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Do abyssal scavengers use phytodetritus as a food resource? Video and biochemical evidence from the Atlantic and Mediterranean

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ABSTRACT

Deep-sea benthic communities derive their energetic requirements from overlying surface water production, which is deposited at the seafloor as phytodetritus. Benthic invertebrates are the primary consumers of this food source, with deep-sea fish at the top of the trophic hierarchy. Recently, we demonstrated with the use of baited cameras that macrourid fish rapidly respond to and feed vigorously on large plant food falls mimicked by spinach (Jeffreys et al., 2010). Since higher plant remains are scarce in the deep-sea, with the exception of canyons, where terrestrial material has been observed, these results led us to ask if a more commonly documented plant material i.e. phytodetritus might form a food source for deep-sea fish and mobile scavenging megafauna. We simulated a phytodetritus dump at the seafloor in two contrasting environments (1) the NE Atlantic where carpets of phytodetritus have been previously observed and (2) the oligotrophic western Mediterranean, where the deposition of phytodetritus at the seafloor is a rare occurrence. We recorded the response of the scavenging fauna using an *in situ* benthic lander equipped with baited time-lapse cameras. In the NE Atlantic at 3000 m, abyssal macrourids and cusk-eels were observed ingesting the phytodetritus. The phytodetrital patch was significantly diminished within 2 h. Abundance estimates calculated from first arrival times of macrourids at the phytodetrital patch in the Atlantic corresponded with abundance estimates from video-transect indicating that fish were attracted to the scent of phytodetrital bait. In contrast to this, in the western Mediterranean at 2800 m a single macrourid was observed investigating the phytodetrital patch but did not feed from it. The phytodetrital patch was significantly diminished within 6.5 h as a result of mainly invertebrate activity. At 1900 m, *Lepidion lepidion* was observed near the lander and the bait, but did not feed. The phytodetrital patch remained intact until the end of the experiment. In the deployments in the Mediterranean abundance estimates from first arrival times at the bait, corrected for their body size, were lower than estimates obtained from video-transects and trawl catches. This suggests that the Mediterranean fish were not readily attracted to this food source. In contrast, invertebrates in the Balearic Sea were observed ingesting the phytodetritus bait despite the rare occurrence of phytodetritus dumps in the Mediterranean. Stable isotope values of the fish at both study sites, set within the context of the benthic food web, did not demonstrate a strong trophic link to phytodetritus. Fatty acid profiles of these fish indicated a strong link between their lipid pool and primary producers i.e. phytoplankton, which may be attributed to trophic transfer. The usefulness of fatty acid biomarkers in ascertaining deep-sea fish diets is discussed. Our study suggests that the abyssal grenadier *C. armatus* on the Atlantic Iberian margin is attracted to phytodetritus. However the exact contribution of this food source to the diet of macrourids in this area remains unresolved.

1. Introduction

Phytodetritus forms the basal resource for the majority of deep-sea benthic communities. Phytodetritus is a rich food source mainly comprised of aggregates of intact phytoplankton cells, which sink to the seafloor following phytoplankton blooms in the overlying surface waters (Beaulieu, 2002). The arrival of this resource pulse at the deep-sea floor has been documented in many areas of the world's oceans, and in some areas thick layers of phytodetritus have been documented covering the seafloor e.g. in the equatorial Pacific, the N. Atlantic and the Antarctic (Billett et al., 1983; Hecker, 1990; Smith et al., 1996; de Wilde et al., 1998; Mincks et al., 2005; Nodder et al., 2007). Resource availability is known to control the structure and dynamics of ecological systems (Nowlin et al., 2008), and in deep-sea

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ecosystems phytodetritus has been shown to be significant in both the structuring and functioning of biological communities (Kitazato et al., 2000; Bett et al., 2001; Ruhl et al., 2008). Invertebrate taxa are known to respond rapidly to pulses of phytodetritus (Witte et al., 2003a) and certain species are able to select for the freshest most recently settled particles (Miller et al., 2000; Ginger et al., 2001). In some invertebrate species physiological responses to this food source have also been documented, for example in growth rates, reproduction and recruitment patterns (Sumida et al., 2000; Gage, 2003; Hudson et al., 2003; Wigham et al., 2003).

Conversely, deep-sea fish are reported to be opportunists, feeding and scavenging on invertebrates and carrion (Pearcy and Ambler, 1974; Drazen et al., 2001; Stowasser et al., 2009). Although the abundance, size structure, growth, and swimming speeds of abyssal grenadiers (family Macrouridae), being among the most common deep-sea fish, appear to be influenced by surface productivity (Pearcy et al., 1982; King and Priede, 2008, Priede et al., 1994, 2003; Bailey et al., 2006; Kemp et al., 2008), phytodetritus itself is not considered as a viable resource for these fish (Drazen, 2002; Bailey et al., 2006). Much of the evidence for the dietary preferences of deep-sea fish has been derived from stomach contents or biochemical analyses e.g. stable isotopes and fatty acids. There are, however, limitations to both methods. Stomach content analyses provides only snapshots of information on the most recent feeding events and are difficult to obtain for deep-sea fish since hydrostatic decompression results regularly in regurgitation of prey. Stable isotope and fatty acid (FA) analyses, which provide time-averaged dietary information as food items are incorporated into tissues over time, may easily overlook short-term incidental opportunistic feeding actions.

Dietary items, which may be consumed for short periods may either be under-represented or missed using above methods. Using baited time-lapse cameras mounted on benthic landers, Jeffreys et al. (2010) observed that abyssal grenadiers are attracted to, and vigorously eat from vegetable bait (spinach). These experiments were the first offering vegetable food instead of carrion, e.g. mackerel, which has thus far been used in combination with baited cameras to attract deep-sea fish and estimate their abundances (Bailey et al., 2007). Since higher plant remains are scarce in the deep-sea, with the exception of canyons, which may transfer terrestrial material to the deep-sea, the response of the grenadiers in the experiments of Jeffreys et al. (2010) raised the question of whether the more commonly observed phytodetrital plant material in the deep-sea, might be a food source for deep-sea fish and scavenging mobile megafauna.

Here we describe baited camera experiments to test the response of deep-sea fish and mobile invertebrates to a simulated pulse of phytodetritus in two contrasting ecosystems: the eutrophic NE Atlantic and the oligotrophic western Mediterranean. Specifically we ask: (a) are deep-sea fish and invertebrates attracted to an experimental phytodetritus deposition, (b) do they consume the phytodetrital bait and (c) can assimilation of phytodetritus consumption be detected using stable isotopes and fatty acids? We attempt to further delineate the link between surface water production and the ecology of fish and organisms.

2. Materials and methods

2.1. Study areas

The Iberian margin (NE Atlantic) is characterized by high annual surface water productivity $\sim$220 g C m^{-2} yr^{-1} (Joint et al., 2002) resulting from intense seasonal wind-driven coastal upwelling occurring during the spring (Epping et al., 2002). Production can be further enhanced by dispersal of filaments of these productive waters up to 250 km offshore, (van Weering et al., 2002) and phytodetritus has been documented at the seafloor during May and September, off La Coruña, NW Iberian margin (Lavaleye et al., 2002). Conversely, the Balearic Sea, western Mediterranean is characterized by lower annual surface water productivity $\sim$160 g C m^{-2} yr^{-1}, with peaks in production occurring during the spring and autumn (Estrada, 1996). Records of phytodetritus in the deep Mediterranean Sea are scarce, being restricted to canyons and trenches (Riauxgobin et al., 1995; Boetius et al., 1996).

In order to investigate the response of deep-sea demersal fish to a pulse of phytodetritus we conducted four baited camera experiments, during two research cruises, one deployment at the Iberian margin and three deployments in the Balearic Sea (Table 1). All deployments were carried out during November 2009, during which there was no visual or chemical (phytopigment) evidence of recent deposition of phytodetritus at the seafloor at any of the stations during this period. Mean chlorophyll-*a* values were low: 0.004 μg g^{-1} at 1200 m and 0.001 μg g^{-1} at 1900 and 2800 m in the Balearic Sea, whereas values of 0.004 μg g^{-1} were measured at 3000 m on the Iberian margin. Average current speeds recorded during each deployment were $\sim$2.1, 3.8 and 4.2 cm s^{-1} at 1200, 1900, 2800 m in the Balearic Sea and 4.0 cm s^{-1} at 3000 m at the Iberian margin.

2.2. Baited camera deployments

We used a NIOZ ALBEX benthic lander (Duineveld et al., 2004), consisting of an aluminum tripod frame with 12 glass Benthos floats, two acoustic releasers and a single 250-kg ballast weight. The lander carried a Nortek$^{\text{TM}}$ Aquadopp current meter and a custom video system consisting of 2–3 digital cameras each lit by 20 W white halogen lamps (Fig. 1). Camera 1 was positioned to record activity at the bait, whilst, camera 2 was positioned opposite the baited carrousel facing away from the lander frame in order to record fish around the frame, possibly attracted merely to the frame or the lights. Camera 1 recorded the response of mobile consumers to the bait during the first 30 min of each experiment and following this, a 15-s video clip every 20 min. Camera 2 recorded during the first 30 min of each experiment a 15-s video clip every 5 min, and following this a 15-s video clip every 20 min. In the experiments conducted in the Balearic Sea an additional camera (camera 3) recorded activity at the bait, this camera recorded a 60-s video clip every 5 min for the entire duration of pulse 1 only at all depths. This camera 3 also recorded the entire duration of pulse 2 at the 2800 m station in the Balearic Sea.

Table 1
Details of baited camera deployments: region, depth, position and deployment duration in hours are given. The duration of each phytodetrital pulse, P1 and P2, are given in hours.

Station #	Date	Depth (m)	Position	Deployment duration	Pulse duration
Iberian margin 83	02/11/09	2908	41.72°N, 10.67°W	21.6	P1=8.6, P2=11.6
Balearic Sea 07	11/11/09	2778	39.23°N, 05.59°W	33.6	P1=16.9, P2=16.5
Balearic Sea 80	20/11/09	1880	39.24°N, 04.18°W	17.7	P1=8.8, P2=8.7
Balearic Sea 66	19/11/09	1175	39.61°N, 04.16°W	21.7	P1=11.7, P2=9.7