Not whale-fall specialists, Osedax worms also consume fishbones

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Abstract

Marine annelid worms of the genus Osedax exploit sunken vertebrate bones for food. To date, the named species occur on whale or other mammalian bones, and it is argued that Osedax is a whale-fall specialist. To assess whether extant Osedax species could obtain nutrition from non-mammalian resources, we deployed teleost bones and calcified shark cartilage at approximately 1000 m depth for five months. Although the evidence from shark cartilage was inconclusive, the teleost bones hosted three species of Osedax, each of which also lives off whalebones. This suggests that rather than being a whale-fall specialist, Osedax has exploited and continues to exploit a variety of food sources. The ability of Osedax to colonize and to grow on fishbone lends credibility to a hypothesis that it might have split from its siboglinid relatives to assume the bone-eating lifestyle during the Cretaceous, well before the origin of marine mammals.

Keywords: Annelida; Siboglinidae; teleost bones

1. INTRODUCTION

Osedax [1] is a group of annelids occurring widely in the world’s oceans [2]. The females use a ‘root’ system hosting heterotrophic γ-proteobacteria for nutrition from sunken bone [3,4], whereas males are non-feeding dwarfs [5]. Osedax differs from other relatives in Siboglinidae (Frenulata, Vestimentifera and Sclerolinum), which exploit chemosynthetic endosymbionts and do not exhibit sexual size dimorphism [6]. The times at which Osedax split from other siboglinids and diversified into its modern lineages remain unresolved, owing to ambiguities in molecular clock calibrations [2], and debate regarding the diversity of bones on which these worms can subsist. For instance, Glover et al. [7] defended the hypothesis that Osedax is a ‘whalebone specialist’, discounting as ecologically irrelevant the discovery that Osedax could exploit the bones of terrestrial boids [8,9].

An intuitively attractive ‘Eocene Osedax’ hypothesis is that Osedax split from a common ancestor with Sclerolinum/Vestimentifera about 45 million years ago (Ma), following the Eocene origin of Archaeocete whales [10]. The most recent common ancestor (MRCA) of modern Osedax lineages would then date to about 26 Ma (Late Oligocene), coincident with the diversification of baleen whales [11]. The recent discovery of Osedax-like borings in the fossilized bones of small, toothed mysticetes from the early Oligocene (30 Ma) is consistent with this hypothesis [12]. However, this fossil finding does not exclude an alternative ‘Cretaceous Osedax’ hypothesis based on a slower molecular clock [2]. According to this hypothesis, Osedax split from a common ancestor with Sclerolinum/Vestimentifera about 130 Ma, and its MRCA began to diversify about 75 Ma (Late Cretaceous). Cretaceous marine vertebrates that could have fed Osedax include mosasaurs [13], plesiosaurs [14], turtles [15] and birds [16], as well as cartilaginous and teleost fishes [17,18]. A problem with the Cretaceous Osedax hypothesis stems from the 20 Myr gap after the Cretaceous-Tertiary extinction event (k-T event), when marine vertebrates may have been scarce [2]. Although large-bodied teleosts also suffered mass extinction at this time, they might have provided sustenance for Osedax, as several extant teleost clades diversified during the Palaeocene, e.g. carangoids, scombroids, sphyraenids and xiphioids [17,19]. Other marine vertebrates also survived the K–T event, with birds, turtles and cartilaginous fishes available for Osedax consumption [15,16,20]. Indeed, Oligocene fossil evidence suggests that Osedax may have exploited the bones of large flightless marine birds [16]. Nonetheless, Osedax has only been observed living on mammalian bones [7–9]. In this study, we deployed teleost bones and shark cartilage as a critical test of the ‘whale-fall specialist’ hypothesis to see whether Osedax may obtain nutrition from non-mammalian bones.

2. MATERIAL AND METHODS

Wire cages were deployed via ROV Ventana (on R/V Point Lobos) on 13 February 2010. Upon recovery, the cowbones showed specimens of Osedax roseus [5] and two as yet undescribed species; ‘yellow patch’ and ‘nude-palp-E’ [2]. Each of these Osedax species could obtain nutrition from non-mammalian bones [7–9]. In this study, we deployed teleost bones and shark cartilage as a critical test of the ‘whale-fall specialist’ hypothesis to see whether Osedax may obtain nutrition from non-mammalian bones.

3. RESULTS

Upon recovery, the cowbones showed specimens of Osedax roseus [5] and two as yet undescribed species; O. ‘yellow patch’ and O. ‘nude-palp-E’ [2]. Each of these Osedax species occurs on the nearby blue whale carcass [21]. Although the small teleost vertebrae exhibited no traces of Osedax, the large teleost vertebrae hosted Osedax. A large vertebra from cage no. 1 hosted a mature (with spawned eggs) specimen

References

of *O. roseus* (GenBank JF509949), with four dwarf males in the lumen of her tube (figure 1a,b,d–h), and two specimens of *O. yellow patch* (not shown, GenBank JF509950-51). The large teleost vertebrae from cage no. 2 had five specimens (e.g. figure 1c) of *O. nude-palp-E* (GenBank JF509952-56). The shark jaws and vertebrae had disintegrated, with only some teeth and the outer calcareous matrix remaining.

Roots of the *O. roseus*, *O. yellow patch* and *O. nude-palp-E* specimens were visible as discolouration beneath the fish bone surface (figure 1b–d). Dissection of the superficial bone revealed *Osedax* roots that radiated laterally away from a worm’s trunk in a layer beneath the superficial lamellar bone (figure 1c,e,g). Interspersed among roots of the *O. roseus* specimen (figure 1e) was a soft granular white material (figure 1g) that remains.

Figure 1. (a) Cages prior to deployment; (1) ‘large’ teleost vertebrae (approx. 2 cm diameter centrum); (2) ‘small’ teleost vertebrae (approx. 5 mm diameter); (s) half a lower jaw and vertebrae (approx. 5 mm diameter) from a small Mako shark; and (c) sections of cow femur. (b) Two large teleost vertebrae from cage no. 1, with a mature female *Osedax roseus* specimen (GenBank JF509949). (c) Neural spine of large teleost vertebra from cage no. 2 with female *Osedax* ‘nude-palp-E’ (1,2) with sediment-covered tubes. Arrows indicate roots of specimen 1. Roots from specimen 2 can also be seen extending outward beneath the tube. (d) Large teleost vertebra in (b) occupied by *O. roseus*. (e) Same *O. roseus* with the veneer of bone overlying the root system dissected away to reveal her green roots. (f) Crown of the preserved female *O. roseus* with two spawned eggs (arrows). (g) Detail of root system shown in (e) with surrounding white dissolved bone matrix. (h) Junction of the trunk and crown of female *O. roseus* in (d). Arrows indicate two of four dwarf males found in her tube.
to be characterized. The processes of bone demineralization and nutrient extraction by Osedax are poorly understood, but similar deposits have not previously been noted in mammalian bones.

DNA sequencing from the O. roseus specimen verified the presence of 16S sequences (GenBank JF509946-48) typical of symbiotic PI phenotype (99% similarity with GenBank DQ11537-42) isolated from adjacent whalebone O. roseus [3]. Root extracts from the O. yellow patch and O. nuda-palp-E were small and contaminated by environmental microbes. Endosymbionts associated with these two Osedax species remain to be characterized.

4. DISCUSSION
The present finding helps to resolve an apparent paradox generated from prior considerations of genetic demography of Osedax. A restriction to living on whalebones seemed inconsistent with our earlier findings of very high mitochondrial DNA sequence diversity in Osedax, where there are large ‘genetically effective’ population sizes [2,5,22]. Although whale carcasses surely provide large and persistent habitats for modern Osedax, they might not provide the most abundant or widespread food resource. The ability of Osedax females to acquire suitable endosymbionts, recruit dwarf males and produce eggs by consuming teleost bones suggests that they may survive in a range of habitats outside the breeding and feeding grounds and migratory paths of whales.

Sedimentation will probably bury and make small bones inaccessible at shallow near shore localities [7,21], but offshore deep-sea habitats exhibit slower sedimentation and bioturbation rates [23,24]. Larger bones, as used in our study, may well remain accessible to Osedax, however it could be argued that fishbones in cages might be considered unnatural. The actions of large scavengers could have a marked effect on the availability of fishbones for Osedax by eating or otherwise destroying them. Evidence to date however suggests that bones may often be left available.

Camera-based studies on unenclosed teleost remains (e.g. [25]) showed that scavenging fishes and invertebrates removed the flesh but left bones behind, even after 20 days of deployment [26].

While the bones deployed in this study were protected from larger scavengers, they were on or close to the sediment surface, and the 5 mm mesh did not exclude other animals such as lysianassid amphipods that can interfere with Osedax colonization [21]. The smaller carangid vertebrae were not colonized, and the shark cartilage was destroyed, so additional experiments will be needed to ascertain whether these substrates are suitable for Osedax. Nonetheless, the capacity of Osedax to exploit larger fishbones suggests the worms may be capable of exploiting an immense resource that constantly falls to the seafloor globally. Even if fishbones provide ephemeral resources and many are lost to scavengers or burial, these highly fecund and rapidly growing worms [5,27] should be able to exploit at least a portion of this resource.

The role that Oceanospirillales bacterial endosymbionts play in the extraction and processing of nutrients is not understood, but all Osedax species studied to date appear to host them, along with diverse epibionts [3,4]. Osedax acquire their endosymbionts anew each generation from environments in which the aposymbiotic larvae settle [27]. The endosymbionts associated with the O. roseus from fishbone were from the same lineages previously isolated from O. roseus on whalebones [3]. Thus, the Osedax/Oceanospirillales association is successful on bones from vertebrates only distantly related to mammals. Scambred bones also have high fat content (20%), although it is confined to a large single space in each vertebra and not distributed throughout the bone [28]. The shallow roots observed here suggest that the present Osedax worms were engaged in extracting collagen, as has been suggested for Osedax living on mammalian bones [3,29].

Our understanding of Osedax phylogeny [2] shows that the three species recovered from fishbones effectively span the diversity of the group. This capacity of disparate Osedax lineages to exploit mammalian and teleost bones suggests that a generalist ability to exploit vertebrate bones may be an ancestral trait. Exploitation of fishbones removes a significant obstacle to the Cretaceous Osedax hypothesis. These bone-eating worms may have expanded their feeding niche several times to exploit the bones of large marine vertebrates as they successively colonized the world’s oceans from land. We suggest that whalebones are but one of a long series of food sources that Osedax has exploited and continues to exploit.

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