

The influence of changing food supply on the lipid biochemistry of deep-sea holothurians

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Abstract

The biochemical response of three species of deep-sea holothurian (*Oneirophanta mutabilis*, *Pseudostichopus villosus*, and *Psychropotes longicauda*) to temporal variation in food supply at the Porcupine Abyssal Plain (PAP; ~4850 m water depth in the NE Atlantic) was studied over a period of 22 months. Lipid contents of *P. longicauda* showed a strong positive correlation with the contents of lipids in the surficial sediments (0–5 mm; Spearman rank correlation, $R_s = 1.0$, $P < 0.001$). *O. mutabilis* did not show the same trend in total lipid, but there was an apparent enrichment of sterol in both particulate organic matter (POM) arriving at the sea floor in September–October 1997 and the tissues of *O. mutabilis*, suggesting that this species can respond to changing availability of food resources. Lipid contents of *P. villosus* did not vary temporally, probably because this species feeds on deeper layers of sediment, which show little or no temporal variation in lipid composition or concentration. The biochemical response of holothurians to variations in food supply appears to depend on their feeding mode. Changes in the quantity and quality of organic matter have the potential to change deep-sea benthic community structure.

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1. Introduction

In the deep sea, small organisms, particularly the bacteria and prokaryotic meiofauna, such as the benthic foraminifera, can respond rapidly to the supply of particulate organic matter (POM; Lochte and Turley, 1988; Gooday and Turley, 1990; Gooday, 1993). Until recently, the response of large metazoans was considered to be much less rapid because of their longer generation times. However, experimental work has indicated that the influx of POM is preferentially taken up by macrofauna

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when it first arrives on the sea bed (Witte et al., 2003) and seasonal pulses have been shown to trigger reproduction and growth in some species (Tyler et al., 1982; Lampitt, 1990; Campos-Creasy et al., 1994). A study of the Porcupine Abyssal Plain (PAP) in the north-eastern Atlantic Ocean showed for the first time, a major population change in the megafauna and macrofauna that impacted the abyssal sedimentary environment (Billett et al., 2001; Bett et al., 2001; Ginger et al., 2001; Galéron et al., 2001). Termed the “*Amperima* Event” (Billett and Rice, 2001), the dramatic increase in the abundance of the holothurian *Amperima rosea*, amongst other species, led to the rapid removal of POM arriving seasonally at the sea floor over a period of days rather than months, as observed previously at the same location (Bett et al., 2001). Concomitant changes in the abundance, size, sexual maturity and fecundity of other holothurians species, were considered to reflect the changing environment on the PAP sea floor (Billett et al., 2001; Ramirez-Llodra et al., 2005) and their feeding selectivity and efficiency (Wigham et al., 2003).

The response of holothurians to food availability most likely reflects their feeding mode (Billett et al., 1988; Roberts et al., 1996, 2001), rate of locomotion (Roberts et al., 2001), gut anatomy (Penry and Jumars, 1986; Roberts et al., 1996, 2001), tentacle structure (Roberts et al., 1996, 2001), efficiency of organic matter (OM) absorption (Sibuet et al., 1982; Pfannkuche et al., 1999; Miller et al., 2000) and requirement and turnover of specific organic substrates in their bodies (Ginger et al., 2000, 2001).

Different species are likely to respond in different ways to pulses of food supply and/or food availability, because some organisms respond physiologically (e.g. reproduction) to food enrichment whilst others do not (Tyler, 1988). For example *A. rosea* selectively assimilates specific sterols and carotenoids (Ginger et al., 2000; Wigham et al., 2003) and shows temporal variability in its polyunsaturated fatty acid (PUFA) content (Hudson et al., 2004).

The distribution of POM arriving at the deep-sea floor tends to be patchy and is rare for most of the year at the PAP. The manner in which species forage and their effectiveness in exploiting and assimilating OM may drive their responses to variations in food supply. The hypothesis tested here is that the biochemical composition of holothurians varies in response to the periodic enrichment of POM at the deep-sea floor, and that this

may influence species population dynamics at the PAP (Billett et al., 2001). Three dominant species of holothurian at the PAP, *Oneirophanta mutabilis*, *Pseudostichopus villosus*, and *Psychropotes longicauda* (Billett, 1991; Billett et al., 2001), were studied over a period of 22 months between July 1997 and April 1999. These species were chosen as they were the most abundant animals; furthermore, they have different gut anatomies (Roberts et al., 1996), morphologies (Hansen, 1975), rates of locomotion (Roberts et al., 2000) and tentacle structures (Roberts et al., 2000), which presumably leads them to exploit different parts of the sedimentary OM. Lipids were chosen as the primary biochemical targets because they are functionally involved in energy storage (fatty acids as triacylglycerols), in hormonal regulation (e.g. steroids) and cell membrane structure and function (polyunsaturated acids, steroids) (Ginger et al., 2000).

2. Materials and methods

2.1. Study sites and sample collection

Samples were collected at the PAP (48°50'N 16°30'W; ~4850 m water depth, ~270 km southwest of Ireland) in the northeast Atlantic Ocean (Billett and Rice, 2001).

Three holothurian species, *O. mutabilis*, *P. villosus* and *P. longicauda*, were collected by otter-trawl (OTSB14; Rice et al., 1990) during cruises of RRS *Discovery* (July 1997, March 1998 and October 1998) and RRS *Challenger* (October 1997, and April/May 1999). Hereafter the cruises will be referred to as July 1997, October 1997, March 1998, October 1998 and April 1999.

On recovery of the trawls, animals that were in good condition were selected and stored in chilled seawater (4 °C). The animals were dissected within 2 h in a cold room (6 °C). After dissection, body wall samples were stored in clean, aluminium foil wrapped, pre-weighed petri dishes.

Sediment cores were sampled in replicate (i.e. from different deployments) using a multi-corer (Barnett et al., 1984). Cores were sliced on recovery from the sea floor in 7 sections (0–5, 5–10, 10–20, 20–30, 30–40, 40–50 and 50–60 mm).

All samples were stored in freezers (–80 to –60 °C) on board ship. Samples were packed with dry ice to be transported to the laboratory where samples were freeze-dried (–60 °C; 10^{–2} T; 24 h). Once dry, samples were frozen in liquid nitrogen

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