) of about 13 mm diameter that were packed into tin capsules. Sediments for $\delta^{13}C$ analyses (POM_{sed}) were initially weighed (~5 mg) directly in silver capsules; the carbonate fraction was then removed by treatment with 1 M HCl followed by drying (60 °C until constant weight). $\delta^{15}N$ analyses of sediments were carried out directly on bulk powdered samples of 15–20 mg placed into tin capsules.

Stable isotope measurements of biological, POM_{wat} and POM_{sed} samples were carried out by a ThermoFisher Flash EA 1112 elemental analyzer coupled to a Thermo Electron Delta Plus XP isotope ratio mass spectrometer (IRMS) at the geochemistry laboratory of the IAMC-CNR Institute at Naples (Italy). Samples were run against blank cups and known urea standards (analytical grade urea of certificated isotopic composition). Three capsules of urea were analysed at the beginning of each sequence, and one capsule was analysed every six samples, in order to compensate for potential machine drift and as a quality control measure. Experimental precision (based on the standard deviation of replicates of the internal standard) was <0.2‰ for $\delta^{15}N$ and <0.1‰ for $\delta^{13}C$. $\delta^{13}C$ and $\delta^{15}N$ values were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (vPDB) and atmospheric N_2 standards, respectively, according to the following formula:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard})-1]10^3, \text{ where } R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N.$$

A minimum of three replicates (when sufficient samples were available; in a few cases only one sample was processed) were analysed for each of the taxa per survey (Table 1), and each replicate included just one individual in order to reduce pseudo-replication (Hurlbert, 1984). Only in the case of *Harpinia* spp., several individuals were pooled to obtain sufficient mass for the isotope measurement. Also POM_{wat} and POM_{sed} samples were analysed in triplicate.

2.3. Gut content and pigment analyses

The gut contents of 12 species (species marked with § in Table 1) collected during the cruises were also analysed. In order to obtain a general and qualitative view of the diet composition, the guts of some specimens (from 2 to 10 specimens for each species) were examined under a compound microscope (×100–×600). Information obtained on gut contents of species analysed is summarised in Cartes et al. (2009) and also reported in Table 1.

Reverse phase high pressure liquid chromatography (HPLC) analysis was used to determine phytopigments in the stomach contents of three species (*A. longicallus*, *Bryssopsis lyrifera* and *Calocaris macandreae*), in a total of 34 specimens (mean size of *A. longicallus* = 19.2 mm ± 0.6 SD; *B. lyrifera* = 30 mm ± 5 SD; mean carapace length of *C. macandreae* = 9.5 mm ± 0.3 SD). These species were chosen as indicators of suspension-deposit feeding (based on literature and our own data) for which the analysis of gut contents is often of little use since the impossibility to identify the composition of detritus ingested. A sub-sample of gut contents from individuals frozen immediately (−20 °C) after capture was taken using forceps or a Pasteur pipette. All samples were processed according to Witbaard et al. (2000): extracted in 3 ml 100% methanol by mechanical grinding, filtered through Whatman GF/F filters and 0.2 ml of the pigment extract was injected into a Hewlett Packard series 1100 HPLC with a C_8 BDS 3 μm Hypersil, IP column (Thermo Electron). The following HPLC protocol is detailed in Brunet et al. (2006). The mobile phase was composed of two solvent mixtures: methanol:aqueous ammonium acetate (70:30) and methanol. Pigments were detected spectrophotometrically at 440 nm using a Hewlett Packard photodiode array detector model DAD series 1100. Fluorescent pigments were detected in a Hewlett Packard standard FLD cell series 1100 with excitation and emission wavelengths set at 407 and 665 nm, respectively. Determination and quantification of pigments were based on pigment standards from the D.H.I. Water & Environment Group (Denmark).

2.4. Environmental variables

CTD casts were performed at each station using a SBE 32 coupled with a fluorometer and a transmissometer, approximately at the same locations where biological and POM_{sed} samples were collected. Values of temperature, salinity, fluorescence and turbidity were recorded for each CTD profile. The values of these variables at 5 m below the surface and at 5 m above the sea bottom (5 mab) were also obtained.

Phytoplankton pigment concentration (PPC, mg Chl a/m^3), obtained from NASA (http://reason.gsfc.nasa.gov/Giovanni), was used as an indicator of the productivity of the area. Monthly average readings of PPC at the positions of the bottom trawls were used, considering different lag intervals before the sampling periods (simultaneously and 1, 2 and 3 months before). Sea-surface temperature was obtained from the same web source. Mean monthly flow volumes at the mouths of the two main rivers discharging in the area, the Besòs and Llobregat, were obtained from http://aca-web.gencat.cat/aca/appmanager/aca/aca/. Total organic matter (%TOM) contents of collected sediments, calculated as the difference between dry weight (DW: 60 °C to constant weight) and ash weight (500 °C in a furnace for 2 h), were also obtained.

2.5. Data analyses

Isotope data were normally distributed, thus they were not transformed for univariate and multivariate analyses. $\delta^{13}C$ values of POM_{sed} and POM_{wat} were tested for differences among surveys (seasons), depth stations (650 vs. 800 m) and POM carrier (POM_{sed} vs. POM_{wat}) by means of one-way ANOVA.

In order to identify groups of species, a hierarchical cluster analysis (Euclidean distance, average grouping methods) was performed on $\delta^{13}C$ and $\delta^{15}N$ mean values per species and per sampling date (month) (Davenport and Bax, 2002; Le Loc'h and

Hily, 2005; Grall et al., 2006). The groups obtained were compared with postulated trophic groups based on literature (see Table 1) and on our own data, i.e. active suspension feeders (ASF), surface deposit-feeders (SDF), sub-surface deposit feeders (SSDF), mixed diet (Mix) and carnivores (Carn), as given in Table 1 and also Cartes et al. (2009).

Permutational univariate ANOVAs (PERMANOVA: Anderson et al., 2008) were performed on the same matrix to compare groups identified based on knowledge of gut contents. Analyses were performed separately for δ^{13}C and δ^{15}N in order to identify which isotopes were driving the clusters. When the statistics proved significant outputs, a pair-wise comparison was done on the average δ^{13}C and δ^{15}N of these groups. Significance was set at $p = 0.05$ and p-values were obtained using 9999 permutations, under unrestricted permutation of raw data, which is recommended when there is only one factor.

Correlations were used to assess the strength of association between δ^{15}N and δ^{13}C data across all sampled materials (see Polunin et al., 2001) and then to contrast periods of water column homogeneization (February/April = B1-B08/B2) vs. stratification (June–July/October = B3-B4). The rationale behind these combinations is that the whole megafaunal assemblages (including fish, large decapods, cephalopods and megabenthos) changed as a function of the water column conditions (e.g. homogenised vs. stratified; Papiol et al., 2008). Only those species for which data from at least three surveys were available were included in these analyses.

Since no significant differences were detected between samples collected at 650–800 m in February 2007 (B1) and those from February 2008 (B08), in terms of species composition, abundance, biomass and also isotopic values, the isotopic signatures of specimens from the two periods (February 2007 and February 2008) were merged by replicate and indicated as B1.

Finally δ^{15}N and δ^{13}C data recorded at each station/sampling period were compared with environmental variables using Spearman's correlation coefficients, separately, and using the BIOENV routine available in PRIMER6 (Clarke and Warwick, 1995) in order to find the best match between the two isotopic values and the environmental variables. For those analyses, only those species analysed in both periods (February/April vs. June–July/October) were considered. Before the analysis, a draftsman plot (Clarke and Warwick, 1995) was performed on environmental variables in order to look at collinear variables and to reduce the number of environmental variables to be used in the following analyses.

All the analyses were performed using PRIMER6 and PERMANOVA+ (Clarke and Warwick, 1995; Anderson et al., 2008) and STATISTICA 6 software.

3. Results

3.1. *Isotope analysis*

Nitrogen isotope signatures of POM_{wat} could not be quantified by the IRMS, because they were lower than the detection limit of the instrument. POM_{wat} δ^{13}C values varied seasonally (ANOVA test $F_{3,8} = 22.96$, $p < 0.001$; SNK post hoc test: February < April = June/July < October), being more negative during February ($\delta^{13}C = -26.40 \pm 0.41$), increasing in April and June/July ($\delta^{13}C = -22.88‰ \pm 0.04$ SD and $-23.01‰ \pm 0.56$ SD) and finally being more positive during October ($\delta^{13}C = -21.23 \pm 1.41$).

δ^{15}N values of POM_{sed}, both at 650 and 800 m depths, were more enriched during February and October, and depleted by comparison during April and June–July (Table 2). Differences in δ^{15}N values of POM_{sed} were significant only at 800 m (Table 2). δ^{13}C of POM_{sed} varied seasonally at 650 m, being significantly more depleted during June–July than in the other seasons (Table 2). Similarly, at 800 m δ^{13}C of POM_{sed} during June/July was rather more depleted than those recorded in the other three surveys (Table 2). No significant differences were detected in both δ^{15}N and δ^{13}C values of POM_{sed} between 650 and 800 m samples. Similarly, no significant difference was found when tested for POM carriers (POM_{wat} vs. POM_{sed}).

δ^{15}N and δ^{13}C values of other possible food sources (remains of wood, tree leaves and *P. oceanica*) collected from 650 to 800 m depths are reported in Table 2. As expected, the δ^{13}C values of wood and tree leaves were highly depleted (i.e. terrigenous signal).

High values of %TOM were observed at both 650 and 800 m depths in June–July, while the maximum value of %TOM was recorded at 800 m in April (Fig. 2). Both high values of %TOM and

Table 2

Isotopic signatures of the potential food sources on the Catalan slope during BIOMARE surveys (mean ± standard deviation) and results of one-way ANOVA tests on POM_{sed}.

δ^{15}N	February	April	June/July	October
Tree leaves*	5.15 (1.01)	–	2.75	4.59
Wood remains	1.23	–	–	1.65
P. oceanica leaves	–	–	5.38	–
POM_{sed} 650 m	3.44 (0.13)	2.71(0.69)	2.52 (0.31)	3.47 (0.26)
POM_{sed} 800 m	3.70 (0.60)	2.29 (0.05)	3.03 (0.54)	3.67 (0.29)
	One-way ANOVA		SNK post hoc test	
POM_{sed} 650 m	ns		–	
POM_{sed} 800 m	$F_{3,8} = 7.19$; $p < 0.05$		February = June/July = October > April	
δ^{13}C	February	April	June/July	October
Tree leaves*	−27.58 (0.90)	−28.35 (1.32)	−27.90 (0.12)	−27.93
Wood remains	−28.07 (0.64)	−26.83 (0.61)	−27.02 (2.13)	−27.42 (0.09)
P. oceanica leaves	−14.52	–	−16.59	–
POM_{sed} 650 m	−22.21 (0.23)	−22.38 (0.05)	−23.74 (0.09)	−22.34 (0.05)
POM_{sed} 800 m	−22.39 (0.09)	−22.28(0.09)	−22.66 (0.01)	−22.27 (0.07)
	One-way ANOVA		SNK post hoc test	
POM_{sed} 650 m	$F_{3,8} = 94.84$; $p < 0.001$		February = April = October > June/July	
POM_{sed} 800 m	$F_{3,8} = 20.9$; $p < 0.001$		February = April = October > June/July	

ns = not significant.

B1 = February samples; B2 = April; B3 = June–July 2007 and B4 = October 2007

* Leaves of beech (*Fagus sylvatica*) and holm oak (*Quercus ilex*).

^{13}C-depletion in sediments (POM$_{sed}$) observed in early July could be indicators of a terrigenous origin of food.

δ^{13}C values of macro-megabenthic species ranged from −21.3‰ (juveniles of the thalassiinid shrimp *C. macandreae*) to −14.5‰ (the sipunculid *Sipunculus norvegicus*). δ^{15}N ranged from 4.0‰ (the ophiuroid *Amphipholis squamata*) to 12.1‰ (*M. musculus*) (see Table 1). Surface-deposit feeders (*Aporrhais serresianus*, *A. squamata*, *Amphiura chiajei*, both juveniles and adults of *C. macandreae*, *Aspidosiphon muelleri* and *Lumbrinereis* sp) and active suspension feeders (*A. longicallus* and *Scalpellum scalpellum*) had low δ^{15}N values. The other surface deposit feeders (*Alpheus glaber*, Capitellidae) and taxa with a mixed diet (*Harpinia* spp. and nemerteans) showed intermediate δ^{15}N values. Sub-surface deposit feeders had high δ^{15}N values, comparable to those of carnivores. Thus, although the difference (Δ^{15}N) between the mean δ^{15}N values of SSDF and the δ^{15}N of their potential basal source (POM$_{sed}$) was ca. 6.3‰, their trophic position could be similar to SDF. Carnivores showed high δ^{15}N values: among them the decapod *Paromola cuvieri* and polychaetes of the Oenonidae family occupied the highest trophic position.

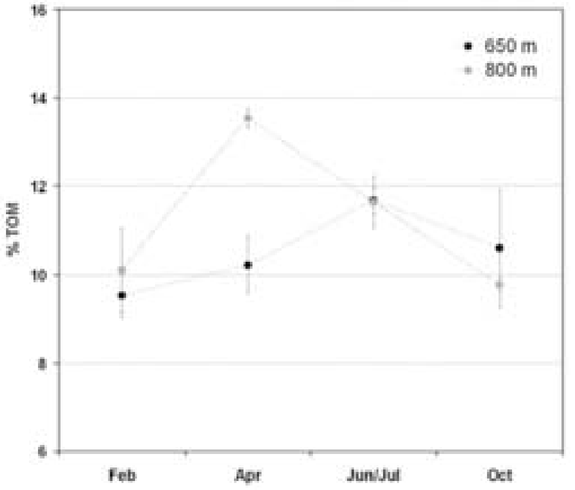


Fig. 2. Temporal variations of total organic matter (%TOM) at two depth stations over the Catalan slope: black symbols indicate samples collected at 650 m and grey symbols are samples at 800 m. Vertical bars represent standard deviations.

The trophic groups identified by cluster analysis (Fig. 3) were partially in agreement with other information on feeding habits (Table 1), with the exception of SSDF and *M. intestinalis*. The cluster analysis based on δ^{15}N and δ^{13}C identified two main groups, I and II, and two subgroups within II (IIA and IIB). Group I included mostly selective SDF: the ophiuroids *A. chiajei* and *A. squamata*, juveniles of *C. macandreae* and the polychaete *Lumbrinereis* sp., but also the cirriped *S. scalpellum* (ASF) and the amphipod *Harpinia* sp., which were classified as a species with a mixed diet, since it can act as a SDF or a scavenger. Group II comprised the remaining species. Subgroup IIA included SDF (including capitellid polychaetes, adults of *C. macandreae*, *A. serresianus* and *A. muelleri*), taxa with a mixed diet such as nemerteans (that can be carnivores and/or scavengers), ASF such as the bivalve *A. longicallus* and carnivores of low trophic level such as *Nephrops norvegicus*, *Monodaeus couchii* and aphroditid polychaetes, which can also act as scavengers. Group IIB was also heterogeneous, including (1) taxa preying on benthic resources (including meiofauna), such as polychaetes of the genus *Nephtys*, (2) large benthic decapods such as *P. cuvieri* and *G. longipes* and (3) a group of SSDF (the holothuroid *M. musculus*, the sipunculid *S. norvegicus*, the echinoid *B. lyrifera* and polychaetes of Maldanidae family). This Group IIB showed more enriched δ^{15}N and δ^{13}C values than SDF. An exception was the SDF *M. intestinalis*; the association of this species with the Carn/SSDF group was probably related with the greater depth at which *M. intestinalis* was collected (1400–1600 m) compared to the other SDFs. Within group II, *M. musculus* clustered separately, because of its high δ^{15}N value.

Average stable isotopic δ^{15}N differed significantly among trophic groups identified by cluster analysis (univariate PERMANOVA main test $F_{4,35}=7.96$, $p<0.001$), while δ^{13}C did not. The pair-wise comparisons showed significant differences between the

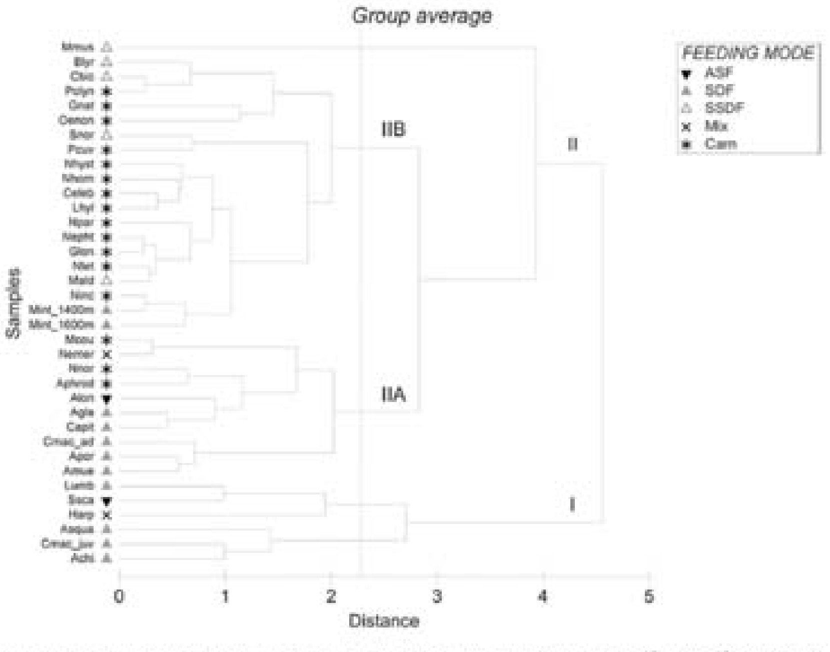


Fig. 3. Hierarchical clustering (Euclidean distance of untransformed data subjected to pair-averaged grouping) of δ^{13}C and δ^{15}N for 34 epibenthic and infaunal taxa. Roman numerals at the tree branches identify groups of taxa belonging to different trophic guilds. Abbreviations of species as in Table 1. ASF = active suspension feeders; SDF = surface deposit feeders; SSDF = sub-surface deposit feeders; Mix = species with a mixed diet; Carn = carnivores. Dashed line represents a distance between groups of 2.3.

Table 3
Results of PERMANOVA pair-wise tests comparing δ^{15}N values of postulated feeding groups based on 9999 permutations.

Groups	t
Carn, SDF	4.55***
Carn, ASF	3.57**
Carn, Mix	2.08ns
Carn, SSDF	1.47ns
SDF, ASF	0.14ns
SDF, Mix	0.83ns
SDF, SSDF	3.35**
ASF, Mix	3.08ns
ASF, SSDF	2.80*
Mix, SSDF	1.93ns

ASF = Active suspension feeders; SDF = surface suspension feeders; SSDF = sub-surface suspension feeders; Carn = carnivore; Mix = mixed diet.

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 4
Spearman correlation of δ^{15}N and δ^{13}C values with environmental variables recorded for each collection of megabenthic epifauna.

	Valid	Spearman	p-level
δ^{15}N			
Temperature 5 mab	112	−0.42	***
Salinity 5 mab	112	−0.25	**
Turbidity 5 mab	112	0.22	*
Chl a 1 month	114	0.41	***
Chl a sim	114	0.31	***
%TOM sediment	67	0.28	*
River discharge sim	114	0.28	**
δ^{13}C			
Salinity 5 mab	113	0.20	*
Turbidity 5 mab	113	0.22	*
Chl a 1 month	115	0.19	*
River discharge two months	115	0.23	*

Only significant correlations are given. %TOM = % Total Organic Matter; Chl a = surface chlorophyll a concentration; mab = metres above the bottom; sim = value recorded simultaneously to sampling.

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

isotopic signatures of ASF/SDF and SSDF and between ASF/SDF and carnivores (Table 3).

3.2. Relationship between δ^{13}C and δ^{15}N data in food webs

The overall correlation between δ^{15}N and δ^{13}C was weak but significant ($R^2 = 0.11$, $p < 0.05$).

ANCOVA analysis did not prove significant differences between δ^{13}C vs. C/N values among seasons ($F_{4,134} = 2.24$, $p = 0.07$), and mean C/N values were similar throughout the seasons.

Correlations of δ^{15}N and δ^{13}C for species in common between the two different water column conditions (stratified vs. homogenised) were weaker when the water column was stratified ($R^2 = 0.03$) than when it was homogeneous ($R^2 = 0.18$); the same results were obtained when we considered normalised δ^{13}C values (according to the equation proposed by Post et al. (2007)), although correlations were even weaker.

3.3. Correlation with environmental variables

δ^{15}N values were positively correlated ($p < 0.001$) with the concentration of Chl *a* recorded simultaneously 1 month before the sampling, and also with river discharge ($p < 0.01$) (see Table 4).

δ^{15}N values were negatively correlated with temperature at 5 mab and salinity at 5 mab. δ^{13}C values were positively correlated (indicating more enriched δ^{13}C) with salinity and turbidity recorded at 5 mab and the concentration of Chl *a* recorded 1 month before sampling (Table 4). The BIOENV routine showed that the best correlation between isotopic signatures and environmental variables was obtained with two variables (salinity and Chl *a* both recorded at 5 mab: $R = 0.140$) or alternatively with only one variable (salinity at 5 mab: $R = 0.124$).

3.4. Gut content and pigment analyses

Based on trophic information in Cartes et al. (2009), *A. longicallus* was classified as an active suspension feeder, while *C. macandreae* and *B. lyrifera* were deposit feeders. In general there was a high amount of degraded chlorophyll pigments (phaeophorbides and phaeophytine) in the three species (particularly in *B. lyrifera*), due to the degradation of photopigments during their passage through the water column or on sediment surface, as well as when grazed by the fauna (Fig. 4a).

Among the three species analysed, *A. longicallus* yielded the lowest pigment content; both degraded chlorophyll products and non-degraded pigments occurred, probably a reflection of its feeding mode (suspension feeding). The presence of a great variety of non-degraded pigments (Fig. 4b), although occurring in low quantity,

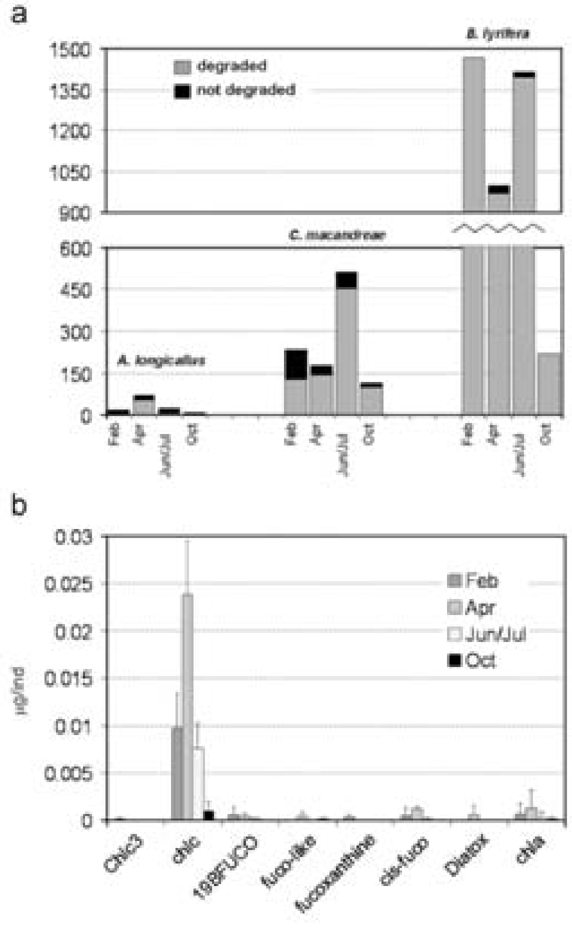


Fig. 4. Temporal variations of (a) degraded chlorophyll pigments (phaeophorbides and phaeophytines) and non-degraded pigments (chlorophylls and carotenoids) found in *Abra longicallus*, *Calocaris macandreae* and *Bryssopsis lyrifera* and (b) non-degraded phytoplanktonic pigments found in *Abra longicallus*. Whiskers indicate standard deviations.

indicates the exploitation of fresh food sources in comparison with the other two species. Being more narrowly dependent on the downward flux, the suspension feeding *A. longicallus* yielded a higher quantity of pigments during April than during the rest of the year (Fig. 4a and b). The most abundant pigments were chlorophyll *c* and carotenoids from the fucoxanthin family. These were more abundant during February and April than during June–July and October, indicating the consumption of brown algae, such as diatoms.

In *C. macandreae* the highest pigment values were recorded during B3 (Fig. 4a), mainly attributed to degraded products of chlorophyll *c* and astaxanthine. These suggest a diet based on astanxathin-containing animals and brown algae, possibly already present in the gut content of the animals. During February and April we observed higher pigment diversity and the occurrence of many non-degraded pigments, mainly from the fucoxanthin family (19B-fucoxanthine and fucoxanthine) and chlorophyll *c* that indicates brown algae (for instance, diatoms or prymnesiophytes). Pigments occurring in *B. lyrifera* gut contents were all highly degraded throughout the sampling period. Also for this species, the pigment analyses were also consistent with the feeding mode in this SSDF species, which was probably eating already degraded pigments.

4. Discussion

4.1. *Food sources off the Catalan slope*

The deep sea is assumed to be a food-limited environment with organisms subsisting on organic material derived from surface productivity. However, in our study, isotopic signatures and pigments identified two main POM vectors as food for macro-megabenthic invertebrates: advective and vertical fluxes. Due to the transport of terrestrial material to depth along submarine canyons, the Catalan Sea slope (CSS) receives considerable amounts of particulate organic matter, some of it of high quality, at depths of ca. 1600 m (Cartes et al., 2002). River discharges are important sources of these terrestrial organics (Cartes et al., 2009). We found evidence of this advective flux in POM_{wat} at 800 m ($\delta^{13}C = -26.4‰ \pm 0.4$) and in terrestrial plant remains (particularly beech, *Fagus sylvatica*, and holm oak, *Quercus illex*) with $\delta^{13}C$ values ranging between −26.8‰ and −28.4‰. These occurred frequently at the bottoms of slopes and represented typical Mediterranean terrestrial $\delta^{13}C$ values (Vidal-Sanchez et al., 2009).

POM arriving to the CSS was more likely to be of direct terrestrial origin, or consisting of degraded phytodetritus linked to phytoplankton production, than originated from continental shelf habitats (e.g. seagrasses). Indeed, although *Posidonia oceanica* beds are located close to Besòs and Berenguera canyons head and seagrass remains were found at slope bottoms, the contribution of *P. oceanica* in the trophic web seems rather low, as indicated by the low proportion of seagrass in guts of shrimps from this area (<5% of volume: Cartes et al., 2009). As a further evidence, average $\delta^{13}C$ values of *P. oceanica* were more enriched (ranging between −14.5‰ and −16.6‰) than those of the deposit feeders analysed (e.g. *M. musculus* and *M. intestinalis*: −16.9‰ and −16.3‰, respectively). Conversely, the $\delta^{13}C$ of POM_{sed} (average −22.7‰ at 650 m and −22.4‰ at 800 m) was within the range of $\delta^{13}C$ values for marine phytoplankton (−18‰–24‰; Fry and Sherr, 1984), while the $\delta^{13}C$ of POM_{wat} found in February ($\delta^{13}C = -26.4‰$) suggested terrigenous input.

Fresh food for suspension feeders was abundant only during the brief post-bloom period and was extremely sparse during the remainder of the year (Iken et al., 2001). Hence, for most of the year suspension feeders may be dependent on resuspended material (as observed by Lampitt (1985) in NE Atlatic). Pigments in guts of key species on the Catalan slope were generally degraded. Only in the case of the active suspension feeder *A. longicallus* did we find chlorophyll *c* in guts, mainly in February and April 2007, the periods of maximum surface primary production (satellite data; Estrada, 1996). On the seafloor, fresh POM occurs as greenish fluffy lumps or mats ('fluff') that become mixed with the superficial sediment layer by benthic storms, tidal movement and bioturbation (e.g. Smith, 1992), and become the principal food source for all surface deposit feeders (SDF). Depending on the amount of sedimented matter, sediment reworked by bioturbation and the feeding activity of larger animals incorporates only a relatively small fraction of this material into deeper sediments, making it available to sub-surface deposit feeders (SSDF) (Lisitsyn and Vinogradov, 1982). The main variation in $\delta^{13}C$ in sediments was observed on the Catalan slope between April and June–July, with ^{13}C depletion of POM_{sed} within Besòs canyon (Fig. 2). The occurrence of advective fluxes in the area is also suggested by the significant positive correlation found between ^{13}C depletion and river runoff (two months before isotope analyses). Thus ^{13}C depletion in spring–early summer seems to be dependent on the advective flux (with a delay of two months). All of these points reinforce the idea that phytodetritus inputs are not the main food source for the Catalan slope benthic community but that there is an important terrigenous contribution mainly transported seaward along the Catalan canyons, in agreement with previous studies of the northwestern Mediterranean slope bottoms (Buscail et al., 1990, based on sediment traps) and with the greater megabenthos biomass on Catalan slopes compared to the insular slopes of the Balearic Basin (Cartes et al., 2009).

4.2. *Food web structure*

Like gut-content data, stable isotopes have several limitations in elucidating the complex dynamics of food webs. Among these, there is the resolution of only broad categories of prey organisms by $\delta^{15}N$ and/or $\delta^{13}C$ values (Polunin and Pinnegar, 2002). This is particularly true for deep-sea communities, where primary food sources arrive from the photic zone after being remineralised, enriched and degraded by microbial activity, potentially reducing the chances of correctly identifying types of source material (Pinnegar and Polunin, 1999).

Our study is the first attempt to unravel the trophic web structure of benthic species in the Mediterranean, so comparable data are scarce except for some species, e.g. *G. longipes* and *N. norvegicus* (Polunin et al., 2001). Comparisons with data from congeneric species (i.e. *Molpadia blakei*, Sipunculida as a whole taxon) outside the Mediterranean (Iken et al., 2001) can be made, but this has some limitations due to geographical and depth differences in isotopic signatures.

Nevertheless, the isotopic signatures of the bulk of our target species fit well with gut content findings in the literature and with our own data (see Table 1). The cluster analysis placed carnivores at the highest trophic levels of the benthic food web (excluding sub-surface deposit feeders—SSDF), while active suspension feeders (ASF) and surface deposit feeders (SDF) were at the lowest levels. ASF and SDF can be identified by their lower $\delta^{15}N$ values: they either feed on different size classes of the available POM, including small particles usually exhibiting very low $\delta^{15}N$ (Rau et al., 1990), or they rely on different microbial food sources. ASF compete directly with SDF for the limited POM food source (e.g. *A. longicallus* ingesting non-degraded chlorophylls), intensifying the trophic competition as observed in other geographic areas (Iken et al., 2001). A first discrepancy between isotopic signatures and gut content findings in the literature was represented by the position of the SDF species *M. intestinalis* among those with more enriched $\delta^{15}N$ and $\delta^{13}C$ values. This apparent inconsistency is likely related to the depth range of collection of this elasipod holothurian, which lives between 1400 and 1600 m (Cartes et al., 2009), deeper than the other species analysed. The $\delta^{15}N$ of benthic POM consumers increases with water depth (Polunin et al., 2001; Mintenbeck et al., 2007). This results from excretion of nitrogen depleted in ^{15}N with the corresponding enrichment in ^{15}N of the residual material during bacterial degradation of POM (Macko et al., 1986). Microbial consumption is thus reflected in an increase of POM $\delta^{15}N$ with depth.

In our study we found significant differences in $\delta^{15}N$ values between SDF and SSDF, indicating that the latter feed on more refractory and frequently recycled material (Iken et al., 2001), in contrast to SDF, which ingest much of the labile organic matter deposited on the seafloor prior to extensive microbial processing (DeMaster et al., 2006). This may explain why SSDF showed high $\delta^{15}N$ and $\delta^{13}C$ values and clustered with carnivores. Among SSDF, deep-sea holothurians may exploit the bacteria directly as a food source or they may use the bacteria indirectly to provide them with the essential nutrients not available otherwise (Deming et al., 1981; Deming and Colwell, 1982; Eardly et al., 2001), leading to a high $\delta^{15}N$ in holothurians' tissue and an enrichment of $\delta^{13}C$ values. Additionally, compounds with high nutritional quality (i.e. N rich) are readily available in the seafloor sediments of the CSS (Amaro et al., 2009, 2010), which explains the high abundance of the holothurian *M. musculus* locally in the Catalan area (Cartes et al., 2009) as well as in the Nazaré canyon (Amaro et al., 2009).

The pattern of carbon enrichment found for *M. musculus* was also found in other SSDF species analysed in our study: (i) the irregular urchin *B. lyrifera*, which is reported to feed selectively on carbon- and nitrogen-rich particles (Hollertz, 2002), and to rework relatively large volumes of sediment (Hollertz and Duchêne, 2001) by living burrowed 20 mm below the surface of the substratum, (ii) the burrowing sipunculid *S. norvegicus* and (iii) the maldanid polychaete *Chirimia biceps*. Biodeposition processes, dependent on the suspension feeding fauna that actively remove particles from the water column and deposit them as faeces either within or on the top of the sediment (Graf and Rosenberg, 1997), may further enrich the organic matter ingested by deposit feeders (Thomsen and Flach, 1997).

Among carnivores, an important group was represented by polychaetes of the families Nephtydae, Polynoidae (*Harmothoe* spp.) and Oenonidae, which exhibited very high $\delta^{15}N$ values, comparable to those of top predators such as fish (Polunin et al., 2001; Fanelli and Cartes, 2010). The high $\delta^{15}N$ values observed in carnivorous polychaetes are consistent with the idea that deep-benthic food webs are highly complex compared to pelagic ones (Cartes et al., 2008; Fanelli and Cartes, 2010). These predators may rely on either benthic and suprabenthic prey from the benthic boundary layer, as in the cases of the Norway lobster *N. norvegicus*, which consumes mainly nektobenthic decapods, euphausiids and peracarids (Cristo and Cartes, 1998), and the crab *G. longipes*, which feeds on endobenthic crustaceans such as *C. macandreae*, the isopod *Natatolana borealis*, nektobenthic decapods and pteropods (Cartes, 1993).

Regarding trophic levels in deep-sea benthic ecosystems, it seems unrealistic to use a single fractionation factor to characterise the food web structure (Caut et al., 2009). The values of 2.75‰, proposed by Caut et al. (2009), based on 268 estimates of $\Delta^{15}N$ from reviewed papers, e.g. the difference between the isotopic composition of a consumer with respect to its diet) or of 3.1‰ (as calculated according to the equation proposed by the authors for invertebrates) were consistent with the dietary information available for carnivores, ASF and SDF. Large decapods such as *N. norvegicus* and *G. longipes* (with $\delta^{15}N$ signature of 7.1‰ and 9.2‰, respectively) consume prey (e.g. *C. macandreae*, *A. longicallus*; Cristo and Cartes, 1998; Cartes, 1998; this study) for which $\delta^{15}N$ signature ranged between 4.7‰ and 6.3‰, providing an average fractionation of ~2.6‰. Additionally, $\Delta^{15}N$ values found for ASF and SDF ranged from 2.4‰ (SDF) to 3.1‰ (ASF) and so were close to the two values proposed above. On the other hand, this value seemed inappropriate for SSDF, for which differences between animals and their diet (POM_{sed}) exceed 6‰ (e.g. the case of *M. musculus*). Thus, assuming a fractionation value of between 2.75‰ and 3.1‰ (except for SSDF), three trophic levels were identified among epibenthic and infaunal invertebrates of the Balearic Basin (from the lowest level occupied by SDF and ASF to the uppermost levels with *P. cuvieri* and Oenonidae among predators).

The significant overlap in nitrogen isotopic values between feeding groups, as observed in previous studies (Iken et al., 2001), may be an indicator of vertical niche extension (across trophic levels), a likely feature in severely food limited systems. On the other hand, according to the high fractionation factor found for SSDF (high difference between $\delta^{15}N$ of SSDF and $\delta^{15}N$ of POM_{sed}), it is likely that the recycled or bacterially degraded material consumed by this group (Amaro et al., 2010) may be the start for a new food chain with a different basal N rather than a continuation of an existing food chain. However, further studies will be necessary to better understand the mechanism of isotope incorporation in SSDF tissues, especially *M. musculus*. This species, like others of the genus *Molpadia* (i.e. *M. blakei*, Iken et al., 2001), has enteric bacteria that may break down refractory compounds, which can then be assimilated by the holothurians (Roberts et al., 2001).

The only study of deep megabenthos similar to ours was carried out at the Porcupine Abyssal Plain (PAP; 4840 m; Iken et al., 2001), where the lowest $\delta^{15}N$ value was found for the ophiuroid *Ophiocten hastatum* ($\delta^{15}N=10.7$‰) and the highest in the holothuroid *M. blakei* ($\delta^{15}N=16.2$‰, excluding the $\delta^{15}N$ value of 17.7‰ found for the polychaete *Nicon* sp.). Our results were, as expected, less enriched in $\delta^{15}N$ (between 4.1‰ for *A. squamata*, and 12.1‰ for *M. musculus*) than at PAP, because of the lower depth of our study (650–1100 m at CSS vs. 4840 m at PAP). It is interesting that closely related taxa marked the extremes of the trophic gradient at both sites (an ophiuroid at the lowest, *Molpadia* spp. at the highest). The range of all $\delta^{15}N$ values was greater in our area ($\Delta\delta^{15}N=7.8$‰) than at PAP ($\Delta\delta^{15}N=5.5$‰), which is surprising considering the impoverishment of Mediterranean deep-sea benthos (Pérès, 1985; Cartes et al., 2009) compared to the NE Atlantic. A possible explanation for this apparent discrepancy might be that we worked on fauna collected adjacent to submarine canyons, thus animals exploiting two different basic food sources (including both marine phytodetritus and terrestrial vegetal remains).

4.3. Temporal variations in isotopic signatures: influence of environmental variables

As shown by weak $\delta^{13}C$–$\delta^{15}N$ correlations, there were clear differences in the coupling of benthos with peaks of new production (nitrate-based production or export production) during periods of stratification and homogenity of the water column. High $\delta^{13}C$–$\delta^{15}N$ correlations likely indicate a single food source (e.g. in deep-sea communities; Cartes et al., 2007) and suggest pulses of new production. In contrast, weak correlations (low R^2 values) point to a wide array of sources of production (Polunin et al., 2001).

Over Catalan slopes, the weakest $\delta^{13}C$–$\delta^{15}N$ correlations in macro-megabenthic fauna occurred in the summer (end of June–July), two months after the peak of river discharge in the area in April (Papiol et al., 2008). This suggests a link (with a delay of two months) between $\delta^{13}C$ signal in tissues of invertebrates and peaks of river discharge, according to the idea that river discharge provides a more mixed food pulse, especially terrestrial input. The role of river flows is consistent with the negative correlation found between $\delta^{13}C$ values of dominant benthic species and the amount of river discharge recorded two months before the sampling. In addition, the maximum amount of organic matter (%TOM) in sediments was recorded two months after the peak of river discharge in April, and the %TOM peak also coincided with depletion in POM_{sed} $\delta^{13}C$ (Fig. 2 and Table 2).

The particular oceanographic conditions of the Mediterranean influence the quantity and quality of POM reaching deep waters. The approximately constant temperature around 13 °C at 150 m

(Hopkins, 1985) enhances rapid degradation of organic matter throughout the water column (Wishner, 1980). As a consequence, most of the organic matter transported as vertical flux appeared degraded in the guts of CSS benthic fauna. The occurrence of a higher quantity of pigments during April in the active suspension feeder *A. longicallus* is consistent with a quick response to the phytoplankton bloom in February–March (Estrada, 1996). The most abundant accessory pigments present in February–April were indicative of the consumption of phytodetritus derived from brown algae (Chl *c*), diatoms (Cis-fucoxanthine, diatoxanthine and Chl *c*) and prymnesiophytes (fucoxanthine derivatives, Chl *c*), dominant in phytoplankton assemblages during the late winter–early spring bloom over the CSS (Estrada, 1991; Estrada et al., 1999).

C. macandreae also takes advantage of the food derived from surface primary production from February to March, as indicated by the high pigment diversity in their stomach contents in February and April. However, unlike *A. longicallus*, the occurrence of a higher quantity of pigments in June–July in *C. macandreae* (a SDF), together with the high percentage of degraded pigments, is consistent with the idea that deposit feeders respond later and probably more weakly than suspension feeders to the input of phytodetritus from vertical flux. Finally, the almost exclusive occurrence of degraded pigments in *B. lyrifera* confirms our previous observations based on isotopic signatures, which pointed to the exploitation by SSDF of highly recycled, degraded POM.

δ^{15}N values were also related to other temporal variables, e.g. the structure of the water column. Thus, benthos showed more depleted δ^{15}N values during water-column stratification (summer–autumn), i.e. with increase in temperature and salinity than during strong mixing. This is consistent with the findings of Jennings and Warr (2003) who report depleted δ^{15}N in the scallop *Aequipecten opercularis* in summer. During summer, ammonia excreted by zooplankton that are depleted in δ^{15}N is likely to be an important nitrogen source for phytoplankton (Owens et al., 1990). Zooplanktons are known to become relatively depleted in δ^{15}N when ammonia, rather than nitrate from riverine sources, is the main nitrogen source for their phytoplankton prey (Mullin et al., 1984). This is also consistent with data from the area near Corsica where δ^{15}N values of surface plankton were much higher in spring than in autumn (Michener and Schell, 1994). Turbulent mixing and upwelling caused by offshore winds in spring bring nitrate high in δ^{15}N to the surface where it is taken up by phytoplankton (Michener and Schell, 1994). As this mixing and upwelling cease, the surface waters rapidly become oligotrophic and primary production is based on recycled ammonium depleted in ^{15}N (Polunin et al., 2001).

Higher δ^{15}N values of the analysed species were also associated with higher water turbidity, which may be linked to the formation of nepheloid layers (Puig and Palanques, 1998) by the resuspension of POM. Over the Catalan slope, water turbidity, which in turn is related to a homogeneous water column, was higher in February–April near the seafloor (Puig and Palanques, 1998). In contrast, in a stratified water column, a thermocline may act as a physical barrier to the downward particle flux.

In conclusion, over the Catalan slope, proximity to the mainland means that the benthic community is influenced by advective inputs from strong river discharge and associated events such as nepheloid layer formation in and near submarine canyons (Puig and Palanques, 1998), in addition to vertical flux. Under these conditions, high quantities of POM can settle on the seabed of the Catalan slope, especially through canyons (Rowe et al., 1982; Vetter and Dayton, 1998) that channel this advective flux. This explains why detritus feeders (e.g. *C. macandreae*, *M. musculus* and *B. lyrifera*) were dominant among macro-megabenthic invertebrates on the Catalonian side of the basin (Cartes et al., 2009), in contrast to the insular slope and the Algerian basin (Cartes et al., 2004; Fanelli et al., 2009), which are less influenced by advective fluxes.

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CHAPTER 4 - FOOD WEB STRUCTURE AND SEASONALITY OF SLOPE MEGAFAUNA IN THE NW MEDITERRANEAN ELUCIDATED BY STABLE ISOTOPES: RELATIONSHIP WITH AVAILABLE FOOD SOURCES

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Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: Relationship with available food sources

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ABSTRACT

The food-web structure and seasonality of the dominant taxa of benthopelagic megafauna (fishes and decapods) on the middle slope of the Catalan Sea (Balearic Basin, NW Mediterranean) were investigated using the carbon and nitrogen stable isotope ratios of 29 species. Macrofauna (infauna, suprabenthos and zooplankton) were also analysed as potential prey. Samples were collected on a seasonal basis from 600 to 1000 m depth between February 2007 and February 2008. The fishes and decapods were classified into feeding groups based on the literature: benthic feeders (including suprabenthos) and zooplankton feeders, the latter further separated into migratory and non-migratory species. Decapods exhibited depleted δ^{15}N and enriched δ^{13}C compared to fishes. Annual mean δ^{13}C of fishes ranged from -19.15‰ (*Arctozenus risso*) to -16.65‰ (*Phycis blennoides*) and of δ^{15}N from 7.27‰ (*Lampanyctus crocodilus*) to 11.31‰ (*Nezumia aequalis*). Annual mean values of δ^{13}C of decapods were from -18.94‰ (*Sergestes arcticus*) to -14.78‰ (*Pontophilus norvegicus*), and of δ^{15}N from 6.36‰ (*Sergia robusta*) to 9.72‰ (*Paromola cuvieri*). Stable isotopes distinguished well amongst the 3 feeding guilds established *a priori*, pointing to high levels of resource partitioning in deep-sea communities. The trophic structure of the community was a function of the position of predators along the benthic–pelagic gradient, with benthic feeders isotopically enriched relative to pelagic feeders. This difference allowed the identification of two food webs based on pelagic *versus* benthic consumption. Prey and predator sizes were also important in structuring the community. The most generalised seasonal pattern was δ^{13}C depletion from winter to spring and summer, especially amongst migratory macroplankton feeders. This suggests greater consumption of pelagic prey, likely related with increases in pelagic production or with ontogenic migrations of organisms from mid-water to the Benthic Boundary Layer (BBL). δ^{15}N enrichment was detected in periods of water column stratification, particularly amongst benthic feeder fishes. Megafauna relied on a single source of nutrition after peaks in surface production, presumably marine snow. Conversely, a larger array of food sources, probably from advection, sustained the community in periods of water column stratification. Benthic feeder δ^{13}C values of both taxa were positively correlated with fluorescence measured 5 m above the seabed and negatively correlated with total organic carbon in the sediments, both being food sources for deposit feeding macroinfauna. Macroplankton feeder δ^{13}C values were linked to environmental variables related to vertical transport from surface production, *i.e.* lipids and chlorophyll and their degradation products, likely due to their stronger reliance on sinking phytodetritus through consumption of planktonic prey.

1. Introduction

Food availability has been described as controlling megafauna community structure in deep marine ecosystems (Gage and Tyler, 1991), which may be especially true in oligotrophic areas such as the Mediterranean Sea (Cartes, 1998a; Cartes and Maynou, 1998; Papiol et al., 2012). This conjecture led us to study the trophic relations of megafauna in the Balearic Basin.

Traditional studies of food web dynamics have used gut content analyses to elucidate aspects of community structure (*e.g.* Carrassón and Cartes, 2002; Cartes et al., 2007; Jennings et al., 2002; Madurell and Cartes, 2005). Gut contents reflect food consumed at particular points in time and space, and they provide a great deal of information on gut fullness variation and on specification of prey and trophic effects of their density on distribution of both food sources and consumers. Nevertheless, this approach has limitations (Fanelli and Cartes, 2008; Fry, 2006; Pinnegar and Polunin, 2000) that are especially intense for deep-sea food webs as a result of sampling constraints *e.g.* hydrostatic decompression regularly results in regurgitation of prey in some deep-sea fish. Additionally, whilst gut

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content analysis of secondary consumers is useful for assessing prey consumption and selectivity, it does not reveal the end members sustaining megafauna communities, specifically not the origin (terrestrial *versus* marine) of organic matter (OM).

Stable nitrogen (N) and carbon (C) isotope ratios are commonly used as indicators of trophic level and organic matter source in aquatic ecosystems (*e.g.* Davenport and Bax, 2002; Iken et al., 2001; Pinnegar and Polunin, 2000) and can be used to differentiate assimilated food from that initially ingested (Guiguer et al., 2002; Persic et al., 2004; Reñones et al., 2002). Stable isotope analyses (SIA) can characterise in a general fashion food assimilated over a considerable period (Hesslein et al., 1993), and thus they are less subject to temporal bias than gut content analyses. SIA are useful in identifying food pathways and trophic interactions within complex ecosystems (Davenport and Bax, 2002; Fry et al., 1987; Iken et al., 2001). Stable nitrogen isotopes have been used to identify the relative trophic position of organisms within the food web (Hobson and Welch, 1992; Mincks et al., 2008; Vander Zanden et al., 1996). Nitrogen isotope ratios of animals in the $\delta^{15}N$ format are enriched on average by 3‰ compared with their diet (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001; Post, 2002; McCutchan et al., 2003; Caut et al., 2007). Carbon isotopes are widely used as indicators of sources of primary production in the ecosystem (Fry, 2006; Michener and Lajtha, 2007). Different potential sources (*e.g.* terrestrial *versus* marine) of carbon have different $\delta^{13}C$ signatures and have been described for the NW Mediterranean Sea (Fanelli et al., 2011a; Meyers, 1997; Pinnegar and Polunin, 2000). Animal $\delta^{13}C$ is typically enriched by 1.1‰ or less per trophic level within oceanic systems (*e.g.* France and Peters, 1997; Michener and Lajtha, 2007). Given the constraints and paucity of gut-content data, stable isotopes are useful in elucidating the structure of deep-sea food webs.

In food-limited environments, such as the NW Mediterranean slope, co-occurring species typically develop strategies for reducing or avoiding food competition, and niche segregation amongst fishes is mainly driven by trophic resource partitioning (Macpherson, 1981; Ross, 1986). Pairs of species with high dietary overlap segregate along the depth gradient (Carrassón and Cartes, 2002; Cartes, 1998a; Fanelli and Cartes, 2010). The middle slope of the NW Mediterranean Sea, located between ~600 m and ~1200 m, is characterised by homogeneous benthopelagic communities along the Catalonian coast (Abelló et al., 1988; Cartes and Sardà, 1993; Cartes et al., 2009; Fanelli et al., 2012; Stefanescu et al., 1993, 1994). The vertical distributions and sizes of available food resources have been identified as main factors driving resource partitioning amongst the megafauna of this depth range (Carrassón and Cartes, 2002; Cartes, 1998a). Fishes and decapods generally employ different trophic strategies (Cartes and Sardà, 1993; Haedrich et al., 1980) in respect to prey selection (mainly affected by prey size). These taxa are considered to have mixed diets of benthic and mesopelagic prey (Cartes et al., 1994; Mauchline and Gordon, 1986), but species in both groups have distinct preference toward one of these categories. Seasonal changes in dietary composition of deep-sea megafauna species have already been documented (Cartes, 1994; Cartes et al., 2008; Fanelli and Cartes, 2008, 2010; Madurell and Cartes, 2005), for example to at least 1200 m in *Aristeus antennatus* (Cartes, 1994), and have been linked to seasonality of prey (*e.g.* Cartes et al., 2002a). Prey consist of the BBL macrofauna (zooplankton, suprabenthos and infauna) that vary seasonally according to changes in organic matter (OM) inputs that they channel to higher trophic levels. Moreover, several studies have linked the temporal dynamics of certain organic compounds with biological cycles and abundances of meiofaunal and macrofaunal groups (Cartes et al., 2002b; Mamouridis et al., 2011; Riaux-Gobin et al., 2004).

Organic matter inputs to the deep-sea change seasonally in both amount and composition (Beaulieu, 2002; Cartes et al., 2002b; Miquel et al., 1994; Smith et al., 1996, 2008). In the deep NW Mediterranean Sea they are mainly transferred through downward flux of what is loosely referred to as "marine snow" (*e.g.* Sumich, 1999) from the epipelagic zone. Marine snow is a combination of aggregated detrital material (*e.g.* exopolymers, mucous, phytoplankton, plankton exoskeletons, faecal pellets and bacteria) and zooplankton (*e.g.* Beaulieu, 2002; Miquel et al., 1994). Flux of marine snow decreases with depth (Miquel et al., 1994; Sumich, 1999) and varies seasonally, mainly due to changes in surface production (SP) (Rice et al., 1994; Riemann, 1989; Thiel et al., 1990) and water column conditions (Miquel et al., 1994). Surface production in the NW Mediterranean peaks during a late winter surface bloom, whereas there is a deep chlorophyll maximum (DCM) in open waters during the stratified period (Estrada, 1991). Water column stratification takes place from April to November (Papiol et al., 2012). In the study area, advective fluxes, such as in nepheloid layers in submarine canyons, are also key processes affecting food availability at bathyal depths. They both channel significant amounts of sediment and associated OM from the shelf across the slope (Buscail et al., 1990; Palanques et al., 2006) and resuspend OM from the bottom (*cf.* Monaco et al., 1990; Shepard et al., 1974). The submarine canyons are also subject to strong seasonality related to discharges of continental run-off (Buscail et al., 1990; Monaco et al., 1990), to cascading events in the Gulf of Lions affecting the NW Spanish coast, and to varying conditions in the water column (Canals et al., 2006). The distinction between the vertical and the horizontal fluxes involves deliveries of distinctive organic compounds to bathyal depths (*e.g.* phytosterols and polyunsaturated fatty acids, biomarkers of phytoplankton, are associated to vertical flux of phytodetritus; Jeffreys et al., 2009a) and different liabilities of their transported OM (Buscail et al., 1990). Whilst the presence of phytoplankton pigments and lipids is most probably associated with marine snow and phytodetritus inputs (Buscail et al., 1990; Cartes et al., 2002b; Fabiano et al., 1993), organic carbon may be transported by either of the fluxes (Miquel et al., 1994; Monaco et al., 1990). As inputs of distinct food sources vary seasonally, isotopic signatures associated with those sources also present seasonal variation (Michener and Lajtha, 2007). The seasonal variations in the fluxes of OM imply different availability of organic compounds to consumers, and the relationship between $\delta^{13}C$ *versus* $\delta^{15}N$ can be a useful indicator of whether one or more end members support biological communities (Fanelli et al., 2011a; Polunin et al., 2001). Weak correlations between $\delta^{13}C$ and $\delta^{15}N$ are indicative of an array of possible sources of production. Conversely, strong correlations are indicative of a single type of primary source (Polunin et al., 2001).

Studies using stable isotopes of food web structure and seasonal changes are relatively common in shallow waters (*e.g.* Carlier et al., 2007; Cummings et al., 2011; Davenport and Bax, 2002; Pinnegar and Polunin, 2000), but such knowledge of bathyal depths is considerably limited. In the deep sea, studies of temporal dynamics of food web structure using stable isotopes have focussed on specific taxa (*e.g.* pandalid shrimps: Fanelli and Cartes, 2008; fishes: Stowasser et al., 2009; Fanelli and Cartes, 2010; cephalopods: Fanelli et al., 2012) or macrofauna groups (*e.g.* suprabenthos: Madurell et al., 2008; Fanelli et al., 2009; benthos: Iken et al., 2001; Fanelli et al., 2011a; zooplankton: Fanelli et al., 2011b), but such studies on megafaunal communities have been few (Cartes et al., 2007; Jeffreys et al., 2009b; Mincks et al., 2008; Polunin et al., 2001). The only previous study in the Mediterranean was by Polunin et al. (2001), who worked in an insular area in the SW Mediterranean. Jeffreys et al. (2009b) investigated the trophic ecology of megafauna at the Pakistan Margin, although they restricted the analyses to the benthic compartment. Also, Cartes et al. (2007) worked in the Cantabrian Sea (Le Danois Bank) on decapod crustaceans. All these workers considered information from wider depth ranges, and they compared only two sampling periods. Additionally, Mincks et al. (2008) studied the Antarctic megabenthic food web at the continental shelf around 600 m including three different seasons. Furthermore, the influences of vertical *versus* horizontal fluxes and associated OM availability on macrofauna in different seasons has been investigated (Cartes et al., 2002b; Fanelli et al., 2011a,b), but transfer of these sources to megafauna and the associated seasonal patterns in food webs remain little known (Polunin et al., 2001; Stowasser et al., 2009).

The main objectives of this study were to:

i) describe the general structure and seasonal changes of the food-web of the middle slope and
ii) associate feeding trends and resource use within the megafaunal community to available food sources at bathyal depths.

We also discuss the extent to which stable isotopes yield inferences for the food-web structure similar to those based on gut-content data.

2. Materials and methods

2.1. Sampling of fauna

Benthopelagic megafauna were collected using bottom trawls on the continental slope of the Catalan Sea (Balearic Basin, NW Mediterranean) at depths ranging from 423 to 1175 m within the project BIOMARE. Five multidisciplinary surveys were performed seasonally between February 2007 and February 2008 (2007: February, April, June/July and October; 2008: February). Three stations in the fishing ground known as *Serola* were sampled seasonally along the *ca.* 650, 800 and 1000 m isobaths, except in April when no samples were collected from 1000 m. In addition, sampling was performed inside the Besòs submarine canyon, a site at *ca.* 600 m depth on the southern wall locally called *El Buscarró* ground, also on a seasonal basis. The mid-slope between 650 and 800 m is commonly exploited by red-shrimp trawlers, except for *El Buscarró* ground, which has not been fished since the 1990s. The part of the slope below 900 m is free of any trawling activity in the Balearic Basin (Cartes et al., 2004; Maynou, 2008). Details of the sampling campaigns can be found at Papiol et al., (2012).

Samples of three compartments of macrofauna were obtained simultaneously, also on a seasonal basis. Briefly, infauna were collected from the top 20 cm of sediment with a Box-Corer (box area = 0.065 m^2; 3–7 replicates at each station) and sieved through 0.5 mm filters; suprabenthos in the sediment-water interface (0–1.5 m above the sea bottom) were taken with a Macer-GIROQ suprabenthic sledge (hauling time *ca.* 10 min); and zooplankton in the water column near the seabed (*ca.* 10–50 m above the seabed) were taken with horizontal hauls of a WP2 net (Fraser, 1966) that was closed at depth with a CT1000 General Oceanics opening-closing system (hauling time *ca.* 10 min). Mesh size in both the sledge and the net was 0.5 mm.

2.2. Sampling of sediment

Samples of surface sediment (0–2 cm depth) for analysis of particulate organic matter (POM_{sed}) were collected with a multicorer from the 600 and 800 m stations throughout the sampling period to determine C and N contents and isotopic ratios. Sediment was immediately frozen at −20 °C for later analysis.

2.3. Faunal analyses

All benthopelagic megafauna collected were identified to species level, counted, measured and weighed, either on board or at the laboratory when further identification was necessary or when masses were not large enough for precise weighing. Specimens were immediately frozen at −20 °C for future isotopic analyses.

Macrofauna samples were immediately frozen at −20 °C and later sorted in the laboratory as quickly as possible, identified to species level and prepared for analyses.

2.4. Stable isotope analyses (SIA)

Megafauna species selected for isotopic analyses were those dominant in terms of both abundance and biomass in the area (Papiol et al., 2012; Table 1), and only fishes and decapods were considered for the present study, since they are the two dominant taxa in the deep Mediterranean (Cartes et al., 2004). White muscle tissue from fishes and caudal muscle from decapods (the muscle of chelae for crabs *Geryon longipes*, *Monodaeus couchii* and *Paromola cuvieri*) was obtained for the analyses. Representing macrofauna, caudal muscle of mysids and euphausiids was extracted. The whole body (except the shell) was used for the benthic bivalve *Abra longicallus*. For species from which muscle could not be removed from the exoskeleton, entire individuals were used (*e.g.* amphipods, cumaceans). In those cases, single individuals were used when mass was sufficient. Otherwise, several individuals uniform in sex and maturity were pooled to attain the minimum mass required.

Samples were dried to constant weight at 60 °C, then ground to fine powder. For carbon isotope analysis in species with carbonate structures (*e.g.* exoskeleton in gammariids), one sub-sample was acidified by adding 1 M HCl drop-by-drop to remove inorganic carbonates (the cessation of bubbling was used as a criterion to determine the amount of acid to add; Jacob et al., 2005), and then samples were dried again at 60 °C for 24 h. Carbonate removal is required because carbonates have a less negative $\delta^{13}C$ than organic carbon (De Niro and Epstein, 1978).

Lipid extraction prior to stable isotope analysis has been suggested by some authors because tissue rich in lipids is relatively depleted in $\delta^{13}C$ (Michener and Lajtha, 2007). We chose not to defat our samples based on the threshold C/N of 3.5 proposed by Post et al. (2007) for aquatic animal samples. Furthermore, defatting removes possible seasonal signals of phytodetritus inputs, considering its high lipid content (Fabiano et al., 1993, 2001). Since one of our objectives is to analyse seasonal trends in isotopic signals, we used non-defatted samples for direct comparison with the available literature (Cartes et al., 2007; Fanelli and Cartes, 2008, 2010; Polunin et al., 2001) and for investigation of natural signals of fresh food inputs. Nevertheless, since C/N is a relatively good surrogate for tissue lipid content (*i.e.* samples containing more lipids have higher C/N; Tieszen et al., 1983), C/N was measured simultaneously during stable isotope analysis, and $\delta^{13}C$ values were normalised for lipid concentration according to the equation of Post et al. (2007): $\delta^{13}C$ values of untreated samples (not defatted) were converted to $\delta^{13}C$ normalised ($\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99\ C/N$). Temporal trends of untreated and normalised $\delta^{13}C$ were then compared. Additionally, the relationship between C/N ratios and the $\delta^{13}C$ values was explored by means of ANCOVA analysis, with season as the covariate.

Biological samples were weighed (*ca.* 1 mg of dry weight) in tin cups. Sediments for $\delta^{13}C$ analyses (POM_{sed}) were initially weighed (*ca.* 5 mg) directly in silver capsules; the carbonate fraction was then removed by treatment with 1 M HCl followed by drying (60 °C until constant weight). $\delta^{15}N$ analyses of sediments were carried out directly on bulk-powdered samples of 15–20 mg placed into tin capsules.

Stable isotope measurements of biological and POM_{sed} samples were carried out by a ThermoFisher Flash EA 1112 elemental analyser coupled to a Thermo Electron Delta PlusXP isotope ratio mass spectrometer (IRMS) at the geochemistry laboratory of the IAMC-CNR Institute at Naples (Italy). Detailed procedure can be found in Fanelli et al., 2011a.

Experimental precision (based on the standard deviation of replicates of the internal standard) was 0.2‰ for $\delta^{15}N$ and 0.1‰ for $\delta^{13}C$. $\delta^{13}C$ and $\delta^{15}N$ values were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 standards, respectively, according to the following formula:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample}/R_{standard}\right) - 1\right], \text{ where } R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N$$

Table 1

Megafauna species analysed for stable isotopes of C and N and number of individuals analysed in each sampling period, size of the individuals, mean annual values of $\delta^{15}N$ and $\delta^{13}C$ ± standard deviations. Trophic guild attributed to each species is also specified: *B* = benthos feeders; *mM* = migratory macroplankton feeders; *nmM* = non-migratory macroplankton feeders. Size of Osteichthyes and Chondrichthyes expressed as total length except for Macrouridae, expressed as preanal length; size of Decapoda expressed as cephalothorax length. Feb = February 2007 and 2008; Apr = April 2007; Jun/Jul = June/July 2007; Oct = October 2007.

Class/Order	Family	Species	Code	Feb	Apr	Jun/Jul	Oct	Size (cm)	$\delta^{15}N$	$\delta^{13}C$	Trophic guild
Decapoda	Aristeidae	*Aristeus antennatus*	Aa	4	4	4	4	4.28 ± 0.21	9.50 ± 0.64	−15.70 ± 0.62	*B*
	Crangonidae	*Pontophylus norvegicus*	Pn	4	3	4	3	0.96 ± 0.09	8.99 ± 0.26	−14.87 ± 0.43	*B*
	Geryonidae	*Geryon longipes*	Gl	3	2	4		5.70 ± 0.37	9.13 ± 0.94	−15.59 ± 0.12	*B*
	Homolidae	*Paromola cuvieri*	Pc			4		8.92 ± 0.42	9.72 ± 0.60	−14.90 ± 0.15	*B*
	Nephropidae	*Nephrops norvegicus*	Nn	4	3	4	4	3.67 ± 0.41	7.43 ± 0.59	−16.85 ± 0.51	*B*
	Polychelidae	*Polycheles typhlops*	Pt	4	4	4	3	3.06 ± 0.21	8.73 ± 0.45	−15.75 ± 0.45	*B*
	Xanthidae	*Monodaeus couchii*	Mc			3		0.95 ± 0.06	7.57 ± 0.57	−15.58 ± 0.50	*B*
	Pasiphaeidae	*Pasiphaea multidentata*	Ps		3	3	3	3.06 ± 0.15	7.02 ± 0.82	−18.36 ± 0.62	*mM*
	Sergestidae	*Sergestes arcticus*	Sa	2		2	3	1.19 ± 0.17	6.72 ± 0.24	−18.94 ± 0.26	*mM*
		Sergia robusta	Sr	3	3	3	3	1.70 ± 0.18	6.36 ± 0.51	−18.18 ± 0.55	*mM*
	Galatheidae	*Munida tenuimana*	Mt	4	3	4	3	1.08 ± 0.02	7.42 ± 0.32	−14.98 ± 0.66	*nmM*
	Oplophoridae	*Acantephyra eximia*	Ae	3	4	4	4	2.76 ± 0.13	8.19 ± 0.51	−17.13 ± 0.75	*nmM*
	Pandalidae	*Plesionika acantonothus*	Pa		3		4	1.50 ± 0.05	7.02 ± 0.65	−16.59 ± 0.73	*nmM*
		Plesionika martia	Pm	4	3	5	4	2.13 ± 0.11	7.70 ± 0.55	−16.92 ± 0.48	*nmM*
Osteichthyes	Bythitidae	*Cataetyx alleni*	Ca			3		7.17 ± 0.15	7.84 ± 0.27	−16.32 ± 0.75	*B*
	Moridae	*Lepidion lepidion*	Ll	3	3	3	3	17.28 ± 2.03	9.98 ± 0.36	−17.05 ± 0.81	*B*
		Mora moro	Mm	2	1	4		32.37 ± 3.20	10.10 ± 0.55	−17.74 ± 0.33	*B*
	Scorpaenidae	*Helicolenus dactylopterus*	Hd	3	3	4	3	24.81 ± 0.68	9.57 ± 0.37	−17.55 ± 0.38	*B*
	Chauliodontidae	*Chauliodus sloani*	Cs		3	2		23.47 ± 1.42	9.00 ± 0.84	−18.82 ± 0.32	*mM*
	Myctophidae	*Lampanyctus crocodilus*	Lc	4	3	4	3	14.69 ± 0.85	7.27 ± 0.74	−16.87 ± 1.10	*mM*
	Paralepididae	*Arctozenus risso*	Ar				3	7.00 ± 0.71	7.89 ± 0.39	−19.15 ± 0.69	*mM*
	Stomiidae	*Stomias boa*	Sb		3	4		14.96 ± 4.48	9.18 ± 0.71	−18.58 ± 0.31	*mM*
	Alepocephalidae	*Alepocephalus rostratus*	Al	2		3	3	33.67 ± 4.80	10.19 ± 0.47	−17.96 ± 0.68	*nmM*
	Gadidae	*Micromesistius poutassou*	Mp	3	4	4	3	26.56 ± 1.35	10.00 ± 0.63	−17.85 ± 1.06	*nmM*
		Phycis blennoides	Pb	4	3	5	4	26.44 ± 1.01	10.24 ± 0.48	−16.65 ± 0.43	*B*
		Phycis blennoides(juveniles)	Pj	3	3	3	3	18.65 ± 1.43	9.80 ± 0.88	−18.53 ± 1.09	*B*
	Macrouridae	*Hymenocephalus italicus*	Hi	3	3	3	3	4.05 ± 0.09	8.26 ± 0.33	−15.03 ± 0.45	*nmM*
		Nezumia aequalis	Na	2	2	2	2	3.81 ± 0.45	11.31 ± 0.27	−17.08 ± 0.75	*B*
		Trachyrhynchus scabrus	Ts	3	3	4	4	13.13 ± 0.78	10.15 ± 0.76	−16.90 ± 0.46	*B*
		Trachyrhynchus scabrus (juveniles)	Tj	3	3	4	3	7.41 ± 0.49	9.95 ± 0.68	−16.99 ± 0.39	*B*
Chondrichthyes	Scyliorhinidae	*Galeus melastomus*	Gm	4	3	4	5	51.30 ± 1.47	9.33 ± 0.41	−17.04 ± 0.37	*nmM*
		Galeus melastomus (juveniles)	Gj	3	3	5		24.72 ± 1.45	8.28 ± 0.71	−16.29 ± 0.53	*nmM*

A minimum of three replicates were analysed for each of the taxa per survey (Table 1), replicates consisting of animals of similar size. Also, POM_{sed} samples were analysed in triplicate.

Total organic carbon (TOC) and total nitrogen (TN) of sediments were determined from the CO_2 and N produced by combustion using the Thermo Electron Flash EA 1112 elemental analyser.

2.5. Lipid analyses

A modified Bligh and Dyer method (Alfaro et al., 2006; Bligh and Dyer, 1959) was used for lipid extractions from sediments. About 2 g wet weight sediment were used for each extraction, including three replicates for each sample at each collection station. Tricosanoic acid was added to each sample as an internal standard (1 ml of 22 mM solution in hexane). Samples were extracted ultrasonically for 20 min with a one phase methanol:chloroform solvent mixture (2:1, 15 ml, v/v). A bilayer mixture was formed by adding equal volumes (5 ml) of chloroform and 1 M NaCl. Lipids were transferred into the lower chloroform phase under centrifugation (5 min at 2000 rpm). The separated chloroform layer was dried under a nitrogen stream to obtain the total lipid extract, which was weighed. Lipid amounts are reported as percentage of sediment dry weight.

2.6. Pigment analyses

Phytoplankton pigments in sediments were analysed as indicators of OM from surface production (SP) in the area. Reverse-phase high-pressure liquid chromatography (HPLC) analysis was used to determine phytopigments in sediments at the two depths sampled in each sampling period. Three replicates of each sample were analysed, each consisting of 1 g of sediment (wet weight). All samples were processed according to Witbaard et al. (2000): extraction in 3 ml 100% methanol by mechanical grinding, filtration through Whatman GF/F filters and injection of 0.2 ml of the pigment extract into a Hewlett Packard series 1100 HPLC with a CBDS 3 mm Hypersil, IP column (Thermo Electron). The following HPLC protocol is detailed in Brunet et al. (2006). The mobile phase was composed of two solvent mixtures: methanol:aqueous ammonium acetate (70:30) and methanol. Pigments were detected spectrophotometrically at 440 nm using a Hewlett Packard photodiode array detector model DAD series 1100. Fluorescent pigments were detected in a Hewlett Packard standard series 1100 FLD cell with excitation and emission wavelengths set at 407 and 665 nm, respectively. Determination and quantification of pigments were based on pigment standards from the D.H.I. Water & Environment Group (Denmark).

2.7. Environmental variables

Casts were performed at each station with an SBE 32 CTD coupled with a fluorometer, at the same locations where biological and POM_{sed} samples were collected. Values of fluorescence were recorded for each CTD profile at 5 m above the sea bottom (5 mab).

2.8. Data analyses

Factorial ANOVA with a crossed design considering sampling sites and surveys was used to test spatial and temporal differences amongst environmental variables and sediment organics.

Isotope data were normally distributed, thus they were not transformed for univariate and multivariate analyses.

Megafauna species were classified into *a priori* trophic groups bearing in mind trophic guilds from extensive studies based on gut content analyses (Carrassón and Matallanas, 1989; Carrassón et al., 1992, 1997; Cartes, 1994, 1998a; Cartes and Abelló, 1992; Cartes et al., 2002a; Macpherson, 1978, 1979; Stefanescu and Cartes, 1992). Groups established were: i) decapods and fishes and ii) feeders on zooplankton and benthos (including suprabenthos) (*B*). Zooplankton feeders were further separated into migratory (*mM*) and non-migratory species (*nmM*). The trophic group attributed to each species are listed in Table 1. For macrofauna, species grouped by trophic guild and faunal compartment (infauna, zooplankton and suprabenthos) were used (Appendix A). *Calocaris macandreae* was considered as macrofauna, given the great importance it has in the diets of megafauna (Cartes, 1994; Cartes and Carrassón, 2004). It is the only detritivorous decapod crustacean included in the present study (Fanelli et al., 2011a). *Abra longicallus* was also considered as infaunal prey for megafaunal groups, representing the trophic guild of active suspension feeders (ASF) (Fanelli et al., 2011a).

Mean annual values of δ^{15}N and δ^{13}C (and standard deviations) were calculated in order to compare megafauna species or macrofauna groups.

First, to identify trophic groups of megafaunal species, a hierarchical cluster analysis (Euclidean distance, average grouping methods) was performed on δ^{15}N and δ^{13}C mean annual values of megafaunal fishes and decapods. To illustrate observed similarities or dissimilarities (distances) between the groups resulting from the cluster analyses, multidimensional scaling (MDS) analysis was carried out on the same isotopic data. Permutational Multivariate ANOVA (PERMANOVA; Anderson et al., 2008) was applied to the same data matrix to test the significance of differences amongst feeding groups established *a priori*, with Monte Carlo sampling (Anderson and Robinson, 2003) employed to increase the number of permutations. Second, a δ^{15}N–δ^{13}C plot was made for δ^{15}N and δ^{13}C mean annual values of the megafauna species, the macrofaunal groups and POM$_{sed}$ to give an overview of the trophic structure of the ecosystem.

Further analyses were performed on seasonal data, looking for seasonal trends in community structure of secondary consumers (fishes and decapods). For this purpose, we only considered species from the slope for which data from at least three surveys were available. A total of 8 decapod species and 9 fish species were studied seasonally (Table 3). Temporal analyses were performed separately for each of the feeding groups of fishes and decapods established *a priori*. Temporal trends in macrofaunal groups were also described, only including the species present in all 4 surveys (Appendix A). Since no significant differences in isotopic values were detected between samples collected in February 2007 and those from February 2008, the isotopic signatures of specimens from the two years (2007 and 2008) were merged and indicated as February. Temporal changes in δ^{15}N and δ^{13}C isotopic signatures of the different groups of fishes, decapods and macrofauna were explored by means of PERMANOVA. Temporal differences were tested for each element between consecutive seasons.

Correlations were used to assess the strength of association between δ^{15}N and δ^{13}C data across all megafauna and macrofauna (see Fanelli et al., 2011a, b; Polunin et al., 2001) as a function of season.

Stable carbon isotope signatures recorded at each station/sampling period were compared with *in situ* fluorescence and sediment organics using non-parametric multivariate multiple regression analyses, which were based on Euclidean distances. These analyses were carried out using the routine DISTLM with forward procedure in PERMANOVA + (Anderson et al., 2008) and model selection was based on minimising Akaike's Information Criterion (AIC). Variables used were fluorescence$_{5mab}$, δ^{13}C signature of POM$_{sed}$, and TOC%, C/N and total lipids in sediments. We also used the sum of chlorophylls and their degradation pigments (*i.e.* phaeophytins and phaeophorbids) as general indicators of phytodetritus amount, and fucoxanthin as an indicator of diatoms (Vidussi et al., 2000 and references therein). Before the analyses, a draftsman plot (*i.e.* scatter plots of all pairwise combinations of variables) (Clarke and Warwick, 1995) was applied to fluorescence and sediment organics to identify whether any were strongly correlated and thus provided redundant information. Redundant variables ($\rho > 0.70$) were discarded, simplifying the matrix.

All statistical analyses were performed using PRIMER6 and PERMANOVA + (Anderson et al., 2008; Clarke and Warwick, 1995) and STATISTICA 6 softwares.

3. Results

3.1. Organic matter sources

3.1.1. Isotopic and elemental composition of sedimentary organic matter (POMsed)

Seasonal values of δ^{15}N and δ^{13}C of POM$_{sed}$ are detailed in Fanelli et al. (2011a). In short, δ^{15}N values of POM$_{sed}$ varied from 2.52‰ to 3.47‰ at 650 m and from 2.29‰ to 3.70‰ at 800 m. No significant seasonal changes ($p > 0.05$) were detected at 650 m. At 800 m, δ^{15}N values of POM$_{sed}$ were significantly depleted ($p < 0.05$) in April relative to the rest of samplings. δ^{13}C of POM$_{sed}$ were between −22.21‰ to −23.74‰ at 650 m and −22.27‰ to −22.66‰ at 800 m, being significantly depleted ($p < 0.01$) during June–July at both depths (Fig. 1a).

TOC% values in sediments can be found in Papiol et al. (2012). Briefly, TOC% in sediments at 600 m was highest in February and lowest in June, increasing afterwards. An inverse trend was found at 800 m (Fig. 1b).

TN% followed the same temporal trends as TOC% at both sites (Fig. 1c). C/N of sediment was close to constant around 5 throughout the year at both stations, except for the sampling in June/July at 600 m, when values were nearly 10 (data not shown as a figure).

3.1.2. Total lipids

Total lipid content followed temporal trends similar to those of TOC and TN. Minimum lipids were observed at 600 m in June/July, when maximum lipids were observed at 800 m (Fig. 2a). No significant differences were observed between consecutive seasons or between stations ($p > 0.05$).

3.1.3. Pigment analyses

Chlorophyll and phaeopigment (pheophytins and pheophorbides) concentration in sediments ranged between 0.016 μg g^{-1} in April at 600 m and 0.005 μg g^{-1} in the same month at 800 m. Although temporal changes were never significant ($p > 0.05$), at 600 m concentration of chlorophylls and degradation products were lowest in February and greater during the rest of the year, with maxima in April and October. At 800 m, minimum concentration was in April, and it increased afterwards (Fig. 2b).

Fucoxanthin concentration in sediments was slightly greater at 600 m compared to 800 m, except in February. Seasonally, fucoxanthin concentration changed significantly from February to April at 800 m ($t = 4.04$; $p < 0.05$), when a minimum was observed, and from April to June/July ($t = 3.30$; $p < 0.05$) (not displayed in the figure).

3.1.4. Fluorescence 5 m above the sea bottom

Values and seasonal trends in fluorescence measured 5 m above the sea bed (Chla$_{5mab}$) were similar at the two depths sampled. Maximum fluorescence was observed in February (Fig. 2c) relative to the low values of both April and June/July.

3.2. Characterisation of functional feeding groups

Temporal trends in δ^{13}C$_{untreated}$ and δ^{13}C$_{normalised}$ by species were parallel. Also, ANCOVA model between C/N ratios and the δ^{13}C values, with season as the covariate was not significant ($p > 0.05$). Hence, we have analysed the δ^{13}C$_{untreated}$ data.

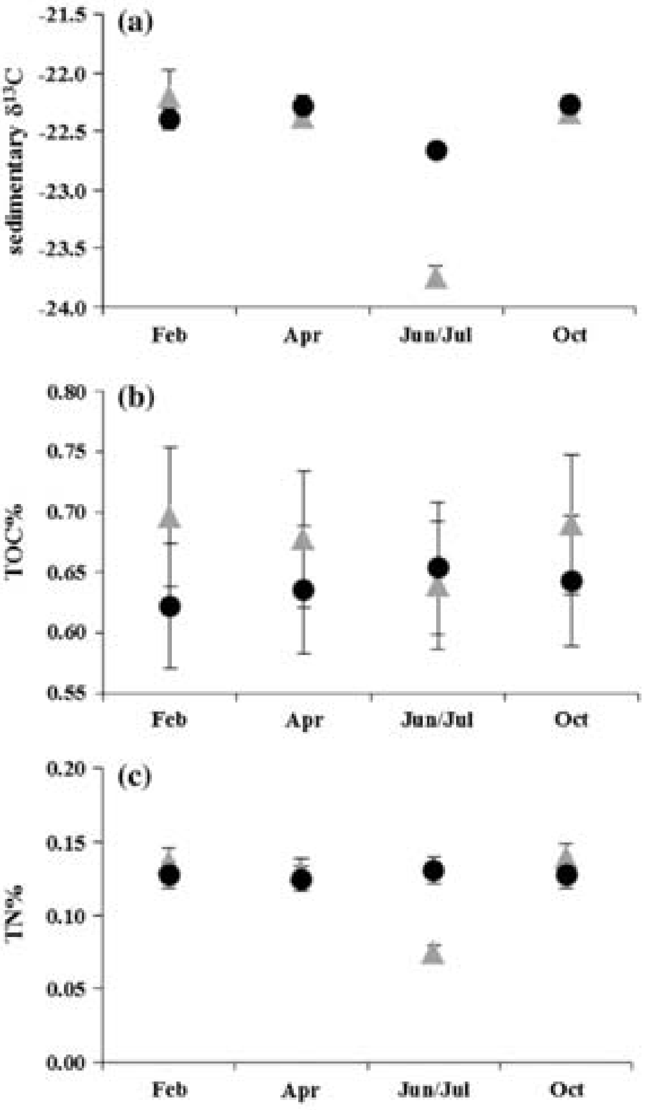

Fig. 1. Temporal variations in (a) $\delta^{13}C$ of sedimentary organic matter (POM_{sed}), (b) total organic carbon (TOC%) and (c) total nitrogen (TN%)in sediments for stations at two depths over the Catalan slope: grey triangles indicate samples collected at 600 m, and black circles samples at 800 m. Vertical bars represent standard deviations.

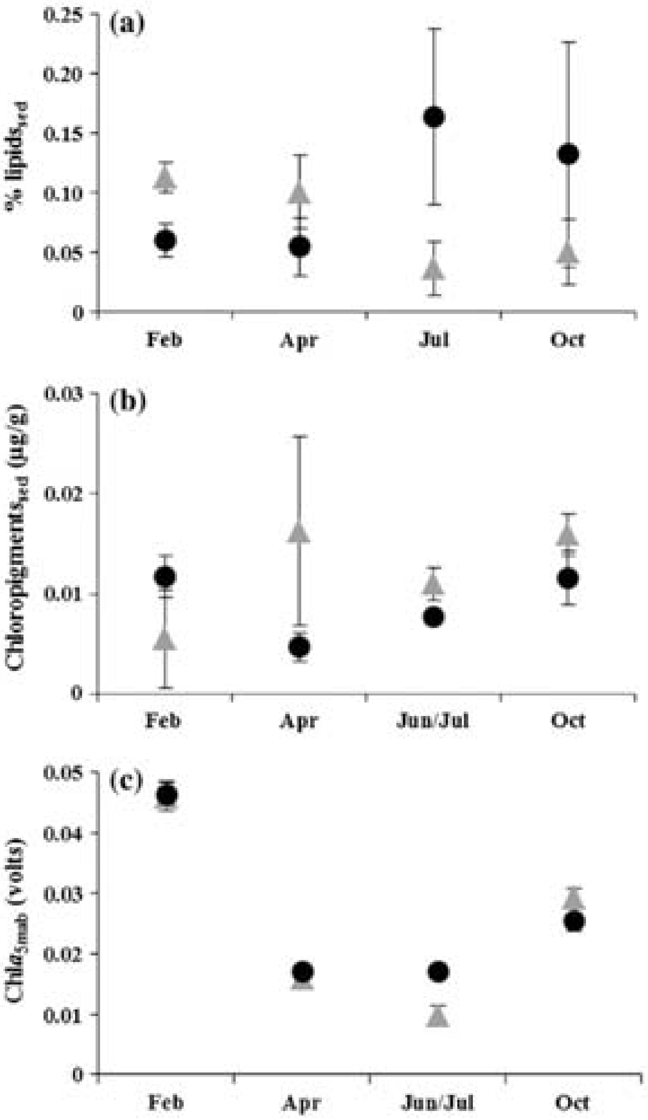

Fig. 2. Temporal variations in (a) total lipids and (b) chloropigments (*i.e.* chloropgylls, phaeophytins and phaeophorbids) in sediments (sed), and (c) fluorescence measured 5 m above the sea bottom ($Chla_{5mab}$) at two depths over the Catalan slope: grey triangles indicate samples collected at 600 m, black circles samples at 800 m. Vertical bars represent standard deviations.

Mean annual values of $\delta^{15}N$ and $\delta^{13}C$ signatures are detailed in Table 1.

The MDS analysis performed on $\delta^{15}N$ and $\delta^{13}C$ data showed that trophic preference toward benthic or pelagic prey was the main factor structuring assemblages (Fig. 3). Combining the results of cluster analysis with the MDS ordination, we observed that grouping of the species of both decapods and fishes coincided in general with the feeding groups established *a priori*, and a PERMANOVA test performed on these feeding guilds showed that their isotopic $\delta^{15}N$ and $\delta^{13}C$ composition differed significantly (*pseudo*-$F_{5,31} = 8.43$; Monte Carlo $p < 0.001$), except for non-migratory macroplankton feeders (*nmM*) and the benthic feeder (*B*) fishes, and for the migratory macroplankton-feeding (*mM*) decapods and fishes.

For decapods, three groups were obtained. Out of the 14 decapod species analysed, only two of them were clustered in a group different from that established *a priori*: the Norway lobster *Nephrops norvegicus*, *a priori* classified as *B*, was grouped with the *nmM* decapods; an opposite shift was observed for the galatheid *Munida tenuimana*.

Fishes were also grouped according to their feeding guild, and two groups were obtained (Fig. 3). The *mM* fishes made up one group, the *nmM* and *B* species the other. Although included in the same group, a gradual segregation was observed amongst *nmM* and *B* species. Out of the fifteen fish species analysed (three of them divisible into two size classes) only four (*i.e.* the *Hymenocephalus italicus* and the juveniles of *Galeus melastomus* classified as *nmM*, the *mM* feeder *Lampanyctus crocodilus*, and the *B Cataetyx alleni*) were clustered with decapod crustaceans.

3.3. General food web structure

3.3.1. Megafauna

The main segregation of species in respect to stable isotope signatures was between the two taxa under study, fishes and decapods ($p < 0.001$) (Fig. 4). In general, even for species in the same trophic guilds, decapods had more depleted $\delta^{15}N$ and more enriched $\delta^{13}C$ than fishes (Table 1; Fig. 4).

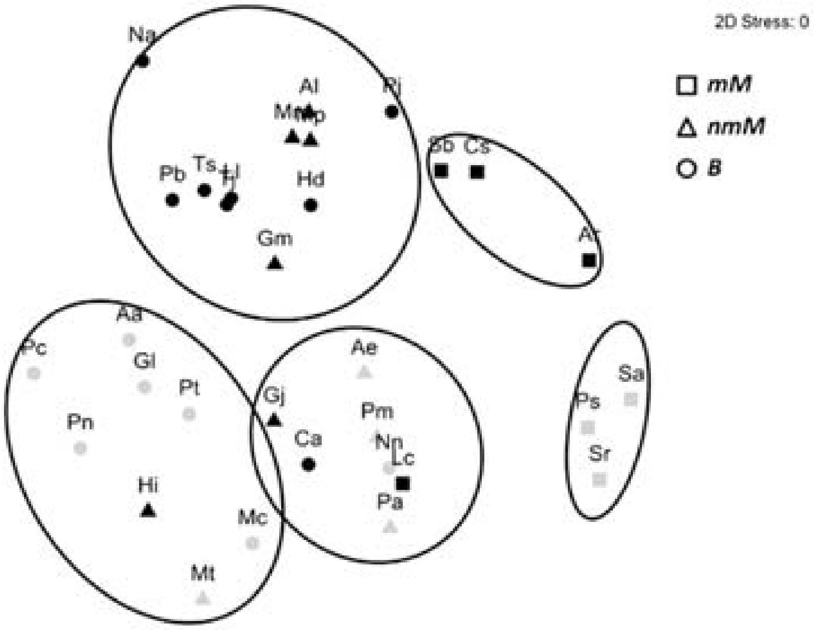

Fig. 3. MDS ordination plot of mean annual values of $\delta^{15}N$ and $\delta^{13}C$ for 14 decapod species and 15 fish species (3 of the fish are represented by two size classes) based on Euclidean distance. Overlaid ovals define clusters at Euclidean distance of 1.6. Data points are identified by feeding mode: *mM* = migratory macroplankton feeders; *nmM* = non-migratory macroplankton feeders; *B* = benthos feeders. Black symbols are fishes, grey symbols are decapods. For species codes see Table 1.

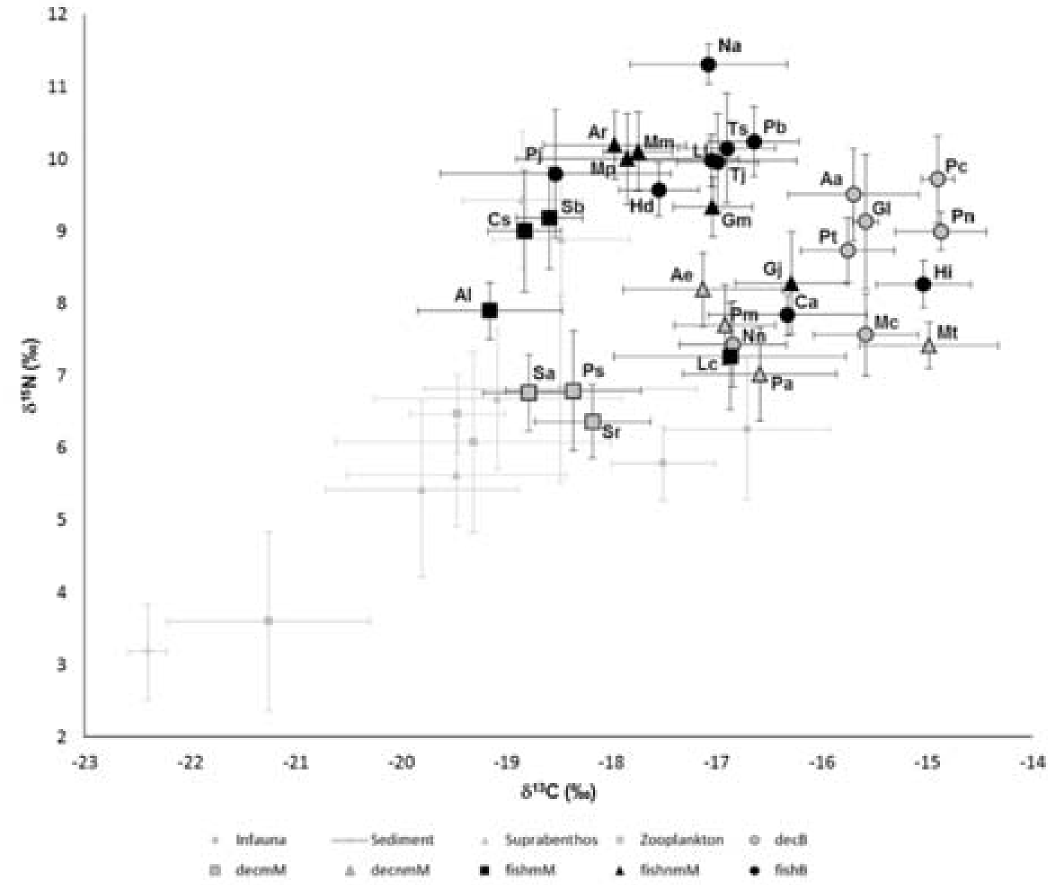

Fig. 4. Scatterplot of annual mean $\delta^{15}N$ (‰) versus $\delta^{13}C$ (‰) values of each species analysed, feeding guilds of fishes (black) and decapods (grey) are designated by distinct symbols. Vertical and horizontal bars are Standard deviations. Species codes as in Table 1. Dec = decapods; mM = migratory macroplankton feeders; nmM = non-migratory macroplankton feeders; *B* = benthos feeders.

mM decapods had the most depleted $\delta^{15}N$ signatures amongst all secondary consumers, particularly the sergestid *Sergia robusta* with the most depleted $\delta^{15}N$ (6.36‰) amongst all megafauna (Table 1; Fig. 4). The other sergestid included in the present study, *Sergestes arcticus*, had the most depleted $\delta^{13}C$ (−18.94‰) amongst all decapods. *nmM* had intermediate values of both stable isotopes, and *B* had the most enriched. Maximum $\delta^{15}N$ amongst decapods was 9.72‰ in the brachyuran crab *Paromola cuvieri*, and maximum $\delta^{13}C$ was −14.87‰ in *Pontophylus norvegicus*, the most enriched $\delta^{13}C$ amongst all megafauna.

As for decapods, the *mM* fishes had depleted $\delta^{15}N$ and $\delta^{13}C$, with the most depleted signatures of $\delta^{13}C$ amongst all megafauna in *Arctozenus risso* (−19.15‰), and of $\delta^{15}N$ amongst all fishes in *Lampanyctus crocodilus* (7.27 ‰). Species belonging to the *nmM* and *B* groups had similar $\delta^{15}N$ (group means were 9.84 ± 0.45‰ and 9.88 ± 0.91‰ respectively), and mainly differed in their $\delta^{13}C$ signatures, which were in general more enriched in *B*. The most enriched $\delta^{13}C$ amongst *B* was in adults of *Phycis blennoides* (−16.65‰), and most enriched $\delta^{15}N$ of fishes was in *Nezumia aequalis* (11.31‰), which also had the most enriched $\delta^{15}N$ of all megafauna. The species of fishes that were grouped with decapods by the MDS (Fig. 3) had the combination of depleted $\delta^{15}N$ and enriched $\delta^{13}C$ usually observed in decapods in general (Table 1; Fig. 4). Accordingly, most depleted $\delta^{15}N$ and most enriched $\delta^{13}C$ amongst fishes were for two of these species: $\delta^{15}N$ of 7.27‰ in the myctophid *L. crocodilus* and $\delta^{13}C$ of −15.03‰ in the macrourid *H. italicus*.

3.3.2. Macrofauna

In general, the most depleted isotopic ratios were for zooplankton groups (Table 2; Fig. 4): most depleted $\delta^{15}N$ and $\delta^{13}C$ amongst all macrofauna were observed for zooplankton feeding on POM (3.60‰ and −21.25‰ respectively).

Isotopic signatures for macroinfauna were obtained from Fanelli et al. (2011a), and were most enriched amongst all macrofauna for both isotopes analysed (Table 2; Fig. 4).

Suprabenthos generally had isotopic signatures between those of zooplankton and macroinfauna, with ratios more depleted for primary consumers, *i.e.* surface deposit feeders (SDF) ($\delta^{15}N = 5.43‰$ and $\delta^{13}C = -19.80‰$) and omnivores ($\delta^{15}N = 5.62‰$ and $\delta^{13}C = -19.47‰$), than for scavengers ($\delta^{15}N = 8.89‰$ and $\delta^{13}C = -18.47‰$) and parasites ($\delta^{15}N = 9.42‰$ and $\delta^{13}C = -18.84‰$). Suprabenthic parasites presented the most enriched $\delta^{15}N$ amongst all macrofauna.

3.4. Seasonal changes in food web structure

A list of the species and macrofauna groups used in the temporal analyses, as well as mean seasonal values of $\delta^{15}N$ and $\delta^{13}C$ of each species and macrofauna group, can be found in Table 3.

3.4.1. Megafauna

For decapods, main PERMANOVA tests performed on seasonal $\delta^{13}C$ signatures for each of the three trophic guilds were significant for *B* (*pseudo*-$F_{3,49} = 7.51$; $p < 0.001$) and *mM* (*pseudo*-$F_{3,18} = 3.57$; $p < 0.05$). Pairwise comparisons revealed significant differences in $\delta^{13}C$ signatures of *B* between February and April ($t = 3.51$; $p < 0.01$), and between October and February ($t = 3.38$; $p < 0.01$). In general, $\delta^{13}C$ of benthic feeders was enriched in February, compared to other sampling periods (Table 3; Fig. 5). $\delta^{13}C$ of the *mM* group was almost significantly different in April and June/July ($t = 2.52$; $p = 0.051$) and in October and February ($t = 2.24$; $p = 0.050$). In this group, $\delta^{13}C$ was enriched in periods of water column homogeneity (February and April) (Table 3; Fig. 5) and depleted during stratification (June/July and October). PERMANOVA on $\delta^{13}C$ of *nmM* decapods revealed no significant changes during the whole period ($p > 0.05$). The main PERMANOVA test on $\delta^{15}N$ was only significant for *mM* group (*pseudo*-$F_{3,19} = 4.22$; $p < 0.05$), and a pairwise test revealed changes between April and June/July ($t = 3.91$; $p < 0.01$), values being depleted in the latter. Additionally, $\delta^{15}N$ of *B* was different in October from February ($t = 2.36$; $p < 0.05$), with more enriched values observed in October (Fig. 5). Isotopic signatures of *nmM* did not vary during the sampling period ($p > 0.05$).

Table 2
Mean annual values of $\delta^{15}N$ and $\delta^{13}C$ of the different trophic groups of macrofauna and of sedimentary organic matter (POM_{sed}) ± standard deviations. Trophic groups established for each macrofaunal compartment are also specified: CZ = carnivores on zooplankton; Omn = omnivores; P = parasites; Scav = scavengers; ScavMix = scavengers combining carnivorous behaviour; SDF = surface deposit feeders; POM = feeders on particulate organic matter; SSDF = sub-surface deposit feeders; ASF = active suspension feeders.

Macrofauna	$\delta^{15}N$	$\delta^{13}C$
Suprabenthos		
CZ*	6.68 ± 0.97	−19.08 ± 1.17
Omn*	5.62 ± 0.70	−19.47 ± 1.04
P	9.42 ± 0.95	−18.84 ± 0.57
Scav	8.89 ± 0.89	−18.47 ± 0.65
ScavMix*	6.82 ± 1.30	−18.48 ± 1.29
SDF*	5.43 ± 1.22	−19.80 ± 0.91
Zooplankton		
CZ*	6.08 ± 1.24	−19.31 ± 1.31
Omn*	6.45 ± 0.45	−19.46 ± 0.45
POM*	3.60 ± 1.24	−21.25 ± 0.96
Infauna		
SSDF*a	9.57 ± 0.15	−14.51 ± 0.31
SDF*a	5.78 ± 0.51	−17.50 ± 0.49
ASF*a	6.26 ± 0.98	−16.71 ± 0.78
Primary food sources	$\delta^{15}N$	$\delta^{13}C$
POM_{sed}*a	3.17 ± 0.67	−22.40 ± 0.18

* Seasonal samples available.
[a] From Fanelli et al., 2011a.

Only *mM* fishes had significant seasonal variation in $\delta^{13}C$ signatures according to a PERMANOVA main test (*pseudo*-$F_{3,15} = 73.56$; $p < 0.001$). In this group, $\delta^{13}C$ signatures changed amongst all sampling periods, with most enriched $\delta^{13}C$ in June/July and most depleted $\delta^{13}C$ in October (Fig. 5). However, $\delta^{13}C$ was significantly enriched in October samples of *B* group compared with June/July ($t = 2.12$; $p < 0.05$). As for *nmM* decapods, PERMANOVA revealed no significant changes in the $\delta^{13}C$ of *nmM* fishes throughout the year ($p > 0.05$). For $\delta^{15}N$, the overall PERMANOVA was not significant for any of the feeding groups. Pairwise comparisons revealed a change in $\delta^{15}N$ of *B*, again between June/July and October ($t = 2.51$; $p < 0.05$), this being enriched in the latter.

3.4.2. Macrofauna

Amongst zooplankton, significant seasonal changes were only observed amongst the group feeding on POM, which had significantly depleted $\delta^{13}C$ in February compared to other periods (Table 3). A common pattern of most enriched $\delta^{15}N$ in June/July was observed in all feeding groups, although it was significant only for omnivores.

Amongst infauna, $\delta^{13}C$ was significantly enriched in February in the ASF *A. longicallus* (Table 3). For the SDF species *C. macandreae*, $\delta^{13}C$ underwent significant depletion from April to June/July, when it was minimal. $\delta^{15}N$ values of *A. longicallus* were maintained throughout the whole period, whereas they differed amongst all seasons in *C. macandreae*, which had enriched $\delta^{15}N$ in February and June/July and depleted $\delta^{15}N$ in April and October.

In suprabenthos, a generalised enrichment was observed in $\delta^{13}C$ from February to April (Table 3), which was most accentuated in omnivores and carnivores on zooplankton. After April, the enrichment in $\delta^{13}C$ of omnivores continued, although not significantly, to June/July, and then abruptly decreased to most depleted values. In the rest of the groups $\delta^{13}C$ suffered depletion from April to June/July, then maintained to October. In contrast to $\delta^{13}C$, $\delta^{15}N$ varied significantly in all groups. All groups presented parallel temporal trends of $\delta^{15}N$ enrichment from February to April and June/July and then enriched

Table 3

Mean seasonal values of δ^{15}N and δ^{13}C of megafauna species and macrofauna groups ± standard deviations. For codes of megafauna species and macrofauna groups see Tables 1 and 2.

	δ^{15}N				δ^{13}C			
	February	April	June/July	October	February	April	June/July	October
Decapods								
Benthic feeders (*B*)								
A. antennatus	8.60 ± 0.76	9.44 ± 0.34	9.63 ± 0.58	10.25 ± 0.23	−14.73 ± 0.27	−15.89 ± 0.49	−15.64 ± 0.36	−16.21 ± 0.42
P. norvegicus	9.02 ± 0.29	8.93 ± 0.12	8.69 ± 0.25	9.13 ± 0.28	−14.58 ± 0.48	−14.98 ± 0.19	−15.66 ± 0.48	−15.01 ± 0.22
P. typhlops	8.50 ± 0.11	8.31 ± 0.12	8.98 ± 0.41	8.87 ± 0.51	−15.52 ± 0.28	−16.27 ± 0.19	−15.52 ± 0.59	−15.78 ± 0.36
Non-migrator macroplankton feeders (*nmM*)								
A. eximia	8.47 ± 0.45	7.93 ± 0.30	7.94 ± 0.59	8.35 ± 0.50	−16.21 ± 0.15	−18.09 ± 0.11	−17.20 ± 0.55	−17.25 ± 0.68
M. tenuimana	7.53 ± 0.33	7.32 ± 0.24	7.53 ± 0.48	7.29 ± 0.28	−15.89 ± 0.05	−15.06 ± 0.67	−14.36 ± 0.23	−14.83 ± 0.14
P. martia	7.61 ± 0.43	7.35 ± 0.60	7.89 ± 0.64	7.89 ± 0.51	−16.91 ± 0.46	−16.87 ± 0.37	−16.93 ± 0.72	−16.98 ± 0.04
Migrator macroplankton feeders (*mM*)								
S. arcticus	7.19 ± 0.50		6.53 ± 0.40	6.45 ± 0.47	−18.52 ± 0.48		−19.22	−18.90 ± 0.35
S. robusta	6.03 ± 0.06	7.45 ± 0.25	6.38 ± 0.47	6.04 ± 0.11	−17.49 ± 0.24	−17.93 ± 0.59	−18.64 ± 0.14	−18.46 ± 0.08
Fishes								
Benthic feeders (*B*)								
H. dactylopterus	9.35 ± 0.00	9.60 ± 0.23	9.73 ± 0.26	9.63 ± 0.50	−17.86 ± 0.04	−17.53 ± 0.23	−17.66 ± 0.64	−17.25 ± 0.13
L. lepidion	10.06 ± 0.12	10.22 ± 0.23	9.74 ± 0.27	10.18 ± 0.36	−16.57 ± 0.20	−16.82 ± 0.33	−18.02 ± 0.24	−15.89 ± 0.81
N. aequalis	11.50 ± 0.37	10.40 ± 0.27	11.30 ± 0.26	11.32 ± 0.34	−15.96 ± 0.62	−17.58 ± 0.75	−16.81 ± 0.92	−17.34 ± 0.57
P. blennoides	10.23 ± 0.52	10.32 ± 0.41	9.77 ± 0.47	10.52 ± 0.36	−16.17 ± 0.26	−16.92 ± 0.35	−16.85 ± 0.39	−16.42 ± 0.33
T. scabrus	9.77 ± 0.55	9.65 ± 0.57	9.65 ± 0.50	10.71 ± 0.60	−16.96 ± 0.44	−16.77 ± 0.07	−17.24 ± 0.22	−16.89 ± 0.75
Non-migratory macroplankton feeders (*nmM*)								
G. melastomus	9.23 ± 0.05	9.35 ± 0.58	9.18 ± 0.31	9.53 ± 0.40	−16.79 ± 0.27	−16.88 ± 0.29	−17.61 ± 0.11	−16.93 ± 0.37
H. italicus	8.28 ± 0.32	8.16 ± 0.30	8.71 ± 0.13	8.08 ± 0.24	−14.97 ± 0.35	−15.63 ± 0.27	−14.81 ± 0.20	−14.71 ± 0.31
M. poutassou	10.65 ± 0.15	9.64 ± 0.60	9.70 ± 0.64	9.88 ± 0.10	−16.81 ± 0.47	−17.77 ± 0.15	−18.96 ± 0.71	−18.92 ± 0.41
Migratory macroplankton feeders (*mM*)								
L. crocodilus	8.23 ± 0.89	7.12 ± 0.09	6.79 ± 0.37	7.00 ± 0.04	−17.22 ± 0.07	−16.43 ± 0.10	−15.86 ± 0.28	−18.47 ± 0.42
Macrofauna								
Infauna								
ASF	6.73 ± 0.41	6.58 ± 0.74	6.54 ± 0.25	6.87 ± 0.22	−16.78 ± 0.25	−16.04 ± 0.15	−16.59 ± 0.36	−16.79 ± 0.08
SDF	6.05 ± 0.29	5.50 ± 0.08	6.30 ± 0.38	5.33 ± 0.51	−17.18 ± 0.62	−17.35 ± 0.11	−17.99 ± 0.10	−17.38 ± 0.68
Suprabenthos								
CZ	6.27 ± 0.74	8.17 ± 0.43	6.95 ± 0.43	6.44 ± 0.36	−19.43 ± 0.46	−18.04 ± 0.05	−18.73 ± 0.38	−19.07 ± 1.08
Omn	5.21 ± 0.22	6.62 ± 0.33	4.96 ± 0.45	6.01 ± 0.19	−20.23 ± 0.20	−18.51 ± 0.37	−18.08 ± 0.40	−20.28 ± 0.04
ScavMix	6.75	6.72 ± 0.51	6.55 ± 0.63	9.63 ± 0.19	−19.43 ± 0.39	−19.08 ± 1.34	−19.56 ± 0.95	−18.70
SDF	5.41 ± 0.81	7.13 ± 0.85	5.73 ± 0.97	6.54 ± 0.99	−19.52 ± 0.18	−19.35 ± 0.78	−20.59 ± 0.76	−19.95 ± 0.22
Zooplankton								
CZ	5.70 ± 1.51	5.55 ± 1.02	6.30 ± 1.16	6.16 ± 1.15	−19.81 ± 1.14	−19.32 ± 0.89	−19.53 ± 1.01	−19.34 ± 0.75
Omn	6.54 ± 0.57	6.13	6.97 ± 0.47	6.21 ± 0.61	−19.31 ± 0.75	−19.31	−19.45 ± 0.18	−19.81 ± 0.22
POM	2.79 ± 0.81	2.26 ± 0.52	2.69 ± 0.10	2.12 ± 0.32	−22.00 ± 0.19	−21.15 ± 0.52	−21.39 ± 0.18	−21.08 ± 0.29

δ^{15}N maintained to October. An exception was the mixed scavenger group, for which δ^{15}N maintained around 6.75‰ from February to June/July and enriched to 9.63‰ in October. Temporal oscillations within feeding groups were greater for suprabenthos than for the other macrofaunal compartments.

3.4.3. Seasonal trends in δ^{15}N–δ^{13}C correlations

Correlations between δ^{15}N and δ^{13}C followed similar temporal trends in the same trophic guilds of fishes and decapods (Fig. 6), and were higher for benthic feeders of both taxa compared to the rest of feeding groups. The maximal correlations of the year were observed in winter for all groups. Correlations decreased slightly in all groups from February to April, and all continued to decrease to June/July, except for a small increase in *B* decapods. After June/July, correlations declined to a yearly minimum in October; those declines were of different magnitude for each trophic guild.

3.5. Correlation of δ^{13}C signatures of megafauna with environmental variables and sediment organics

For decapods, DistLM performed on δ^{13}C of *B* explained 37% of total variance, with variables selected including TOC% and Chla_{5mah} (Table 4). No significant model was found for *nmM* decapods. For *mM* decapod crustaceans, 47% of total variance was explained by lipids in the sediment.

Regarding fishes of group *B*, TOC% and Chla_{5mah} were again explanatory variables (Table 4), which accounted for 13% of total variance. DistLM for *nmM* fishes explained 55% of total variance, with selected variables including C/N of POM$_{sed}$, TOC% and chloropigments (*i.e.* chlorophylls and their degradation products) in the sediments. For *mM* fishes, 95% of total variance was attributed to δ^{13}C of POM$_{sed}$, amount of chloropigments and content of lipids in sediments.

4. Discussion

This is one of the first attempts to describe food webs for deep-sea benthopelagic megafauna and seasonal trophic changes at a multispecies level. We observed great differences between fish and decapods, the former usually with higher trophic levels. Within each taxon, the community was structured as a function of the position along the benthic–pelagic gradient where megafauna species found their prey. Seasonal changes in community structure were ultimately driven by changes in food reaching bathyal depths. Influence of vertical and horizontal fluxes of organic matter varied seasonally and differed amongst species from the various trophic guilds. Although we studied benthopelagic megafauna from the middle slope of the NW Mediterranean Sea, most of the

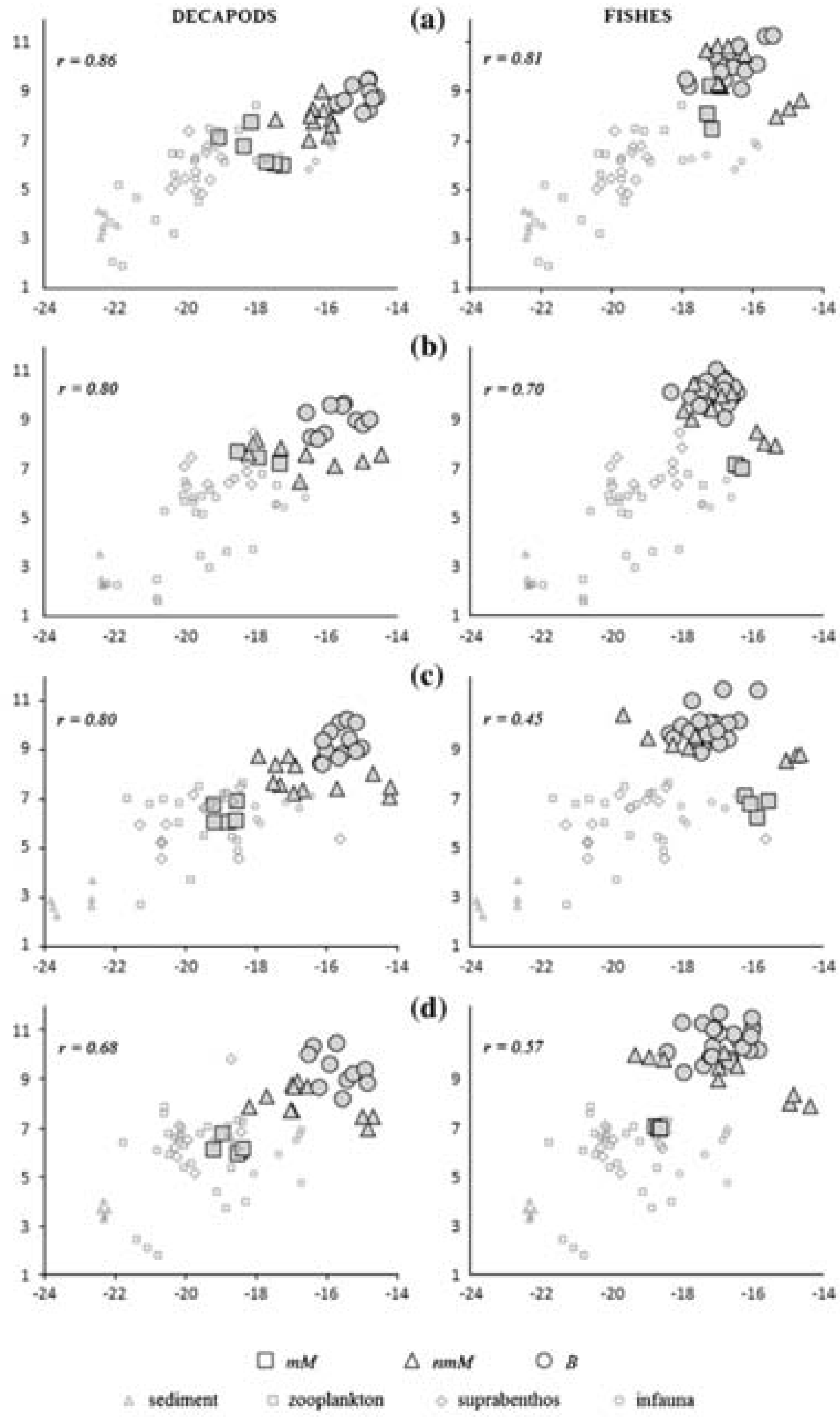

Fig. 5. $\delta^{15}N$–$\delta^{13}C$ scatterplot of megafauna (decapods and fishes), macrofauna and sediments for (a) winter, (b) spring, (c) summer and (d) autumn. Correlations as product-moment (r) correlation are presented. mM = migratory macroplankton feeders; nmM = non-migratory macroplankton feeders; B = benthos feeders.

species/genera considered in our study are widely distributed in the deep sea (e.g. *Nezumia* spp., *Lampanyctus* spp., *Acanthephyra eximia*, *Polycheles typhlops*, *Munida tenuimana*), so our results may apply to a broad context beyond the Mediterranean.

4.1. General food web structure of megafauna

The two main megafaunal taxa under study, fishes and decapods, were clearly trophically segregated: fishes on average with higher trophic levels than decapods ($\delta^{15}N$ values for fishes ranged from 7.27‰ to 11.31‰ and for decapods from 6.36‰ to 9.72‰), coinciding with dietary data from gut contents (Cartes and Carrassón, 2004). Several studies have revealed a strong positive correlation between body size and $\delta^{15}N$ (Cartes and Carrassón, 2004; Jennings et al., 2002), although relationships were weaker between species than within species (Jennings et al., 2001). However, decapods, with smaller mean sizes than fishes, consume a variety of smaller prey items (e.g. Cartes, 1998a; Fanelli and Cartes, 2004) with lower trophic levels

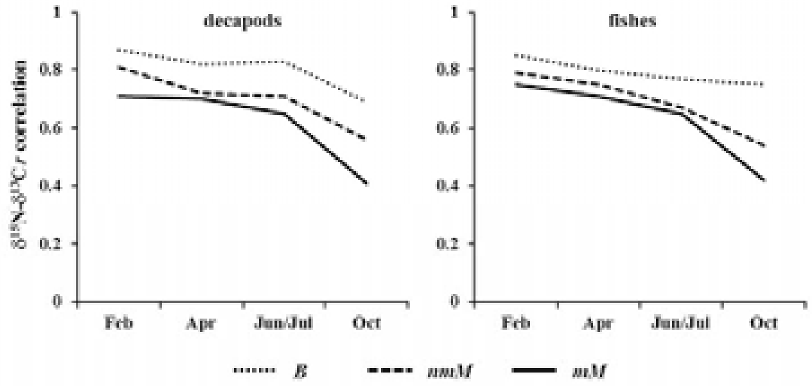

Fig. 6. Seasonal trends in $\delta^{15}N$–$\delta^{13}C$ product-moment (*r*) correlations for the different feeding guilds established for megafauna throughout the sampling period.

(Fanelli et al., 2011a, b; Polunin et al., 2001). Fish diets tend to include larger amounts of fishes, decapods and cephalopods (*e.g.* Carrassón et al., 1992; Morte et al., 2002), usually with higher $\delta^{15}N$ (Fanelli et al., 2012; own results) that has accumulated in more food web steps. $\delta^{13}C$ was enriched in decapods compared to fishes, especially amongst *B* groups of both taxa. The generally greater dominance of benthic prey in the diets of decapods compared to those of fishes from the same trophic guild (see dietary references above) likely accounts for their $\delta^{13}C$ enrichment. At bathyal depths, enriched $\delta^{13}C$ has been described for benthic macrofauna in comparison to zooplankton (Polunin et al., 2001; Fanelli et al., 2011a, b; Kürten et al., 2012; Mincks et al., 2008; our results) as a result of the consumption of microorganisms, meiofauna and refractory organic matter (Amaro et al., 2009; Gooday and Turley, 1990; Iken et al., 2001; Mincks et al., 2008; Roberts et al., 2001). Accordingly, plankton-feeding fishes and decapods (*e.g. Pasiphaea multidentata, Stomias boa*) showed similar $\delta^{13}C$ values due to the high consumption of planktonic prey and the minor contribution of benthic species to their diets (Cartes, 1993b; Roe and Badcock, 1984).

Our data differ from those reported by Polunin et al. (2001) for megafauna from the Balearic Islands. On one hand, organisms from the Catalan Sea slope generally exhibited depleted $\delta^{15}N$ by 2–3‰. Depletion in sedimentary $\delta^{15}N$ from the Catalan Sea slope (Fanelli et al., 2011a; our results) compared to the Balearic Islands (by −2.5‰; see Jeffreys et al., 2011) suggests that it is a variation in the food source, rather than a difference in TL of the large consumers in the areas' food webs (Polunin et al., 2001), what leads to depleted consumer isotope ratios in the Catalan Sea slope. Besides organic matter from surface production, terrigenous matter and matter exported from the shelf contribute to food inputs to the Catalan Sea slope (Fanelli et al., 2011a), leading to sedimentary $\delta^{15}N$ depletion. Instead, $\delta^{15}N$ values in surficial sediments of the Balearic Islands close to 4‰ are typical of phytoplankton (Pantoja et al. 2002, Harmelin-Vivien et al. 2008) and point to vertical inputs from surface production as main food source. Therefore, differences in food sources are likely related to the relative contribution of river discharges in each area (Cartes et al., 2004). The $\delta^{15}N$ depletion in the food source of the Catalan Sea slope would propagate through ascending trophic levels, as evidenced by depletion in $\delta^{15}N$ by ~1–2‰ of some macrofaunal groups (Fanelli et al., 2009, 2011b). Additionally, greater sampling depths (Mintenbeck et al., 2007) and larger sizes of organisms of the same species (Jennings et al., 2002) in the work by Polunin et al. (2001) (Polunin, N.V.C and Pinnegar, J.K. personal communication) should contribute to the relative enrichment in $\delta^{15}N$ observed amongst megafauna of the Balearic Islands. The same species of megafauna on the Catalan Sea were generally $\delta^{13}C$-enriched relative to those of the Balearic Islands (Fanelli and Cartes, 2008; Fanelli and Cartes, 2010; Polunin et al., 2001), but no $\delta^{13}C$ enrichment was observed in primary consumer macrofauna (Fanelli et al., 2009, 2011b). Therefore, this phenomenon may rather be explained by the greater dominance of enriched benthic prey in the diet of megafauna from the Catalan Sea Slope (*e.g.* comparing diets of *Plesionika martia* in the Catalan Sea Slope: Cartes, 1993a; and in the Balearic Islands: Fanelli and Cartes, 2008; and of *A. antennatus* in the Catalan Sea Slope: Cartes, 1994; and in the Balearic Islands: Cartes et al., 2008) likely related to greater abundance of benthos (Cartes et al., 2004, 2009; Maynou and Cartes, 2000).

Table 4
Summary results of distance-based permutational multivariate regression analysis (DistLM) for $\delta^{13}C$ stable isotope signatures of different trophic guilds of decapod crustaceans and fishes with *in situ* trophic indicators. Total variability explained is in bold. Chla5mab = fluorescence 5 m above the sea bed; sed = sediment; TOC% = percentage of total organic carbon in sediments.

Predictor	AIC	Pseudo-*F*	P value	% variability	% total	res. df
Decapods						
Benthic feeders (*B*)						
TOC%	−68.294	22.35	<0.001	31.77	31.77	48
$Chla_{5mab}$	−70.480	4.10	0.052	5.48	**37.25**	47
Non-migratory macroplankton feeders (*nmM*)						
No significant model						
Migratory macroplankton feeders (*mM*)						
$Lipids_{sed}$	−31.168	17.15	<0.001	47.44	**47.44**	19
Fishes						
Benthic feeders (*B*)						
$Chla_{5mab}$	−73.657	5.99	0.016	6.89	6.89	81
TOC%	−77.206	5.53	0.022	6.02	**12.91**	80
Non-migratory macroplankton feeders (*nmM*)						
C/N $atomic_{sed}$	18.766	11.32	0.002	22.96	22.96	38
TOC%	6.271	16.16	0.001	23.42	46.38	37
$Chloropigments_{sed}$	1.298	6.86	0.014	8.58	**54.96**	36
Migratory macroplankton feeders (*mM*)						
$\delta^{13}C_{sed}$	−3.851	12.18	0.004	46.52	46.52	14
$Chloropigments_{sed}$	−27.821	52.89	<0.001	42.93	89.45	13
$Lipids_{sed}$	−37.262	12.53	0.003	5.39	**94.84**	12

4.2. Feeding guilds and resource use

Within each taxon, species exploiting similar resources presented similar combinations of $\delta^{15}N$ and $\delta^{13}C$, and the main trophic differentiation depended upon the level in the water-sediment interface where specific fish and decapods found their prey, as shown in other dietary studies (Carrassón and Cartes, 2002; Cartes, 1998a). We established trophic guilds based on detailed information on diets of both bathyal crustaceans and fishes in the western Mediterranean (see references above). Resulting trophic groups were benthic feeders (*B*) and macroplankton feeders, with migratory (*mM*) and non-migratory (*nmM*) species treated separately in the latter group. Although these classifications of species are simplifications, because of the high diversity of prey consumed (Cartes and Carrassón, 2004; Macpherson and Roel, 1987; Mauchline and Gordon, 1991), the guilds established did prove to be segregated in terms of δ^{15}N and δ^{13}C, confirming that trophic guilds consist of species exploiting relatively distinct classes of resources (Jaksic, 1981). Greater overlap of trophic guilds amongst fishes, essentially of *nmM* with *B*, compared to decapods suggested more similar diets. Indeed, greater dietary overlap occurs amongst benthic and benthopelagic feeders (Carrassón and Cartes, 2002; Macpherson, 1981) than amongst pelagic feeders. However, through SIA we could not identify the niche dimensions (*e.g.* swimming capacity, size of prey consumed) that could be important in establishing resource partitioning (Carrassón and Cartes, 2002; Macpherson, 1979), especially amongst fishes that have access to a large array of prey types and sizes (Cartes, 1998a; Cohen et al., 1993).

For both taxa, *B* species were located closer to the top of the trophic web, whilst *mM* species were at the other extreme presenting the most depleted δ^{15}N and δ^{13}C. The *mM* consists of mesopelagic species that feed on planktonic prey and perform diel vertical migrations for feeding, *e.g.* pasipheid shrimps (Cartes, 1993b). Planktonic macrofauna are mainly influenced trophically by OM from surface production (Fanelli et al., 2011b) that is depleted in both δ^{15}N and δ^{13}C in comparison to recycled sedimentary OM (Fanelli et al., 2011a; Mincks et al., 2008). *nmM* occupied an intermediate position in the food web based on isotope composition, indicating that these species consume both benthic- and plankton-derived material (Davenport and Bax, 2002; Pinnegar and Polunin, 2000). Both δ^{13}C and δ^{15}N became more enriched in species with more benthic diets (Cartes et al., 2007; Iken et al., 2001). The weak discrimination amongst species within the fish *B* group was likely due to the high complexity of the benthic food web, which has several trophic levels amongst macroinfaunal organisms living in the top few centimetres of the sediment (Fanelli et al., 2011a; Iken et al., 2001). Therefore, we could not resolve subtle differences in the diet of benthos-feeding fishes, for which stomach content analysis remains an irreplaceable methodology. Yet, SIA was very effective for identifying the trophic positions of organisms within the BBL community.

The strong isotopic segregation between pelagic and benthic feeders suggests the existence of two trophic webs with different starting points. The use of the same baseline to estimate trophic levels of species therefore appears rather inadequate (in agreement with Post, 2002; Fanelli et al., 2009). As recommended by Vander Zanden and Fetzer (2007), we considered a species of zooplankton feeding on POM as a baseline for the pelagic food web, *i.e.* the thecosomate gastropod *Cymbulia peroni*, which is very abundant over the middle slope of the Catalan Sea (Papiol et al., 2012) and has an annual mean δ^{15}N of 2.6‰ (representing TL 2). Instead, the baseline for the benthic food web should likely be represented by small, selective, surface deposit feeders (TL 2) such as the dominant suprabenthic cumacean *Leucon longirostris* or the ophiuroid *Amphipholis squamata* (Fanelli et al., 2011a), with mean annual δ^{15}N of 4.6‰ and 4.1‰, respectively. Assuming a trophic enrichment of *ca.* 3‰ per TL (Caut et al., 2007; Minagawa and Wada, 1984; Post, 2002), both trophic webs would have 3 trophic levels, with *Alepocephalus rostratus* and *Nezumia aequalis* as top predators for the pelagic and the benthic web, respectively.

Size was also important in community structuring of fishes and decapods (to a lesser extent); organisms of different sizes feed on prey of different sizes. Small fish species, *i.e. Hymenocephalus italicus*, *Cataetyx alleni*, and juveniles of *Galeus melastomus*, had enriched δ^{13}C and depleted δ^{15}N compared to large fishes. Small fishes, with relatively low swimming capacity, seemed to select prey from the water–sediment interface of the BBL (Carrassón and Cartes, 2002). Therefore, δ^{13}C enrichment in small fishes is likely related to specialised consumption of relatively enriched benthos or suprabenthos, whilst consumption of smaller prey (with depleted δ^{15}N) may account for their δ^{15}N depletion. Amongst decapods, larger species within trophic guilds had more enriched δ^{15}N than smaller ones (*e.g. G. longipes versus M. couchi*). Direct correlation between size and trophic level (δ^{15}N) was not always apparent; prey type and degree of specialisation were also important factors setting δ^{15}N. As in studies in other areas (Cartes et al., 2007; Polunin et al., 2001), we observed very high trophic level for the small crangonid shrimp *Pontophilus norvegicus* and for the relatively small macrourid *N. aequalis*; both are *B* species with remarkable contributions of polychaetes to their diets (Cartes et al., 2007; Fanelli and Cartes, 2010; Macpherson, 1979). Accordingly, Fanelli et al. (2011a) measured δ^{15}N of 14 different taxa of polychaetes that ranged between 6‰ and 8‰.

Additionally, species potentially feeding on very similar prey (as derived from δ^{13}C signatures) (*e.g. P. martia* and *A. eximia*, *M. poutassou* and *A. rostratus*) have different bathymetric centres of distribution (Cartes, 1998a; Papiol et al., 2012). Even though our samples came from a relatively narrow depth stratum, bathymetric segregation also contributed to community structuring, probably enhancing resource partitioning and minimising competition (Carrassón and Cartes, 2002; Cartes, 1998a, 1998b; Macpherson, 1981). Minimisation of competition in resource use may be essential to ecological success of species in food-limited environments (Iken et al., 2001; Jeffreys et al., 2009b), and is probably a crucial factor allowing dominance of decapods and fishes in the deep Mediterranean (Cartes and Carrassón, 2004; Papiol et al., 2012).

4.3. Influence of food inputs

4.3.1. Seasonal changes in resource use

The strong correlations between δ^{15}N and δ^{13}C (February to June/July) (Fig. 5a–c; Fig. 6) followed peaks of surface production (SP), observed in the study area between February and April (see satellite data in Mamouridis et al., 2011). This points to OM from the photic zone, from phytoplankton to mesozooplankton production, being the main source of food supporting the community (Beaulieu, 2002; Buscail et al., 1990; Miquel et al., 1994; Sanchez-Vidal et al., 2009). Dependence of deep-sea megafauna on surface production has been already reported both at bathyal (Polunin et al., 2001) and abyssal (Drazen, 2008; Stowasser et al., 2009) environments. Fanelli et al. (2011a, b) discussed the dependence of both the bathyal benthic and zooplanktonic macrofaunal communities on material derived from SP (*i.e.* phytoplankton and associated zooplanktonic production) in periods of water column homogeneity, with macrofauna channelling the OM to megafauna (Cartes and Maynou, 1998; Stowasser et al., 2009). Weaker correlations occurring under conditions of water column stratification and low production, in October (Fig. 6) for all trophic guilds, indicates a wide array of sources of production sustaining the assemblages (Fanelli et al., 2011a,b) once the main yearly input from surface production has decreased. In this period, advective phenomena have been documented in the study area (authors' unpublished data) that may increase the array of food sources available by carrying materials from the shelf and by resuspending OM from the bottom (Nittrouer et al., 2006).

Amongst trophic guilds, the most generalised pattern was δ^{13}C depletion from winter to spring and summer, a tendency especially significant in *mM* decapods. This phenomenon suggests more dependence on pelagic production. On one hand, the general pattern of depletion could be associated with increased availability of gelatinous or small plankton in winter-spring (Cartes, 1998b; Cartes et al., 2010a) and, on the other hand, with great abundance of mesopelagic macroplankton/micronekton crustaceans in summer (Cartes et al., 1994, 2010b). This agrees with the fact that strong seasonal changes in the diet of slope-dwelling fishes are due to oscillations in pelagic resources that show larger seasonal fluctuations than benthic prey (Cartes et al., 2010b; Iken et al., 2001; Mamouridis et al., 2011; Mauchline and Gordon, 1991). On the other hand, ontogenic migrations from mid-water to the BBL linked to changes in the diet from more pelagic to benthic dietary habits have been reported for some species (*mM*) (*e.g. Lampanyctus crocodilus*: Stefanescu and Cartes, 1992; *Pasiphaea multidentata*: Cartes, 1993b). Therefore, arrival of organisms from the mesopelagic domain could account for some of the $\delta^{13}C$ depletion observed under stratified conditions (summer–autumn).

Regarding trophic level of benthopelagic assemblages, we found a tendency toward enriched $\delta^{15}N$ in October under stratified conditions that was especially apparent amongst fish of group *B*. $\delta^{15}N$ enrichment is consistent with greater availability (and consumption) of $\delta^{15}N$-enriched suprabenthic prey in summer (Fanelli et al., 2011a,b; own results) and again with large macroplankton–micronekton in summer–autumn (Cartes, 1998b, 2010a). In fact, fishes rely intensely on suprabenthos for feeding (Carrassón and Cartes, 2002; Fanelli and Cartes, 2010; Morte et al., 2002), and some *B* fish can transitorily change trophic guild in order to take advantage of seasonally abundant pelagic resources (*e.g.* Macpherson, 1981; Carrassón and Cartes, 2002; Cartes et al., 2008). Accordingly, bathyal megafauna seem to show strong preference toward pelagic prey when they are available. The selection of such switching is probably enhanced by the high energetic value of pelagic prey (Cartes, 1998a,b; Madurell and Cartes, 2005). This pattern of enrichment was not observed in all group *B* fish, and only 3 (*Helicolenus dactylopterus*, *Trachyrhynchus scabrus* and *Phycis blennoides*) out of 5 species evidenced $\delta^{15}N$ enrichment in the summer–autumn period. More detailed explanation of species-specific dynamics requires a parallel analysis of dietary changes of species based on gut contents. Outside the objectives of this paper, that will be performed in the future.

Despite the importance of the input of new production after the late winter–spring SP bloom, seasonal changes in $\delta^{15}N$ did not amount to the canonical changes of trophic level that are generally assumed to be *ca.* 2.4 to 3‰ (Caut et al., 2007, 2009; Minagawa and Wada, 1984; Post, 2002), but oscillations in $\delta^{15}N$ were rather low ∼1‰, and the basic structure of deep-sea food webs (*e.g.* its length) scarcely varied during the year. Deep-sea food webs are based on complex interactions amongst species, which in general have very diversified diets and high levels of ommnivory (dietary $H' > 5$ for *Aristeus antennatus*: Cartes, 1994). Those factors will reflect in isotopic signatures over time, depending on the tissue turnover rates of the species. Linked to this, smaller seasonal oscillations in $\delta^{15}N$ of fishes with respect to decapods seem to be related with different rates of assimilation and the time required for equilibration of isotopes, which depend on the trophic levels and/or sizes of taxa (see Hesslein et al., 1993; Schmidt et al., 2003; Sweeting et al., 2005). Large long-lived teleosts and elasmobranchs have lower turnover rates than small short-lived decapods, especially some of the macrozooplankton we have analysed (*e.g.* Sergestidae, *mM*), with longevity around 1–2 years (Franqueville, 1971).

4.3.2. Fluxes of POM sustaining the community

Previous discussion points to changes in the type of prey consumed as the main factor driving seasonality in the isotopic signals of the highest trophic levels in the Catalan Sea. Changes in the diet of megafauna have been associated to availability of their prey in the environment (Cartes et al., 2008; Fanelli and Cartes, 2008). Accordingly, seasonal changes of megafauna assemblages structure are mainly coupled to seasonal changes of zooplankton and SP (Cartes, 1998b; Papiol et al., 2012). Peaks of different macrofauna compartments have been linked to the input of organic compounds associated with the fluxes of POM (*e.g.* benthos: Buscail et al., 1990; meiofauna: Cartes et al., 2002b; copepods: Riaux-Gobin et al., 2004). Here we attempted to find main relationships between megafauna (fish and decapods) and the different fluxes of POM (vertical and advective) by linking different compounds to the $\delta^{13}C$ signatures of predators. These links most likely occur through consumption of prey that rely on specific inputs of OM, as observed by Stowasser et al. (2009).

Temporal trends in isotopic signatures of both group *B* fishes and decapods were associated (in DISTLMs) to TOC% in sediments and $Chla_{5mab}$, the last being related with phytodetritus deposition as documented over the Catalan slope (Riaux-Gobin et al., 2004). These two variables exert great influence on population dynamics of benthic macrofauna, *i.e.* infauna and suprabenthos, main prey of group *B* megafauna. High $Chla_{5mab}$ in February, from the arrival of OM derived from phytoplankton bloom (Beaulieu, 2002), favoured the proliferation of macroinfaunal taxa feeding at the sediment-water interface over the slope, *e.g.* *Abra longicallus* (Fanelli et al., 2011a). The same peak of $Chla_{5mab}$ enhances proliferation of the main prey taxa (*i.e.* copepods and euphausiid larvae) for carnivorous suprabenthos (Buscail et al., 1990; Cartes et al., 2001, 2002b), even as deep as 2300 m on the northwestern Mediterranean slope (copepod nauplii: Guidi-Guilvard et al., 2007), which take an increasing role in the diet of group *B* fishes after February.

TOC% is generally considered a good indicator of the quality and availability of food for benthos (Beaulieu, 2002; Danovaro et al., 1995). Abundance and biomass of benthic organisms are directly related to the amount of food reaching the sediment surface (Gooday and Turley, 1990 and references therein), and TOC% was linked to higher densities of deposit feeders along the Catalan slope (Cartes et al., 2010a; Mamouridis et al., 2011).

TOC% was also an explanatory variable for *nmM* fishes, together with C/N of sediments. Although C/N has often been associated with lipid content, this was not fully supported by our data, because we observed very different temporal patterns between these two variables. Instead, C/N∼5 during most of the period points to highly nutritive and easily degradable OM of marine origin (Buscail et al., 1990). Maximum C/N in June/July inside canyons (C/N∼10) suggests arrival of terrigenous OM (Meyers, 1997); either degraded or largely remineralised. Due to the very mixed nature of the diets and behaviours of *nmM* group animals, significant models were obtained for fish but not for decapods.

Additionally, phytoplankton pigments had substantial importance in explaining the dynamics of isotopic composition for macroplankton feeders (both *mM* and *nmM*), due to their stronger link to vertical inputs of POM through their zooplankton prey (Beaulieu, 2002; Fanelli et al., 2011b; Riaux-Gobin et al., 2004). Isotopic dynamics of *mM* (both fish and decapods) were also related with lipids in the sediment. Additionally, for the *mM* fish, $\delta^{13}C$ of sediment OM and the sum of all chlorophylls (degraded and undegraded) were also important. Lipids are important constituents of phytodetritus (Fabiano et al., 1993, 2001), with high and easily degradable energetic content. Given the significant amounts of lipids in phytodetritus and marine snow (Riaux-Gobin et al., 2004), input of phytodetritus after the surface bloom constitutes an organic flux of a large amount of labile OM (Buscail et al., 1990; Riaux-Gobin et al., 2004), which may sustain the rapid metabolism of planktonic fauna, the main prey of *mM* megafauna (Buscail et al., 1990; Gooday and Turley, 1990).

Deposition of chloropigments in the sediment after spring under low turbidity conditions, suggests they might be available in winter-spring near the water–sediment interface, where they might be ingested by zooplankton. In the Gulf of Lions, nauplius abundance has important interannual variations related with turbidity conditions and the flux of particles over the slope (Guidi-Guilvard et al., 2007). In agreement, high turbidity, associated to the formation of nepheloid layers in winter and spring, was reported in the Catalan Sea (Papiol et al., 2012; Puig and Palanques, 1998).

5. Conclusions

Trophic web dynamics deduced from stable isotopes yield similar temporal patterns (homogenised *versus* stratified water column conditions) as have been found by gut content analysis of the structure of fish and decapod communities. Strong correlations between $\delta^{15}N$ and $\delta^{13}C$ were observed in periods of water column homogeneity (February and April, following peaks of surface primary production), whilst weaker correlations were observed in July and October (stratified waters). The latter indicates a diversification of sources of production. Species tend to be organised in trophic guilds from depleted (groups *mM*, *nmM*) to enriched (groups *B*) δ^{13}C. Segregation amongst guilds was clearer in decapods than in fish, because decapods occupy a lower trophic level (on average), and they are closer to primary food sources. Most generalised seasonal patterns of δ^{13}C depletion and δ^{15} N enrichment agree with the patterns of macrofauna production and availability for megafauna. As important constituents of phytodetritus, lipids found in sediments and Chla$_{Smab}$ were explanatory variables for the δ^{13}C composition of megafauna, especially for the *mM* groups, whilst %TOC explained seasonal isotope variability in *B* groups, with less evident relationships for *nmM* groups due to the mixed nature of their diets. The indicators of the importance of inputs of material from surface production to the dynamics of megafauna, together with the pattern observed in δ^{13}C–δ^{15} N correlations, emphasised the large contribution of material derived from the SP bloom in sustaining bathyal megafauna. Some general tendencies in deep sea food-webs can be deduced by SIA. However, revealing the detailed species-specific trends will require the analyses of gut-contents that are still in progress (authors' unpublished data).

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Appendix A. Groups of macrofauna with abbreviations for species included in each group, their prey and specification of the sources of information

Group	Species	Main prey	Source
Suprabenthos			
Carnivore on zooplankton (Supra-CZ)			
Amphipoda	*Nicippe tumida*	Copepods	Fanelli et al., 2009
Amphipoda	*Rhachotropis caeca**	Copepods	Cartes et al., 2001
Amphipoda	*Rhachotropis grimaldii**	Copepods	Cartes et al., 2001
Amphipoda	*Rhachotropis rostrata*	Copepods	Cartes et al., 2001
Amphipoda	*Syrrhoe affinis*	Copepods, gelatinous	Fanelli et al., 2009
Picnogonida	*Pallenopsis scoparia*		
Omnivore (Supra-Omn)			
Mysidacea	*Boreomysis arctica**	Crustaceans, detritus, phytoplankton	Cartes and Sorbe, 1998
Predator (Supra-P)			
Isopoda	*Gnathia maxillaris*		Fanelli et al., 2009
Scavenger (Supra-Scav)			
Isopoda	*Natatolana borealis*	Scavenger	Kaim-Malka, 1997
Scavenger Mix (Supra-ScavMix)			
Amphipoda	*Eusirus longipes**		
Amphipoda	*Scopelocheirus hopei*	Detritus, Polychaeta	Cartes et al., 2001
Amphipoda	*Tmetonyx similis**		
Surface Deposit Feeder (Supra-SDF)			
Amphipoda	*Bathymedon acutifrons*		
Amphipoda	*Bathymedon banyulsensis*		
Amphipoda	*Bathymedon longirostris*	Detritus, foraminiferans	Cartes et al., 2001
Amphipoda	*Bruzelia typica**	Detritus	Fanelli et al., 2009
Decapoda	*Calocaris macandreae* (small)		
Amphipoda	*Harpinia* spp.	Detritus, meiobenthos	Fanelli et al., 2009
Cumacea	*Leucon longirostris*	Detritus, meiobenthos	Cartes et al., 2001
Cumacea	*Makrocylindrus gibraltarensis*		
Isopoda	*Munnopsurus atlanticus*	Detritus, foraminiferans	Elizalde et al., 1999; Cartes et al., 2001
Amphipoda	*Oediceropsis brevicornis**		
Amphipoda	*Tryphosites alleni**	Detritus	Fanelli et al., 2009
Amphipoda	*Tryphosites longipes**	Detritus	Fanelli et al., 2009
Zooplankton			
Carnivore on zooplankton (Zoopl-CZ)			
Osteichthyes	*Argyropelecus hemygimnus*		Kinzer and Schulz, 1988
Siphonophora	*Chelophyes appendiculata**		Purcell, 1981
Osteichthyes	*Cyclothone braueri**	Copepods, ostracods	Fanelli et al., 2009
Osteichthyes	*Cyclothone pygmaea*		Fanelli et al., 2009
Chaetognatha	Chaetognatha*		Pearre, 1980
Copepoda	*Candacia tenuimana*		
Mysidacea	*Eucopia hanseni*		Hopkins et al., 1994
Decapoda	*Gennadas elegans**	Copepods	Cartes et al., 2002a
Osteichthyes	*Lampanyctus crocodilus* (juveniles)		Stefanescu and Cartes, 1992
Euphausiacea	*Nematoscelis megalops**	Copepods	Fanelli et al., 2009
Hydrozoa	*Periphylla periphylla**		Sørnes et al., 2008
Omnivore (Zoopl-Omn)			
Euphausiacea	*Meganycthiphanes norvegica**		Onsrud and Kaartvedt, 1998
Feeding in Particulate Organic Matter (Zoopl-POM)			
Copepoda	*Calanus helgolandicus*	Phytoplankton	Corner et al., 1972
Gastropoda	*Cavolinia inflexa*		Gilmer and Harbison, 1986
Gastropoda	*Cymbulia peroni**		Gilmer, 1972
Amphipoda	*Euprimno macropa*		Madin and Harbison, 1977
Thaliacea	*Pyrosoma atlanticum*		Drits et al., 1992

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CHAPTER 5 - REGULATION OF THE FEEDING DYNAMICS AND REPRODUCTIVE CYCLES OF BENTHOPELAGIC FISH ON NORTHWEST MEDITERRANEAN CONTINENTAL SLOPES BY FOOD AVAILABILITY

Regulation of the feeding dynamics and reproductive cycles of benthopelagic fish on northwest Mediterranean continental slopes by food availability

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Abstract

Trophic dynamics and biological cycles of fish from the middle slope of the Catalan Sea (Balearic Basin, NW Mediterranean) have been investigated. Samples were collected on a seasonal basis from 600 to 1000 m depth between February 2007 and February 2008. Gut contents of 7 species from several families were analysed and weights of gonads and livers and C/N ratios of muscle were measured. Additionally, food availability was estimated through analyses of densities of potential prey and of indicators of organic matter sources. The trophic structure of the community was a function of the size of predators and of the bentho-pelagic gradient of the water-sediment interface where megafauna find their prey. Fish species fed upon benthos, hyperbenthos and zooplankton, showing preference towards one of these categories. We established three trophic groups: benthic feeders, non-migrator macroplankton feeders and small-sized fish, the latter group mainly feeding on hyperbenthos and small macroplankton. Dietary overlap increased from April to June/July among benthos feeders and small-sized fish, which consistently changed diets from April to June/July. Benthos feeders increased consumption of hyperbenthos and detritivores, and small-sized fish increased consumption of more mobile hyperbenthic and macroplanktonic prey. Among planktivores, dietary overlap was low and increased in June/July concurring with greatest feeding intensities. Dietary overlap decreased back in October, when diets of macroplankton feeders changed significantly to eating mesopelagic decapod species of different sizes. Feeding intensity (gut fullness, *F*) was related with food availability. The *F* values of benthos feeders were related to TOC% in the sediments, to surface production 2 months before the sampling, and to the abundance of benthic/hyperbenthic polychaetes and mysids. For plankton consumers, lipids in the sediment were the most important explanatory variable, and *F* was also related to the abundance of the mesopelagic shrimp *Pasiphaea* spp. *F* of small fish species was also related to C/N of muscle. Food availability partially controlled temporal trends in gonadosomatic index. Also, increased feeding intensity preceded increases in gonadosomatic index, but different reproductive strategies and energy use were deduced from the relationships between the gonadosomatic and different biological indices in different species. Most fishes reproduced between autumn (October) and spring (April/May), with different timing of reproduction between species feeding on the same prey resources.

Keywords: Deep Sea, benthopelagic fish, diet, reproduction, seasonality, food availability.

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1. Introduction

The bathyal domain of the Catalan Sea (NW Mediterranean) is a food-limited environment with communities of megafauna dominated by benthopelagic fish and decapod crustaceans. Decapod crustaceans dominate the middle slope of the NW Mediterranean Sea in terms of numerical abundance, and fishes represent the largest biomass among all megafauna (Cartes and Sardà, 1992; Stefanescu et al., 1994; Papiol et al., 2012). Despite this difference, these two taxa of the middle slope around Catalan canyons consume similar amounts of food annually and play leading roles in the consumption of virtually all macrobenthic and macroplanktonic production (Cartes and Maynou, 1998). Over the middle slope, fish communities are dominated by relatively small species, such as macrourids and *Phycis blennoides* (Stefanescu et al., 1994), with diets of benthic and hyperbenthic macrofauna. Only large specimens of some species (e.g. *P. blennoides* and *Trachyrhynchus scabrus*: Macpherson, 1978; 1979) and some sharks (Fanelli et al., 2009) also prey on larger fauna (decapods, cephalopods and other fishes). Dominant fish species on the middle slope have mixed diets based on benthic and mesopelagic prey, although with a distinct preference toward one of these categories (Mauchline and Gordon, 1986; Fanelli and Cartes, 2010). In general, there are high levels of trophic resource partitioning over the middle slope of the Mediterranean Sea, allowing species to coexist despite the oligotrophy of the ecosystem (Macpherson, 1981; Carrassón and Cartes, 2002; Madurell and Cartes, 2006; Papiol et al., 2013). Usually, species inhabit and feed at different depths in the water column and feed on different prey sizes (Carrassón and Cartes, 2002). Nevertheless, seasonal changes in dietary composition of deep-sea fish take place (Madurell and Cartes, 2005; Fanelli and Cartes, 2010) and resource partitioning is weaker during some periods due to transitory abundance peaks of specific prey (Macpherson, 1981). In the northwestern Mediterranean, consumption of pelagic prey follows the significant seasonal fluctuations in abundance of pelagic macroplankton relative to benthic macrofauna (Mauchline and Gordon, 1991; Iken et al., 2001; Cartes et al., 2010a; Mamouridis et al., 2011). However, seasonal variations in macrofaunal prey do not affect all predators equally, and responses are stronger and faster in species consuming pelagic prey rather than in benthos feeders situated at the top of deep-sea trophic webs (Macpherson, 1981; Fanelli and Cartes, 2010).

Fluctuations in the abundance of macrofauna are related to variations in the organic matter (OM) inputs upon which they feed (Cartes et al., 2002; Guidi-Guilvard et al., 2007). In the study area, the main OM input to bathyal depths is the vertical flux of particles originating near the surface (Fanelli et al., 2011a,b), which is greatest after the late winter surface blooms when the water column is homogeneous. Low particle flux is associated with periods of stratification that usually extend from April to November (Miquel et al., 1994). Additionally, advective currents through submarine canyons in the study area play a role in food availability, either by carrying organic matter across the slope or by resuspending OM from the upper sediment layers. These advective fluxes also vary seasonally with discharge rates of continental run-off (Monaco et al., 1990; Buscail et al., 1990), with cascading events in the Gulf of Lions and with changing water column conditions along the NW Spanish coast (Canals et al., 2006; Palanques et al., 2006; Cartes et al., 2010b). They are greatest in spring and least in summer.

In a fairly constant physical environment such as the deep Mediterranean Sea (Hopkins, 1985), the temporal oscillations in food availability have often been proposed as drivers of the biological cycles of deep-sea species (Cartes and Carrassón, 2004). That agrees with the idea that seasonal reproductive processes respond to the natural fluctuations in environmental factors (Gage and Tyler, 1991). An expectation that biological processes would be constant in the theoretically constant deep-sea environment (Orton, 1920) has been revised over recent decades, and both seasonal and continuous reproductive patterns have been found in slope fauna, and specifically among fish (Gage and Tyler, 1991; Martino et al., 2001; Rotllant et al., 2002; Drazen, 2002a; Tsikliras et al., 2010). The relationship between biological cycles and cyclic food availability on the middle slope of the NW Mediterranean Sea has been established repeatedly for macrofaunal groups (Cartes and Sorbe, 1996; 1998; Cartes, 1998a). Among megafauna, cyclic recruitment patterns of detritivorous species have been linked to pulses of food (Ginger et al., 2001; Hudson et al., 2004; Howell et al., 2004), but few studies have tackled this issue in deep-water predators. Some authors have related the biological cycle of bathyal benthopelagic shrimps to changes in their feeding habits (Fanelli and Cartes, 2008; Cartes et al., 2008), showing greater consumption of energetic prey during gonad development in pre-reproductive periods. Biological cycles of benthopelagic shrimps have also been related to vertical fluxes of organic matter reaching bathyal depths (Puig et al., 2001; Cartes et al., 2008), and delayed responses to blooms in surface production have been observed. Nevertheless, this issue remains largely unexplored in deep-sea benthopelagic fish (Drazen, 2002a).

Studies on the biological cycles of fish have usually focused on single species or species from the same families, and reproduction studies for species from different families have barely been addressed. Mainly based on shelf and pelagic fish species, Tsikliras et al. (2010) described a global pattern of spawning by fish in the Mediterranean Sea in spring and summer months. Nevertheless, no consistent pattern has been found in reproductive timing of deep-sea fishes, and distinctive species-specific timing of biological cycles of coexisting slope fish is usual (Massutí et al., 1995; Rotllant et al., 2002). If food availability was the most important factor controlling reproduction at bathyal depths, synchronised reproductive cycles of cohabiting species with contemporary inputs of organic might be expected. Therefore, the species-specific timing observed suggests that seasonal availability of energy does not affect all species reproductive processes equally. The diverse interspecific responses to seasonality in relation to the feeding preferences (Macpherson, 1981; Fanelli and Cartes, 2010) of each species could have some effect on their timings of reproduction. In addition, some biological aspects related to energy allocation and use could be responsible for these differences. Besides, segregation of spawning in time and/or space could be useful for avoiding competition among offspring and thus increasing reproductive success. In fact, current data seem to indicate the existence of a common pattern of partitioning in recruitment grounds according to season and/or depth of closely related species.

In our study of middle-slope fish we aimed to

i) identify the trophic and reproductive seasonal patterns of the whole fish assemblage,
ii) determine the coupling between the trophic dynamics and the reproductive cycles,
iii) determine the main food sources driving their trophodynamics and reproductive cycles.

2. Materials and methods

Data describing diets and gut fullness of seven species of dominant benthopelagic fish of the middle slope of the Catalan Sea (Balearic Basin, NW Mediterranean Sea: Fig. 1) were obtained using bottom trawls and analysed on a seasonal basis over a one-year period.

2.1. *Study area and sampling strategy*

Five multidisciplinary surveys distributed in the four seasons of a calendar year were performed between February 2007 and February 2008 (BIOMARE B1, B2, B3, B4 and B08) at depths ranging from 423 to 1175 m within the project BIOMARE.

Fig. 1. Study area and sampling sites (grey)

Three stations in an open slope area located on the fishing ground known as *Serola* were sampled along the isobaths close to 650, 800 and 1000 m, except in April when no samples were collected from 1000 m. In addition, sampling was performed inside the Besòs submarine canyon, a site locally called *El Buscarró* ground at *ca.* 600 m depth along the canyon's southern wall. Two different fishing gears were used for sampling. Nineteen hauls were performed using a semi-balloon otter trawl (OTSB-14) (Merrett and Marshall, 1981) from the oceanographic vessel *García del Cid*. Twelve hauls were carried out on board the commercial vessel *Stella Maris* III with a commercial trawl (CT), gear locally called "*bou*". Features of these trawls are detailed by Cartes et al. (2009). Samples collected by OTSB-14 were in taken in February, April, June/July and October 2007, and February 2008. Details of the OTSB-14 samplings can be found in Papiol et al. (2012). The CT was only used at two stations (*Buscarró* at *ca.* 600 m and *Serola* at *ca.* 800 m), and those tows were performed on dates close to OTSB-14 tows (2007: March 6th, May 11th, June 25th, July 19th, September 17th and December 28th).

All hauls were carried out during daytime (06:58h – 20:55h GMT). The time on bottom of each haul ranged between 45 and 90 min at a towing speed around 2.6 knots.

Samples of surface sediment (0–2 cm depth) for analysis of particulate organic matter (POM_{sed}) were collected with a multicorer from the 600 and 800 m stations throughout the sampling period. Sediment was immediately frozen at -20 ºC for later analysis.

2.2. *Analyses of stomach contents and biological parameters.*

All benthopelagic megafauna collected was identified to species level, counted, measured and weighed, either on board or at the laboratory. Specimens were immediately frozen at -20 ºC for future analyses.

At the laboratory, we analysed the biological parameters of 1503 fish belonging to the seven species dominating the slope assemblage (Table 1). Only adult individuals of most species were selected for analysis, but we distinguished two age classes (juveniles and adults) for *Galeus melastomus* and *Trachyrhynchus scabrus*. All individuals were sexed and weighed (±0.001 g), and total length (mm) (pre-anal length in the case of macrourids) was recorded. Stomach content, liver and gonads were removed and weighed (±0.001 g). The food items were identified to species or to the lowest feasible taxonomic level, and their weight after drying with blotting paper was recorded to the nearest 0.1 mg. Although analysis of gut contents has limitations

(Pinnegar and Polunin, 2000; Fry, 2006; Fanelli and Cartes, 2008) that are especially intense for the deep-sea (e.g. hydrostatic decompression regularly results in regurgitation of prey in some deep-sea fish), they provide a great deal of information on gut fullness variation, on specification of prey and of trophic effects of the density and distribution of both food sources and consumers. Intestine contents were analysed for species in which a significant number of stomachs were everted (i.e. juveniles and adults of T. scabrus, and adults of Phycis blennoides). Prey in intestines were more broken and digested than those in stomachs, but hard parts (otoliths, mandibles, etc.) allowed prey identification, sometimes to species level. Due to greater digestion, prey remains in intestines were strongly mixed, and direct prey weighing was impossible in practice. For this reason, for intestines the percentage volume of each prey was estimated by the subjective points method (Swynnerton and Worthington, 1940).

White muscle tissue from fishes was sampled for analyses of organic carbon and nitrogen. Samples were dried to constant weight at 60 ºC, then ground to fine powder. Total organic carbon (TOC) and total nitrogen (TN) were determined from the CO2 and N2 produced by combustion using a Thermo Electron Flash EA 1112 elemental analyser.

2.3. *Analyses of sediment organics*

TOC of sediments (TOC_{sed}) was determined by the same procedure employed for muscle tissue. TOC amounts are reported as percentage of sediment dry weight.

Total lipid content of sediments ($lipids_{sed}$) was also analysed following a modified Bligh and Dyer method (Bligh and Dyer, 1959; Alfaro et al., 2006). Lipid amounts are reported as percentage of sediment dry weight.

In addition, phytoplankton pigments in sediments were analysed as indicators of OM from surface primary production in the area by means of reverse-phase high-pressure liquid chromatography (HPLC).

For all sedimentary analyses, three replicates were analysed for each sample at each collection station in each season. Details of the analyses of sediment organics can be found in Papiol et al. (2013).

Table 1. Fish species examined in the present study. Length ranges (TL = total length; PAL = pre-anal length), mean weight (± standard deviation) number of specimens dissected for measuring biological parameters, number of females dissected for measuring biological parameters, number of stomach contents analysed (number of intestine contents analysed in brackets) by season (win=winter; spr=spring; sum=summer; aut=autumn). Trophic guild (mM=migrator macroplankton feeders; nmM=non-migrator macrolankton feeders; B=benthos feeders) from literature and source are also indicated.

Species	Size (mm)		Mean weight (g)	Season	Dissected	Females	Diet	Trophic guild	Source
Galeus melastomus adults	300-605	TL	297 ± 179					nmM	Carrassón et al., 1992; Fanelli et al., 2007
				win	50	14	41		
				spr	11	8	11		
				sum	42	16	40		
				aut	55	25	54		
Galeus melastomus juveniles	150-300	TL	45 ± 19					nmM	Carrassón et al., 1992; Fanelli et al., 2007
				win	65		52		
				spr	41		34		
				sum	47		39		
				aut	32		23		
Hymenocephalus italicus	30-50	PAL	7 ± 2					nmM	Macpherson, 1979
				win	39	19	19		
				spr	18	12	8		
				sum	91	52	60		
				aut	22	10	20		
Lampanyctus crocodilus	100-180	TL	20 ± 10					mM	Stefanescu and Cartes, 1992.
				win	51	28	31		
				spr	42	21	20		
				sum	130	38	76		
				aut	40	7	20		

Micromesistius poutassou	200-350	TL	120 ± 57					nmM	Macpherson, 1978a
				win	48	19	12		
				spr	17	12	12		
				sum	15	9	10		
				aut	31	24	18		
Nezumia aequalis	22-58	PAL	27 ± 14					B	Macpherson, 1979; Carrassón and Matallanas, 1989
				win	42	20	28		
				spr	13	8	10		
				sum	45	16	31		
				aut	21	19	19		
Phycis blennoides	150-400	TL	147 ± 96					B	Macpherson, 1978b
				win	32	8	5 (22)		
				spr	28	13	4 (17)		
				sum	41	20	14 (23)		
				aut	36	15	12 (34)		
Trachyrhynchus scabrus adults	95-150	PAL	71 ± 53					B	Macpherson, 1979
				win	21	12	6 (20)		
				spr	18	8	4 (12)		
				sum	33	12	2 (32)		
				aut	89	43	7 (85)		
Trachyrhynchus scabrus juveniles	50-94	PAL	22 ± 10					B	Macpherson, 1979
				win	51		7 (17)		
				spr	49		8 (25)		
				sum	55		6 (32)		
				aut	42		4 (38)		
Total					1503	508	767 (357)		

2.4. *Environmental variables*

Casts were performed at each station with an SBE-32 CTD coupled with a fluorometer. Locations were the same as those where biological and POMsed samples were collected. Values of fluorescence were recorded for each CTD profile at 5 m above the sea bottom (5 mab).

Phytoplankton pigment concentration (PPC, mg Chl*a* m^{-3}), obtained from *http://reason.gsfc.nasa.gov/Giovanni*, was used as a rough index of surface primary production in the area. We used monthly average ppc values at the bottom trawl positions coincident with sampling, and 1, 2 and 3 months before sampling (Cartes et al., 2004).

2.5. *Data analysis*

Two-way PERMANOVA with a crossed design considering sampling sites and surveys as factors was used to test spatial and temporal differences among environmental variables and sediment organics.

Abundances of the megafauna species analysed and of potential prey species were standardized to a common swept area of 1 ha (ind ha^{-1}), according to the values proposed by Cartes et al. (2009).

2.5.1. *Trophic data*

The dietary composition was analysed for the 767 individuals with stomachs containing food (Table 1). Intestine contents of 357 individuals of *Phycis blennoides* and *Trachyrhynchus scabrus* were also analysed, and stomach and intestine contents were compared to investigate whether they could be analysed together. The contribution of each prey item to the diets was standardised to total fish weight. Analysis of similarities (ANOSIM) between intestine and stomach contents of the same individuals was performed using Bray-Curtis similarity index (Field et al., 1982) after square-root transformation of diet proportions by weight. Given the significant differences found between contents of the two organs (ANOSIM $p<0.05$), seasonal patterns were studied based on intestine contents, because available stomach contents provided inadequate dietary description.

Stomach fullness (%*F*) was used to measure feeding intensity and was calculated as:

$$\%F = 100 \text{ (stomach content weight / predator weight).}$$

C/N ratios were calculated for muscle tissue, since C/N is a relatively good surrogate for tissue lipid content (i.e. samples containing more lipids have higher C/N; Tieszen et al., 1983).

Diet diversity across the year as a whole was calculated for each species based on the Shannon-Wiener *H´* index.

2.5.2. *Biological indices*

Two indices were calculated for describing the overall physiological condition of the fish (Lloret and Planes, 2003). The hepatosomatic index (HSI) was calculated as a proxy for energy reserves stored in the liver: HSI = 100 (liver weight/body weight). The gonadosomatic index (GSI) is often considered as a surrogate for reproductive effort (Jakobsen et al., 2009), and it was calculated as: GSI =100 (gonad weight/body weight). All weights were wet weights. Taking into consideration that females allocate more energy to reproduction than males (Wootton, 1998; Tsikliras et al., 2010) and that the liver plays an important role in energy storage, HSI and GSI were only estimated for adult females.

2.5.3. *Overall diet of species*

Diet was analysed for each species in each haul of each survey. Between 8 and 26 individuals (a “sample”) were analysed per haul for all species. For the 20% of hauls analyzed with low numbers of individuals (<8), specimens from different hauls within the same survey were pooled to attain minimum sample sizes of 8 individuals (the minimum representative samples for diet analysis obtained from cumulative curves, see Cartes, 1991 for further details). For each diet category (prey type) in each sample, prey biomass was standardised to an equivalent for 10 individuals.

To identify overall trophic interactions among fish species, a hierarchical cluster analysis (average grouping method) was performed on the square-root transformed biomass data using the Bray-Curtis similarity index (Field et al., 1982). To illustrate observed similarities or dissimilarities (distances) between the groups resulting from the cluster analyses, multidimensional scaling (MDS) analysis was carried out on the same data matrix. The groups obtained were compared with postulated trophic groups based on the literature (Table 1). Analysis of similarities (ANOSIM) between the different groups obtained by cluster analysis was performed on the same resemblance matrix to test significance of segregation between the groups. SIMPER analysis was performed to identify characteristic prey for each group obtained by cluster analysis and to calculate the degree of similarity/dissimilarity among diets of the different groups of species.

2.5.4. *Seasonal intraspecific variations*

Seasonal variations in diets of each species were measured by applying a one-way PERMANOVA (Anderson, 2001) to square-root transformed proportional biomass data of individual stomach contents based on the Bray-Curtis similarity index. Additionally, temporal trends in prey consumption (biomass) were studied by merging all replicates from the same season.

Two-way permutational univariate ANOVA with a crossed design considering both sex (adult males and females) and survey as factors was used to test sexual differences in fullness. Pairwise tests were performed when the interaction between the two factors was significant in order to allocate the source of variation. One-way permutational univariate ANOVAs (Anderson, 2001) based on Euclidean distances were adopted to test seasonal changes in fullness, C/N, GSI and HSI after arcsine transformation in order to approximate Normality. While permutational ANOVA was designed for multivariate analysis of distance matrices, it can be used for univariate ANOVA. Because we have only one dependent variable in the analysis and use Euclidean distances, the resulting sums of squares and F-ratios are the same as Fisher's univariate F-statistic in traditional ANOVA. Significance was set at $p = 0.05$; p values were obtained using 9999 permutations of residuals under a reduced model (Anderson, 2001).

2.5.5. *Seasonal changes in interspecific relationships*

Affinities between diets of the different species in each season were calculated using the quantitative Schoener index (α) (Schoener, 1974).

2.5.6. *Drivers of fullness and biological cycle*

A draftsman plot (i.e. scatter plots of all pairwise combinations of variables) (Clarke and Warwick, 1995) was applied to environmental variables to identify whether any of them were strongly correlated, thus providing redundant information. Redundant variables ($r > 0.70$) were discarded, simplifying the matrix for later Generalised Linear Models.

In order to identify which variables explained patterns of fullness and GSI, values of fullness and GSI were compared with independent explanatory variables by means of Generalised Linear Models (GLMs) after normalising the dependent variables by arcsine transformation (Sokal and Rohlf, 1995). GLMs for fullness were calculated on each of the trophic groups obtained by cluster analyses using mean values of fullness per haul and species. GLMs for GSI were calculated on each species using GSI per individual (not mean per haul) in order to increase sample size. GLMs are flexible generalisations of ordinary least squares regression. A GLM generalises linear regression by allowing the linear model to be related to the response variable via a link function and by allowing the magnitude of the variance of each measurement to be a function of its predicted value. The distribution family used was Gaussian with identity link. The models were computed by adding single terms based on minimising Akaike's Information Criterion (AIC) and only including variables that were significant ($p<0.05$). Both in the fullness and the GSI models we included environmental variables: i) surface phytoplankton pigment concentration (PPC) simultaneous with and 1, 2 and 3 months before the sampling, ii) fluorescence$_{5mab}$; iii) TOC$_{sed}$%, iv) lipids$_{sed}$% and v) the sum of sediment chloropigments (chlorophylls and their degradation products). Chloropigments were used as general indicators of the quantity of phytodetritus (Vidussi et al., 2000 and references therein). Standardised abundances of potential prey of megafaunal fish caught with the OTSB-14 (i.e. sergestid and pasipheid shrimps, brachyuran crabs, benthic shrimps including *Calocaris macandreae* and *Alpheus glaber*, nektobenthic decapods - mainly pandalids and *Acantephyra eximia*, mesopelagic myctophids and benthopelagic fish - including *P. blennoides*, *Symphurus ligulatus* and macrourids, cephalopods, euphausiids, mysids, isopods and polychaetes) were also included in the model, as were density, and predator mean size and W (biomass/abundance) or individual size and W (in the case of models for GSI). Species and sampling depths were included as factors. For the models of GSI, fullness, C/N ratio and HSI were also included, as they are indicators of energy consumption and availability in the organism. Considering fullness is an immediate reflection of what is consumed, we compared fullness with variables sampled simultaneously. Given that gonad growth has some delay in relation to the food ingested or the energy stored in the organism, values of GSI were compared with variables sampled simultaneously and those form the previous sampling. For previous biological indices, mean values per sampling station were used because we considered the animals sampled in each season as a cohort from the same population.

All statistical analyses were performed using PRIMER6 and PERMANOVA+ (Clarke and Warwick, 1995; Anderson et al., 2008), R 2.14.2 (http://www.r-project.org/) and STATISTICA 6 and XLSTAT software.

3. Results

3.1. *Organic matter sources*

Results for spatial and temporal trends of TOC_{sed}% and surface primary production are detailed in Papiol et al. (2012) and lipids and pigments in sediments and fluorescence 5 m above sea bottom are reported in Papiol et al. (2013). Those are not repeated here, as they are taken into account only for GLMs development.

3.2. *Overall diet of species*

3.2.1. *Resource partitioning*

The MDS analysis performed on dietary data shows that both the position of predators along a benthos–plankton gradient, that is the distribution of their prey in the near-bottom water column, and size of predators are the main structuring factors (Fig. 2).

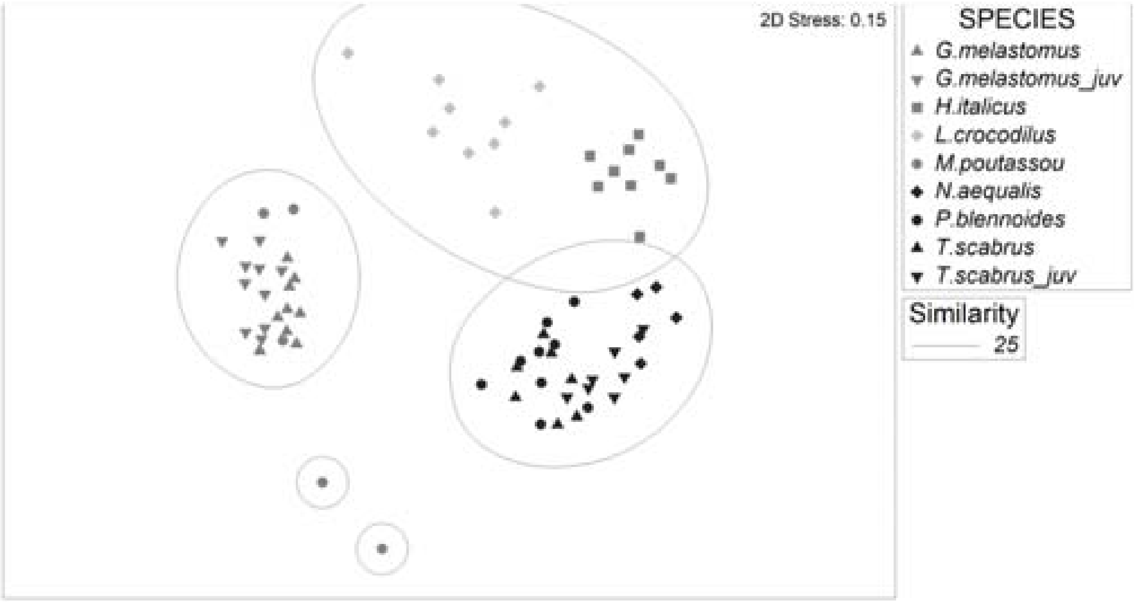

Fig. 2. MDS ordination plot of stomach contents of the different fish species per haul, based on Bray-Curtis resemblance matrix of square-root transformed prey weight data. Data points are identified by species and by trophic guilds from the literature (Table 1): black = benthos feeders; dark grey = non-migratory macroplankton feeders; light grey = migratory macroplankton feeders. Circles indicate cluster overlay at 25% of similarity.

Combining the results of cluster analysis with the MDS ordination we distinguish three groups at 25% similarity. Species classified as benthos feeders (*B*) from the literature (*P. blennoides*, *Nezumia aequalis* and both categories of *T. scabrus*) cluster together at the right side of the MDS, while non-migrator macroplankton feeders (*nmM*) (*Micromesistius poutassou* and both size classes of *Galeus melastomus*) cluster on the other side. The small macrourid *Hymenocephalus italicus*, classified *a priori* as *nmM*, groups with the migrator-macroplankton feeder (*mM*) *Lampanyctus crocodilus*, constituting a group that comprises the *small-sized* fish species. All groups of species obtained by cluster analyses were statistically distinct (ANOSIM R=0.897; p<0.001).

SIMPER reveals that dissimilarities between all the groups obtained from cluster analyses are well above 75%, and greatest dissimilarities are between the group containing benthic feeder species and that containing the large *nmM M. poutassou* and *G. melastomus* (90.24%). For benthic feeders, 51.50% of the diet was accumulated by the benthic shrimp *C. macandreae*, the hyperbenthic isopods *M. atlanticus* and *N. borealis*, hyperbenthic eusirid gammariids and the crab *Monodaeus couchii.* For the *nmM*, 54.09% of the diet was characterised by pasipheid shrimps and mesopelagic fish, mainly myctophids. Main prey of the group of small fish (i.e. *L. crocodilus* and *H. italicus*) were the hyperbenthic mysid *Boreomysis arctica* and the hyperbenthic isopod *N. borealis*, which represented 53.73% of the diet.

3.2.2. *Dietary diversity*

The greatest dietary diversities were observed among benthos feeders, with *H'* ranging from 4.18 bits in *P. blennoides* to 4.84 bits in *N. aequalis*. Dietary diversities in adults and juveniles of *T. scabrus* were 4.60 and 4.66 bits respectively. For macroplankton feeders, diversities were usually lower, with the lowest diversity among all species observed in *M. poutassou* (*H'*=2.57 bits). Diet diversity among adults and juveniles of *G. melastomus* were 3.86 and 4.09 bits respectively. Diet diversity among small fish were within the ranges found in non-migrator macroplankton feeders: in *L. crocodilus* diet diversity was 3.37 bits and in *H. italicus* it was 3.91 bits.

3.3. *Intraspecific seasonal variations*

3.3.1. *Seasonal trends in diets*

Statistical significance estimates for seasonal variations in dietary composition can be found in Table 2.

Table 2. Results of PERMANOVA pair-wise tests comparing diet composition of each fish species in consecutive seasons based on 9999 permutations. *t* values and p-level significance (*p<0.05; **p<0.01; ***p<0.001; *n.s.* = not significant) indicated.

Species	Feb-Apr	Apr-Jul	Jul-Oct	Oct-Feb
N. aequalis	1.75*	1.42*	*n.s.*	1.65*
P. blennoides	*n.s.*	*n.s.*	*n.s.*	*n.s.*
T. scabrus (adults)	*n.s.*	1.57*	*n.s.*	*n.s.*
T. scabrus (juveniles)	2.39***	1.77*	1.65*	2.08**
H. italicus	2.21*	1.72*	*n.s.*	*n.s.*
L. crocodilus	*n.s.*	1.46*	*n.s.*	1.56*
G. melastomus (adults)	1.60*	*n.s.*	2.19***	1.60*
G. melastomus (juveniles)	1.68*	1.50*	1.68*	1.61*
M. poutassou	*n.s.*	*n.s.*	1.82*	2.28**

Benthos feeders

Consumption of polychaetes was rather constant throughout the year in all benthos feeders.

Seasonal changes in diet of *N. aequalis* were significant (*pseudo-*$F_{3,87}$= 2.61; p<0.001), and stomach contents differed significantly between all consecutive samplings (p<0.05), except between June/July and October. The most abundant prey in the diets of *N. aequalis* during the whole study were benthic polychaetes and gammarids (especially *Rhachotropis* spp.), the former being more abundant in the first half of the year and the latter in the second half (Fig. 3). Hyperbenthic isopods were also consumed all through the year, especially in April (*N. borealis*) and October (*M. atlanticus*). Ophiuroids were important diet items in February, as were *C. macandreae* from February to June/July and mysids (namely *B. arctica*) in October.

Intestine content of *P. blennoides* was homogenous through the whole period, and no significant changes were observed. Main prey in the four periods sampled were the brachyuran crab *M. couchii* and hyperbenthic isopods, mainly represented by *N. borealis* from February to June/July and by *M. atlanticus* in October (Fig. 3). *Boreomysis arctica*, benthic decapods (*C. macandreae* and *Alpheus glaber*) and benthic polychaetes (families Polyonidae and Nephtyidae) were secondary prey. Additionally, non-mesopelagic fish were consumed from February to June/July.

Intestine contents of adults of *T. scabrus* varied seasonally (*pseudo-*$F_{3,148}$=2.43;

$p<0.05$), although most prey consumed were present in all four seasons, i.e. *M. couchii*, hyperbenthic isopods, namely *N. borealis*, *C. macandreae*, polychaetes, hyperbenthic gammarids and non-mesopelagic fish (Fig. 3). In February *N. borealis* was the dominant prey, and, in addition to the species mentioned, we found *Pasiphaea* spp. Although changes to April were not significant, *N. borealis* was replaced by *M. couchii* and *Pasiphaea* spp. by mysids (mainly *B. arctica*), which were also part of the diet in June/July and October. Dietary changes from April to June/July were statistically significant. In June/July, isopods, *C. macandreae* and polychaetes were the most abundant prey. Changes to October were not significant, although *Pasiphaea* spp. were again important prey.

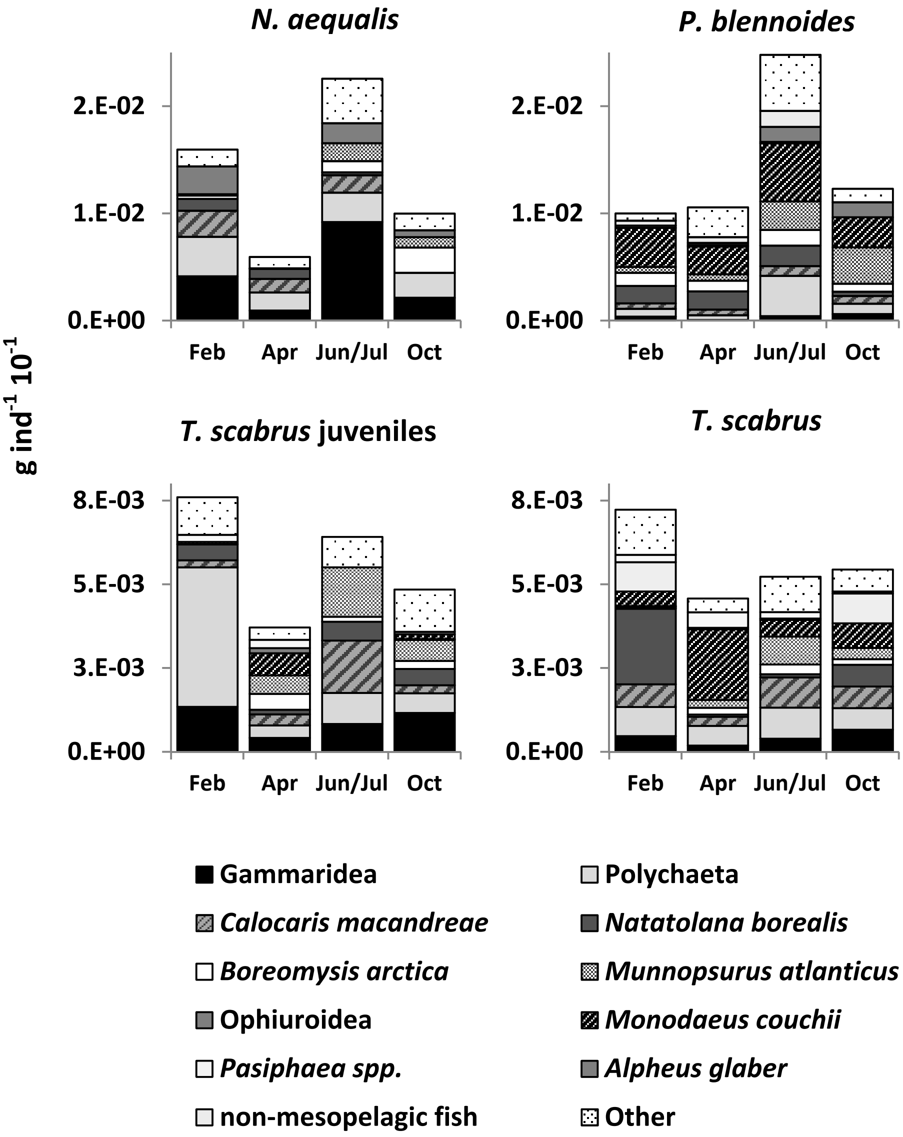

Fig. 3. Diet composition (by weight) of benthos feeder fishes in each sampling period.

Diet also changed significantly for juveniles of *T. scabrus* (*pseudo*-$F_{3,111}$=3.64; p<0.001) and varied between all consecutive samplings, as occurred in *N. aequalis*. Benthic polychaetes were consumed in all seasons, and constituted more than half of the diet in February, when hyperbenthic gammarids and cyprinid ostracods were also important (Fig. 3). In April, no prey item dominated and diet was constituted of hyperbenthic gammarids, *C. macandreae*, *M. couchii*, hyperbenthic isopods (mainly *M. atlanticus*), benthic polychaetes and mysids (essentially *B. arctica*). *Munnopsurus atlanticus* and *C. macandreae* acquired greater importance in June/July. In October, *C. macandreae* was replaced by hyperbenthic gammarids.

Non-migrator macroplankton feeders

The diet of adults of *Galeus melastomus* was mostly composed of *P. multidentata*, *M. couchii*, cephalopods and mesopelagic fish (Fig. 4). Adults of *G. melastomus* changed diet seasonally (*pseudo*-$F_{3,145}$=3.07; p<0.001). In February the diet was dominated by pasipheid shrimps with brachyuran crabs in second place, but a great variety of prey were observed. Diet significantly changed to April, when *G. melastomus* mainly consumed cephalopods and brachyuran crabs, with small changes in June/July to consumption of more pelagic prey (i.e. pasipheids and mesopelagic fish). In October, diet was strongly dominated by pasipheid shrimps. Dietary changes between October and February were also statistically significant.

The diet of juvenile *G. melastomus* also changed seasonally (*pseudo*-$F_{3,147}$=2.433; p<0.001), and varied significantly between all consecutive samplings. Consumption of pasipheids was rather constant during the whole year (Fig. 4).Mesopelagic fish, essentially the mictophids *L. crocodilus* and *Ceratoscopelus maderensis*, were the most important prey in the first half of the year. In February we also observed considerable amounts of cephalopods, which were partially substituted by the euphausiid *M. norvegica* in April. Cephalopods were the second ranking prey after pasipheid shrimps in June/July, and in October the diet was dominated by *M. norvegica*.

Diet of *Micromesistius poutassou* also changed seasonally (*pseudo*-$F_{3,51}$=2.62; p<0.001), although samples from October were the only ones statistically different from the rest. Mesopelagic fish (mainly myctophids) were very important prey from February to June/July, constituting virtually the entire diet in February (Fig. 4). In April, mesopelagic fish were secondary and the main prey were pasipheids, a ranking that reversed again in June/July. Sergestids dominated in October.

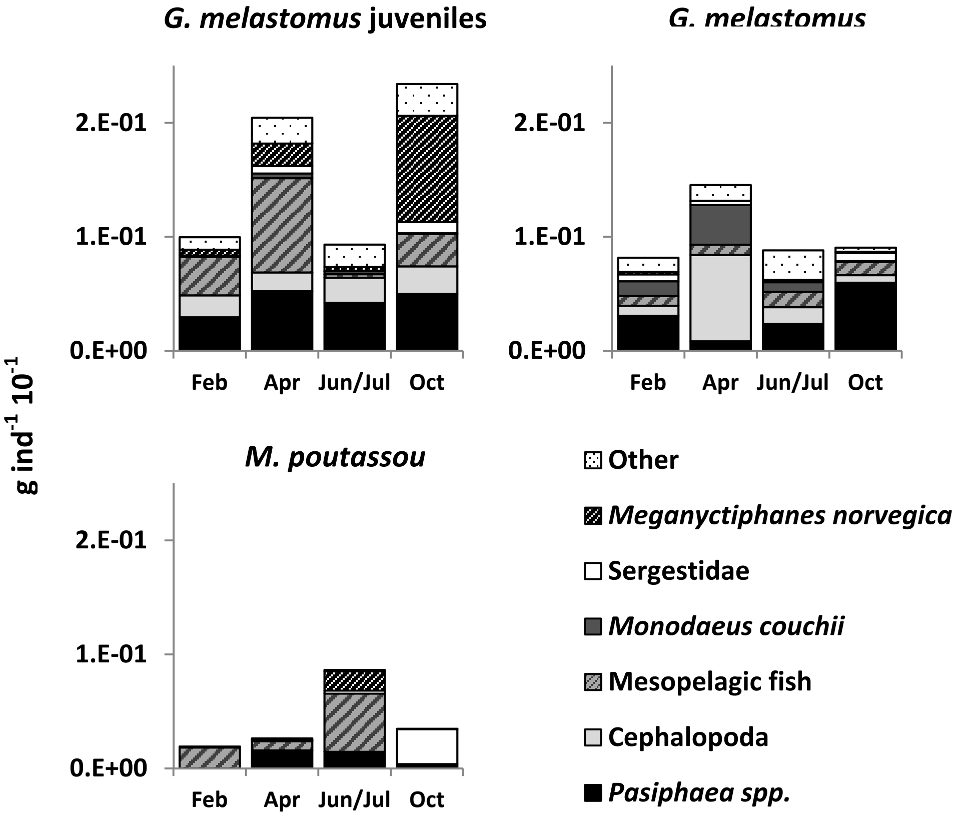

Fig. 4. Diet composition (by weight) of non-migratory macroplankton feeder fishes in each sampling period.

Small-sized fish

Hyperbenthic prey, namely *B. arctica*, gammarids and *N. borealis*, were the main prey of *H. italicus* all year around (Fig. 5), but dietary composition changed seasonally (*pseudo-*$F_{3,108}$=2.65; p<0.01). Their diet in February and April consisted of the prey above mentioned, with changed proportions between those two periods being statistically significant. That difference is attributable to the presence of calanoid copepods in stomach contents in February and to a marked dominance of *B. arctica* in April. Also, gammarids consumed in February were oedicerotids, lyssianassids and *Rhachotropis* spp., but in April we only observed lyssianassids. Changes were also significant from April to June/July, when the shrimp *Processa canaliculata* (category "Other" in Fig. 5), some cumaceans and calanoid copepods were incorporated as prey. Consumption of calanoids persisted to October, and *P. canaliculata* was replaced by euphausiids, essentially *M. norvegica*.

Diet of *L. crocodilus* also changed seasonally (*pseudo-*$F_{3,146}$=1.75; p<0.05), although main prey were always sergestid shrimps, euphausiids and *B. arctica* (Fig. 5). Changes were not significant between February and April but the euphausiid *M. norvegica* dominated in February and sergestid shrimps in April. Changes from April to June/July were significant, with *B. arctica* and other unidentified mysids (category "Other" in Fig. 5) increasing in the diet. *Nematoscelis megalops* was consumed in June/July and *M. norvegica* was consumed again in October. Sergestids also regained importance in October, although not significantly.

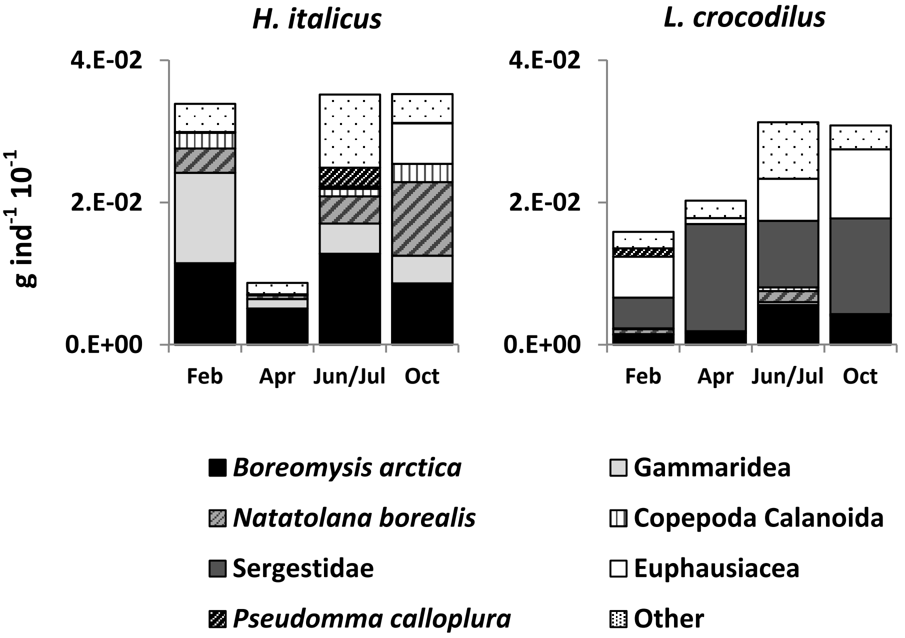

Fig. 5. Diet composition (by weight) of small-sized fish species in each sampling period.

3.3.2. *Seasonal trends in fullness*

The interaction between the two factors (sex and survey) of the two-way ANOVA performed on fullness of each species was never significant ($p>0.05$). Likewise, no significant pair-wise comparisons were found, thus fullness of males and females could be analysed jointly.

Fullness of the benthos feeder *N. aequalis* was greatest in June/July and October and lowest in February and April (Fig. 6), although the changes were not statistically significant. Fullness of *P. blennoides* peaked in June/July and significantly declined afterwards to October, remaining low during the rest of the year. For both size classes of *T. scabrus*, fullness was greatest in February, and was low the rest of the year, changes not being significant. Fullness of *T. scabrus* was lower than that of the other benthos feeders.

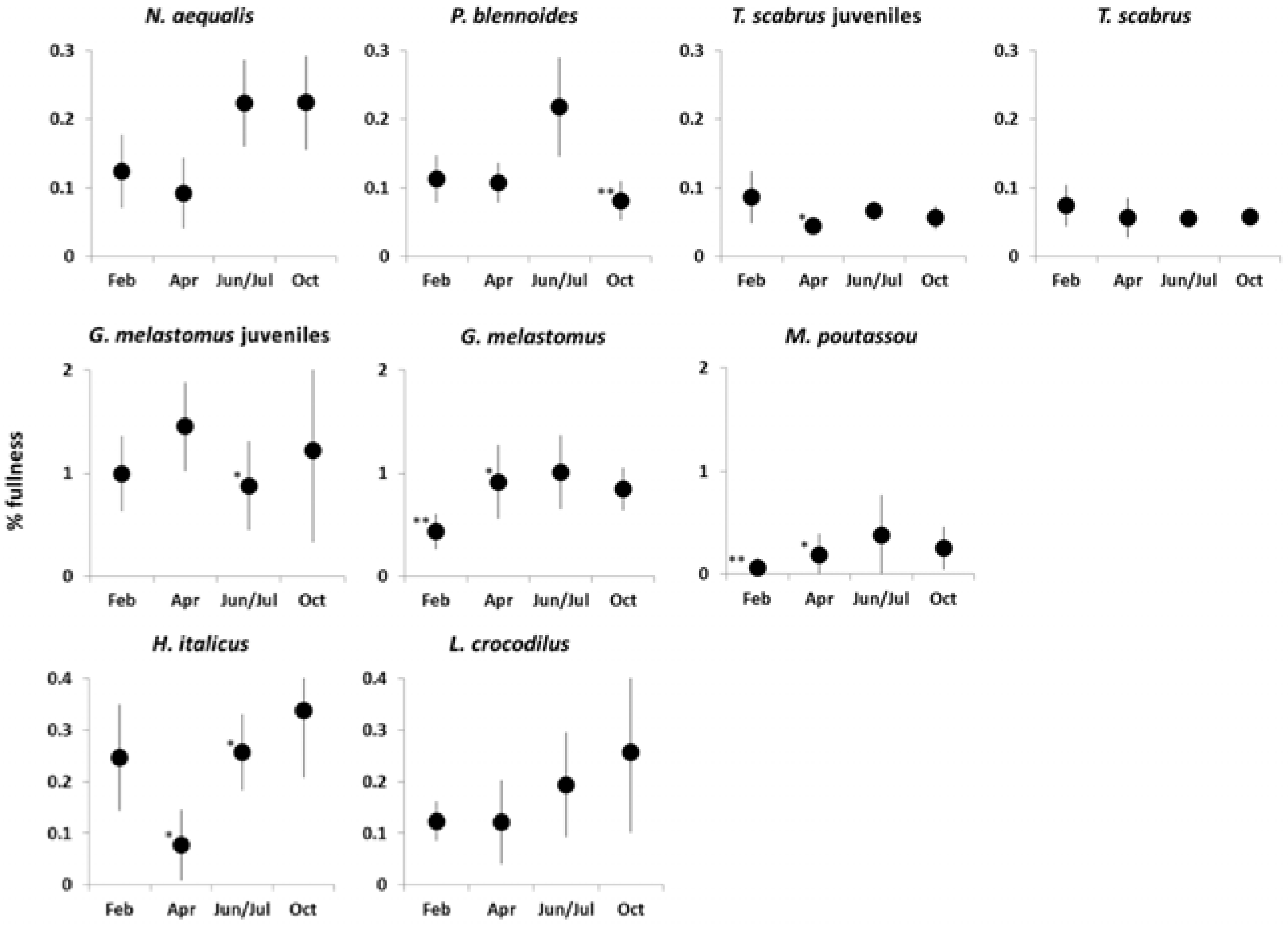

Fig. 6. Seasonal trends in %fullness (F) of the different fish species. Vertical bars indicate 95% confidence intervals. Asterisks indicate significant differences with preceding sampling: *p<0.05; **p<0.01; ***p<0.001.

Adults of *G. melastomus* and *M. poutassou* both presented greatest fullness in June/July (Fig. 6), although these maxima were not significant. Relatively high fullness was maintained in October, and significantly lowest fullness occurred in February for both species. Fullness of *G. melastomus* was greater than that of *M. poutassou*. Fullness of juveniles of *G. melastomus* was generally greatest among all *nmM* species, peaking in April and significantly decreasing to a minimum in June/July.

Hymenocephalus italicus and *L. crocodilus* followed a similar temporal pattern of increasing fullness from April to October (Fig. 6); minimum fullness in April was significant in *H. italicus*. In February fullness was high in *H. italicus* but low in *L. crocodilus*.

3.3.3. *Seasonal trends in C/N ratio of muscle*

Results on C/N are summarized in Table 3. The muscle C/N of *N. aequalis* was significantly greater in October than in February, and remained similar in other seasons. For this macrourid, we did not have results in June/July. Both *P. blennoides* and *T. scabrus* had greatest muscle C/N in April, followed by significant decreases to minima in June/July. *Galeus melastomus* had greatest C/N in June/July and lowest C/N in April, the decrease from February to April being the only significant change. Muscle C/N of *M. poutassou* remained relatively high from February to June/July, and then was significantly lower in October. Its C/N values for October and February differed significantly. Muscle C/N of *H. italicus* remained constant throughout the whole period. In contrast, *L. crocodilus* C/N increased significantly from February to April, increased more by June/July, and then decreased significantly such that C/N was similar in October and February.

Table 3. C/N ratio of muscle tissue of the different fish species by season. Feb=February; Apr=April; Jun/Jul=June/July; Oct=October.

	Feb	Apr	Jun/Jul	Oct
G. melastomus	2.29	2.13	2.38	2.23
H. italicus	3.92	4.04	3.90	3.83
L. crocodilus	2.70	3.35	3.86	2.79
M. poutassou	2.34	2.51	2.26	1.19
N. aequalis	2.29	2.25		2.78
P. blennoides	1.95	2.45	1.85	2.30
T. scabrus	2.94	3.24	2.09	2.95

3.3.4. *Seasonal trends in biological indices*

Out of the seven species studied, five presented a trend of maximum HSI followed by maximum GSI (Fig. 7). In *L. crocodilus* and *T. scabrus* the pattern was the opposite. Among species feeding upon similar trophic resources, peaks in GSI usually occurred at different times.

Benthos feeders

Greatest GSI of the benthos feeders *N. aequalis* and *T. scabrus* were observed in February, with the significant increases from October to February. The GSI of *N. aequalis* decreased gradually to June/July, but not significantly, and that of *T. scabrus* decreased abruptly and significantly in April (Fig. 7). In contrast, GSI of *P. blennoides* was low from February to June/July, then peaked in October, presenting wide sampling variation in that sampling period. The HSI values of benthos feeders usually followed temporal trends opposite to those of their GSI values. Oscillations in HSI of *N. aequalis* were not very large, but greatest HSI occurred in October, when low GSI was observed. During winter, HSI declined significantly to its lowest values in February, simultaneous with the year’s highest GSI. In *P. blennoides*, HSI was low from February to April, increased significantly to June/July, and then decreased again by October. *Trachyrhynchus scabrus* did not follow the same trends. Its high GSI in February was not accompanied by low HSI, but the February HSI was significantly lower than in April when GSI had strongly decreased. HSI decreased significantly after April to an October minimum.

Non-migrator macroplankton feeders

Galeus melastomus had its significantly highest GSI in October, and a secondary peak was observed in April (Fig. 7). The GSI of *M. poutassou* was significantly lowest in April, maintained to June/July and increased from October to February. The HSI of *G. melastomus* changed in parallel with its GSI, though a significant maximum was observed in April. The lowest HSI of *M. poutassou* occurred in February and the greatest in June/July, though changes in that index were not significant.

Small-sized fish

Hymenocephalus italicus had a profile of high GSI from February with a slightly greater, but significant, maximum in June/July. Its GSI then decreased sharply and significantly by October (Fig. 7). The GSI of *L. crocodilus* was greatest in February, lower in April and

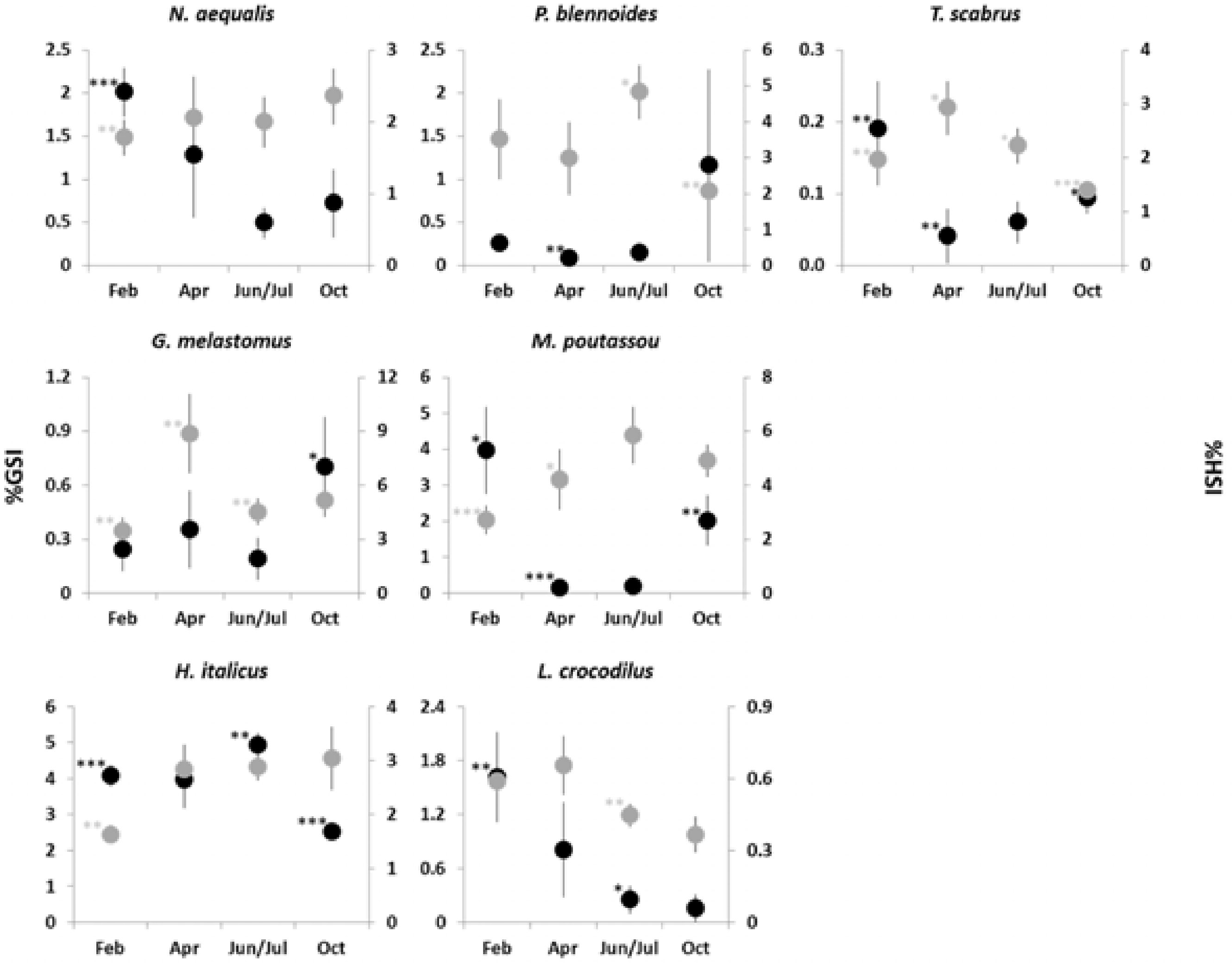

Fig. 7. Seasonal trends in gonadosomatic index (%GSI) (black) and hepatosomatic index (%HSI) (grey) of females of the different fish species. Vertical bars indicate 95% confidence intervals. Asterisks indicate significant differences with preceding sampling: *$p<0.05$; **$p<0.01$; ***$p<0.001$.

very low in June/July and October. The HSI of *H. italicus* was high from April to October and significantly low in February. The relationship between HSI and GSI of *L. crocodilus* was distinct from all other species in the present study. Its HSI was high in February and April, simultaneous with high GSI; then both indexes were significantly low in June/July and October.

3.4. *Seasonal changes in interspecific relationships*

Although dietary overlap values between species were rather low throughout the whole year, lowest overlap between species from all the feeding groups was generally in February (Table 4). In macroplankton feeders, dietary overlap between juveniles and adults of *G. melastomus* and was greater in February and June/July, and of juveniles of *G. melastomus* and *M. poutassou* was greater in April and October. Between both adults of *G. melastomus* and *M. poutassou* it was greatest in June/July. In benthos feeders and in small-sized fish, overlap was generally lower in February and April and greater in June/July and October.

3.5. *Drivers of fullness*

The generalised linear models (GLMs) performed on fullness data for each trophic group identified by the hierarchical cluster analysis revealed that fullness of benthos feeders was negatively correlated to density of the individuals and to abundances of mysids and benthic polychaetes (Table 5). In contrast, benthos-feeders fullness was positively related to surface production two months before the sampling and to TOC% in sediments. The GLM for benthos feeders explained 53% of the total variation. The model for the non-migrator macroplankton feeders *G. melastomus* and *M. poutassou* explained 64% of the total variation and revealed that fullness varied from species to species, being lowest in *M. poutassou* and greatest in juveniles of *G. melastomus* (Table 5). Additionally, lipids in the sediment were inversely correlated with fullness, while positive correlation was observed between fullness and the abundance of *Pasiphaea multidentata*. For *H. italicus* and *L. crocodilus*, the GLM explained 80% of the total variation and included C/N ratio and lipids as explanatory variables, the former positively and the latter negatively correlated to fullness (Table 5).

3.6. *Relationship between biological cycle and food availability*

The GLM performed on the GSI of females of *N. aequalis* explained 63% of the total variation. Density, weight and previous HSI were positively related to GSI, and total organic carbon in sediments in the precious sampling was negatively correlated with

Table 4. Diet overlap for the seven benthopelagic fish species using Schoener's Index by season. Gmel=*G. melastomus*; Gmelj=*G. melastomus* juveniles; Hita=*H. italicus*; Lcro=*L. crocodilus*; Mpou=*M. poutassou*; Naeq=*N. aequalis*; Pble=*P. blennoides*; Tsca=*T. scabrus*; Tscaj=*T. scabrus* juveniles.

FEBRUARY	Gmel	Gmelj	Hita	Lcro	Mpou	Naeq	Pble	Tsca	Tscaj
Gmel	1	0.57	0.00	0.24	0.13	0.02	0.28	0.23	0.04
Gmelj		1	0.00	0.30	0.34	0.00	0.07	0.16	0.02
Hita			1	0.19	0.00	0.30	0.26	0.18	0.23
Lcro				1	0.06	0.10	0.18	0.07	0.06
Mpou					1	0.00	0.03	0.03	0.02
Naeq						1	0.25	0.34	0.42
Pble							1	0.38	0.25
Tsca								1	0.32
Tscaj									1

APRIL	Gmel	Gmelj	Hita	Lcro	Mpou	Naeq	Pble	Tsca	Tscaj
Gmel	1	0.28	0.00	0.10	0.19	0.04	0.26	0.29	0.22
Gmelj		1	0.00	0.12	0.62	0.04	0.11	0.03	0.05
Hita			1	0.10	0.02	0.08	0.17	0.09	0.19
Lcro				1	0.12	0.01	0.13	0.07	0.10
Mpou					1	0.02	0.08	0.03	0.02
Naeq						1	0.31	0.20	0.32
Pble							1	0.45	0.50
Tsca								1	0.59
Tscaj									1

JUNE/JULY	Gmel	Gmelj	Hita	Lcro	Mpou	Naeq	Pble	Tsca	Tscaj
Gmel	1	0.61	0.01	0.02	0.39	0.01	0.28	0.18	0.05
Gmelj		1	0.02	0.08	0.30	0.01	0.16	0.14	0.04
Hita			1	0.30	0.01	0.32	0.23	0.26	0.32
Lcro				1	0.04	0.12	0.12	0.16	0.12
Mpou					1	0.01	0.04	0.01	0.01
Naeq						1	0.21	0.39	0.42
Pble							1	0.55	0.38
Tsca								1	0.66
Tscaj									1

OCTOBER	Gmel	Gmelj	Hita	Lcro	Mpou	Naeq	Pble	Tsca	Tscaj
Gmel	1	0.47	0.02	0.11	0.28	0.02	0.05	0.21	0.05
Gmelj		1	0.17	0.24	0.54	0.00	0.03	0.21	0.06
Hita			1	0.26	0.17	0.33	0.14	0.25	0.32
Lcro				1	0.62	0.13	0.11	0.06	0.12
Mpou					1	0.00	0.02	0.09	0.02
Naeq						1	0.33	0.35	0.57
Pble							1	0.46	0.48
Tsca								1	0.57
Tscaj									1

Table 5. Generalised Linear Models performed on fullness of fish considering the trophic groups obtained by cluster analyses. D.f. = degrees of freedom. $PPC_{2months}$=Phytoplankton pigment concentration at surface 2 months before the sampling; TOC_{sed}%=total organic carbon in sediments; $Lipids_{sed}$%=lipids in sediment; Polychaetes=density of polychaetes; Mysids=density of mysids; *P. multidentata*=density of *Pasiphaea multidentata*.

	Explained dev.	Residual dev.	% Explained	*F*	Sign of correlation	p-value
Benthos feeders						
NULL		0.003				
Density	0.0004	0.003	12.88	8.834	(-)	0.006
$PPC_{2months}$	0.0004	0.002	14.00	9.603	(+)	0.004
Polychaetes	0.0003	0.002	11.18	7.670	(-)	0.009
Mysids	0.0003	0.002	8.29	5.686	(-)	0.023
TOC_{sed}%	0.0002	0.001	7.03	4.821	(+)	0.035
			53.36			
D.f. 37						
AIC = -265.27						
Small fish species						
NULL		0.009				
Muscle C/N	0.0032	0.005	59.32	16.496	(+)	0.001
$Lipids_{sed}$%	0.0011	0.004	20.88	5.807	(-)	0.025
			80.21			
D.f. 24						
AIC = -137.63						
Non-migrator macroplankton feeders						
NULL		0.035				
Species	0.0155	0.020	43.81	16.260		0.000
$Lipids_{sed}$%	0.0032	0.017	8.93	6.627	(-)	0.016
P. multidentata	0.0039	0.013	10.89	8.081	(+)	0.008
			63.63			
D.f. 31						
AIC = -147.35						

GSI (Table 6). The GLM for *P. blennoides* revealed that heavier individuals had greater GSI, and that HSI enhanced GSI growth afterwards. Also, greater GSI was observed with low surface production in the previous month. The GLM for *P. blennoides* explained 56% of total deviance. A GLM revealed that the GSI of *T. scabrus* was greater in larger animals, after greater availability of lipids in the sediments and one month after greater surface production. Instead, greater availabilities of TOC in

Table 6. Generalised Linear Models performed on gonadosomatic index of the seven species of benthopelagic fish. Species: Gmel=*G. melastomus*; Hita=*H. italicus*; Lcro=*L. crocodilus*; Mpou=*M. poutassou*; Naeq=*N. aequalis*; Pble=*P. blennoides*; Tsca=*T. scabrus*. *F*-value and significances specified (*p<0.05; **p<0.01; ***p<0.001). Sign of the correlation indicated in parentheses. D.f. = degrees of freedom. Factors: Density= density of each fish species; PPC$_{1\ \text{month}}$=Phytoplankton pigment concentration at surface on month before the sampling; TOC$_{\text{sed}}$%=total organic carbon in sediments; Lipids$_{\text{sed}\%}$=lipids in sediment; *M. norvegica*=density of *Meganyctiphanes norvegica*; 1 survey=value from the preceding sampling survey; densities of different potential prey sampled with the bottom trawl also indicated.

	Species						
Factor	Naeq	Pble	Tsca	Hita	Lcro	Gmel	Mpou
Size			64.51^{***} (+)	4.55^{*} (+)	14.89^{***} (+)		
Weight	4.95^{*} (+)	53.18^{***} (+)				58.31^{***} (+)	
Density	32.05^{***} (+)			4.49^{*} (-)		7.92^{**} (+)	
Fullness$_{\text{1survey}}$				15.05^{***} (-)			
HSI$_{\text{simult.}}$					8.34^{**} (+)		
HSI$_{1\ \text{survey}}$	34.31^{***} (+)	5.30^{*} (+)					7.45^{**} (+)
Muscle C/N							49.24^{***} (-)
PPC$_{1\ \text{month}}$		4.55^{*} (-)	4.38^{*} (+)			4.50^{*} (-)	13.31^{***} (+)
Lipids$_{\text{sed}}$%$_{\text{1survey}}$			4.15^{*} (+)	9.24^{**} (+)			
TOC$_{\text{sed}}$%$_{1\ \text{survey}}$	3.08^{*} (-)		34.51^{***} (-)				
M. norvegica$_{\text{1survey}}$					132.32^{***} (+)		
% explained	62.67	55.77	68.70	33.22	74.23	68.16	62.50
AIC	-201.56	-209.18	-146.30	-316.42	-269.68	-188.77	-164.05
D.f.	46	53	53	71	57	36	45

sediments were unfavourable for GSI increase. The GLM explained 69% of total GSI deviance of *T. scabrus*.

The GLM of *G. melastomus* explained 68% of the total deviance of its GSI. Heavier individuals of *G. melastomus* had greater GSI, and individuals with greater GSI were associated with greater densities of the species (Table 6). GSI was greater after greater surface production. In the case of *M. poutassou*, the GLM explained 62% of the total deviance, and the model showed positive relationships between GSI and previous surface production and HSI, and negative relationships between GSI and muscle C/N.

The GLM for *H. italicus* GSI explained 33% of its total deviance, showing that its GSI was greater at lower population densities. Its GSI was also greater in larger individuals and after greater availability of lipids in the sediment and lower fullness (Table 6). For *L. crocodilus*, the GLM showed that greater HSI was related with greater GSI, which was also observed in larger individuals. Greater availability of *M. norvegica* favoured the GSI increase. The GLM model explained 74% of the total GSI deviance of *L. crocodilus*.

4. Discussion

4.1. *Feeding guilds*

As already reported for slope megafauna of the NW Mediterranean, both prey and predator size have a strong influence on the diets of fish (Macpherson, 1981; Carrassón and Cartes, 2002). In addition, fish species feed at different levels in the water column above the sea bottom (Carrassón and Cartes, 2002; Papiol et al., 2013). Diets of deep-sea fish are diversified, and species exploit mesopelagic, hyperbenthic and benthic prey as resources. However, each species showed some preference towards one of these prey taxa. Hence, trophic guilds/groups can be deduced, as shown by Carrassón and Cartes (2002) from diets and by Papiol et al. (2013) from stable isotope ratios. We obtained three trophic groups consisting in large benthic feeders, large macroplankton feeders and small fish, the latter mainly feeding on hyperbenthos and small zooplankton. In general, we obtained results for fish diets that agree with previous studies (see Table 1). The only exception was the macrourid *Hymenocephalus italicus*, sometimes considered as a non-migrator macroplankton feeder (*nmM*) (e.g. Macpherson, 1979), which was found to feed mainly on hyperbenthic fauna (mysids, gammarids and isopods) with occasional consumption of the macroplanktonic euphausiid *Meganyctiphanes norvegica.* The latter events must be associated with aggregation of this prey close to the bottom at the end of its life cycle (Cartes et al., 2010a). In general, our dietary analyses point to greater contributions of hyperbenthos to fish diets than previously thought (e.g. *Trachyrhynchus scabrus*; Macpherson, 1979), most likely due to the extensive knowledge of hyperbenthic fauna achieved for the deep Mediterranean in recent years (Cartes et al., 2001; 2011). For a given species, trophic segregation among coexisting individuals of different sizes is also important (Carrassón and Cartes, 2002), probably decreasing intraspecific competition for food. Adults, greater in size and with higher natatory capacity, usually feed on larger and more mobile prey (e.g. *P. blennoides*: Macpherson, 1978; Gallardo-Cabello, 1979), as observed in the macrourid *Trachyrhynchus scabrus* and the shark *Galeus melastomus*, the latter with adults preying on cephalopods.

Feeding intensity (fullness) of *nmM* feeders was greater than that of benthos feeders (*B*), especially among sharks. Fish that feed on macroplankton have greater natatory capacity for foraging in the water column; they are active swimmers with higher metabolic rates (Koslow, 1996; Maynou and Cartes, 1998; Drazen, 2002b). Greater feeding intensity may supply the necessary energy for maintaining higher metabolism. In agreement, high daily rations have been found previously in the sharks *G. melastomus* and *Etmopterus spinax* (Madurell and Cartes, 2005) in the Mediterranean. Mesopelagic prey are also more energy-rich than benthic species (Blaber and Bulman, 1987; Zagami et al., 1991; Madurell and Cartes, 2005; Brey et al., 2010), which may contribute to satisfying the higher energy demands of swimming fish.

4.2. *Seasonal trophic dynamics*

Interspecific dietary overlap was in general low among the mid-slope fish, and we observed a pattern of lowest dietary overlap concurring with lowest feeding intensities (e.g. among small-sized fish in April, among benthic and macroplankton feeders in February). Contrary to the trends found by Macpherson (1981), overlap among benthos feeders increased after spring (summer/autumn), coinciding with pronounced changes in dietary composition. The same temporal trends were observed among the small-sized fish *L. crocodilus* and *H. italicus*. This pattern seems related with a greater contribution of hyperbenthos to their diets after spring, when it is more available as previously reported by Madurell and Cartes (2006) for some species in the Mediterranean Sea. Still, species from each of the feeding guilds (i.e. large benthic feeders and small-sized fish) shifted diets to exploitation of distinct taxa. Among benthic feeders, greater consumption of hyperbenthic gammarids and isopods and of the benthic decapod *Calocaris macandreae* was detected in summer, matching their greater availability (Cartes, 1998a; Mamouridis et al., 2011). In contrast, small-sized fish, increased ingestion of more mobile hyperbenthos (i.e. *Boreomysis arctica* and *Pseudomma calloplura*: Cartes and Sorbe, 1995) and nektobenthic species (i.e. *P. canaliculata*: Cartes et al., 1994) in summer and preyed more importantly upon the mesopelagic euphausiid *M. norvegica* in autumn (Sardou et al., 1996; Cartes et al., 1998a; 2010). Increased dietary overlap in autumn due to consumption of *M. norvegica* has been reported previously, and was attributed to the consumption of a resource that peaks in abundance (Macpherson, 1981; Cartes, 1998b). Consistently, juveniles of *G. melastomus* also preyed upon *M. norvegica* in autumn. Among adults of non-migrator macroplankton feeders (*G. melastomus* and *M. poutassou*) great size differences led to a generalised low dietary overlap. This was greatest in summer concurring with greatest feeding intensities (Cartes et al., 1998a; 2010). Main dietary changes among macroplankton feeders were observed afterwards, in autumn, when this assemblage shifted diets to feed mainly on mesopelagic crustaceans. We still observed the influence of size in this feeding pattern (Carrassón and Cartes, 2002), with the larger predator *G. melastomus* preferentially consuming *Pasiphaea multidentata* and the smaller *M. poutassou* preying upon sergestid shrimps

The above discussed peaks in availability of some prey, presumably led to greater feeding intensities (fullness) in summer that usually persisted to autumn. Consistently, temporal trends in *F* were related with indicators of food sources of such prey. Among benthos feeders, feeding intensity was greater two months after the peak of surface production (PPC) when there was greater TOC% in the sediments. That likely supports increases of some taxa (e.g. small copepods, foraminiferans, meiofauna in general) that quickly respond to nutrient inputs (Buscail et al., 1990; Gooday and Turley, 1990, Danovaro, 1995; Cartes et al., 2002; 2003). That initial trophic step may in turn increase densities of carnivorous/omnivorous hyperbenthos (e.g. the isopod *Munnopsurus atlanticus*; amphipods: *Rhachotropis* spp.) and detritus feeders (*C. macandreae*) (Cartes et al., 2001) in summer. Those are important prey of fish such as *N. aequalis*. Thus, fresh inputs of organic matter to bathyal depths are quickly transformed (in *ca.* 2 months) into food for benthic-feeding fish by a variety of pathways through trophic webs. Additionally, some key prey (polychaetes and mysids), representing intermediate steps in the transfer of energy through trophic webs, entered significantly as explanatory variables of *F* in GLM models for benthos feeders. The only exception to the summer maxima of feeding intensity was *T. scabrus,* which exhibited no remarkable seasonal changes in feeding intensity (based on intestine contents). Probably due to the large number of pyloric caecae of *T. scabrus* (Carrassón and Matallanas, 1994) its intestine contents were rather liquidified (Buddington and Diamond, 1986) and only hard body parts of prey remained. Hence, feeding intensity may not be properly estimated in *T. scabrus*. Suggesting likely seasonal variation, analysis of values of stomach fullness of adults of *T. scabrus* showed lowest feeding intensity in February (0.03%) and greatest in October (0.57%). Unfortunately, non-everted specimens were insufficient in April and June/July. In contrast, lesser digestion of intestine content in *P. blennoides* (with lower pyloric caeca density), allowed a reliable estimation of feeding intensity in that species with a peak in summer. As further evidence of reliability of our gut content estimates, observed seasonal homogeneity in the dietary composition of *P. blennoides* is in agreement with previous studies (Macpherson, 1977).

The *F* of small-sized fish was basically related with C/N in muscle and lipids in sediments, the latter also being important for macroplankton feeders. Greater *F* in *H. italicus* and *L. crocodilus* was linked to enhanced storage of lipids in muscle (C/N ratio), indicating that increased ingestion allowed a relatively quick storage of energy in the muscle tissue. Also, *F* of small-sized fish and of non-migrator macroplankton feeders increased after lipid deposition in sediments. Lipids are easily degradable, highly energetic compounds abundant in phytodetritus (Fabiano et al., 1993; 2001), which constitutes the main food for the macroplanktonic community (Fanelli et al., 2011b). Hence, increases in the availability and subsequent consumption of macroplanktonic prey after lipid deposition are expected. Consistently, trends in abundance of the mesopelagic decapod *P. multidentata* were positively correlated to fullness of macroplankton feeders, pointing to greater exploitation of a resource when it is more available. Besides, greater *F* among small fish coincided with greater consumption of mesopelagic crustaceans. The high lipids, and therefore high energetic content, of planktonic macrofauna (Blaber and Bulman, 1987; Madurell and Cartes, 2005; Brey et al., 2010) may be important in supplying the necessary energy for maintaining the high metabolism of their predators, as mentioned above and in line with results on predator carbon stable isotope ratios (Papiol et al., 2013). Exploitation of macroplankton when abundant was not only restricted to macroplankton feeders, and some species (e.g. *T. scabrus* or *H. italicus*) seasonally changed trophic guild to use this largely available food source (Cartes, 1998b). Generalised increase of dependence of the benthopelagic community of the middle slope of the Catalan Sea on mesopelagic production after winter-spring was also detected through depletion of its δ^{13}C signature (Papiol et al., 2013).

Seasonal variations in diet composition of large benthos feeders (*P. blennoides* and *T. scabrus*) were less than those observed in large macroplankton feeders (*G. melastomus* and *M. poutassou*). This pattern has been reported previously to be a consequence of the greater variation in abundance and composition of pelagic macroplankton compared with benthic macrofauna (Mauchline and Gordon 1991; Iken et al. 2001; Cartes et al., 2010a; Mamouridis et al., 2011). Our results point to prey availability as an important driver of feeding intensity and diet composition. Some authors have suggested that seasonal changes in feeding intensity and diet composition of megafauna are not only driven by fluctuations in food availability but also by the need to cover different energy requirements at different times of year. More specifically, it has been argued that deep-sea shrimps shift to more energetic diets in pre-reproductive periods in order to match the energy demands for gonadal development (Cartes et al., 2008; Fanelli and Cartes, 2008; 2010). Contrarily, Madurell and Cartes (2005) found general seasonal stability in the energy content of the diet composition of demersal fish in the eastern Ionian Sea and suggested that animals simply eat more when they need more energy. Considering the differences in the feeding patterns of adults and juveniles of the same species (i.e. differences in the shifts in dietary composition and in fullness trends), some influence of the reproductive period in the feeding patterns of adult fish cannot be discarded.

4.3. *Relationship between trophic dynamics and reproduction*

In a thermally stable environment such as the deep Mediterranean, continuous biological processes were once expected (Orton, 1920), but both seasonal and continuous reproductive patterns have since been found in slope megafauna (e.g. Massutí et al., 1995; Rotllant et al., 2002; Cartes et al., 2008) and in the present study. Seasonality in reproduction responds to natural fluctuations in environmental factors (Gage and Tyler, 1991), and the main seasonal fluctuations in the area are associated with pulses of food reaching bathyal depths. Consistently, GSI of fish from the present study was associated with abundances of trophic resources and specific prey, which are known to fluctuate temporally in the NW Mediterranean Sea related to seasonality in OM inputs (Cartes and Sorbe, 1996; 1998; Cartes, 1998a; Cartes et al., 2002; Guidi-

Guilvard et al., 2007). Among most mid-slope fish (excluding *N. aequalis*) GSI was partially controlled by indicators of the vertical flux from surface production, implying rapid transfer and use of vertical production to deep-sea predators of different trophic guilds, probably through diel vertical migrations of macroplankton (e.g. pasipheid shrimps: Cartes, 1993). This was observed not only among strictly pelagic feeders, but also in some benthos/hyperbenthos feeders (*T. scabrus*, *H. italicus*) that shifted their diets and consumed macroplankton in autumn (October), prior to the beginning of their GSI increases in winter (February). Organic material from the photic zone is the main food source supporting the bathyal and abyssal faunal communities, especially pelagic species, and the seasonal variations in this food input provoke important changes in such communities (Polunin et al., 2001; Drazen, 2008; Stowasser et al., 2009; Fanelli et al., 2011a,b; Papiol et al., 2013). The response of GSI to indicators of surface production varied among species. The temporal patterns in GSI differed among species within the same feeding guild, pointing to successive and non-overlapping spawning. Therefore, even though the seasonality in food inputs exerts some control to biological cycles of deep-sea species, other factors contribute to regulation of the timing of reproduction. This is coherent with the idea that temporal (or spatial) segregation in reproduction is an adaptive strategy for avoiding interspecific competition among offspring (Sabatés et al., 2007; Tsikliras et al., 2010).

High GSI during most of the year in the two smaller macrourids *N. aequalis* and *H. italicus* suggests a continuous (or almost continuous) pattern of reproduction for the two species and is consistent with previous observations (Massutí et al., 1995; D'Onghia et al., 1996). Protracted spawning is considered to be an adaptive strategy aimed at ensuring that at least some of the larvae will encounter favourable conditions for survival and growth (Sherman et al., 1984). It could be one factor contributing to the great abundances of *Nezumia* spp. and *H. italicus* over Mediterranean continental margins (Stefanescu et al., 1994; Madurell et al., 2004; Papiol et al., 2012). In both *N. aequalis* and *H. italicus*, the main increase in feeding intensity preceded their increases in GSI, pointing to food consumption, and thus food availability (see above), as the trigger for reproduction. Partitioning of available prey between the two species probably enables a certain degree of reproductive succession, deduced from their different timing of the initial increase in GSI: (from June/July to October in *N. aequalis*; from October to February in *H. italicus*). Maintenance of high feeding intensity through protracted seasons in *N. aequalis* and *H. italicus* indicates continuous reliance on food available in the environment, rather than intermittent reliance on body reserves, which is characteristic of iteroparous fish species with protracted spawning periods (Murua and Saborido-Rey, 2003). Moreover, low seasonal oscillations of the HSI and the C/N ratio of muscle in *N. aequalis* and *H. italicus* point to low usage of body reserves (Lambert and Dutil, 1995; Drazen, 2002b).

Reproduction by continuous mating and egg deposition, with peaks of activity in both winter and summer, has previously been described for the oviparous catshark *Galeus melastomus* in the Mediterranean Sea and the Atlantic (Costa et al., 2005; Rey et al., 2005), which is in agreement with our trends in its GSI. As in the two small macrourids, we observed high feeding rates during most of the year. Nevertheless, *G. melastomus* presented marked oscillations in HSI and muscle C/N, which peaked in April and June/July respectively. The HSI increase coincided with an increase in *F* and with ingestion of very energetic prey (i.e. cephalopods: Madurell and Cartes, 2005), suggesting energy storage in liver. Subsequent increase of muscle C/N with continued high feeding intensity points to later storage of lipids in muscle. This differential storage of energy is possible through the ability of sharks to selectively deposit lipids into different tissues (Pethybridge et al., 2010). Deep-water sharks function differently than bony fish with protracted reproductive cycles, which rely on energy from food immediately available in the environment for sexual maturation. In chondrichthyes, and more specifically scyliorhinids, the liver plays an important role in energy storage for fuelling reproduction (Pethybridge et al., 2010), and we think *G. melastomus* may be largely using this energy source for maintaining the all-year-round vitellogenic activity reported by Capapé and Zaoualli (1977).

We observed that population density played an important role in the reproductive cycles of some species, especially those with protracted spawning. Positive correlations between GSI and density of *N. aequalis* and *G. melastomus* suggest aggregations for reproduction. These two species present a bigger-deeper trend in size distribution, and the relationship of GSI with weight of individuals suggests that large, reproducing adults may aggregate at specific depths (Massutí et al., 1995; Morales-Nin et al., 2003). In contrast, mature individuals of *H. italicus* do not aggregate for reproduction, and body size is uniformly distributed along its bathymetric range (Massutí et al., 1995).

Patterns of seasonal reproduction in mid-slope fish of the NW Mediterranean have already been described for *T. scabrus* (Motais et al., 1960; Massutí et al., 1995; D’Onghia et al., 1996; Fernández-Arcaya et al., 2012), *P. blennoides* (Rotllant et al.,

2002) and *M. poutassou* (Matarrese et al., 1998; Sbrana et al., 1998; Martino et al., 2001), and agree with the temporal patterns we found in GSI. Iteroparous species with short spawning seasons mostly depend on their body reserves for gonad maturation (Murua and Saborido-Rey, 2003), and we observed correspondingly large oscillations in HSI and C/N from muscle. Moreover, opposed trends between HSI and GSI are attributable to the importance of the liver in providing energy for gonad development (Lambert and Dutil, 1995; Marshall et al., 1999).

We observed parallel temporal trends of increase in fullness and HSI, both preceding gonad growth (GSI) in the two gadids (i.e. *M. poutassou* and *P. blennoides*). As a matter of fact, temporal patterns in GSI were positively related to previous patterns in HSI. Greater feeding intensity in pre-reproductive periods evidently enabled energy storage in the liver (e.g. Lambert and Dutil, 1995), which was later used for gonad development, as discussed for *P. blennoides* by Gallardo-Cabello (1979) and as observed in the Atlantic cod (Marshall et al., 1999). While muscle C/N of *P. blennoides* remained rather constant throughout the year, the great decrease observed from June /July to October in muscle C/N of *M. poutassou* pointed to usage of energy stored in the muscle. The muscle lipid may well have been metabolised to sustain the high activity of this natatory species during gonad development from nutriment stored in the liver.

Also for *T. scabrus* and *L. crocodilus*, greatest feeding intensity preceded gonad growth (if we assume a composite year), pointing once more to a direct relationship between food consumed and reproduction. In addition, phytodetritus inputs may favour gonad growth afterwards in both species, likely related to the ingestion of mesopelagic crustaceans observed in both species before maturation. Nevertheless, these species had different strategies of energy storage and reproduction than those discussed above. In both species, greatest feeding intensity was in autumn (October), and it seems to have promoted the growth of both the gonad and the liver. Moreover, we unexpectedly observed a peak of HSI *after* greatest GSI. This temporal scheme does not agree with previously published patterns of energy use and storage, and further studies on these species would help us to understand the variety of population maintenance strategies employed by fish living under restricted food availability.

We observed a common trend of reproduction between late autumn and spring/early summer that did not follow the main Mediterranean pattern of spawning in spring and summer (see Tsikliras et al., 2010 for a review). This most typical pattern is mainly based on fish from coastal zones, early stages of which generally feed on phytoplankton and zooplankton from the photic zone and/or the Deep-Chlorophyll-Maximum (Sabatés et al., 2007). Little is known about the ecology of early stages of bathyal fish, although production of buoyant pelagic eggs has long been considered typical (Gage and Tyler, 1991; Merret and Barnes, 1996; Ådlandsvik et al., 2001) and the recruitment of juveniles to depth has been described for some species as occurring months after the spawning period (Massutí et al., 1995; 1996). The early spawning of bathyal fish may be timed to match both the peak in surface production and the formation of the thermocline. Larvae hatching in the winter-spring period in shallower layers of the water column most probably find maximum abundance of POM from surface production in this period (Miquel et al., 1994). Also, early downward vertical migration of small individuals can allow them to reach depths below the thermocline before it is formed (May-June: Papiol et al., 2012), thus avoiding the difficulty of transiting such a barrier. However, in deep studies of early stages of bathyal fish species would be required in order to clearify this issue.

Conclusions

The mid-slope fish community of the NW Mediterranean has high levels of resource partitioning that are related to their size, swimming capacity and to the energetic demands of metabolism, growth and reproduction. Partitioning decreases in periods of superabundant prey, and seasonal changes in fish diets are coupled to cycles of secondary production. Consistently, feeding intensity (*F*) is linked to food availability. Feeding intensity of benthos-feeders is linked to food sources (TOC%) and to surface production (2 months prior to *F* peaks). The link is through enhanced benthos (and hyperbenthos) production. The *F* of plankton-feeding fish is mainly linked to lipids both in the sediment and the muscle of fish. Association to lipids in sediment, probably related with phytodetritus deposition, may be because of consumption of mesopelagic prey that relies on this phytodetritus. Greatest *F* precedes gonad maturation for most fish species; thus changes in food availability appear to trigger the reproductive cycles of benthopelagic fish. Probably related with an optimization of food partitioning, we observed a clear temporal segregation in the reproductive cycles of fish species feeding on similar resources. Spawning was mostly concentrated from autumn to spring. Given that, it seems that food for adults is more important than resource partitioning for the offspring, which may find enough food in water column features such as the slope Intermediate Nepheloid Layer before formation of thermocline (late spring).

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CHAPTER 6 - LINKING FEEDING DYNAMICS AND REPRODUCTIVE CYCLES OF DECAPOD CRUSTACEANS WITH FOOD AVAILABILITY ON THE NORTHWEST MEDITERRANEAN CONTINENTAL SLOPES

Linking feeding dynamics and reproductive cycles of decapod crustaceans with food availability on the northwest Mediterranean continental slopes

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Abstract

Trophic dynamics and biological cycles of decapods from the middle slope of the Catalan Sea (Balearic Basin, NW Mediterranean) have been investigated. Samples were collected on a seasonal basis from 600 to 1000 m depth between February 2007 and February 2008. Stomach contents of the 6 most abundant species were analysed and weights of gonads and livers were measured. Each species had a distinctive diet but they mainly fed upon benthos and zooplankton. Dietary overlap was greater among macroplankton feeders than among benthos feeders. Dietary overlap among both macroplankton feeders and among the different classes of the endobenthos feeder *Aristeus antennatus* was lowest in April. Among macroplankton feeders it was greatest in February, and among *A. antennatus*, in October. Diet of macroplankton feeders mainly changed from February to April, related to the maximum of secondary mesopelagic production. Diets of *A. antennatus* changed between all consecutive seasons and this species exploited different types of prey, from benthos to hyperbenthos and zooplankton, according to their availability. Generalised greater dietary diversity coincided with lowest dietary overlap in April in macroplankton feeders, and the opposed situation was observed in *A. antennatus*. Feeding intensity (stomach fullness, *F*) was related with food availability. Based on Generalised Linear Models, the *F* of macroplankton feeders was related to dietary diversity, to the density of mesopelagic fish and to indicators of surface production. For *A. antennatus*, densities of benthic prey (i.e. *C. macandreae* and benthic polychaetes) were important explanatory variables of trends in *F*, which were also related to surface production and to densities of stomiiforms. Size was also an important factor defining prey selection and trends of *F* in *A. antennatus*. We observed different timing of gonad maturation (high gonadosomatic index) between species feeding on the same prey resources, but planktotrophic larvae were released in summer, and lecitotrophic larvae in winter-spring. The gonadosomatic index of mid-slope decapods was related to indicators of the vertical flux from surface production. Increased feeding intensities usually preceded gonad maturation, and hepatosomatic index depletion was also observed parallel to gonad increase. Different relationships between food intake, and energy storage and reproductive indicators pointed to other biological processes affecting importantly the energetic balance required for reproduction to take place.

Keywords: *Deep Sea, benthopelagic decapods, diet, reproduction, seasonality, food availability.*

1. Introduction

Decapod crustaceans are the most abundant taxon on the Mediterranean slopes (Cartes and Sardà, 1992; D’Onghia et al., 2003; Politou et al., 2008), and more specifically in the Catalan Sea (NW Mediterranean Sea) (Cartes and Sardà, 1992; Cartes, 1993a; Papiol et al., 2012), where the distribution and composition of benthopelagic decapod assemblages has been extensively studied. In this area, three depth zones characterised by different decapod assemblages have been identified: the upper, the middle and the lower slopes (Abelló et al., 1988; Abelló and Valladares, 1988; Cartes and Sardà, 1992; Cartes, 1993a), which coincide with the different depth strata defined by Pérès (1985) for the bathyal Mediterranean. The middle-slope assemblage, located between ~600 and ~1200 m, is characterised by high diversities of benthic and nektobenthic decapod species and some typical bathypelagic species that coexist (Cartes and Sardà, 1993). This assemblage is dominated by the benthic shrimps *Aristeus antennatus* and *Calocaris macandreae*, but assemblage composition varies seasonally and high densities of mesopelagic shrimps are observed in spring over the upper and the middle slopes (Cartes et al., 1994). Given the thermohaline stability of the deep Mediterranean (below ~200 m) (Hopkins, 1985), changes in assemblage structure are attributed to fluctuations in food availability (Cartes, 1998JMBAUK; Papiol et al., 2012).

Most decapod species inhabiting the middle slope of the Catalan Sea are secondary consumers mainly feeding on macrofauna (Cartes, 1993b-e; 1994; Fanelli and Cartes, 2008). Together with fish, they consume virtually all macrobenthic and macroplanktonic production (Cartes and Maynou, 1998), thus food constitutes a limited resource. In such conditions, minimisation of competition in food use may be essential to ecological success of species (Margalef, 1974; Jeffreys et al., 2009) and is probably a crucial factor allowing dominance of decapods in the deep Mediterranean. Even though dominant decapod species on the middle slope have mixed diets based on small sized benthopelagic and mesopelagic prey (Cartes and Maynou, 1998; Cartes and Carrassón, 2004), dietary overlap is held to be low and high levels of food partitioning take place (Cartes, 1998). Usually, species inhabit and feed at different levels of the sediment-water interface, preying upon different prey taxa. Contrary to that observed in fish (Macpherson, 1981), dietary overlap among decapods is lower among benthic species than among benthopelagic species, which has been attributed to greater diversities of benthic (Mamouridis et al., 2011) and hyperbenthic (Cartes et al., 2003) prey with respect to zooplankton (Cartes et al., 2010). Nevertheless, seasonality in the abundances of the different prey types causes changes in the feeding and diets of their predators (e.g. Cartes, 1994; Cartes et al., 2008; Fanelli and Cartes, 2008). Species may expand their foraging niche in order to survive to transitory resource limitation and/or to gain competitive advantage over other species (Jeffreys et al., 2009). As a result, resource partitioning can decrease due to exploitation of a peaking resource by several species (Macpherson, 1981; Cartes, 1998). In the northwestern Mediterranean, seasonal consumption of macroplankton by coexisting species has been observed and has been related to the large seasonal fluctuations in abundance of pelagic macroplankton compared to benthic macrofauna (Mauchline and Gordon, 1991; Iken et al., 2001; Cartes et al., 2010; Mamouridis et al., 2011). Otherwise, dietary overlap may remain high, as species can use the same food resources in different seasons.

Seasonal changes in availability of macrofauna respond to variations in food inputs to bathyal depths (Cartes et al., 2002; Guidi-Guilvard et al., 2007; Mamouridis et al., 2011). The main food input sustaining the majority of deep benthopelagic communities is marine snow originated at surface (Tyler, 1988; Graf, 1989; Smith et al., 1996; Drazen et al., 2004; Stowasser et al., 2009), which reaches bathyal depths through vertical transport. Dependence of deep communities on organic matter derived from surface production has also been reported in the NW Mediterranean Sea (Polunin et al., 2001), where the importance of this food source varies seasonally (Fanelli et al., 2011a,b; Papiol et al., 2013). Flux of marine snow is greater after the late winter surface blooms when the water column is homogeneous. Low particle flux is associated with periods of stratification that usually extend from April to November (Miquel et al., 1994). In addition to inputs of marine snow, food availability in the continental slope of the Catalan Sea is also determined by local influence of advective currents through submarine canyons that convey organic matter across the slope (Buscail et al., 1990; Palanques et al., 2006) and resuspend OM from the upper sediment layers (*cf.* Shepard et al., 1974; Monaco et al., 1990). Advective fluxes are greatest in spring and least in summer, related to hydrologic processes taking place in shelf areas (Monaco et al., 1990; Buscail et al., 1990; Canals et al., 2006; Palanques et al., 2006).

The temporal oscillations in food availability are likely the drivers of the biological cycles of fauna in a constant physical environment such as the deep Mediterranean. That agrees with the idea that seasonal reproductive processes respond to the natural fluctuations in environmental factors (Gage and Tyler, 1991). It has been reported that different macrofauna groups from the NW Mediterranean slope have biological cycles coupled to cyclic food availability (Cartes and Sorbe, 1996; 1998; Cartes, 1998a). Among megafauna, reproduction and recruitment processes of some detritivore species respond to pulses of food (Ginger et al., 2001; Hudson et al., 2004; Wingham et al., 2003; Howell et al., 2004). Nevertheless, few studies have related food availability with the reproductive cycles of deep-water predators. Biological cycles of benthopelagic shrimps have been associated to vertical fluxes of organic matter reaching bathyal depths (Puig et al., 2001), and delayed responses to blooms in surface production have been observed (Cartes et al., 2008; Fanelli and Cartes, 2008; Briones-Fourzán et al., 2010). The time lag between the physiological response of secondary consumers and the organic matter inputs is attributable to the additional trophic step between them. Consistently, the biological cycles of some bathyal benthopelagic shrimp species were related to changes in prey consumption (Cartes et al., 2008; Fanelli and Cartes, 2008). These studies focused on a single species or on congeneric species that are bathymetrically segregated but such work considering coexisting species has not been performed. If food availability were the most important factor controlling reproduction at bathyal depths, one would expect that reproductive cycles of cohabiting species with contemporary inputs of organic matter were synchronised. Contrarily, both seasonal and continuous reproductive cycles have been found in coexisting benthopelagic decapod crustaceans. Moreover, a pattern of successive reproductive cycles among middle-slope species has been described (Company et al., 2003). A similar phenomenon was observed among dominant benthopelagic fish species from the middle-slope of the Catalan Sea (Papiol et al., this volume). Reproductive cycles of these fishes were defined by patterns of feeding and energy allocation, which were ultimately driven by prey availability and use. For decapods, it is known that the success in maturation and spawning depends on their nutritional status before maturation (Teshima et al., 1988). An optimal dietary balance is required: the dietary intake of energy substrates in addition to energy reserves of the body must exceed the maintenance and activity costs of an animal in order to have sufficient energy to invest in reproduction, somatic growth or moulting (Harrisson, 1990).

In our study of middle-slope decapod crustaceans we aimed to

i) analyse the partitioning of trophic resources previously described at a seasonal scale and identify the trophic patterns of the whole assemblage,
ii) relate their trophic dynamics with their reproductive cycles,
iii) determine the main food sources driving their feeding dynamics and reproductive cycles.

2. Materials and methods

Data describing diets and gut fullness of six species of dominant benthopelagic decapod crustaceans of the middle slope of the Catalan Sea (Balearic Basin, NW Mediterranean Sea) were obtained using bottom trawls and analysed on a seasonal basis over a one-year period.

2.1. *Study area and sampling strategy*

Five multidisciplinary surveys distributed in the four seasons of a calendar year were performed between February 2007 and February 2008 (BIOMARE B1, B2, B3, B4 and B08) at depths ranging from 423 to 1175 m within the project BIOMARE. Three stations in an open slope area were sampled along the isobaths close to 650, 800 and 1000 m, except in April when no samples were collected from 1000 m. In addition, sampling was performed inside the Besòs submarine canyon, a site locally called *El Buscarró* ground at *ca.* 600 m depth along the canyon's southern wall. Nineteen hauls were performed using a semi-balloon otter trawl (OTSB-14) (Merrett and Marshall, 1981) in February, April, June/July and October 2007, and February 2008. Details of the OTSB-14 samplings can be found in Papiol et al. (2012). Twelve hauls were carried out with a commercial trawl only at two of the stations (*ca.* 600 m and *ca.* 800 m), and those tows were performed on dates close to OTSB-14 tows (2007: March 6th, May 11th, June 25th, July 19th, September 17th and December 28th). All hauls were carried out during daytime. The time on bottom of each haul ranged between 45 and 90 min at a towing speed around 2.6 knots.

Samples of surface sediment (0–2 cm depth) for analysis of particulate organic matter (POM_{sed}) were collected with a multicorer from the 600 and 800 m stations throughout the sampling period. Sediment was immediately frozen at -20 ºC for later analysis.

2.2. *Analyses of stomach contents and biological parameters.*

All benthopelagic megafauna collected was identified to species level, counted, measured and weighed, either on board or at the laboratory when further identification was necessary or when sample mass was not large enough for precise weighing. Specimens were immediately frozen at -20 ºC for future analyses.

At the laboratory, we analysed the biological parameters of 1564 decapod crustaceans belonging to the six species dominating the slope assemblage (Table 1; Cartes et al., 1994). Only adult individuals of most species were selected for analysis, but we distinguished two size classes (small and large) for *Aristeus antennatus*. This is the only species presenting a marked sexual dimorphism, mature females achieving larger sizes than males, thus, the size class of small individuals consisted of mature males and immature females that were analysed separately. All individuals were sexed and weighed (±0.001 g), and cephalothorax length (mm) was recorded. Sexual maturity of females was determined macroscopically according to five stages of gonadal development: I: immature; II: resting gonads; III, IV and V: 3 stages of recrudescent gonads, i.e. from the initial stages of gametogenesis up to the stage prior to spawning of eggs (Company et al., 2003). Presence of eggs in pleopods was also logged. For females of *A. antennatus*, seven gonadal stages of gonad maturation were determined: I: undeveloped, II: undeveloped/resting, III: developing, IV: maturation, V: advanced maturation, VI spawning, VII: post-spawning (Demestre and Fortuño, 1992). Stomach content, liver and gonads were removed and weighed (±0.001 g). The food items were identified to species or to the lowest feasible taxonomic level, and their percentage volume was estimated by the subjective points method (Swynnerton and Worthington, 1940). Most decapods use their mandibles to crush their food and have plates in their stomachs that will further grind and process the food for digestion. For this reason, prey remains were strongly broken and mixed, and direct prey weighing was impossible in practice.

2.3. Analyses of sediment organics

TOC of sediments (TOC_{sed}) was determined by the same procedure employed for muscle tissue. TOC amounts are reported as percentage of sediment dry weight.

Total lipid content of sediments ($lipids_{sed}$) was also analysed following a modified Bligh and Dyer method (Bligh and Dyer, 1959; Alfaro et al., 2006). Lipid amounts are reported as percentage of sediment dry weight.

In addition, phytoplankton pigments in sediments were analysed as indicators of OM from surface primary production in the area by means of reverse-phase high-pressure liquid chromatography (HPLC).

For all sedimentary analyses, three replicates were analysed for each sample at each collection station in each season. Details of the analyses of sediment organics can be found in Papiol et al. (2013).

2.4. Environmental variables

Casts were performed at each station with a SBE-32 CTD coupled with a fluorometer. Locations were the same as those where biological and sediments samples were collected. Values of fluorescence were recorded for each CTD profile at 5 m above the sea bottom (5 mab).

Phytoplankton pigment concentration (PPC, mg Chl*a* m^{-3}), obtained from http://reason.gsfc.nasa.gov/Giovanni, was used as a rough index of surface primary production in the area. We used monthly average PPC values at the bottom trawl positions coincident with sampling, and 1, 2 and 3 months before sampling (Cartes et al., 2004).

2.5. Data analysis

Two-way PERMANOVA with a crossed design considering sampling sites (i.e. depth) and surveys (i.e. seasons) as factors was used to test spatial and temporal differences among environmental variables and sediment organics.

Table 1. Decapod species examined in the present study. Length ranges (CL = cephalotorax length), number of specimens dissected for measuring biological parameters, number of stomach contents analysed, number of females dissected for measuring biological parameters by season (win=winter; spr=spring; sum=summer; aut=autumn). Trophic guild from literature and source are also indicated (B=benthos feeders; nmM=non-migratory macroplankton feeders; mM=migratory macroplankton feeders).

Species	CL (mm)	Season	Dissected	Females	Diet	Trophic guild	Source
Aristeus antennatus large	30-50					B	Cartes and Sardà, 1989; Cartes et al., 2008
		win	76	73	56		
		spr	58	58	43		
		sum	73	72	51		
		aut	80	77	57		
Aristeus antennatus small	20-30					B	Cartes, 1994; Cartes et al., 2008
		win	43		29		
		spr	48		42		
		sum	124		60		
		aut	158		77		
Acantephyra eximia	24-33					nmM	Cartes, 1993b
		win	35	32	32		
		spr	9	7	8		
		sum	76	49	68		
		aut	35	26	29		
Munida tenuimana	8-19					nmM	Cartes, 1993c
		win	42	22	34		
		spr	49	22	36		
		sum	21	7	15		
		aut	28	11	20		

Pasiphaea multidentata	25-45					mM	Cartes, 1993d; Fanelli and Cartes, 2008
		win	81	55	46		
		spr	29	23	19		
		sum	70	46	33		
		aut	8	7	4		
Plesionika martia	15-25					nmM	Cartes, 1993e; Fanelli and Cartes, 2008
		win	74	29	54		
		spr	55	24	37		
		sum	72	35	39		
		aut	67	22	47		
Polycheles typhlops	20-40					B	Cartes and Abelló, 1992
		win	53	41	19		
		spr	17	8	5		
		sum	47	32	15		
		aut	36	24	10		
Total			1564	801	985		

Abundances of the megafauna species analysed and of potential prey species were standardized to a common swept area of 1 ha (ind ha-1), according to the values proposed by Cartes et al. (2009a).

2.5.1. *Trophic data*

The dietary composition was analysed for 976 individuals with stomachs containing food (Table 1). The contribution of each prey item to the diets was standardised to total individual weight.

Stomach fullness (*F*) was used to measure feeding intensity and was calculated as: *F* = 100 (stomach content weight / predator weight).

2.5.2. *Biological parameters*

Two indices were calculated for describing the overall physiological condition of the decapods. The hepatosomatic index (HSI) was calculated as a proxy for energy reserves stored in the liver (George and Patel, 1956; Gibson and Barker, 1979): HSI = 100 (liver weight/body weight). The gonadosomatic index (GSI) is often considered as a surrogate for reproductive effort (e.g. Tuck et al., 1997; Cartes et al., 2008), and it was calculated as: GSI =100 (gonad weight/body weight). All weights were wet weights. Taking into consideration that females allocate more energy to reproduction than males and that the liver plays an important role in energy storage (Rosa and Nunes, 2003a; Guijarro et al., 2008), HSI and GSI were only estimated for adult females.

In order to compare the duration of the annual reproductive periods, percentage of females with recrudescent gonads (Stages III to V; Stages III to VI in *A. antennatus*) and percentages of ovigerous females were calculated in relation to the population of adult females by survey.

2.5.3. *Overall diet of species*

Diet was analysed for each species in each haul and survey. Between 8 and 22 individuals (a “sample”) were analysed per haul for all species. For the hauls analysed with low numbers of individuals (<8), specimens from different hauls within the same survey were pooled to attain minimum sample sizes of 8 individuals (30% of the total samples). For each diet category (prey type) in each sample, prey biomass was standardised to an equivalent of 10 individuals.

To identify overall trophic interactions among fish species, a hierarchical cluster analysis (average grouping method) was performed on the square-root transformed biomass data using the Bray-Curtis similarity index (Field et al., 1982). To illustrate observed similarities or dissimilarities (distances) between the groups resulting from the cluster analyses, multidimensional scaling (MDS) analysis was carried out on the same data matrix. The groups obtained were compared with postulated trophic groups based on the literature (Table 1). Analysis of similarities (ANOSIM) between the different groups obtained by cluster analysis was performed on the same resemblance matrix to test significance of segregation between the groups. SIMPER analysis was performed to identify characteristic prey for each group obtained from cluster analysis and to calculate the degree of similarity/dissimilarity among diets of the different groups of species.

Diet diversity across samples was calculated for each species using the Shannon-Wiener *H´* index (Shannon and Weaver, 1949).

2.5.4. *Seasonal intraspecific variations*

Two-way permutational multivariate ANOVA with a crossed design considering both sex (adult males and females) and survey as factors was used to test sexual differences in diet composition between immature females and small males of *A. antennatus*.

Seasonal variations in diets of each species were measured by applying a one-way PERMANOVA (Anderson, 2001; Anderson et al., 2008) to square-root transformed proportional biomass data of individual stomach contents based on the Bray-Curtis similarity index. Additionally, temporal trends in prey consumption (biomass) were studied by merging all replicates from the same season.

Seasonal trends in dietary diversity (*H'*) were described.

Two-way permutational univariate ANOVA with a crossed design considering both sex (adult males and females) and survey as factors was used to test sexual differences in fullness in all species. Large and small *A. antennatus* were considered separately. Pairwise tests were performed in order to allocate the sources of variation. One-way permutational univariate ANOVAs (Anderson, 2001) based on Euclidean distances were adopted to test seasonal changes in fullness, HSI and GSI after arcsine transformation in order to approximate Normality (Sokal and Rohlf, 1995). While permutational ANOVA was designed for multivariate analysis of distance matrices, it can be used for univariate ANOVA. Because we have only one dependent variable in the analysis and use Euclidean distances, the resulting sums of squares and *F*-ratios are the same as Fisher's univariate *F*-statistic in traditional ANOVA. Significance was set at $p = 0.05$; p values were obtained using 9999 permutations of residuals under a reduced model (Anderson, 2001).

Seasonal trends in the percentages of mature and ovigerous females were described.

2.5.5. *Seasonal changes in interspecific relationships*

Affinities between diets of the different species in each season were calculated using the quantitative Schoener index (α) (Schoener, 1974).

2.5.6. *Drivers of fullness and biological cycle*

A draftsman plot (i.e. scatter plots of all pairwise combinations of variables) (Clarke and Warwick, 1995) was applied to environmental variables to identify whether any of them were strongly correlated, thus providing redundant information. Redundant variables ($r > 0.70$) were discarded, simplifying the matrix for later Generalised Linear Models.

In order to identify which variables explained patterns of fullness and GSI, values of fullness and GSI were compared with independent explanatory variables by means of Generalised Linear Models (GLMs) after normalising the dependent variables by arcsine transformation (Sokal and Rohlf, 1995). GLMs for fullness were calculated on each of the trophic groups obtained by cluster analyses using mean values of fullness per haul and species. GLMs for GSI were calculated on each species using GSI per individual (not mean per haul) in order to increase sample size. GLMs are flexible generalisations of ordinary least squares regression. A GLM generalises linear regression by allowing the linear model to be related to the response variable via a link function and by allowing the magnitude of the variance of each measurement to be a function of its predicted value. The distribution family used was Gaussian with identity link. The models were computed by adding single terms based on minimising Akaike's Information Criterion (AIC) and only including variables that were significant ($p<0.05$). Both in the fullness and the GSI models we included environmental variables: i) surface phytoplankton pigment concentration (PPC) simultaneous with and 1, 2 and 3 months before the sampling, ii) fluorescence$_{5mab}$; iii) sediment TOC$_{sed}$%, iv) sediment total lipids and v) the sum of sediment chloropigments (chlorophylls and their degradation products). Chloropigments were used as general indicators of the quantity of phytodetritus (Vidussi et al., 2000 and references therein). Standardised abundances of potential prey of megafaunal fish caught with the OTSB-14 (i.e. sergestid and pasipheid shrimps, brachyuran crabs, *Calocaris macandreae*, mesopelagic myctophids and stomiiforms smaller than 50 mm [Cartes et al., 2008], euphausiids, mysids, isopods, hyperiids) were also included in the models, as was dietary diversity and predator's density. Additionally, densities of polychaetes and ophiuroids obtained by means of a Box-Corer in a parallel study (Mamouridis et al., 2011) were used. Also, for the monospecific models performed on GSI, density, size and individual predator W (in the case of models for GSI) and HSI were included as biological variables potentially linked to gonad maturation. Considering fullness is an immediate reflection of what is consumed, we compared fullness with variables sampled simultaneously. Given that gonad growth has some delay in relation to the food ingested or the energy stored in the organism, values of GSI were compared with variables sampled simultaneously and those from the previous sampling. For previous biological indices, mean values per sampling station were used because we considered the animals sampled in each season as a cohort from the same population.

All statistical analyses were performed using PRIMER6 and PERMANOVA+ (Clarke and Warwick, 1995; Anderson et al., 2008), R 2.14.2 (*http://www.r-project.org/*), STATISTICA 6 and XLSTAT software.

3. Results

3.1. *Organic matter sources*

Results for spatial and temporal trends of TOC_{sed}% and surface primary production are detailed in Papiol et al. (2012) and lipids and pigments in sediments and fluorescence 5 m above sea bottom are reported in Papiol et al. (2013). Those are not repeated here, as they are taken into account only for developing GLMs.

3.2. *Overall diet of species*

3.2.1. *Resource partitioning*

The MDS analysis performed on dietary data shows that position of predators along a benthic–pelagic gradient, that is, the distribution of their prey in the near-bottom water column is the main structuring factor (Fig. 1). Combining the results of cluster analysis with the MDS ordination we distinguish three main groups at 20% similarity. Species from both categories of macroplankton feeders established from the literature

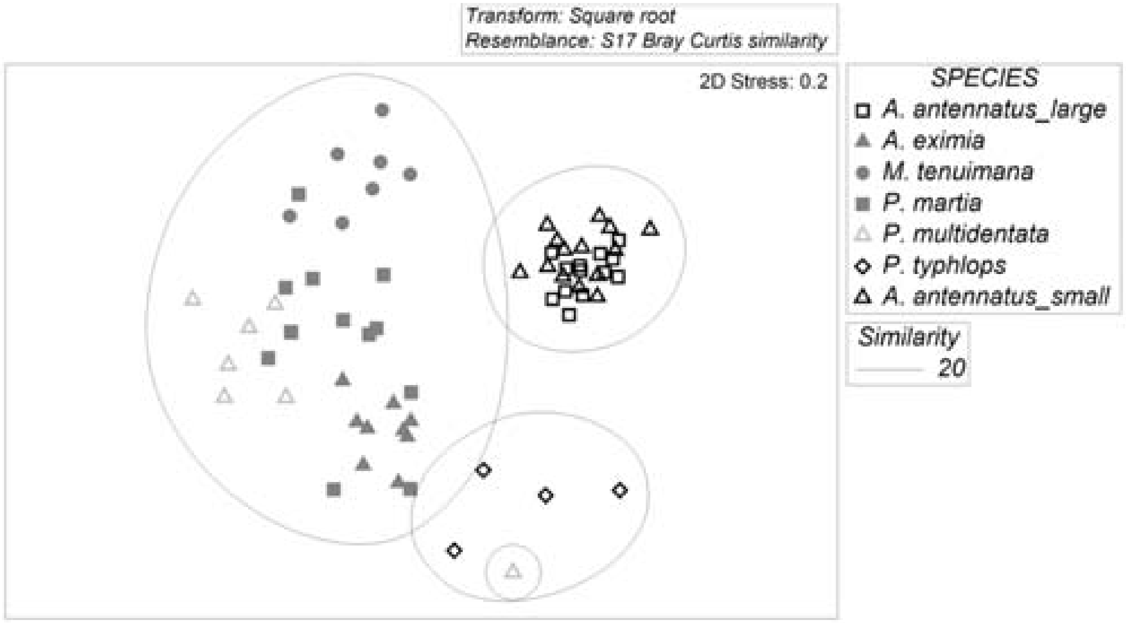


Fig. 1. MDS ordination plot of stomach contents of the different decapod crustacean species per haul, based on Bray-Curtis resemblance matrix of square-root transformed prey weight data. Data points are identified by species and by trophic guilds from the literature (Table 1): black = benthos feeders; dark grey = non-migratory macroplankton feeders; light grey = migratory macroplankton feeders. Circles indicate cluster overlay at 20% of similarity.

(the non-migratory macroplankton feeders (*nmM*) *Munida tenuimana*, *Acantephyra eximia* and *Plesionika martia*, and the migratory macroplankton feeder (*mM*) *Pasiphaea multidentata*) cluster together at the left side of the MDS, and each of the benthic-feeder species (*A. antennatus* and *Polycheles typhlops*) forms another cluster located at the right side of the MDS. *A. antennatus* is located at the top right and *P. typhlops* is at the bottom right. All groups obtained by cluster analyses were statistically distinct (ANOSIM R=0.748; p<0.001).

SIMPER reveals that 67% of the diet of macroplankton feeder species was represented by the euphausiid *Meganyctiphanes norvegica*, the congeneric mesopelagic shrimps *Pasiphaea sivado* and *P. multidentata*, unidentified fish and stomiiforms. The group consisting of the two size categories of the benthic feeder shrimp *A. antennatus* was more homogenous than the rest (average within group similarity=65.3%). Diets of *A. antennatus* were characterised by consumption of polychaetes (principally Nephtydae and *Glycera* sp.), hyperbenthic isopods (essentially, *Natatolana borealis*), bivalves, holothurians, hyperbenthic gammariids, benthic foraminiferans, caudofoveats, fish remains and echinoid remains, accounting for 60% of the cumulative W of the diets.

Diets of *P. typhlops* were characterised by mesopelagic stomiiforms, *A. antennatus* remains, unidentified fish remains and hyperbenthic isopods, accumulating 68% of the diet W. Dissimilarities between diets of the different groups of species obtained by cluster analysis were well above 80%.

3.3. *Intraspecific seasonal variations*

3.3.1. *Seasonal trends in diets*

Statistical significance estimates for seasonal variations in dietary composition can be found in Table 2.

Table 2. Results of PERMANOVA pair-wise tests comparing diet composition of each decapod species in consecutive seasons based on 9999 permutations. t values and p-level significance (*p<0.05; **p<0.01; ***p<0.001; n.s.=not significant) indicated.

	Feb-Apr	Apr-Jun/Jul	Jun/Jul-Oct	Oct-Feb
P. martia	2.459^{***}	ns	2.269^{***}	3.280^{***}
A. eximia	ns	ns	ns	ns
P. multidentata	2.178^{***}	1.431^{*}	-	-
M. tenuimana	1.705^{**}	ns	ns	1.901^{**}
P. typhlops	-	-	ns	1.360^{*}
A. antennatus large	3.121^{***}	1.737^{***}	2.570^{***}	1.822^{***}
A. antennatus small	1.302^{*}	1.889^{***}	2.979^{***}	1.586^{***}

Macroplankton feeders

Diet of the pandalid shrimp *P. martia* changed seasonally (*pseudo*-$F_{3,176}$=5.23; p<0.001), although pasipheid shrimps (i.e. *P. multidentata* and *P. sivado*) were the most important prey in all seasons (Fig. 2). In February pasipheid shrimps, mostly *P. multidentata*, were main prey, representing almost 60% of the food consumed. Diet changed significantly to April, when *P. martia* consumed greater variety of prey, and proportion of pasipheid shrimps in the diet, now primarily *P. sivado*, was less (23%). Mesopelagic fish, i.e. myctophids and stomiiforms, were also abundant in the diet (19%). Changes to June/July were not statistically significant, although consumption of hyperiids, myctophids and *M. norvegica* decreased and was replaced by ingestion of gelatinous zooplankton, benthic polychaetes and the hyperbenthic isopod *N. borealis*. Diet in October differed significantly to that of June/July and main prey was *P. sivado* (46%).

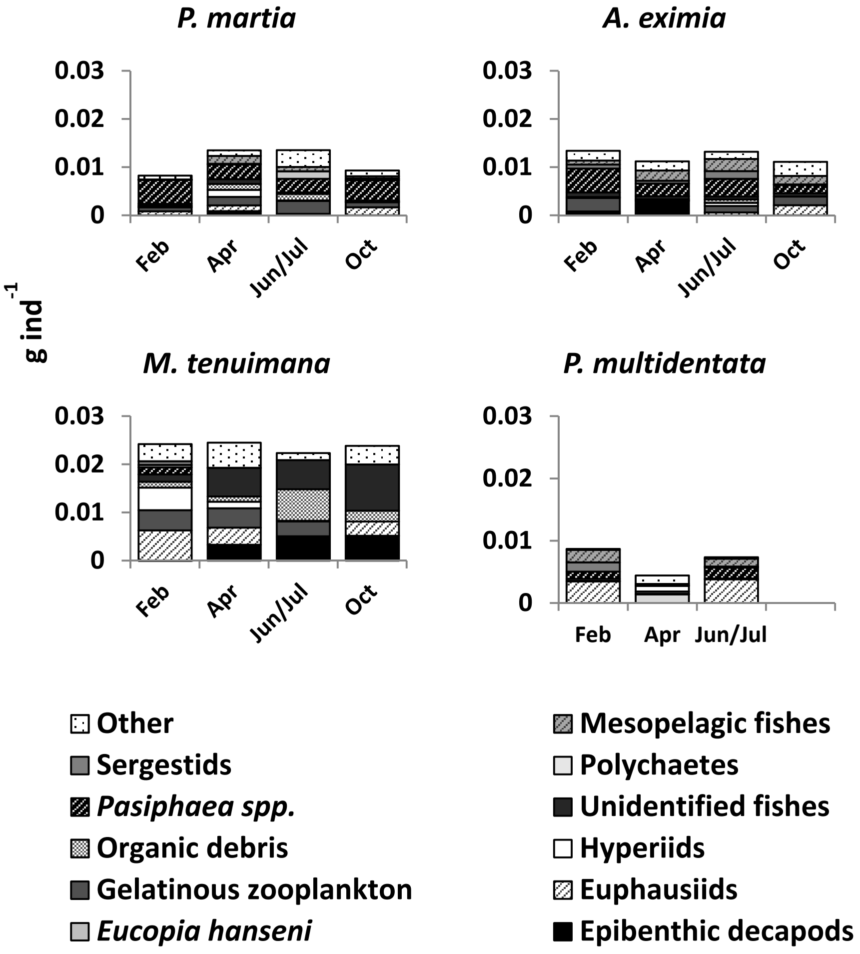


Fig. 2. Diet composition (by weight) of macroplankton feeder decapod species in each sampling period.

Seasonal changes in the diet of the oplophorid shrimp *A. eximia* were not significant ($p>0.05$), and diet did not change significantly between consecutive seasons, being *P. multidentata* the most important prey throughout the year (Fig. 2). In February, *P. multidentata* represented 37% of the food ingested, and second most important prey was gelatinous zooplankton, mainly salps. Consumption of *P. multidentata* decreased in April but was still most important prey together with mesopelagic fish, namely stomiiforms, and *Plesionika* sp. In June/July myctophids, especially *Ceratoscopelus maderensis*, and the sergestid *Sergia robusta* were abundant prey together with *P. multidentata*. In October, main prey was the euphausiid *M. norvegica* and *P. multidentata* was second most important prey in terms of biomass. Mesopelagic fish and the hyperbenthic isopod *N. borealis* represented each more than 10% of the food ingested in this period.

Diet of the pasipheid shrimp *P. multidentata* changed seasonally (*pseudo*-$F_{2,97}$=3.80; p<0.001). In February, *M. norvegica* dominated in the diet of this predator (40%), which also ingested substantial amounts of *Sergestes arcticus*, *P. sivado* and mesopelagic fish, mainly small stomiiforms (Fig. 2). Diet changed significantly to April, when it consisted mainly of the mysid *Eucopia hanseni*, of the benthic shrimp *Calocaris macandreae*, and of hyperiids. Changes to June/July were significant and in this period the diet was again dominated by the euphausiid *M. norvegica*. The rest of the diet was principally composed by *P. sivado* and myctophids, predominantly *L. crocodilus*. Diet in October could not be described due to insufficient number of individuals (4) with stomachs containing food.

Seasonal changes in the diet of the galatheid *M. tenuimana* were statistically significant (*pseudo*-$F_{3,104}$=2.42; p<0.01), and diet in February was different from both diet in the following (April) and the preceding (October, assuming a composite year) seasons. In February, diet of *M. tenuimana* mainly consisted of euphausiids, essentially *M. norvegica* but also *N. megalops*, hyperiids and gelatinous zooplankton, mostly salps and hydrozoans (Fig. 2). In April, main prey consisted of fish remains, and consumption of gelatinous zooplankton maintained, although the siphonophore *Chelophyes appendiculata* was now more important. Consumption of *M. norvegica* was still important, although lower than in February, and *M. tenuimana* and brachyuran crabs were also eaten. Changes to June/July were not statistically significant, but in this period, main food items found in stomachs consisted of organic debris and fish remains. Fish remains were the most abundant food item in October, when *M. tenuimana* also fed on brachyuran crabs and *M. norvegica*.

Aristeus antennatus

For both size categories of *A. antennatus*, seasonal changes in the diet were significant (large: *pseudo*-$F_{3,206}$=6.28; small: *pseudo*-$F_{3,204}$=4.23; both p<0.001) and diet changed between all consecutive seasons (including October and February assuming a composite year).

Benthic polychaetes, especially *Nephtys* sp. and *Glycera* sp., were the dominant prey in all categories of *A. antennatus*, and their consumption was rather constant throughout the year.

Diet of large females of *A. antennatus* was dominated by benthic prey, especially polychaetes in February (Fig. 3). Changes to April were mainly attributable to a large

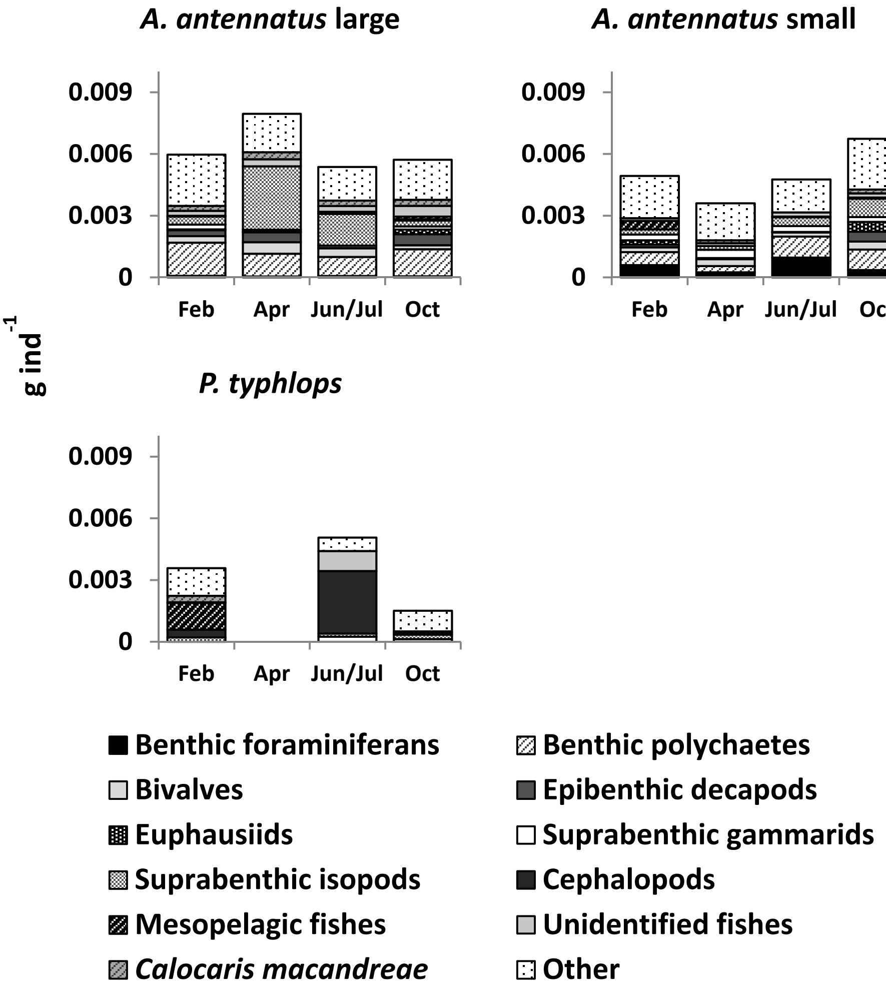


Fig. 3. Diet composition (by weight) of benthos feeder decapod crustacean species in each sampling period.

increase in consumption of hyperbenthic isopods, essentially *N. borealis* (>40% of the diet). This prey still dominated in the diet in June/July. In October consumption of *N. borealis* decreased sharply and diet was dominated by polychaetes again. Brachyuran crabs, holothurians and fish gained importance as prey. In June/July and October some consumption of pasipheid shrimps was also observed.

The interaction between the two factors (sex and survey) of the two-way permutational ANOVA performed on diet composition of small *A. antennatus* was not significant ($p>0.05$), thus seasonal trends in diet composition of individuals of both sexes were analyses jointly. Small *A. antennatus* consumed a wide variety of prey all year long, none of them clearly dominating in the diet (Fig. 3). In February, the most abundant prey were benthic polychaetes, foraminiferans, and ophiuroids. Mesopelagic fish and *M. norvegica* were secondary. In April, consumption of hyperbenthic prey increased, and hyperbenthic gammariids and mysids, namely *Boreomysis arctica*, were the most abundant. Contrarily, ingestion of ophiuroids and polychaetes decreased. Consumption of the hyperbenthic gammariids and mysids decreased in June/July and benthic prey (i.e. polychaetes and benthic foraminiferans) became main prey. Consumption of cumaceans, especially *Leucon longirostris*, also increased in this period. In October, main prey were polychaetes and *N. borealis*, and euphausiids and pasipheid shrimps were also consumed.

Polycheles typhlops

Seasonal changes in the diet were statistically significant (*pseudo*-$F_{2,43}$=1.61; p<0.01). Main prey in February were *C. braueri* and fish eggs, and remains of the shrimp *A. antennatus*, the cephalopod *Histioteuthis reversa* and the benthic shrimp *C. macandreae* were secondary prey (Fig. 3). Diet could not be described in April because of the few stomachs found containing food. In June/July, cephalopod remains were the main food item, constituting more than half of the food ingested. Second most important food item were fish remains. In October this predator mainly preyed upon *M. norvegica* and hyperbenthic prey (i.e. *B. arctica*, *N. borealis* and *Rachotropis* spp.), although changes from June/July to October were not statistically significant. Diet differed significantly between October and February.

3.3.2. *Seasonal trends in fullness*

The interaction between sex and survey of the two-way ANOVA performed on fullness of each species was never significant (p>0.05). Therefore, males and females of all the species were analysed jointly.

Among macroplankton feeders, significant seasonal changes in stomach fullness were only observed between February and April in *P. martia*, when fullness increased to a maximum, decreasing gradually afterwards (Fig. 4). Fullness of *A. eximia* was greatest in February and lowest in October, although changes were not significant. For *P. multidentata* fullness decreased from February to June/July, when it was lowest and it increased afterwards to maximum values in October. *Munida tenuimana* and *P. typhlops* presented parallel temporal patterns of fullness, with similar values within each species between February and June/July and a slight decrease of fullness in October. These changes were not significant either. Fullness of large females of the benthos feeder *A. antennatus* peaked significantly in April and remained constant during the rest of the year. Fullness of small *A. antennatus* increased significantly from

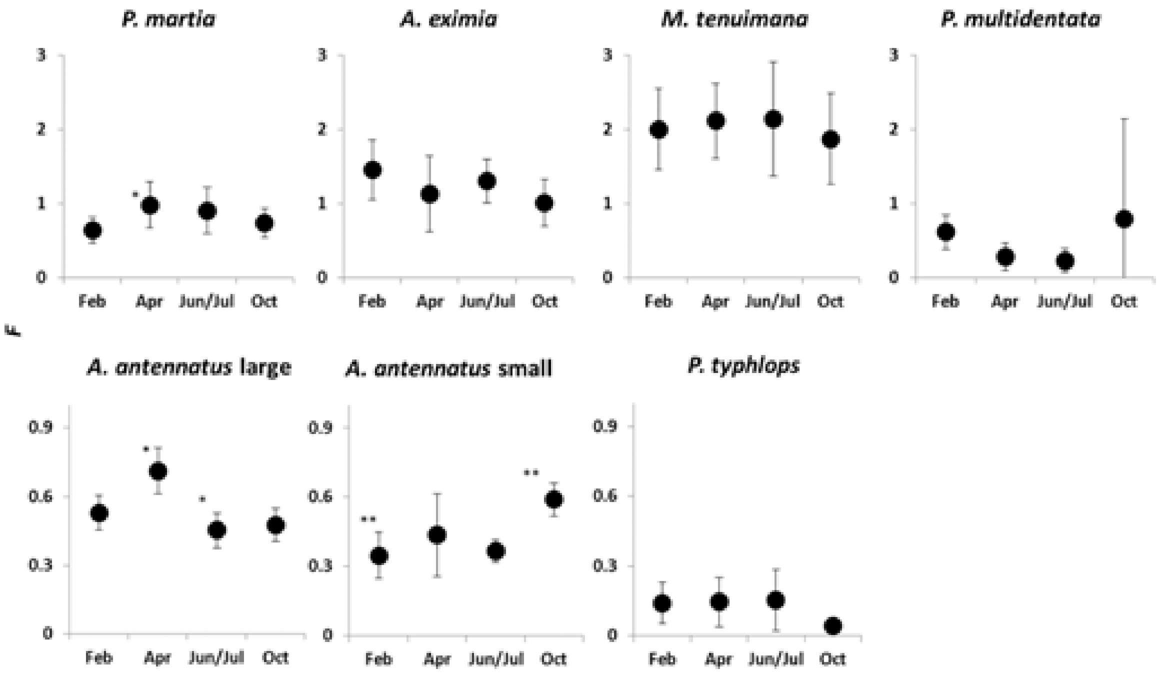


Fig. 4. Seasonal trends in %fullness (F) of the different decapod crustacean species. Vertical bars indicate 95% confidence intervals. Asterisks indicate significant differences with preceding sampling: *p<0.05; **p<0.01; ***p<0.001.

June/July to October, when it was greatest, and decreased in February to minimum values.

3.3.3. *Seasonal trends in dietary diversity*

Diet diversity *H’* among macroplankton feeders followed species–specific temporal trends, and greatest diet diversities seemed to follow one another among the different species (Fig. 5). That is, the diet of *M. tenuimana* was more diverse in February and April and less diverse during the rest of the year, that of *P. martia* was more diverse in April and June/July, and diet diversity in *A eximia* was relatively greater in June/July and October. Diversity (*H’*) of these species was between 2.2 and 4. Dietary diversity in *P. multidentata* was homogenous from February to June/July (*H’*=2.5±0.13). *H’* of both large and small females of *A. antennatus* was lowest in April and gradually increased to October. Instead, for males *H’* was great in February and April, and lowest in June/July. *H’* of *A. antennatus* was the greatest among all species (*H’*=4.4-5.3). Although no value was obtained in April for *P. typhlops*, the pattern of dietary *H’* was similar to that of males of *A. antennatus*. *H’* of diet of *P. typhlops* ranged between 2 and 3.1.

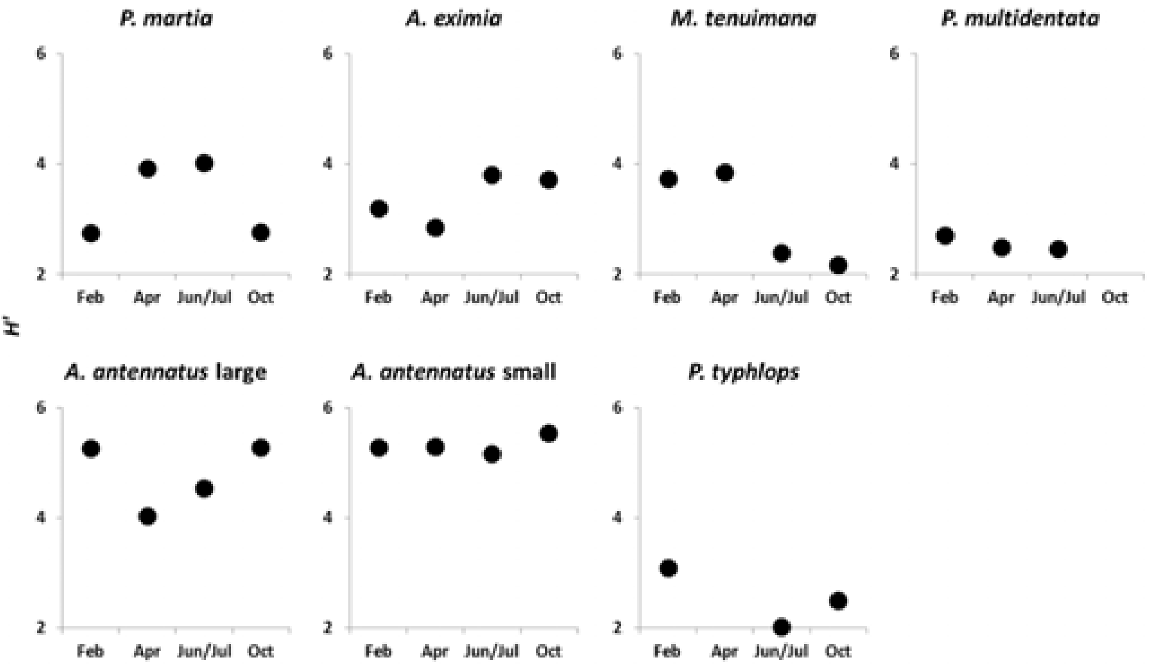


Fig. 5. Seasonal trends in dietary diversity (*H'*) of the different decapod crustacean species.

3.3.4. *Seasonal trends in hepatosomatic index (HSI)*

Greatest HSIs were found in *A. antennatus* and *A. eximia* (from 7.3% to 11.9%) and lowest were in *M. tenuimana* and *P. typhlops* (from 0.3% to 2.5%). *P. martia* and *P. multidentata* presented mid-values of HSI. Significant changes in HSI between consecutive seasons are specified in Figure 6.

Among macroplankton feeders, temporal trends in HSI of *P. martia* and *A. eximia* were parallel, and HSI decreased from February to June/July and increased afterwards (i.e. October) (Fig. 6). HSI of *P. multidentata* increased gradually from February to October, changes being statistically significant between February and April. *Munida tenuimana* had low HSI in February and July, and great HSI in and October.

The HSIs of the benthic-feeders *A. antennatus* and *P. typhlops* were high in February and April, and low in June/July and October. Significant temporal changes were observed in *A. antennatus* but not in *P. typhlops*.

3.3.5. *Seasonal trends in gonadosomatic index (GSI) and percentage of mature and ovigerous females*

In all species, trends in GSI and in the percentage of mature females were parallel.

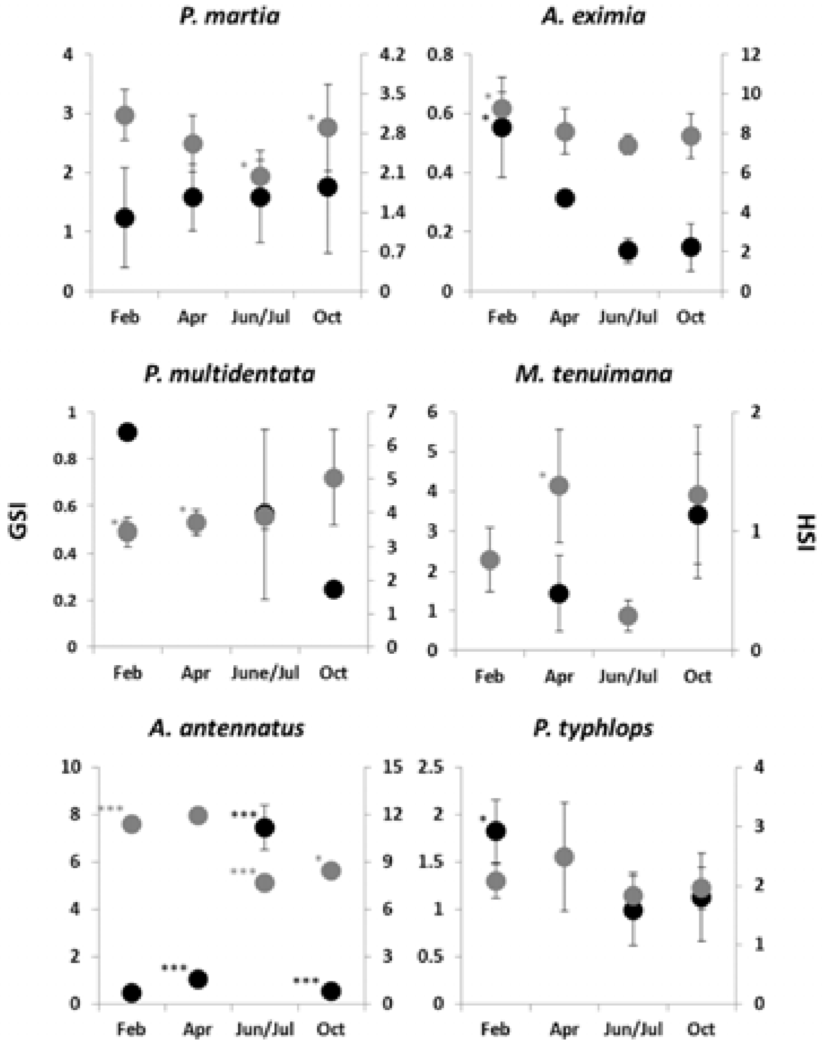


Fig. 6. Seasonal trends in gonadosomatic index (%GSI) (black) and hepatosomatic index (%HSI) (grey) of mature females of the different decapod crustacean species. Vertical bars indicate 95% confidence intervals. Asterisks indicate significant differences with preceding sampling: *p<0.05; **p<0.01; ***p<0.001.

Temporal changes in the GSI of *P. martia* were not significant, due to the high variance in GSI within each sampling period (Fig. 6). This is because *P. martia* has continuous reproduction. In agreement, mature and ovigerous females were observed in all periods (Fig. 7). GSI of *A. eximia* was greatest in February and gradually decreased to June/July and October (Fig. 6). Low within-season variance in GSI was observed, so maturity in the females' population was synchronised. In fact, greatest percentage of mature females was observed in February (Fig. 7), and no mature females were observed in June/July and October. A peak in the percentage of ovigerous females was observed four months after the presence of mature females (June/July). The number of individuals for which GSI of *P. multidentata* was recorded was not large enough to analyse temporal patterns appropriately. Ovigerous females were observed in October and in February to a lesser extent. For *M. tenuimana* GSI had a main peak in October and a secondary peak in April, parallel to the trends in percentages of mature and ovigerous females.

GSI and percentage of mature females of *A. antennatus* had both a sole significant peak in June/July, and variance within each period was very low (Fig. 6). *Aristeus antennatus* is a species that does not carry eggs (Demestre and Fortuño, 1992).

GSI of *P. typhlops* peaked in February and decreased afterwards (Fig. 6), parallel to the trend in the percentage of mature females (Fig. 7). GSI in April was lacking. A peak of ovigerous females was found in June/July, four months after the greatest percentage of mature females.

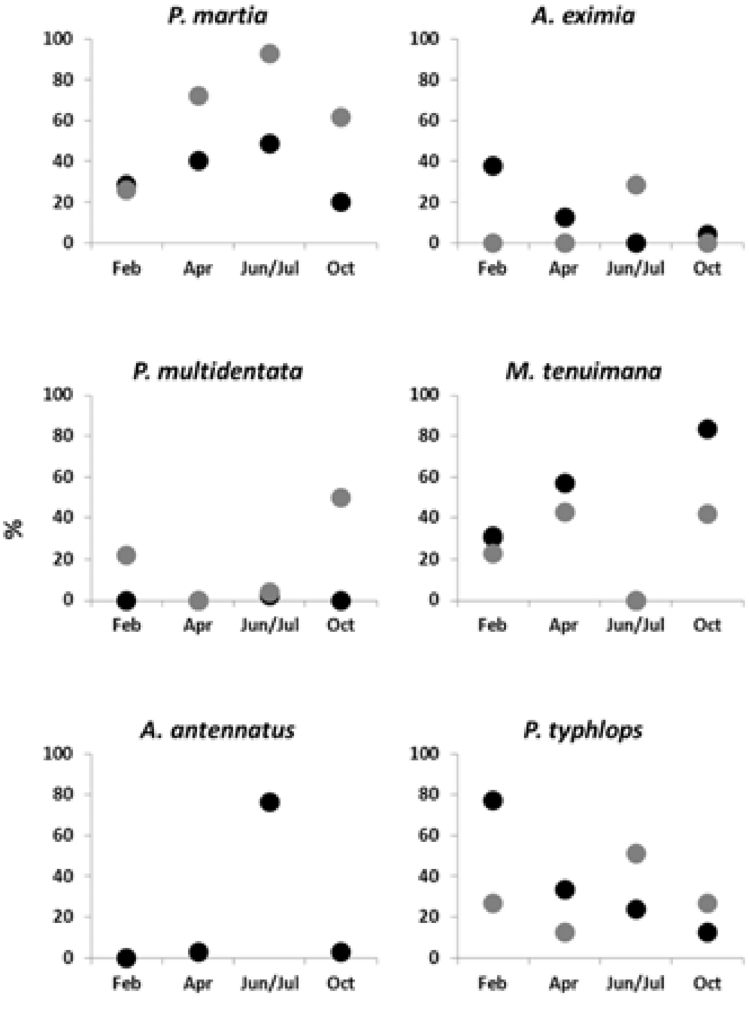


Fig. 7. Seasonal trends in the percentage of maturing (black) and ovigerous (grey) females.

3.4. *Seasonal changes in interspecific relationships*

Dietary overlap was generally low throughout the whole period of the study (Table 3). Among macroplankton feeders overlap was relatively high in February between *P. martia* and *A. eximia* and between *P. multidentata* and *M. tenuimana.* Nevertheless, the most common trend was of relatively greatest overlap between pairs of species in February, decreasing in April and June/July. Overlap increased slightly in October. Dietary overlap between the two size categories of *A. antennatus* was lowest in April and increased to greatest values in October. Although overlap between macroplankton feeders and the benthic-feeder *A. antennatus* was always low, it was greatest in October. Contrarily, temporal trends in dietary overlap between *P. typhlops* and the rest of species were in general greatest in February and lowest in October.

Table 3. Diet overlap for the seven benthopelagic decapod species by season using Schoener's Index. Aant L=*A. antennatus* large; Aant S=*A. antennatus* small; Aexi=*A. eximia*; Mten=*M. tenuimana*; Pmar=*P. martia*; Pmul=*P. multidentata*; Ptyp=*P. typhlops*.

FEBRUARY	Aant L	Aant S	Aexi	Mten	Pmar	Pmul	Ptyp
Aant L	1	0.52	0.12	0.10	0.09	0.01	0.15
Aant S		1	0.16	0.12	0.12	0.02	0.13
Aexi			1	0.29	0.58	0.03	0.19
Mten				1	0.27	0.41	0.11
Pmar					1	0.18	0.10
Pmul						1	0.02
Ptyp							1

APRIL	Aant L	Aant S	Aexi	Mten	Pmar	Pmul
Aant L	1	0.36	0.09	0.12	0.18	0.10
Aant S		1	0.05	0.10	0.11	0.07
Aexi			1	0.03	0.20	0.02
Mten				1	0.26	0.05
Pmar					1	0.08
Pmul						1

JUNE/JULY	Aant L	Aant S	Aexi	Mten	Pmar	Pmul	Ptyp
Aant L	1	0.47	0.10	0.07	0.23	0.03	0.11
Aant S		1	0.09	0.09	0.23	0.02	0.10
Aexi			1	0.06	0.22	0.12	0.07
Mten				1	0.08	0.02	0.20
Pmar					1	0.28	0.06
Pmul						1	0.02
Ptyp							1

OCTOBER	Aant L	Aant S	Aexi	Mten	Pmar	Ptyp
Aant L	1	0.66	0.17	0.17	0.13	0.09
Aant S		1	0.26	0.14	0.15	0.07
Aexi			1	0.21	0.29	0.06
Mten				1	0.23	0.06
Pmar					1	0.07
Ptyp						1

3.5. *Drivers of fullness*

The generalised linear models (GLMs) performed on fullness data for each trophic group revealed that fullness of macroplankton feeders was positively correlated with dietary diversity (*H’*) and predator’s own density, and negatively correlated with surface production 3 months before the sampling and the density of small mesopelagic fish (Table 4). The model explained 47% of the total variation.

For *A. antennatus*, the GLM performed on fullness explained 44% of the total variation and included densities of *C. macandreae*, small stomiiforms (i.e. *A. hemygimnus* and *C. braueri*) and polychaetes, which were positively correlated with fullness (Table 4). Additionally, fullness was inversely correlated to surface production taking place simultaneously to the sampling.

The model for *P. typhlops* was not calculated due to the small number of samples available.

Table 4. Generalised Linear Models performed on fullness of decapods considering the trophic groups obtained by cluster analyses. D.f. = degrees of freedom. H’=dietary diversity; $PPC_{3\ months}$=Phytoplankton pigment concentration at surface 3 months before the sampling; $PPC_{simult.}$= Phytoplankton pigment concentration at surface simultaneously to the sampling. Names of prey taxa indicate their densities.

	Explained dev.	Residual. dev.	Explained dev.	*F*	Sign of correlation	*p-value*
Macroplankton feeders						
NULL		0.050				
H'	0.011	0.040	21.54	15.932	(+)	0.000
$PPC_{3\ months}$	0.004	0.036	7.67	5.676	(-)	0.022
Density	0.006	0.030	11.68	8.640	(+)	0.006
Mesopelagic fish	0.003	0.027	6.39	4.729	(-)	0.036
			47.28			
D.f. 43						
AIC -189.29						
Aristeus antennatus						
NULL		0.004				
C. macandreae	0.001	0.003	24.40	14.860	(+)	0.001
Stomiiforms	0.001	0.003	12.01	7.312	(+)	0.011
$PPC_{simult.}$	0.000	0.002	7.73	4.708	(-)	0.038
Polychaetes	0.000	0.002	8.23	5.013	(+)	0.033
			44.14			
D.f. 33						
AIC -221.27						

3.6. *Relationship between biological cycle and food availability*

The GLM performed on the GSI of females of *P. martia* revealed that 11% of the total variation was explained by a negative correlation between GSI and surface production taking place two months before (Table 5). The GSI of *A. eximia* was greater in larger animals after greater concentrations of lipids in the sediment and after low stomach fullness (Table 5). The GLM performed on the GSI of *A. eximia* explained 54% of the total variation. The GLM for the GSI of adult females of *A. antennatus* included 5 variables that explained 75% of the total variation. The GSI was positively related to surface production taking place three months before the sampling and to abundances of *N. borealis*. GSI was greater at greater densities of adult females of *A. antennatus* and in larger animals, following great stomach fullness. Trends in GSI of adult females of *P. typhlops* were explained by two variables that explained 35% of the total variation. Greater concentration of lipids in the sediments enhanced gonad growth, which was observed in larger animals.

Table 5. Generalised Linear Models performed on gonadosomatic index of the seven species of benthopelagic decapods. F value and significances specified. Sign of the correlation indicated in parentheses. D.f. = degrees of freedom. Factors: Density= density of each decapod species; PPC$_{2\ \text{months}}$ and PPC$_{3\ \text{months}}$=Phytoplankton pigment concentration at surface 2 and 3 months before the sampling; Lipids=lipids concentration in sediments; 1 survey=value from the preceding sampling survey; densities of different potential prey sampled with the bottom trawl also indicated.

	Species							
Factor	*P. martia*		*A. eximia*		*A. antennatus*		*P. typhlops*	
Size			6.92^{*}	(+)	10.76^{**}	(+)	5.89^{*}	(+)
Density					46.16^{***}	(+)		
Fullness$_{\text{1survey}}$			29.24^{***}	(-)	43.31^{***}	(+)		
PPC$_{2\ \text{months}}$	5.85^{*}	(-)						
PPC$_{3\ \text{months}}$					513.37^{***}	(+)		
Lipids$_{\text{1survey}}$			15.82^{***}	(+)			28.66^{***}	(+)
C. borealis$_{\text{1survey}}$					111.92^{***}	(+)		
% explained	10.87		53.60		74.68		35.42	
AIC	-128.54		-256.57		-793.33		-247.34	
D.f.	49		48		251		65	

4. Discussion

4.1. *Feeding guilds*

In agreement with previous studies on trophic relationships in crustacean assemblages from the Mediterranean slope, benthopelagic decapods structured according to the vertical distribution of available food resources near the seabed (Cartes, 1998; Cartes and Carrassón, 2004; Papiol et al., 2013).

We recorded high diversities in diets of deep-sea decapods, indicating exploitation of a great variety of prey. Nevertheless, two main trophic pathways based on mesopelagic or benthic prey consumption can be deduced, as shown by Cartes (1998) from diets and by Papiol et al. (2013) from stable isotope ratios. Dietary results coincided, in general, with previous studies (see references in Table 1). Dietary data did not allow the discrimination between migratory (i.e. *P. multidentata*) and non-migratory (i.e. the *Plesionika martia*, *Acantephyra eximia* and *Munida tenuimana*, feeding close to the sea bottom) plankton feeders (Cartes, 1993d, g). Both groups prey on similar pelagic species, though at different levels of the water column. Benthos feeders (*B*) were strongly segregated; *Aristeus antennatus* mainly foraged on prey that live buried in the substratum or right beneath it (Cartes and Sardà, 1989; Cartes, 1994) and *P. typhlops* restricted to the uppermost level of the bottom sediment and the water layer immediately adjacent to the seabed (Cartes and Abelló, 1992). Among *B*, pelagic prey were also important seasonally, and may act as vectors for surface production and signals for reproduction processes (see below).

A pattern of increasing food consumption with increasing swimming capacity (Maynou and Cartes, 1998; Papiol et al., this volume), which is related to greater metabolic rates (Koslow, 1996; Company and Sardà, 1998; Drazen, 2002), was confirmed: the benthic *P. typhlops* had the lowest feeding intensity, which was greater in nektobenthic species (i.e. *P. martia*, *A. eximia* and *A. antennatus*). The low feeding intensity of the mesopelagic shrimp *P. multidentata* is attributable to its nocturnal feeding behavior mainly in midwater (water levels above the Benthic Boundary Layer) (Cartes, 1993c, d), so when specimens were caught in the daytime stomachs were empty. Differently, greatest feeding intensity of the slow-moving benthic *M. tenuimana* is reinforced by its diurnal feeding (Maynou and Cartes, 1998) linked to the presence of the species' preferred prey items near the bottom (Sardou et al., 1996). Nevertheless, other factors should contribute to the high feeding intensities of *M. tenuimana*, as discussed below.

Related with the swimming capacity of decapods, we observed a pattern of greater HSI in more mobile species and low HSI in low-mobile ones (i.e. *M. tenuimana* and *P. typhlops*). The hepatopancreas (HP) of decapods is considered the main organ for energy storage, providing metabolic energy for the main energy expending processes, i.e. swimming (Gade, 1983; Yu et al., 2009), reproduction (Gibson and Barker, 1979) and moulting (Adiyodi and Adiyodi, 1970). Thus, the HP of species with low natatory capacity may be exempt of storing energy for this purpose, enabling the existence of a small HP.

4.2. *Seasonal variations in resource use and feeding intensity*

We performed over the Catalonian slope novel analyses on seasonal changes in the resource use in deep sea trophic webs. In general, diets of *M* changed from February to April, after the late winter bloom of surface production and particle flux (Miquel et al., 1994). In February, *M* mainly preyed upon *M. norvegica* and *P. multidentata* (Fig. 2), which dominated the macroplankton community in this period of low diversities of macroplankton (Sardou et al., 1996; Cartes, 1998b; Cartes et al., 2010). Expected influence of predator size in prey selection (Cartes, 1993b,d,e) was observed and while *P. multidentata* and *M. tenuimana* preyed upon *M. norvegica*, larger *M* predators (i.e. *P. martia* and *A. eximia*) consumed greater amounts of *P. multidentata*. In addition, the pairs of predators feeding on the same prey (and with high dietary overlap in this period) avoid possible competition by feeding at different times of the day and at different levels of the water column (e.g. *M. tenuimana* and *P. multidentata*: Cartes, 1993c, g), or by being bathymetrically segregated (e.g. *A. eximia* and *P. martia*: Cartes, 1998a). In April, the natatory *A. eximia*, *P. martia* and *P. multidentata* consumed greater amount of different mesopelagic prey. These species must respond to the bloom of secondary production, which is characterized by greater availability of a large variety of plankton (e.g. mesopelagic fish, hyperiids and gelatinous zooplankton: Sardou et al., 1996; Cartes, 1998b; Cartes et al., 2010). Instead, the low-mobile *M. tenuimana* switched diets to greater consumption of prey from the bottom surface, and an increase in the scavenging activity that continues to June/July can be deduced from the presence of fish remains and of organic debris in stomachs (Cartes, 1993c). The temporal patterns in dietary overlap were coupled to the trends in diversity and dominance in the macroplankton community. The availability of a wider array of potential prey (in other words, the lack of a dominant single prey) in April and June/July favored greater partitioning of resources, as revealed by the decrease in dietary overlap. This suggests active prey selection among decapods that should be based, at least to some extent, on prey-predator visual interactions. In October, the dynamics of zooplankton and the dietary composition of *M* were also parallel: the decline in secondary pelagic production and the dominance of *M. norvegica* close to the seabed (Sardou et al., 1996; Cartes et al., 2010) coincided with the greater consumption of the latter, a phenomenon that has been reported in other studies on bathyal benthopelagic megafauna (Macpherson, 1981; Cartes, 1998a). The dominance of *M. norvegica* and *P. multidentata* in October and February brought about greater dietary overlap (i.e. more similar diets).

Seasonal patterns in the feeding intensity within the group of *M* decapods differed, although a trend of great fullness in April and June/July that decreased in October was observed among the non-migratory species. As observed in fish (Madurell and Cartes, 2005; Papiol et al., this volume), great feeding intensity followed the greater availability of prey after the late winter surface bloom. Lower fullness in October was associated to the decrease in small macroplankton production. The peak of fullness of *A. eximia* in February is attributable to the capacity of this species to prey on small *P. multidentata* present over mid-slope depths in this period (authors' unpublished data), which probably owes to its greater size (compared to *P. martia*) (Cartes et al., 1994) and its burst swimming performance (Bailey et al., 2005). Temporal patterns in feeding activity of the own *P. multidentata*, were opposed to those of the non-migratory species above cited (Fig. 4), and seemed coupled to the presence of small pelagic prey, essentially *M. norvegica*, in the water column and the BBL (Sardou et al., 1996; Cartes et al., 2010). Some kind of association must exist between the diet and the seasonal migratory behavior of *P. multidentata*. For example *M. norvegica* should be captured rather at surface/midwater (0-300 m) in February and closer to the bottom (*ca.* 500 m) in October, following the annual migratory cycle of this euphausiid (in the Ligurian Sea: Sardou et al., 1996).

We discussed that pelagic secondary production after the winter-spring bloom enhances the feeding activity of *M* benthopelagic decapods. This idea is reinforced by the relationship found between surface production 3 months before samplings and fullness in GLMs for macroplankton feeders. *M* decapods respond to the winter surface bloom of primary production with this delay (*ca.* 2-3 months) because this may be the time required for biomass increases of their pelagic prey (Fanelli et al., 2011b). The increased flux of particulate organic matter (POM) from surface production in spring-summer (Miquel et al., 1994) along the water column likely enhances the growth of larvae and early stages of macroplankton species found in the epi and mesopelagic zones, which may later perform ontogenetic migrations to the Benthic Boundary Layer with adult stages reaching bathyal depths (e.g. *C. braueri*: Goodyear et al., 1972; *M. norvegica*: Sardou et al., 1996). Particle flux after the surface bloom also favors the proliferation of deep macroplankton from low trophic levels near the bottom (Franqueville, 1971; Sardou, 1996; Cartes, 1998b; Cartes et al., 2010).

The positive relationship between fullness (*F*) of macroplankton feeders and their population density must be associated to feeding aggregations, as found for *Plesionika* spp. (Fanelli and Cartes, 2004). In addition, aggregations of adults for reproduction (e.g. in *P. martia*: Puig et al., 2001; Fanelli and Belluscio, 2003; *P. multidentata*: Company et al., 2001), cannot be excluded and these species generally had a temporal pattern of *F* parallel to that of the gonadosomatic index, as discussed later.

Greater seasonal variations of macroplankton communities with respect to macroinfauna (Mauchline and Gordon 1991; Iken et al. 2001; Cartes et al., 2010; Mamouridis et al., 2011) did not lead to the greater changes in diet composition of *M* compared to *B* that are usually accepted (e.g. Macpherson, 1981; Papiol et al., this volume), and the diet composition of *A. antennatus* varied between all consecutive seasons. Although the diet of *A. antennatus* is mainly based on endobenthos, this species showed the capacity of exploiting a wide spectrum of prey. In April, *A. antennatus* consumed greater amount of hyperbenthos, and in October their diet included pelagic prey that peaked (i.e. fish: Cartes et al., 2010; and *M. norvegica* and *P. multidentata*: Sardou et al., 1996; Cartes, 1998a; Cartes et al., 2010). Consistently, we observed (from GLMs) that feeding intensity of *A. antennatus* was positively related to densities of small mesopelagic fish in the environment. Large expansion of trophic niche by *A. antennatus* was observed in other areas of the western Mediterranean Sea (e.g. north of the Balearic Islands: Cartes et al., 2008) and was detected through stable isotopes (Papiol et al., 2013). This must work as an advantageous strategy for gaining competitiveness over other species, as confirmed by the dominance of *A. antennatus* at middle slope assemblages in most areas in the western Mediterranean (Cartes and Sardà, 1992; Papiol et al., 2012). High diet diversities (*H'*) obtained for *A. antennatus* agree with the classification of this species as a non-specialised hunter (Cartes, 1994). Therefore, diet should reflect the composition of benthos, and great consumption of *N. borealis* by large *A. antennatus* in April and June/July should be associated to its greater availability. Both the presence of fish and cephalopod remains in stomachs of coexisting *N. borealis* in April (authors' personal observation) and the scavenging activity in *M. tenuimana* in the spring-summer period support the possibility of great availability of carrion that would in turn enhance the presence of large *N. borealis* (Kaim-Malka, 1997; Johansen and Brattegard, 1998).

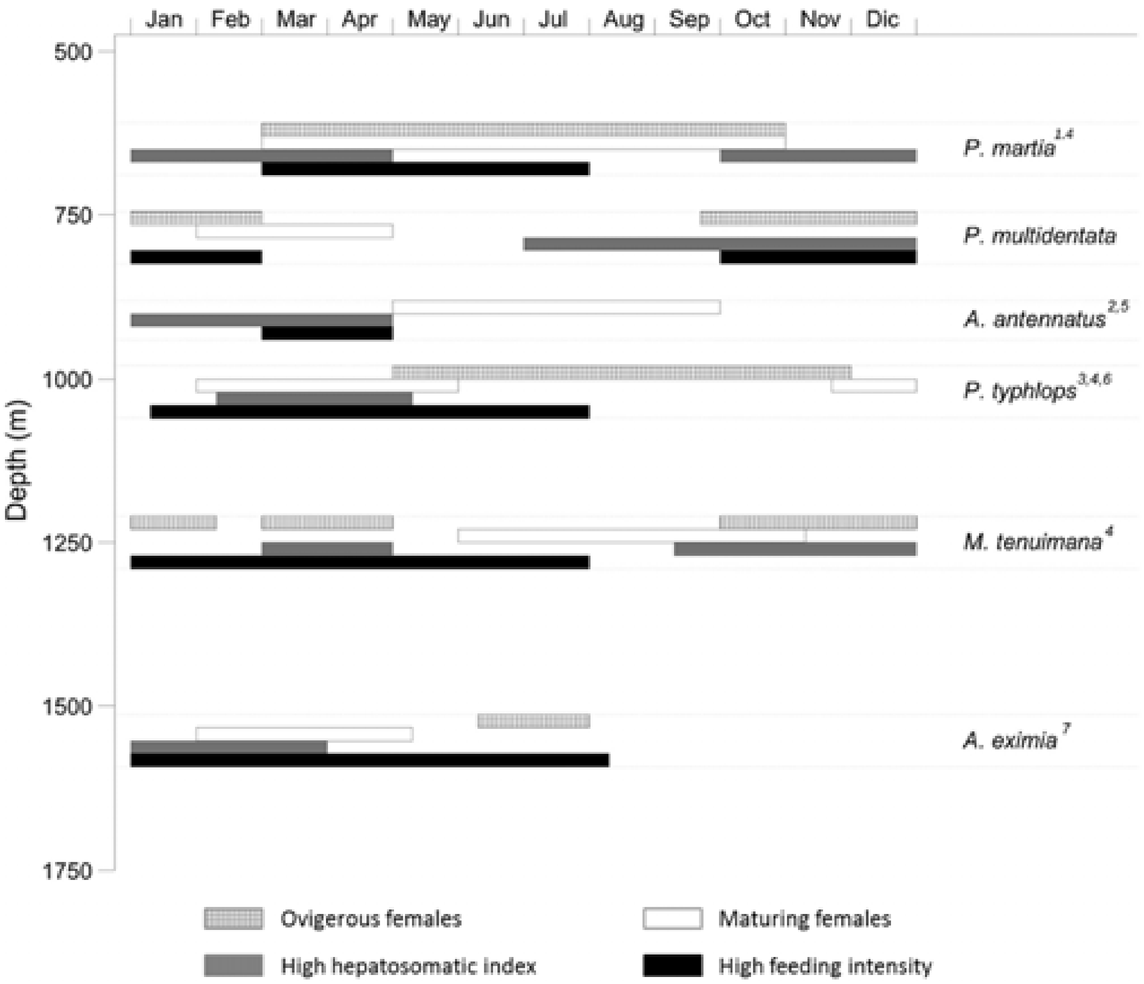
Large and small *A. antennatus* showed different, somehow inverse, temporal trends in feeding activity. Although size had some influence in prey selection by *A. antennatus* (Cartes and Sardà, 1989; own results), this must be associated to the reproductive cycle of this species. While large females increased fullness in April, before the reproductive period starting in May-June (Demestre and Fortuño, 1992) this tendency was not found in small specimens. Ovarian development of *A. antennatus* seems to be induced by copulation in spring (Carbonell et al., 2006; Kapiris and Thessalou-Legaki, 2008), and therefore pre-reproductive increase in fullness in April to meet the energy demands for gonadal development is plausible and has been observed in other areas in decapods (*A. antennatus*: Cartes et al., 2008; *P. martia*: Fanelli and Cartes, 2008) and in fish (Madurell and Cartes, 2005; Papiol et al., this volume). Additionally, some authors have reported greater ingestion of energetic prey accompanying the pre-reproductive increase in food consumption (e.g. Cartes et al., 2008). Therefore, some positive selection on *N. borealis* in April and June/July by large females of *A. antennatus* cannot be discarded. The median size (>20 mm), the burrowing behavior (MacQuart-Moulin and Kaim-Malka, 1994) and the moderate lipid content (152 mg/gDW in the North Atlantic: Zwaan and Skojldal, 1979; 35 mg/gDW in the Catalan Sea: own unpublished data) of *N. borealis*, make this species the most likely source of "extra" energy that *A. antennatus* could use prior to its reproduction in the study area.

Scavenging was important in the feeding activity of (adult) *P. typhlops*, and remains of large cephalopods (*Histioteuthis* sp.) were the main food source in June-July coinciding with the period of maximum fullness. This again suggests great presence of carrion that could be available for consumption to this slow-moving blind species. *P. typhlops* also exploited mobile living prey seasonally, e.g. *M. norvegica* and hyperbenthic peracarids as *B. arctica*, *R. caeca* and *N. borealis*. High predation on *M. norvegica* in autumn was found in previous studies in the same area (Cartes and Abelló, 1992), coinciding with higher abundance of this euphausiid near the bottom (Sardou et al., 1996). This tendency was not detected in October 2007 in *P. typhlops*, and was neither as strong as previously reported in the diet of the benthos feeder *A. antennatus*

(Cartes, 1994). This could be due to interannual changes in euphausiids abundance, euphausiids' scarcity restricting their consumption to more active predators.

4.3. *Relationship between trophic dynamics and reproduction*

After Orton's rule (1920), biological processes ought to be continuous in stable environments such as the Deep Sea. Instead, both seasonal and continuous reproductive patterns have been found among slope decapod crustaceans (e.g. Company et al., 2003; Fanelli and Cartes, 2008; Guijarro et al., 2008; Briones-Fourzán et al., 2010; Gastoni et al., 2010; the present study). Even more, seasonality in reproduction among decapods increases with depth in the Mediterranean Sea (Company et al., 2003). This trend was also observed in the present study (Fig. 8), with the species distributed deeper (i.e. *A. eximia* with average depth distribution > 1000 m; Fanelli et al., submitted) showing high GSI during a shorter period. Seasonality in reproduction responds to natural fluctuations in environmental factors (Gage and Tyler, 1991), which in the study area are associated with variations in food (e.g. PPC, lipids, prey) availability over slope depths. POM from the photic zone is the main food source supporting the bathyal faunal communities, and its importance varies seasonally causing important changes in their structure (Polunin et al., 2001; Drazen, 2008; Stowasser et al., 2009; Fanelli et al., 2011a,b; Papiol et al., 2013). Coherently, GSI of mid-slope decapods was partially controlled by indicators of the vertical flux from surface production (e.g. lipids, PPC 2 and 3 months before sampling), as has been observed previously in other invertebrates (e.g. Bishop and Shalla, 1994; Ginger et al., 2001; Howell et al., 2004; Fanelli and Cartes, 2008). This occurs not only among pelagic feeders, but also among the benthos feeders. The delay in the response of GSI to the vertical organic matter inputs was related to the trophic level and feeding mode of decapods. The GSI of *P. martia*, feeding at lower trophic levels and on pelagic prey (Papiol et al., 2013; own results), responded earlier ($PPC_{2\ months}$ in GLM) to new inputs from surface production than *A. antennatus*, the latter with higher trophic level and therefore with more trophic steps after the primary POM food source. GSI of *A. eximia* and *P. typhlops* was linked to lipids deposited in the sediment. These are indicators of the arrival of phytodetritus and marine snow (Fabiano et al., 2001), which has been recorded in the western Mediterranean as deep as 2070 m (Riaux-Gobin et al., 2004). Both *A. eximia* and *P. typhlops* had highest GSI in February, when they also occupied similar trophic level (Papiol et al., 2013). Lipids are highly energetic and easily degradable organic compounds that may be rapidly transferred through the food web



[1] Maiorano et al., 2002; [2] Demestre and Fortuño, 1992; [3] Maiorano et al., 1998; [4] Company et al., 2003; [5] Cartes et al., 2008; [6] Cabiddu et al., 2008; [7] Gastoni et al., 2010.

Fig. 8. Scheme of the timing in the reproduction, biological and trophic condition of the dominant decapods living along the continental slope in the Balearic Basin. Species are ordered (downwards) by increasing average depth that they inhabit.

via the planktonic prey (i.e. *P. multidentata* for *A. eximia* and *C. braueri* for *P. typhlops*) (Fanelli et al., 2011b). Lipid requirements increase in maturing decapods (Wouters et al., 2001) due to increased lipid amounts in the ovary during ovarian maturation (Kulkarni and Nagabhushanam, 1979; Harrison, 1990; Rosa and Nunes, 2003b). Within species, GSI and brood size increased with female size (Maiorano et al., 2002; Guijarro et al., 2008; Briones-Fourzán et al., 2010).

The response of GSI to indicators of surface production varied among species with similar trophic dynamics (i.e. *P. martia* and *A. eximia*). Related to this, the temporal patterns in GSI differed among species within the same feeding guild, pointing to successive and non-overlapping spawning.

High GSI and presence of ovigerous females during most of the year and especially in summer in *P. martia* suggests a continuous (or almost continuous) pattern of reproduction with a seasonal peak, which is consistent with previous observations (Company et al., 2003; Maiorano et al., 2002). The rest of species from the present study presented pronounced peaks of GSI in some specific seasons suggesting seasonal reproduction, as has already been described (Demestre and Fortuño, 1992; Company et al., 2003; Guijarro et al., 2008; Gastoni et al., 2010). Timing of reproduction observed agreed with the previous findings, with the exception of the galatheid *M. tenuimana*.

Protracted spawning is considered as an adaptive strategy aimed at ensuring that at least some of the larvae will encounter favorable conditions for survival and growth (Sherman et al., 1984). It could be one factor contributing to the great abundance *P. martia* over Mediterranean continental margins (Cartes and Sardà, 1992; Papiol et al., 2012). Temporal trends in feeding intensity and GSI of *P. martia* were rather parallel, and both were *quasi*-opposed to trends in HSI. The parallel temporal trends of feeding intensity and GSI indicate continuous reliance on food available in the environment for gonad maturation, which was observed in some decapods (Rosa and Nunes, 2003a, b) and is also characteristic of iterouparous fish (Murua and Saborido-Rey, 2003). Still, the energy obtained from feeding is transferred to the ovary *via* the hepatopancreas (Gibson and Barker, 1979), and seasonal trends in HSI are defined by the balance between energy incomes and expenditures (Harrison, 1990; Tuck et al., 1997). Therefore, HSI depletion in April and June/July is likely caused by greater energetic expenses than those covered by the food ingested, which are attributable to the high energetic costs of continuous maturation of ovaries and production of eggs (Wehrtmann and Graeve, 1998). Consistently, the decrease in gonad maturation (GSI) after summer concurred with HSI recovery (in autumn). The HSI increase must be reinforced by contemporary consumption of highly energetic prey and by preceding high feeding intensity, a relationship that was also found in the other *M* species.

The pattern of HSI depletion with gonad growth was much more apparent in *A. antennatus* and *P. multidentata* (Fig. 6), both species also preferentially distributed over the middle slope (< 1000 m). Moreover, greater feeding intensity also preceded gonad development. Both patterns are again consistent with the great metabolic costs associated to gonad maturation. Greater gonads (evidenced by the great GSI) in fully mature females of *A. antennatus* (June/July) compared to the rest of species likely explain the greater oscillations both in fullness and HSI. Greater gonads are due to the production of a greater number of eggs associated to reproductive strategy of *A. antennatus*. As the rest of penaeoidean shrimps, *A. antennatus* sheds eggs into the water not attaching them to their pleopods, and greater gonads facilitate the production of increased egg number to compensate high larval mortality. The decline in fullness with gonad size increase could be due to size restriction in the cephalotorax. Regarding *P. multidentata*, production of few large eggs (Company et al., 2003) with great amounts of yolk for the generation of lecitrotrophic larvae requires considerable energy, additional to that required for the swimming activity of this mesopelagic shrimp. Quite different reproductive strategies involving different parental care of the offspring (planktotrophic *vs.* lecitotrophic) in this two species result in similar reproductive success, and both species dominate over the middle slope (Cartes et al., 1994).

In contradiction with this pattern, *M. tenuimana*, with a reproductive strategy similar to that of *P. multidentata* (large eggs and lecitotrophic larvae), had contemporary peaks of HSI and GSI. The great feeding intensities observed in the low-mobile *M. tenuimana* compared to the rest of species coupled with their low energetic requirements for swimming may result in energy intakes that cover the needs for gonad maturation and allow simultaneous accumulation of reserves in the HP (April and October). Low HSI in February and June/July, after the peak in GSI, are probably associated to great consumption of energy during the posthatching moults, which may be highly expensive in this species characterized by a large carapace/body mass ratio and a much calcified carapace.

The two peaks of GSI and of ovigerous females observed in *M. tenuimana* suggest bivoltine reproduction. This does not concur with previous findings in the same area (Company et al., 2003), but agrees with observations made in the Atlantic Ocean (Hartnoll et al., 1992). Differences with the previous study performed in the Catalan Sea (Company et al., 2003) could be due to interannual differences in food availability. Given that ovarian maturation takes place when the adequate balance in the energetic budget is met, low food availability in the study by Company et al. (2003) could derive in univoltinism. Differences in the sign of the North-Atlantic Oscillation index (NAO) between the periods of the two studies could have some influence in this sense (Cartes et al., 2009b), though specific studies would be required in order to confirm this hypothesis.

Acantephyra eximia and *P. typhlops* had parallel temporal trends in reproduction, with a peak of GSI in February and of ovigerous females in June/July. Also, the February reproductive peak coincided with greatest HSI. In this period, both species had great relative feeding intensities and ingested pelagic energetic prey, which may reimburse energy losses for gonad maturation. Although not easy to explain, the decrease of HSI and GSI in June/July, when feeding intensities are still high must owe to some relationship with other processes, most probably to egg spawning and the associated moulting (Raviv et al., 2008). In fact, during and after egg extrusion, both the ovary and the hepatopancreas are typically depleted (Harrison, 1990).

It is commonly accepted that breeding cycles among decapod crustaceans are correlated with seasonal changes in such a way that the offspring are produced at a time most favorable for their survival (Raviv et al., 2008). Despite the different timings of ovarian maturation that we observed (Fig. 8), we found a common pattern in the presence of ovigerous females and therefore the timing of larval eclosion. In species directly producing larvae (i.e. *A. antennatus*) and those carrying relatively small eggs (i.e. *P. martia*, *P. typhlops* and *A. eximia*), larvae were released in summer, while those species with big eggs (i.e. *P. multidentata* and *M. tenuimana*) (Maiorano et al., 2002; Company et al., 2003) carried them in late autumn and early spring, suggesting larvae fed from the environment in the winter-spring period. Given that data on larval stages of deep decapods suggests they migrate to the photic zone in their pelagic phases (Lindley, 1986; Carbonell et al., 2010), this patterns of egg release could be linked to the presence of food in shallower waters during the late winter surface production bloom and/or to the existence of the permanent slope Intermediate Nepheloid Layer (Puig and Palanques, 1998) in late-spring and early summer (Puig et al., 2001). Nevertheless data on larval distribution is scarce and samplings of these studies are usually restricted to shallow waters. Therefore, further seasonal studies considering the entire water column (including de Benthic Boundary Layer) and covering all seasons are required in order to clarify this issue.

The different reproductive patterns observed suggest seasonality in food availability is not the only factor controlling the biological cycle of deep-sea species, and other factors may contribute to regulation of the timing of reproduction (Harrison, 1990), including internal regulation for the production of offspring in the most favorable conditions (Raviv et al., 2008) or the effect of other biological processes affecting the optimal energetic balance needed for reproduction (Harrison, 1990).

As conclusion, we observed that bathyal decapods partition well the available resources in all seasons and that changes in prey availability are critical drivers of seasonal changes in their dietary composition and feeding intensity. In addition, the phase of the reproductive cycle also seems important, and deep decapods increased food consumption and ingestion of some prey, mainly mesopelagic (e.g. euphausiids, Pasiphaeidae, fish) but also hyperbenthic (*N. borealis*) in pre-reproductive periods. Relationships between the biological indicators (GSI, HSI, fullness) here considered varied among decapod crustacean species depending of the variety of life strategies adopted, which at the end can result in similar success in species dominance in deep-sea systems in spite contrasting strategies. Despite all the differences observed, spawning was coordinated to periods with high food inputs, reinforcing the idea that production of offspring in the most favorable conditions also contributes to regulating the timing of reproduction.

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CONCLUSIONS

CONCLUSIONS

Our results allow drawing some conclusions regarding the role of trophic resources in spatio-temporal changes in assemblages, in food web structure, and in the feeding patterns and reproductive dynamics of the benthic and the benthopelagic communities over the Catalan slope:

1. Bathymetric changes in the composition and size distribution of benthopelagic megafauna were attributable to the responses of species to environmental variables correlated with depth (e.g. temperature and salinity) and the decrease in prey availability with depth. Changes consisted in a species replacement with depth and a bigger-deeper (or smaller-shallower) pattern of species' size distribution.

2. Seasonal changes in the composition of benthopelagic fish and decapods mainly depended on water column conditions (stratified vs. homogenised), basically defined by changes in salinity and temperature. The presence/absence of the thermocline may have influence on the dynamics of organic matter inputs reaching the deep sea.

3. Peaks in surface production in February-March and maximum river discharge in April in periods of water column homogeneity, which must have increased the availability of organic matter at bathyal depths, favoured greater densities of megafauna.

4. Peaks of surface primary production in winter and maximum river discharge in April corresponded to a maximum in megafaunal biomass in summer after a time lag of *ca.* 3–5 months. Intermediate peaks of macrofaunal key prey (zooplankton, micronekton and benthic infauna) were observed, which may channel the organic matter inputs to higher trophic levels.

5. Within the benthic community, a wide spectrum of feeding strategies (from active suspension feeders to top predators) and complex food webs consisting of at least 3 trophic levels were deduced from the continuum of values (e.g. $\delta^{15}N$ range of 8‰) of stable isotope ratios found among the macro- and megabenthic fauna.

6. The ^{15}N enrichment of active suspension feeders and surface deposit feeders by *ca.* 3 ‰ with respect to particulate organic matter (POM) in sediments suggests that both feed on sinking particles. The ^{15}N enrichment of sub-surface deposit feeders by *ca.* 6‰ with respect to POM in sediments points to the existence of a parallel and somehow new branch of the food web based on bacteria and refractory and biodeposited material.

7. Generalised weak $\delta^{15}N$-$\delta^{13}C$ correlations in the benthic community indicate that it relies on multiple carbon sources throughout the year: likely different kinds of sinking particles (e.g. marine snow, phytodetritus), sedimented and recycled POM, and macrophyte remains. Even weaker $\delta^{15}N$-$\delta^{13}C$ correlations in October suggest an increase in carbon sources.

8. Both marine and terrestrial inputs from vertical and advective fluxes, respectively, were food sources for macro- and megabenthos, but their importance varied seasonally. Organic matter deriving from the late-winter peak of surface primary production was an important food source for the benthic community under water column homogeneity. Terrestrial inputs channelled through maximal river discharges in April were an additional food source for benthos in summer, after *ca.* 2 months, in periods of low water turbidity near the bottom.

9. Within benthos, coupling with surface inputs differed between species with similar trophic level belonging to different feeding guilds. The analysis of pigments in guts revealed that active suspension feeders (the bivalve *Abra longicallus*) responded earlier than surface deposit feeders (the thalassinid shrimp *Calocaris macandreae*) to the late-winter surface bloom of production.

10. Fish and decapods were segregated from a trophic point of view. Fish had higher $\delta^{15}N$ and lower $\delta^{13}C$ than decapods because they feed upon fauna with higher trophic levels and ingest less amounts of benthic prey.

11. Within fish and decapods, both stable isotopes and dietary studies revealed that the food web was structured as a function of the position along the benthic–pelagic gradient in the sediment-water interface where megafauna species found their prey. Predator size was also important, especially for fish. Large fish and decapods fed either upon benthos or zooplankton. Small fish segregated from large ones and fed mainly upon hyperbenthos and small macroplankton.

12. Strong $\delta^{15}N$-$\delta^{13}C$ correlations observed in the benthopelagic community in periods of water column homogeneity, after peaks of surface primary production, emphasize the importance of OM from the photic zone as their main source of food source. As for benthos, weaker correlations observed under stratified waters, especially in October, indicate the community relied on more diversified food sources, probably from advection.

13. Seasonal changes in the food web structure of benthopelagic megafauna agree with the patterns of macrofauna production. The ^{13}C depletion after winter in migratory macroplankton feeders (e.g. *Sergia robusta*) points to consumption of more pelagic prey. The ^{15}N enrichment in summer among benthos feeders (e.g. *Aristeus antennatus*) suggests greater consumption of enriched hyperbenthic macrofauna.

14. Within the benthopelagic megafauna community, seasonal changes in the prey used were coupled with changes in the availability of different primary food sources depending on the trophic guild considered. Seasonal variations in the food sources used by macroplankton feeders were determined by changes in the amount of lipids and of chlorophyll pigments in sediments, both proxies for phytodetritus inputs. In contrast, in benthos feeders, seasonal changes in food utilisation were explained by changes in total organic carbon (TOC) in sediments and in fluorescence measurements near the seabed.

15. Changes in food availability are critical drivers of seasonal variations in the dietary composition and feeding intensity of fish, with different responses observed between fish of different trophic guilds. Benthos feeders increased feeding activity upon hyperbenthic and deposit feeding macrofauna (*C. macandreae*) in summer, two months after the peak of surface production when more TOC was available in the sediments. Macroplankton feeders increased feeding activity towards more mobile hyperbenthic and planktonic macrofauna after spring, in association with greater inputs of phytodetritus (i.e. greater amounts of lipids in sediments).

16. As for fish, changes in food availability are critical drivers of seasonal variations in the dietary composition and feeding intensity of decapod crustaceans. Macroplankton feeder decapods increased feeding intensity towards zooplankton prey after the late-winter surface production bloom. Feeding intensity of the benthos feeder *A. antennatus* was enhanced by the availability of both benthic and mesopelagic prey. Consistently, diet varied between all consecutive seasons mainly related with the exploitation of hyperbenthic and planktonic macrofauna.

17. Both for fish and for decapods, gonad maturation (i.e. gonadosomatic index - GSI) was associated with abundances of trophic resources and specific prey, suggesting that the availability of specific trophic resources regulates the reproductive cycles, at least partially. Main primary food source controlling GSI was derived from surface production and the associated detrital inputs in species from all feeding guilds, which implies a rapid (*ca.* 2-3 months) transfer and use of water column production to deep-sea predators.

18. Temporal trends in GSI differed among species from the same trophic guild, both among fish and among decapods. This indicates that seasonal availability and use of food do not affect all species reproductive processes equally.

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