Comment

On the role of bone-eating worms in the degradation of marine vertebrate remains

While the study of terrestrial vertebrate taphonomy is well advanced, our knowledge of the fate of large vertebrates in the marine environment is extremely poor, owing to the deep and distant locations of most recently deceased marine organisms. These include the largest animals ever to have existed, the great whales. In recent years, a series of both serendipitous discoveries and planned experimental manipulations have provided some of the first data on the fate of whale remains in the deep sea (Smith 2006). One of the more remarkable discoveries has been a specialized ‘whale-fall’ fauna, including organisms such as *Osedax*, a sessile polychaete worm that is capable of burrowing into whalebones to extract energy through microbial symbioses (Rouse *et al.* 2004; Glover *et al.* 2005). The recent paper in this journal by Jones *et al.* (2008) puts forward the hypothesis that *Osedax* is not specialist on whalebones, based on the observation of *Osedax* growing on cow bones suspended above the seafloor of the Monterey Canyon. In this comment, we show that a range of other observations on the fate of small marine vertebrates do not, as yet, lend any support to this hypothesis.

The enigmatic polychaete genus *Osedax* is now thought to consist of at least 11 known species recorded from the depths of 30–2900 m in both the Atlantic and Pacific oceans (Dahlgren *et al.* 2006; Braby *et al.* 2007; Jones *et al.* 2008; Rouse *et al.* 2008). *Osedax* presents a biogeographic paradox. If whale falls are rare and ephemeral habitats in the marine environment, a restricted distribution might be expected, similar to that recorded for the closely related hydrothermal vent vestimentiferans, which are endemic to the deep Pacific. However, the broad biogeographic range of *Osedax* is similar to that for cold-seep vestimentiferans and shows even greater bathymetric range. Furthermore, the molecular studies of mtCO1 diversity suggest both large global population sizes (Rouse *et al.* 2004), and a high level of haplotype diversity at single sites (Glover *et al.* 2005; Dahlgren *et al.* 2006). The latter point suggests that at any one single location in the ocean, *Osedax* larvae from more than one population may be available to colonize a whale carcass, should it so appear. Three hypotheses can be erected to explain the biogeographic pattern of *Osedax*: (i) whale falls (in the form of whalebones lying on the seabed) are very common on regional scales, as suggested by Smith & Baco (2003), (ii) *Osedax* reproductive output, larval longevity and life-history strategies show specific adaptations for exploiting isolated yet food-rich ephemeral habitats (Rouse *et al.* 2004), and (iii) *Osedax* are able to colonize a wider range of vertebrate remains, such as

the bones of porpoises, pinnipeds and large bony or cartilaginous fish (Jones *et al.* 2008).

The study of deep-sea whalebone decomposition is encumbered with a range of methodological problems that may bias the testing of any hypothesis. Evidence has come from a variety of sources. The earliest known reports of a whalebone fauna were from a whale skull collected in the trawl net of a fisherman off the coast of Aberdeen, Scotland (Marshall 1900), yet trawled material is usually heavily washed and damaged. Another approach, locating a naturally occurring whale fall, requires a tremendous amount of luck and access to many hours of deep-sea submersible or remotely operated vehicle time (Smith *et al.* 1989). These chance-located carcasses are, however, statistically most likely to be in an advanced state of decomposition. A more successful method has been to ballast the remains of dead, stranded whales and sink them at a known location (Smith & Baco 2003). Whalebones can also be implanted on their own, or placed in seawater aquaria, with the conditions controlled for the purpose of the experiment (Dahlgren *et al.* 2006), but these conditions may not be representative of a full-sized whale carcass. Cow bones suspended in the water column approximately 0.5 m above the sediment could not be said to be representative of any known marine habitat, with the exception perhaps of a cow-sized marine mammal skeleton balanced on a submerged rock, a scenario yet to be observed in the deep ocean.

The successful colonization of bone material by *Osedax* is likely to be dependent on a range of ecological factors, including the size and food content of the bone, bone calcification, disturbance or removal by scavenging organisms, competition with bacterial mats and the degree of sedimentation. Even in areas of low sedimentation, bones are likely to settle over time into the sediment through the actions of bioturbating organisms and benthic scavengers. These hypotheses are supported by recent studies of small marine vertebrate remains. Two porpoises and a dolphin, weighing between 50 and 100 kg and placed directly on the seabed at 4800 m in the Porcupine Abyssal Plain were studied over a period of 1–12 days by time-lapse camera (Jones *et al.* 1998). Although the duration of the experiment was almost certainly too short for *Osedax* to have had time to settle, the limited skeletal remains after just 12 days on the seabed, and the likelihood of many of the small bones being scavenged or settling into the sediment, suggests that there would be little available bone material left after three to four weeks. A subsequent time-lapse camera experiment with two porpoises at bathyal depths in the Porcupine Seabight (at comparable depths to the Monterey Canyon sites) showed a distinctly different pattern of species succession

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to that found on larger whales (Kemp *et al.* 2006). The remains were initially consumed by abyssal grenadiers *Coryphaenoides armatus* and later by squat lobsters *Munidopsis crassa*; after six months, almost nothing remained of the carcass, with most of the bones having been consumed or pushed into the sediment by the action of *M. crassa*, and some bones actually being carried off by fish (K. M. Kemp 2001, personal observation). Other recent studies of large food falls in the deep sea include a 10 kg fish parcel (Collins *et al.* 1999), a 29 kg shark (Witte 1999) and tuna (Janßen *et al.* 2000), none of which have yet revealed any *Osedax* populations, despite these tissues being rich in both lipids and collagen, the suggested food source for *Osedax* symbionts (Goffredi *et al.* 2007).

The paper of Jones *et al.* draws attention to the current poor knowledge both of marine vertebrate taphonomy and perhaps crucially, the food quality of the bones themselves. Early estimates for the fat content of whale vertebrae (32–68%) are seemingly based on anecdotal evidence from whalers (Slijper 1962). More recently, direct measurements of 45% lipids in a vertebra of either a blue whale (*Balaenoptera musculus*) or fin whale (*Balaenoptera physalus*), which had been on the sea floor for over 40 years are contradictory, with estimates of 4% in sperm whale (*Physeter macrocephalus*), 9% in dolphin and 27% in fin whale ribs (Tont *et al.* 1977; Honda *et al.* 1984; Schuller *et al.* 2004). More careful measurement and use of these variables will in the future allow us to better understand the potential degradation of bones in the marine environment, with particular relevance to the taphonomy of large marine reptiles such as the plesiosaurs.

Jones *et al.* hypothesize that ‘a variety of mammalian bones provide sufficient sources of nutrition for the growth and reproduction of *Osedax*’. The only evidence to support this statement comes from the cow-tree experiment, which is not a natural scenario. Furthermore, we feel that it is extremely unlikely that terrestrial mammal bones are washed into the ocean on a large enough scale to be significant. While whalebones have often been trawled from the shelf by fishermen (Smith & Baco 2003), other large mammal remains have not been reported despite 57% of the shelf being trawled annually by the global fishing fleet (Watling & Norse 1998). The occasional mammoth bones found in the North Sea were deposited during low seastands when the shelf was a terrestrial grassland habitat (Flemming 2004). Actual taphonomic data on mammoth remains suggest that they are unlikely to be transported significant distances by rivers (Guthrie 1990). Consequently, while *Osedax* is able to colonize the cow-tree experiment, we feel that this indicates nothing more than a similarity in bone composition between cow and whale.

We accept that the absence of evidence cannot in itself lend support to the theory that *Osedax* are exclusively whale-fall specialists. However, there is currently no strong data to support any alternative hypothesis. While some more generalist species of *Osedax* may be able to opportunistically colonize other types of organic-rich bone, ecological factors will most likely preclude colonization in most natural scenarios, which future experimental approaches must be designed to test. While it is functionally interesting that *Osedax* are able to colonize cow bones, hinting at a plasticity in their food specificity, it does not yet shed light on the biogeographic paradox or evolution of the *Osedax* clade.

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REFERENCES

- Braby, C. E., Rouse, G. W., Johnson, S. B., Jones, W. J. & Vrijenhoek, R. C. 2007 Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. *Deep-Sea Res.* **54**(Pt I), 1773–1791. (doi:10.1016/j.dsr.2007.05.014)
- Collins, M. A., Yau, C., Nolan, C. P., Bagley, P. M. & Priede, I. G. 1999 Behavioural observations on the scavenging fauna of the Patagonian slope. *J. Mar. Biol. Assoc. UK* **79**, 963–970. (doi:10.1017/S0025315499001198)
- Dahlgren, T. G., Wiklund, H., Källström, B., Lundälv, T., Smith, C. R. & Glover, A. G. 2006 A shallow-water whale-fall experiment in the north Atlantic. *Cah. Biol. Mar.* **47**, 385–389.
- Glover, A. G., Källström, B., Smith, C. R. & Dahlgren, T. G. 2005 World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic. *Proc. R. Soc. B* **272**, 2587–2592. (doi:10.1098/rspb.2005.3275)
- Goffredi, S. K., Johnson, S. B. & Vrijenhoek, R. C. 2007 Genetic diversity and potential function of microbial symbionts associated with newly discovered species of *Osedax* polychaete worms. *Appl. Environ. Microbiol.* **73**, 2314–2323. (doi:10.1128/AEM.01986-06)
- Guthrie, R. D. 1990 *Frozen fauna of the mammoth steppe: the story of Blue Babe*. Chicago, IL: University of Chicago Press.
- Honda, K., Fujise, Y., Tatsukawa, R. & Miyazaki, N. 1984 Composition of chemical components in bone of striped dolphin *Stenella coeruleoalba*: distribution characteristics of major inorganic and organic components in various bones, and their age-related changes. *Ag. Biol. Chem.* **48**, 409–418.
- Janßen, J., Treude, T. & Witte, U. 2000 Scavenger assemblages under differing trophic conditions: a case study in the deep Arabian Sea. *Deep-Sea Res.* **47**(Pt II), 2999–3026. (doi:10.1016/S0967-0645(00)00056-4)
- Jones, E. G., Collins, M. A., Bagley, P. M., Addison, S. & Priede, I. G. 1998 The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean. *Proc. R. Soc. B* **265**, 1119–1127. (doi:10.1098/rspb.1998.0407)
- Jones, W. J., Johnson, S. B., Rouse, G. W. & Vrijenhoek, R. C. 2008 Marine worms (genus *Osedax*) colonize cow bones. *Proc. R. Soc. B* **275**, 387–391. (doi:10.1098/rspb.2007.1437)
- Kemp, K. M., Jamieson, A. J., Bagley, P. M., McGrath, H., Bailey, D. M., Collins, M. A. & Priede, I. G. 2006 Consumption of large bathyal food fall, a six month study in the NE Atlantic. *Mar. Ecol. Prog. Ser.* **310**, 65–76. (doi:10.3354/meps310065)
- Marshall, J. T. 1900 On a British species of *Myrina*, with a note on the genus *Idas*. *J. Malacol.* **7**, 167–170.
- Rouse, G. W., Goffredi, S. K. & Vrijenhoek, R. C. 2004 *Osedax*: bone-eating marine worms with dwarf males. *Science* **305**, 668–671. (doi:10.1126/science.1098650)
- Rouse, G. W., Worsaae, K., Johnson, S. B., Jones, W. J. & Vrijenhoek, R. C. 2008 Acquisition of dwarf male ‘harems’ by recently settled females of *Osedax roseus* n. sp., (Siboglinidae: Annelida). *Biol. Bull.* **214**, 67–82.

- Schuller, D., Kadko, D. & Smith, C. R. 2004 Use of Pb-210/Ra-226 disequilibria in the dating of deep-sea whale falls. *Earth Planet. Sci. Lett.* **218**, 277–289. (doi:10.1016/S0012-821X(03)00690-3)
- Slijper, E. J. 1962 *Whales*. London, UK: Hutchinson.
- Smith, C. R. 2006 Bigger is better: the role of whales as detritus in marine ecosystems. In *Whales, whaling and ocean ecosystems* (eds J. A. Estes, D. P. DeMaster, D. F. Doak, T. M. Williams & R. L. Brownell), pp. 286–302. Berkeley, CA: University of California Press.
- Smith, C. R. & Baco, A. R. 2003 Ecology of whale falls at the deep-sea floor. *Oceanogr. Mar. Biol.* **41**, 311–354. London, UK: Taylor & Francis Ltd.
- Smith, C. R., Kukert, H., Wheatcroft, R. A., Jumars, P. A. & Deming, J. W. 1989 Vent fauna on whale remains. *Nature* **341**, 27–28. (doi:10.1038/341027a0)
- Tont, S. A., Percy, W. G. & Arnold, J. S. 1977 Bone structure of some marine vertebrates. *Mar. Biol.* **39**, 191–196. (doi:10.1007/BF00387004)
- Watling, L. & Norse, E. A. 1998 Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv. Biol.* **12**, 1180–1197. (doi:10.1046/j.1523-1739.1998.0120061180.x)
- Witte, U. 1999 Consumption of large carcasses by scavenger assemblages in the deep Arabian Sea: observations by baited camera. *Mar. Ecol. Prog. Ser.* **183**, 139–147. (doi:10.3354/meps183139)