Deep-Sea Research II 58 (2011) 970–978

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Distribution, abundance and trail characteristics of acorn worms at Australian continental margins

T.J. Anderson [1,]*, R. Przeslawski [1], M. Tran [1,2]

[1] Marine and Coastal Environment Group, Geoscience Australia, GPO Box 378, Canberra, ACT 2601, Australia
[2] Department of Environmental Sciences, University of Technology, Sydney, Westbourne Street, Gore Hill, New South Wales 2065, Australia

A R T I C L E I N F O

Article history:
Received 27 October 2010
Accepted 27 October 2010
Available online 5 December 2010

Keywords:
Acorn worms
Enteropneusta
depth range
trail behaviour
sediment characteristics
deep-sea

A B S T R A C T

Acorn worms (Enteropneusta), which were previously thought to be a missing link in understanding the evolution of chordates, are an unusual and potentially important component of many deep-sea benthic environments, particularly for nutrient cycling. Very little is known about their distribution, abundance, or behaviour in deep-sea environments around the world, and almost nothing is known about their distribution within Australian waters. In this study, we take advantage of two large-scale deep-sea mapping surveys along the eastern (northern Lord Howe Rise) and western continental margins of Australia to quantify the distribution, abundance and trail-forming behaviour of this highly unusual taxon. This is the first study to quantify the abundance and trail behaviour of acorn worms within Australian waters and provides the first evidence of strong depth-related distributions. Acorn worm densities and trail activity were concentrated between transect-averaged depths of 1600 and 3000 m in both eastern and western continental margins. The shallow limit of their depth distribution was 1600 m. The deeper limit was less well-defined, as individuals were found in small numbers below 3000 down to 4225 m. This distributional pattern may reflect a preference for these depths, possibly due to higher availability of nutrients, rather than a physiological constraint to greater depths. Sediment characteristics alone were poor predictors of acorn worm densities and trail activity. High densities of acorn worms and trails were associated with sandy-mud sediments, but similar sediment characteristics in either shallower or deeper areas did not support similar densities of acorn worms or trails. Trail shapes varied between eastern and western margins, with proportionally more meandering trails recorded in the east, while spiral and meandering trails were both common in the west. Trail shape varied by depth, with spiral-shaped trails dominant in areas of high acorn worm densities (2000–3000 m water depth) while meandering trails were common over a much broader depth range and were the only trails recorded in deep environments >3000 m. While species-specific patterns may in part explain these differences, evidence suggests that nutrient availability is also likely to be an important driving factor, supporting the hypothesis put forward by Smith et al. (2005) that acorn worms meander when searching for food and form a spiral when feeding in a nutrient-rich area.

1. Introduction

Enteropneusts, or acorn worms, are gelatinous marine worm-like organisms represented by at least 100 known species, most of which filter-feed from burrows in intertidal and shelf soft sediments or deposit-feed in the deep-sea (Cannon et al., 2009; Lowe et al., 2004; Smith et al., 2005). Enteropneusts are hemichordates ('half chordates') that have a three-part body plan consisting of an anterior proboscis, followed by a collar and a posterior trunk. They have strong affinities with chordates, as they have a hollow dorsal nerve cord, stomochord, bilateral symmetry, and gill slits (Lowe et al., 2004). As a consequence, acorn worms have been the focus of molecular and genetic studies to investigate the evolutionary origin of chordates and the pathway from invertebrate to vertebrate structures (Arendt et al., 2008; Tagawa et al., 2001).

Until recently, most research on acorn worms focused on intertidal or shelf species; however, deep-sea video and photography have shown that acorn worms are also relatively common in the deep-sea and abyssal regions in oceans throughout the world (Bourne and Heezen, 1965; Smith et al., 2005). While the taxonomy, molecular structure and ecology of shallow water species are well known, very little information is available on deep-sea species as they have only rarely been seen, and only a small number of intact deep-sea specimens have ever been collected (Holland et al., 2005, 2009) due to their fragility and subsequent maceration in deep-sea sampling gear (Smith et al., 2005). Early photographs of

---

* Corresponding author. Tel.: +61 2 6249 9029.
E-mail address: tara.anderson@ga.gov.au (T.J. Anderson).

doi:10.1016/j.dsr2.2010.10.052

deep-sea acorn worms revealed what researchers thought were tentacle-like structures on the collars of these worms that represented a living evolutionary link between enteropneusts and pterobranchs (review in Gage, 2005). Collection of the first intact deep-sea enteropneust, however, refuted this claim, as the animal had no tentacles (Holland et al., 2005). The collection of this single animal, however, identified the presence of a new family (Torquaratoridae) within the group (Holland et al., 2005), and molecular sequencing of several undescribed deep-sea enteropneusts has since revealed that these are closely related to (or possibly even within) Ptychoderidae, a family of large acorn worms (Cannon et al., 2009). Further studies of other deep-water enteropneusts are likely to provide insight into the evolutionary differences between shallow-water infaunal and deep-water epifaunal enteropneusts and may also help to elucidate the origins of vertebrate evolution.

In addition to their evolutionary importance, acorn worms along with other deposit feeders, such as holothurians, are likely to be ecologically important in surface sediment modification and nutrient cycling in deep-sea soft sediment ecosystems (Smith et al., 1993; Uthicke et al., 2009). However, along with many organisms in the deep-sea, little is known about the ecology of enteropneusts or what regulates their distribution and local abundance. Analysis of video and still-photographs provides a promising way to investigate these animals, although until recently, global records were sparse and included only a few individuals from isolated locations, with records from Australian waters poorly represented in the literature (Smith et al., 2005, Fig. 1A). The limited video footage and photography that is available have identified that deep-sea acorn worms, along with holothurians, are often the dominant epibenthic deposit feeders in otherwise visually barren deep-sea plains (Gage, 2005; Smith et al., 2005). Deep-sea acorn worms are also considerably larger than their shallow-water counterparts often up to 1 m in length, and 5 cm thick across the collar (Bourne and Heezen, 1965), while species such as *Balanoglossus* may exceed 2.5 m in length and 1 kg in weight (Jensen et al., 1992). Most deep-sea acorn worms recorded to date, however, are less than 50 cm in length (Cameron, 2005). Acorn worms in these deep-sea environments are thought to move across the seafloor ingesting the surface layers of the sediments with little or no selectivity, to feed on bacteria, microscopic algae, diatoms, and nutrients that have accumulated in the sediments, and to leave behind characteristically shaped faecal trails (Gage, 2005; Holland et al., 2009; Smith et al., 2005). Time-lapse photography of the seabed at 4100 m off Monterey Canyon in central California provided a unique sequence of photographs of a single acorn worm moving forward over the seafloor in a clockwise direction consuming organic material from the sediments leaving behind a four-whorl spiral-shaped faecal trail (Smith et al., 2005). The feeding trail was generated over 39 hours before the animal departed, and the trail degraded rapidly over 8.5 days. The sediment structures generated by acorn worms may also create microenvironments that facilitate colonisation by other organisms (Mauviel et al., 1987).

Deep-sea acorn worms are known to produce several different faecal trail shapes, categorized by Smith et al. (2005) and Holland et al. (2005) as spiral, switchback, meandering, and combinations of these (spiral-switchback, spiral-meandering, and meandering-switchback), which like the worms have been recorded and photographed from numerous deep-sea environments around the world (Bourne and Heezen, 1965, Holland et al., 2005; Smith et al., 2005). The trail shape has not been shown to be species-specific (Smith et al., 2005). Rather, the shape of the trail may reflect behavioural responses to searching for food, or localised feeding. Meandering trails cover greater linear extents, and may indicate the animal is searching for food, while the spiral trails might be used to focus feeding on an area containing comparatively more nutrients (Smith et al., 2005). Time-lapse photography indicates that deep-sea acorn worms swim or float to and away from their benthic trails to a new feeding location (Smith et al., 2005), explaining the absence of entry and departure points on remnant trails. Some species appear to secrete mucous tubes to facilitate demersal drifting (Holland et al., 2009).

Little is known about the local, regional or global distributions of these unusual deep-sea organisms, their relationship with physical gradients in depth or sediment characteristics, or their ecological function in deep-sea environments, and almost no information is available for Australian waters. In this study, we describe the abundance and depth distributions of acorn worms and their characteristic faecal trails in the eastern (LHR) and western continental margins of Australia and examine the importance of physical habitat characteristics on the distribution of deep-sea enteropneusts.

2. Material and methods

2.1. Study areas

Geoscience Australia undertook two marine reconnaissance surveys between 2007 and 2009 to the outer reaches of Australia's Economic Exclusion Zone (EEZ) as part of the Federal Government's Offshore Energy Security Program. These surveys were designed to acoustically map and sample the seafloor in these rarely studied remote deep-sea environments where previously little to nothing was known about the sedimentology, benthic habitats, or deep-sea benthic organisms (Fig. 1B,C; Heap et al., 2009; Daniell et al., 2009; Przeslawski et al., 2011). The first of these surveys was undertaken in offshore eastern Australia in late 2007 (TAN0713: 7 October–22 November) to survey a 25,500 km^2 study area on the northern Lord Howe Rise in the coral sea between latitudes -26^o to -28^o S and longitudes 160^o to 162^o E (Fig. 1C; Heap et al., 2009; Anderson et al., 2011). In 2008-09 a similar study was undertaken along the western continental margin of Australia (GA2476: 25 October 2008–19 January 2009) that surveyed a 166,500 km^2 area between latitudes -21^o to -32^o and longitudes 107^o to 116^o (Fig. 1B; Daniell et al., 2009). These surveys collected a wealth of bio-physical data from canyon-incised slopes, deep-sea basins, seamounts, and volcanic cones (Heap et al., 2009; Anderson et al., 2011; Daniell et al., 2009) and also presented an opportunity to examine the abundance of acorn worms on Australian continental margins.

2.2. Acorn worm data

To quantify acorn worm abundance and trail characteristics, underwater towed-video transects and still photography were analysed from 39 eastern and 44 western margin sites. A range of marine features were surveyed, including five basins (Faust and Capel Basins on the LHR, and Zeehan, Exmouth, and Houtman sub-basins in the west), a deep-sea Plateau (Wallaby (Cuvier) Plateau in the west) and three seamounts (Gifford Guyot in the east, and the Wallaby and Cuvier Seamounts in the west) (Heap et al., 2009; Daniell et al., 2009; and Nichol et al., 2011). At each site an approximately 1-hour towed-video transect of the seabed (typically 1000 m long) was used to characterise the bio-physical composition of the seafloor, and examine the distribution and abundance of deep-sea acorn worms. Specific deployment details of each deep-sea camera system are provided in Heap et al. (2009) and Anderson et al. (2011) (eastern survey) and Daniell et al. (2009) (western survey). On each towed video-transect, substratum type, depth, relief, bedform, and the occurrence of all macro-organisms were recorded within a 15 sec period every 30 sec using the C-BED (Characterisation of the Benthos and Ecological Diversity) protocol described in Anderson et al. (2008) and Nichol et al. (2009). In addition, all individual acorn worms and acorn trails, and a locally abundant small elasipodid holothurian of unknown species (or sea piglets, Family: Elpidiidae), were counted and