Deep-sea whale fall fauna from the Atlantic resembles that of the Pacific Ocean

Paulo Y. G. Sumida, Joan M. Alfaro-Lucas, Mauricio Shimabukuro, Hiroshi Kitazato, Jose A. A. Perez, Abilio Soares-Gomes, Takashi Toyofuku, Andre O. S. Lima, Koichi Ara & Yoshihiro Fujiwara

Whale carcasses create remarkable habitats in the deep-sea by producing concentrated sources of organic matter for a food-deprived biota as well as places of evolutionary novelty and biodiversity. Although many of the faunal patterns on whale falls have already been described, the biogeography of these communities is still poorly known especially from basins other than the NE Pacific Ocean. The present work describes the community composition of the deepest natural whale carcass described to date found at 4204 m depth on Southwest Atlantic Ocean with manned submersible Shinkai 6500. This is the first record of a natural whale fall in the deep Atlantic Ocean. The skeleton belonged to an Antarctic Minke whale composed of only nine caudal vertebrae, whose degradation state suggests it was on the bottom for 5–10 years. The fauna consisted mainly of galatheid crabs, a new species of the snail Rubyspira and polychaete worms, including a new Osedax species. Most of the 41 species found in the carcass are new to science, with several genera shared with NE Pacific whale falls and vent and seep ecosystems. This similarity suggests the whale-fall fauna is widespread and has dispersed in a stepping stone fashion, deeply influencing its evolutionary history.

Whale carcasses are considered the largest organic inputs reaching the deep ocean floor in a single event. Carcasses attract a suite of opportunistic and specialist organisms (see 1 for a review) that feast on the flesh and lipid-rich bones. Specialized organisms have been evolving in these habitats for millions of years since the appearance of large ocean-going whales and other vertebrates before them1–3. Whale falls can thus be considered as sources of evolutionary novelty and biodiversity in the deep-sea, since they form isles of organic enrichment and biodiversity in an extremely food-limited environment1,8.

Based on this faunal overlap, Smith et al.16 theorized that whale falls may act as stepping-stones for faunal dispersal among different chemosynthetic communities, and could contribute to the colonization of new habitats separated by hundreds of kilometers (e.g. hydrothermal vents). In addition, this theory has also deep evolutionary implications. For instance, some of the most abundant symbiont-bearing invertebrates, such as mytilid mussels, evolved from shallow waters probably using organic-fall islands as dispersal stepping stones1,21–27. Despite the importance of evolutionary and ecological relationships among biological communities at different deep-sea chemosynthetic habitats, the biodiversity and biogeography of hydrothermal vents and cold seeps has been by far much more studied. Whale falls are likely to occur worldwide along whale migratory routes as

1Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico, 191, CEP 05508-120, São Paulo-SP, Brazil. 2Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2–15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan. 3Centro de Ciências Tecnológicas da Terra e do Mar (CTTMAR), Universidade do Vale do Itajai, Rua Uruguai, 458, P.O. Box 360, CEP 88302-202, Itajai-SC, Brazil. 4Departamento de Ecologia Marinha, Universidade Federal Fluminense, P.O. Box 100.644, CEP 24001-970, Niterói-RJ, Brazil. 5College of Bioresource Sciences, Nihon University, Kameino 1866, Fujisawa, Kanagawa 252-0880, Japan. Correspondence and requests for materials should be addressed to P.Y.G.S. (email: psumida@usp.br)
well as in whale breeding and feeding areas\(^\text{16,20}\). However, only 7 natural whale carcasses have been studied in detail in the deep-sea since 1989\(^\text{16,20,28–31}\) (although many more have been observed or remotely sampled\(^\text{1}\)). In consequence, the advancement in the understanding of these poorly known communities has been mainly due to time-series studies of artificially implanted whale carcasses on the seafloor\(^\text{1,20,32–36}\).

Most natural and implanted deep-sea whale-fall community studies are from the deep Northeast Pacific Ocean, specifically from the California slope and Monterey Canyon\(^\text{20,29,30}\). Consequently, the paucity of studies on whale falls as well as the scarce data available beyond the Northeast Pacific make biogeographic and evolutionary syntheses of both whale-fall fauna, and other related chemosynthetic communities, challenging\(^\text{1}\).

Here we describe the community composition of the first whale carcass found in the deep Atlantic Ocean (off the S-SE Brazilian continental margin). We show that, although separated by thousands of kilometers, this abyssal Southwest Atlantic whale fall is inhabited by many lineages previously only found in the Pacific chemosynthesis-based communities. In addition, many other chemosynthetically-related genera have their bathymetric and latitudinal ranges expanded. The findings reported here have deep implications for the poorly known biogeography of deep-sea whale-fall communities and suggest a worldwide distribution for some whale-fall specialists.

Results

Physico-chemical characteristics of the study site and whale carcass description. The whale fall was located ca. 700 km from the Brazilian coast at the base of the São Paulo Ridge (SPR; 28° 31.1191′S, 41° 39.4097′W) at a depth of 4204 m (Fig. 1). The surrounding area was characterized by a thin layer (<20 cm) of sediments overlying basaltic rocks. During our study, the area was under the influence of the Antarctic Bottom Water (AABW)\(^\text{37}\) with a temperature of 0.4 °C and salinity 34.7.

Mitochondrial COI analysis revealed that the carcass belonged to an Antarctic Minke whale (Balaenoptera bonaerensis) (99% identity). The sequence was deposited in the DNA Databank of Japan (DDBJ) under the accession number LC106302. This partial carcass was composed of nine small vertebrae, seven of which were standing side by side. Among those, five vertebrae were loosely joined by intervertebral discs (vertebrae 1–5) (Fig. 2). Additionally, five intervertebral discs were scattered around the skeleton. No soft tissues were present on the bones, which were all exposed to the surrounding water (i.e. not covered by sediment). All vertebrae were similar in shape and dimensions (ca. 11.5 cm in diameter) and their anatomical characteristics suggest they belong to the caudal portion of the animal. The sediment underneath bones and discs was dark in color suggesting anoxia.

Qualitative and quantitative analysis of the macrofauna assemblage and species distributions. Only epifaunal organisms larger than ca. 5 mm could be identified and counted in videos. Five phyla were recovered from the study area comprising at least 41 species (Table 1). Nematoda occurred in large numbers both inside bones and in the surrounding sediments and may be represented by more than one species. Nematodes are currently being quantified and will be treated in detail in a later publication.

Polychaetes were the most speciose taxon on both whale bones and soft sediments, with at least 28 species (≈68%), most of which are probably new to science. Among these was a new species of the bone-eating worm Oseadas (Fig. 3C, D). We found at least eight morphotypes of the dorvilleid Ophryotrocha and the new species Capitella iatapiuna\(^\text{38}\) boring into the bones, with the latter also found inhabiting the surrounding sediment sampled with a slurp gun. Three species of polynoid polychaetes, indistinguishable in video analyses, occurred on the surface of bones and sediments (Figs 3E and 4H), with a higher abundance on the former. Interestingly,
antagonistic behavior could be observed in videos, where two polynoids were fighting, possibly for space or food resources (see supplemental video material). Five species of Hesionidae (Hesiocaeca sp. nov., Microphthalmus sp. nov., Pleijelius sp. nov. 1 and 2 and Vrijenhoekia sp. nov.) (Fig. 4I) and two species of cirratulids (Raphidrilus and Tharyx) were also present in both sediment and bone, except for both species of Pleijelius which were found only on bones. Another important species occurring in bones was the chrysopetalid Vigtorniella.

Some polychaetes were found exclusively in sediments surrounding the bones. Among them, one species of Ampharetidae resembling the genus Grassleia (Figs 3C,D and 4G) and a new species of eyeless nereid from the genus Neanthes were abundant (Figs 3F and 4F). Ampharetids dwelt in tubes that were widespread in sediments close to the bones and were only less abundant in videos than Osedax sp. nov. (Table 1) (Fig. 3C,D). Neanthes sp. nov. could not be counted in videos, however it was observed in videos in the anoxic sediment under bones and intervertebral discs coming out the sediment and climbing the bones, without totally leaving its gallery of burrows (Fig. 3F) (supplemental video material).

Among mollusks, a new species of the abyssochrysoid gastropod Rubyspira was present in large numbers (Figs 3B,D,F and 4D) and individuals were quite large in size, attaining up to 3–4 cm in length. The other gastropod was a small species found on the surface of bones (Fig. 3B). Preliminary molecular data place this small gastropod in the family Raphitomidae (Conoidea). Around the skeleton we also found many large empty shells of Rubyspira. No empty shells of the small unidentified gastropod were registered.

Seven species of crustaceans occurred on bones and surrounding sediments (Table 1), including a species of copepod parasitic on Osedax. Munidopsis spp. were found in large numbers being widely distributed up to 1 m away from the carcass (Figs 3B, 3D, and 4F). We found two morphotypes of Munidopsis, one large and one small, which probably represent different species. A total of 295 individuals of both species were counted in videos (Table 1) and observations suggest these organisms feed on bacterial mats (supplemental video material). However, some of the galatheid crabs were also seen processing sediments in their mouthparts. One ovigerous female of the large morphotype was collected, which suggests that at least one of the galatheid species is reproducing on site. The amphipod Stephonix sp. (Figs 3D and 4C) occurred mainly on bones, frequently coming out of the bones or entering into cracks and holes in degraded areas of bones probably produced by Osedax activity (supplemental video material).

A small species of anemone (polyps ca. 1–2 mm in size) was observed forming extensive carpets of thousands of polyps on rocks around the carcass (Figs 3B and 4A). It was probably the most abundant epifaunal organism, with photographs suggesting a density of ca. 10 ind. cm⁻². However, these anemones could not be counted since they could not be resolved in video analyses due to their small size. This anemone was not observed on rocks far from bones.

Discussion

We find a close affinity between the SW Atlantic whale fall fauna with that of the NE Pacific, especially with genera found in the Monterey Canyon and off southern California. We also found a large generic overlap with other chemosynthetic ecosystems. These findings have deep implications for the almost unknown biogeography of whale-fall communities and contrast/conform with patterns proposed for other chemosynthetic communities, such as vents and seeps.
Vent fields can be ephemeral and separated by large distances, occurring mainly along active mid-oceanic ridges and back arc spreading centers (reviewed in42). They show great endemicity and different biogeographic provinces fit well with different ocean basins and their history of geological events (reviewed in39,40). On the other hand, cold seeps may be longer lasting and widespread along all continental margins (e.g.41). These environments, however, do not present such endemicity and other factors such as depth rather than geography may better explain their faunal distributions (e.g.42,43).

Here we show for the first time an inter-basin distribution for many whale-fall specialists and other genera previously only known to occur in other chemosynthetic-based ecosystems (i.e., vents, seeps and wood parcels). Strikingly, some of the fauna found in the present study appears to be related to that of the NE Pacific. Five genera previously only known to occur in other chemosynthetic-based ecosystems (i.e., vents, seeps and wood parcels). Strikingly, some of the fauna found in the present study appears to be related to that of the NE Pacific. Five genera previously only known to occur in other chemosynthetic-based ecosystems (i.e., vents, seeps and wood parcels).

Table 1. Species collected at the SW Atlantic whale fall site at 4204 m depth. Each species is assigned to a location within the habitat. *Only for organisms that could be counted in videos. **Includes eight different species. ***Includes all three polyplacophoran species collected. n.d. = not determined. †Shimabukuro et al., in prep.; △Shimabukuro et al., in prep.; □Silva et al., in prep.; ▲Shimabukuro et al., in prep.; ▼Fujiwara et al., in prep.; ▲Fujiwara et al., in prep.
is the case of the new hesionid polychaetes *Hesiocaeca* sp. nov. (sensu48) and *Pleijelius* sp. nov. 1 and 2, and the spionid *Lindaspio* sp. nov., previously registered in NW Atlantic methane hydrates48, NW Atlantic wood-fall experiments49 and SE Atlantic oil fields50, respectively (Table 2).

These findings support the stepping-stone hypothesis of Smith et al.16 and suggest that dispersal rather than vicariance is a major driver for diversification in whale fall ecosystems (see15,1). In fact, whale falls are likely to occur worldwide although heterogeneously distributed1. Some large baleen whales, such as humpbacks, migrate from high-latitude high-productivity feeding areas to low-latitude low-productivity breeding areas along continental margins in all oceans and to some specific oceanic islands (e.g. Hawaii) (reviewed in52). In addition, other species such as sperm whales, exhibit cosmopolitan distribution and can potentially sink everywhere in the ocean, especially supplying the deep ocean at equatorial latitudes1. In some areas carcasses may be relatively close to each other, e.g., Smith et al.15 estimated average nearest neighbor distances for whale falls from gray whales to occur every 3–16 km in the NE Pacific Ocean.

Figure 3. Distribution of epifauna on the whale fall and surrounding sediments and rocks. (A) General view of the SW Atlantic whale carcass vertebrae 1–7. Note the abundant fauna and the bacterial mats on vertebrae 1–5. A dark echinoid (Echinoidea sp. 1) can be seen on top of vertebra 2; (B) Black basaltic rocks around the whale fall were heavily colonized by dense carpets of anemones (arrow) (up to 10 ind. cm−2). The large gastropod *Rubyspira* sp. nov. lies behind the red palps of *Osedax* sp. nov. Note also the small unidentified gastropods attached to the bone; (C) Red palps and gelatinous tubes of several *Osedax* sp. nov. in vertebra 8. Note the ampharetid polychaete tubes (arrow) and the bone degraded area (arrowhead); (D) Clusters of *Osedax* sp. nov. in vertebrae 6 and 7. On the surrounding sediment, *Rubyspira* sp. nov. and a tube of an ampharetid polychaete (arrow). The small lysianassoid amphipod *Stephontix* sp. lies on the top of the bone (arrowhead); (E) Dense bacterial mats covering vertebrae 2 and 3. Here we can see the small and the large *Munidopsis* and a polynoid polychaete (arrow); (F) The eyeless nereid polychaete *Neanthes* sp. nov. climbing the surface of vertebra 6 (arrow).
Some genera of the whale fall specialists appear to have a worldwide distribution, such as the bone-eating genus Osedax. Osedax rubiplumus illustrates well this idea having been reported in both sides of the Pacific Ocean and even in the Southern Ocean, which suggests a large inter-basin connectivity. Furthermore, the present Osedax phylogeny does not seem to fit any specific geographical or bathymetrical pattern suggesting that dispersion is an important factor for the evolution of Osedax species. Mitochondrial COI data (DDBJ accession
number LC106303) from the new Osedax found in the present work place it near the NE Pacific species O. franki
press (species description currently in prep.). It is the deepest Osedax species found to date, extending the gen
depth range by more than 1300 m 24 and it is the first found in the deep Atlantic Ocean. Similarly, mtCOI studies
(DDBJ accession number LC106304) cluster Rubyspura sp. nov. with the two previously described species (R.
osteovora and R. goffredi n 45), both of them from the Monterey Canyon (NE Pacific). The occurrence of other
Pacific genera in our study, such as Vrijenhoekia and Bathylurida cf. guaymasensis, also supports the idea that
many whale-fall specialist lineages may be distributed worldwide (Table 2).
Thus, it is feasible to imagine a “worldwide whale-fall corridor” along continental margins, somewhat similar
to the distribution of cold-seeps, but also along equatorial areas. Both “corridors” would allow faunal dispersion
by a stepping-stone dispersal mechanism. This mechanism may be important for some chemosynthetic-generalist
invertebrates with worldwide distributions, such as vesicomyid clams 16,55, and also for whale-fall specialists.

Methods

A whale carcass was serendipitously found at 4204 m depth in the Southwest Atlantic Ocean during a Shinkai 6500
dive in April 24, 2013. This finding is a result of the Iatá-Piúna Research Consortium, a collaborative scientific
partnership between Brazil and Japan. The Iatá-Piúna research cruise comprised two legs of the around-the-world
Project Quelle 2013 (Quest for the Limit of Life) of the Japan Agency for Marine-Earth Science and Technology
(JAMSTEC) using R/V Yokosuka.

Video surveys and sampling were carried out during two dives of the deep-sea manned submersible Shinkai 6500
(Dives 1334 and 1336). On each dive, a detailed video survey was made, including whole community sur-
veys and close-ups of the fauna. Owing to the small habitat size, epifaunal organisms larger that ca. 5 mm were
identified to the lowest taxonomic rank possible and quantified in videos. Videos were also used to verify faunal
distribution patterns along the skeleton. Images were processed using the computer program Image 5 6.

Whalebones were collected using the submersible manipulators and the fauna surrounding the area was
retrieved using a slurp gun and maintained in local cold seawater during submersible ascent. Upon arrival on
deck, bones were immediately transferred to a cold room at a constant temperature of 1°C. Bone and sediment
epifauna and infauna were sorted manually and under stereomicroscope. Samples were taken for morphological
identification and molecular (deep-frozen at ~80°C and 99.5% non-denatured ethanol). In addition, samples
were fixed in glutaraldehyde for SEM and TEM analyses.

Sediments were collected using a slurp gun and push corers and were used in the present work only for qual-
itative analysis. Sediment was fixed with 4% formalin (final concentration) in filtered seawater buffered with
sodium tetraborate and stained with 0.05 GL−1. Rose Bengal dye was used to distinguish meiofauna from sediment
particles. Sediment samples for metazoan meiofaunal analysis were treated according to the procedure described
by 8. The samples were washed over 63-μm mesh sieves. The sediment that remained on the 63-μm mesh sieve
was resuspended and centrifuged for 10 min at 800 g with colloidal silica (Ludox HS40; Sigma-Aldrich, St Louis,
MO, USA) to separate meiofauna and other lighter particles from mineral particles. The supernatants were trans-
ferred to flat-bottomed Petri dishes. Rose Bengal-stained organisms were then collected using an Irwin loop 9,
sorted into higher taxa under a binocular.

A piece of a deep-frozen vertebra was used for DNA sequencing to verify the identity of the whale skeleton.
DNA was directly extracted from the bone. The vertebra sample was thoroughly washed in autoclaved and filtered
seawater to eliminate surface contaminants. DNA extraction was conducted using the DNeasy Tissue Kit (Qiagen
Japan, Tokyo, Japan). The cytochrome c oxidase subunit I (COI) gene was amplified by PCR using the Ex Taq PCR Kit (Takara,
Kyoto, Japan). Two oligonucleotide primers (1 μM each) and <1 μg of DNA template were added to the reaction
mixtures. Thermal cycling was as follows: denatured at 96°C for 20 s; annealed at 55°C for 45 s; and extended
at 72°C for 2 min for a total of 35 cycles. The oligonucleotide primer sequences used for this amplification were
LCO1490 and HCO2198 59. The molecular size of the PCR products was checked with 1.2% Agarose S (Nippon
Gene, Toyama, Japan) gel electrophoresis.

DNA sequencing of the amplified COI genes was performed using the BigDye Terminator Cycling Sequencing
Ready Reaction Kit (PE Applied Biosystems, Foster City, CA, USA). The LCO1490 and HCO2198 primers were
used in sequencing reactions. Sequencing was performed using an ABI PRISM 3100 genetic analyzer (PE Applied
Biosystems).

References

1. Smith, C. R., Glover, A. G., Treude, T., Higgs, N. D. & Amon, D. J. Whale-Fall ecosystems: Recent insights into ecology, paleoecology,
and evolution. Ann Rev Mar Sci 7, 571–596 (2015).
2. Kiel, S., Goedert, J. L., Kahl, W. & Rouse, G. W. Fossil traces of the bone-eating worm Osedax in early Oligocene whale bones. P Natl
Acad Sci USA 107, 8656–8659 (2010).
3. McGowan, M. R., Gatesy, J. & Wildman, D. E. Molecular evolution tracks macroevolutionary transitions in Cetacea. Trends Ecol Evol
29, 336–346 (2014).
4. Kaim, A., Kobayashi, Y., Echizenya, H., Jenkins, R. G. & Tanabe, K. Chemosynthesis-based associations on Cretaceous plesiosaurid
carcasses. Acta Palaeontol Pol 53, 97–104 (2008).
5. Kiel, S. Fossil evidence for micro- and macrofaunal utilization of large nekton falls: Examples from early Cenozoic deep-water
sediments in Washington State, USA. Palaeogeogr Palaeoclim Palaeoecol 267, 161–174 (2008).
6. Kiel, S., Kahl, W. & Goedert, J. L. Osedax borings in fossil marine bird bones. Naturwissenschaften 98, 51–55 (2011).
7. Danise, S. & Higgs, N. D. Bone-eating Osedax worms lived on Mesozoic marine reptile deadfalls. Biol Lett 11, 20150072 (2015).
8. Baco, A. R. & Smith, C. R. High species richness in deep-sea chemosynthrophic whale skeleton communities. Mar Ecol Prog Ser
260, 109–114 (2003).
9. Bennett, B. A., Smith, C. R., Glaser, B. & Maybaum, H. L. Faunal community structure of a chemosynthrophic assemblage on whale
bones in the deep northeast Pacific Ocean. Mar Ecol Prog Ser 188, 265–223 (1999).
10. Smith, C. R., Baco, A. R. & Glover, A. Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. *Cah Biol Mar* **43**, 293–297 (2002).

11. Smith, C. R. & Baco, A. R. Ecology of whale falls at the deep-sea floor. *Oceanogr Mar Biol Annu Rev* **41**, 311–354 (2003).

12. Smith, C. R., Bernardino, A. F., Baco, A., Hannides, A. & Altamira, I. Seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30 tonne whale fall in the Northeast Pacific. *Mar Ecol Prog Ser* **515**, 133–149 (2014).

13. Deming, J. W., Reysenbach, A. L., Mako, S. A. & Smith, C. R. Evidence for the microbial basis of a chemoautotrophic invertebrate community at a whale fall on the deep seafloor: Bone-colonizing bacteria and invertebrate endosymbionts. *Microb Res Technol* **37**, 162–170 (1997).

14. Goffredi, S. K., Wilpissenzki, R., Lee, R. & Orphan, V. J. Temporal evolution of methane cycling and phylogenetic diversity of Archaea in sediments from a deep-sea whale-fall in Monterey Canyon, California. *ISME J* **2**, 204–220 (2008).

15. Tress, T. et al. Biogeochemistry of a deep-sea whale fall: Sulfate reduction, sulfide efflux and methanogenesis. *Mar Ecol Prog Ser* **382**, 1–21 (2009).

16. Smith, C. R., Kukert, H., Wheatcroft, R. A., Jumars, P. A. & Deming, J. W. Vent fauna on whale remains. *Nature* **34**, 127–128 (1989).

17. Smith, C. R. & Baco, A. R. Phylogenetic and functional affinities between whale-seep, and vent and chemosynthetic communities. *Cah Biol Mar* **39**, 345–346 (1998).

18. Feldman, R. A. et al. Vestimentiferan on a whale fall. *Biol Bull* **194**, 116–119 (1998).

19. Baco, A. R., Smith, C. R., Peck, A. S., Roderick, G. K. & Vrijenhoek, R. C. The phylogenetic relationships of whale-fall vesicomyid clams based on mitochondrial COI DNA sequences. *Mar Ecol Prog Ser* **182**, 137–147 (1999).

20. Smith, C. R. & Baco, A. R. Ecology of whale falls at the deep-sea floor. *Oceanogr Mar Biol Annu Rev* **41**, 311–354 (2003).

21. Distel, D. L. et al. Do mussels take wooden steps to deep-sea vents? *Nature* **403**, 725–726 (2000).

22. Jones, W. J. et al. Evolution of habitat use by deep-sea mussels. *Mar Biol* **148**, 841–851 (2006).

23. Fujiwara, Y. et al. Extracellular and mixotrophic symbiosis in the whale-fall mussel *Adipopsis pacifica*: A trend in evolution from extra- to intracellular symbiosis. *PLoS ONE* **5**, e11808. doi: 10.1371/journal.pone.0011808 (2010).

24. Miyazaki, J.-I., Martins, L. O., Fujita, Y., Matsumoto, H. & Fujiwara, Y. Evolutionary process of deep-sea *Bathymodiolus* mussels. *PLoS ONE* **5**, e10363. doi: 10.1371/journal.pone.0010363 (2010).

25. Lorion, J.-L. et al. Evolutionary history of *Iasid* sp. Med (Bivalvia: mytilidae), a cold seep mussel bearing multiple symbionts. *Cah. Biol. Mar.* **53**, 77–87 (2012).

26. Lorion, J.-L. et al. Adaptive radiation of chemosymbiotic deep-sea mussels. *Proc. R. Soc. B* **280**, 2013 1243 (2013).

27. Thubaut, J., Puillandre, N., Faure, B., Cruaud, C. & Samadi, S. The contrasted evolutionary fates of deep-sea chemosynthetic mussels (*Bivalvia, Bathymodiolinae*). *Ecol. Evol.* **4**, 4748–4766 (2013).

28. Fujisaka, K., Wada, H. & Okano, H. Torishima whale deep-sea animal community assemblage- new findings by "Shinkai 6500". *J Geoey* **102**, 507–517 (1993).

29. Goffredi, S. K., Paull, C. K., Fulton-Bennet, K., Hurtado, L. A. & Vrijenhoek, R. C. Unusual benthic fauna associated with a whale fall in Monterey Canyon, California. *Deep-Sea Res I* **51**, 1295–1306 (2004).

30. Lundsten, L., Paull, C. K., Schlimging, K. L., McGann, M. & Usler III, W. Biological characterization of a whale-fall near Vancouver Island, British Columbia, Canada. *Deep-Sea Res I* **57**, 918–922 (2010).

31. Amon, D. et al. The discovery of a natural whale fall in the Antarctic deep sea. *Deep-Sea Res II* **92**, 87–96 (2013).

32. Dahlgren, T. G. et al. A shallow-water experiment in the north Atlantic. *Cah Biol Mar* **47**, 385–389 (2006).

33. Braby, C. E., Rouse, G. W., Johnson, S. B., Jones, W. J. & Vrijenhoek, R. C. Bathymetric and temporal variation among *Oseax* bownowms and associated megafauna on whale-falls in Monterey bay, California. *Deep-sea Res I* **54**, 1773–1791 (2007).

34. Fujiwara, Y. et al. Three-year investigations into sperm whale-fall ecosystems in Japan. *Mar Ecol Sci* **28**, 1219–1232 (2007).

35. Glover, A. G. et al. A live video observatory reveals temporal processes at a shelf-depth whale fall. *Cah Biol Mar* **51**, 375–381 (2010).

36. Lundsten, L. et al. Time-series analysis of six whale-fall communities in Monterey Canyon, California. *Deep-Sea Res I* **57**, 1573–1584 (2010).

37. Speer, K. G. & Zenk, W. The flow of Antarctic Bottom Water into the Brazil Basin. *J Phys Oceanogr* **23**, 2667–2682 (1993).

38. Silva, C. F., Shimabukuro, M., Alfaro-Lucas, J. M., Fujiwara, Y., Sumida, P. Y. G. & Amaral, A. C. Z.: A new *Capitella* polychaete worm (Annellida: Capitellidae) living inside whale bones in the abyssal South Atlantic. *Deep-Sea Res I* doi: 10.1016/j.dsr.2013.12.004 (in press).

39. Van Dover, C. L., German, C. R., Speer, K. G., Parson, L. M. & Vrijenhoek, R. C. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* **295**, 1253–1257 (2002).

40. Moalic, Y. et al. Biogeography revisited with network theory: Retracing the history of hydrothermal vent communities. *Syst Biol* **61**, 127–137 (2012).

41. Levin, L.A. Ecology of cold seep sediments: Interactions of fauna with flow, chemistry and microbnes. *Oceanography* **16** (2003).

42. Olu K., Cordes E. E., Fisher C. R., Brooks J. M. & Sibuet M. Biogeography and potential exchanges among the Atlantic Equatorial Belt cold-seep faunas.

43. Pettibone, 1989 (Annelida: Polynoidae).

44. Johnson S. B.

45. Bellan, G., Dauvin, J. C. & Laubier, L. The genus *Lindaspis* (Annelida: Polychaeta: Spionidae), and a new species from an oil field off Congo, western Africa. *J Nat Hist* **37**, 2413–2424 (2003).

46. Glover, A. G., Kallstrom, B., Smith, C. R. & Dahlgren, T. G. World-wide whale worms? A new species of *Oseax* from the shallow north Atlantic. *Proc Royal Soc B* **272**, 2587–2592 (2013).

47. Roman, J. et al. Whales as marine ecosystem engineers. *Front Ecol Environ* **12**, 377–385 (2014).

48. Glover, A. G. et al. Bone-eating worms from the Antarctic: the contrasting fate of whale and wood remains on the Southern Ocean seafloor. *Proc Royal Soc B* **280**, 20131390 (2013).

49. Rouse, G. W., Goffredi, S. K. & Vrijenhoek, R. C. *Oseax*: bone-eating marine worms with dwarf males. *Science* **305**, 668–671 (2004).

50. Tunnichelke, V. & Juniper, S. K. Cosmicopolitan underwater fauna. *Nature* **344**, 300 (1990).

51. Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to Imagej: 25 years of image analysis*. *Nature Met* **9**, 671–675 (2012).
57. Danovaro, R. et al. Major viral impact on the functioning of benthic deep-sea ecosystems. Nature 454, 1084–1088 (2008).
58. Westheide, W. & Purschke, G. Organism processing in Introduction to the Study of Meiofauna (eds Higgins, R.P. & Thiel, H.) 146–160 (Smithsonian Institute Press, 1988).
59. Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotech 3, 294–299 (1994).
60. Pettibone, M. H. Polynoidae and Sigalionidae (Polychaeta) from Guaymas Basin, with descriptions of 2 new species, and additional records from hydrothermal vents of Galapagos Rift, 21 N, and seep site in the Gulf of Mexico (Florida and Louisiana). P Biol Soc Wash 102, 154–168 (1989).
61. Pettibone, M. H. Revision of the genus Macellicephala McIntosh and the subfamily Macellicephalinae Hartmann-Schröder (Polychaeta: Polynoidae). Smithsonian Contrib Zool 229, 71 p. (1976).
62. Dahlgren, T. G., Glover, A. G., Baco, A. & Smith, C. R. Fauna of whale falls: systematics and ecology of a new polychaete (Annelida: Chrysoptelidae) from the deep Pacific Ocean. Deep-Sea Res I 51, 1873–1887 (2004).
63. Wiklund, H., Glover, A. G., Johannessen, P. I. & Dahlgren, T. G. Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. Zool J Linn Soc 155, 774–785 (2009).

Acknowledgements
We are deeply indebted to the various representatives of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), the Japanese Consulate at São Paulo, the Brazilian Ministry of Science and Technology and Innovation, Brazilian Ministry of Foreign Affairs and the Brazilian Navy for helping establishing the Brazil-Japan Marine Science Agreement. We also wish to thank the Master and crews of RV Yokosuka and DSRV Shinkai 6500 for invaluable help at sea. PYGS benefitted from a BIOTA-FAPESP Grant 2011/50185-1 and a CNPq research productivity fellowship 302526/2012-9 to whom he is grateful. We also wish to thank Craig R. Smith (University of Hawaii) for insightful comments that greatly improved the manuscript.

Author Contributions
Collected and processed data: Y.F., P.Y.G.S., K.A., H.K., J.A.A.P., A.S.G., T.T. and A.O.S.L. Performed laboratory analyses and species identification: J.M.A.L., M.S., P.Y.G.S. and Y.F. Wrote paper: P.Y.G.S., J.M.A.L., M.S. and Y.F.

Additional Information
Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Sumida, P. Y. G. et al. Deep-sea whale fall fauna from the Atlantic resembles that of the Pacific Ocean. Sci. Rep. 6, 22139; doi: 10.1038/srep22139 (2016).

This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/