



Research article

Whale fall chemosymbiotic communities in a southwest Australian submarine canyon fill a distributional gap

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ABSTRACT

A whale fall community of chemosymbiotic invertebrates living on cetacean bones has been identified off southwestern Australia during a Remotely Operated Vehicle (ROV) survey at bathyal depths within the Bremer Marine Park, which is part of important marine mammal areas (IMMA) of the Albany Canyon Region. Cetacean bones on the seafloor of the Hood Canyon, consisted of isolated skulls of three species of beaked whales (family Ziphiidae): *Mesoplodon cf. layardii*, *M. grayi*, and *M. hectori*, a few vertebrae, and lower jaws. One of the beaked whale skulls (*Mesoplodon cf. layardii*) was sampled and found to be intensely colonised by hundreds of specimens of a bathymodilinea mussel ("*Adipicola*" s.l.). Live polychaetes (*Phyllochaetopterus*?), skeinimorph gastropods, and amphipods (*Seba*, *Leptamphopus*) colonised the skull bone, which represent a later stage (sulfophilic) of carcass decomposition. The reducing sediment below the skull was inhabited by lucinid (*Lucinoma*) and vesicomid (*Calyptogena*) chemosymbiotic bivalves. Additionally, the sediment thanatocoenosis comprised shells of various other chemosymbiotic bivalves, such as *Acharax*, thyasirids, lucinids, vesicomids, and limpets, representing the complex ecological turnover phases through time in this whale fall chemosynthetic habitat. With one exception, all bones recovered were colonized by bathymodiolinea mussels. This is the first documented case of a chemosynthetic community and associated chemosymbiotic fauna relating to beaked whales, and the first fully documented record of a whale fall community within the Australian Southern Ocean region.

1. Introduction

Cetacean remains, commonly referred to as 'whale falls', are known to be exploited by chemoautotrophic consortia and specialized chemosymbiotic fauna. Whale carcasses that sink to the seafloor provide a localised but extraordinarily large source of energy to the deep-sea ecosystems from scavengers to specialized chemosynthetic -based organisms that inhabit these regions [1,2] In fact, after the initial scavenging stage by fishes and crustaceans, such as amphipods and decapods, the decomposing whale carcass becomes the locus

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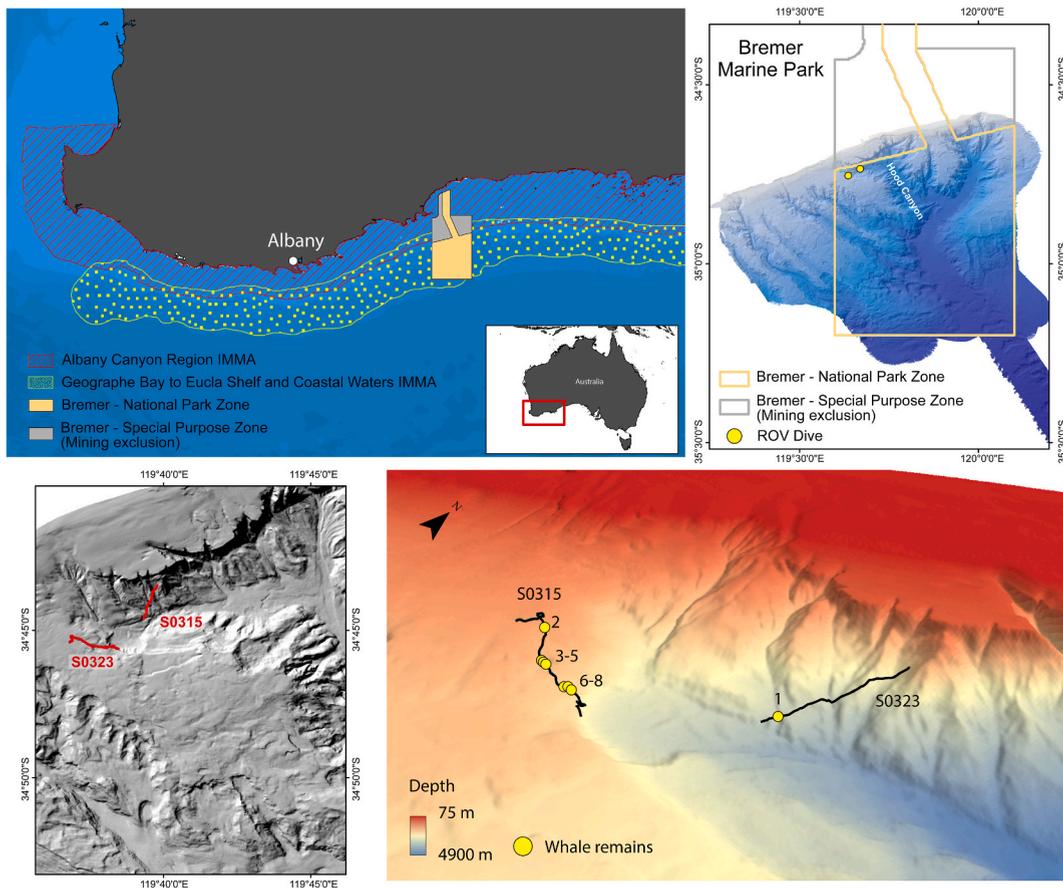


Fig. 1. Location of the two ROV dive sites, 315 and 323, in the Hood Canyon where the whale fall chemosymbiotic communities were found, which are discussed in the text.

of complex pluriannual taphonomic processes, which form sulfidic reducing microhabitats of microbial consortia feeding on its organic components, especially lipids 3–20.

The Hood Canyon is part of the Bremer Canyon systems, a network of submarine canyons incising the southwestern Australian margin 21,22 near the convergence of the southeast Indian Ocean and northwestern limits of the Austral Southern Ocean. This system of canyons was explored during the austral summer of 2020 using the Schmidt Ocean Institute's RV *Falkor* and its ROV, *SuBastian* 23. While the primary goal of the expedition was to find and collect deep-water corals for paleoceanographic and paleoclimatic studies 24, time was also devoted to investigate other interesting biota, including the remains of local megafauna. Notably, this region (Fig. 1) is renowned for its high numbers of seasonally transient or resident large mysticetes and odontocetes, predominantly sperm and killer whales, but also fin, humpback, blue whales, and dolphins, which inhabit the Australian Whale Sanctuary 25 and, more specifically, the Albany Canyon Region IMMA (<https://www.marinemammalhabitat.org/portfolio-item/albany-canyon-region/>) and associated Bremer Marine Park (<https://parksaustralia.gov.au/marine/parks/south-west/bremer/>). The area is also on the migratory route of fin, humpback, blue, and southern right whales 26. Considering the high number of cetaceans in these waters 27, the aggregation of killer whales and the known instances of killer whale predation on beaked whales 28, we anticipated that whale carcasses and skeletons might occur in different stages of preservation on the seafloor within our study area.

The search for whale falls using the ROV *SuBastian* resulted in the discovery of various bones exposed on the seabed at two sites in the Hood Canyon of the Bremer Marine Park, each colonised by a wide variety of chemosymbiotic organisms (<https://www.youtube.com/watch?v=U7LRwVczTas>). Our finding was the first of this type recorded to date from Australian waters, or within the eastern Indian and Austral Southern oceans 23,29. The occurrence of communities related to organic falls in Australian waters was not, however, unexpected given that associated chemosymbiotic organisms (e.g., *Idas*) had been previously collected by trawling surveys (<https://biodiversity.org.au/afd/taxa/Idas>) and were reported from New Zealand waters 30. Recently, Georgieva et al. 31 described in detail the polychaetes from the skull of a pilot whale trawled off eastern Australia. The scope of our study is to provide the first insights into the communities associated with a natural whale fall recorded in-situ offshore southwest Australia.

Table 1
Typology and georeferenced locations of whale bones found in the Hood Canyon, Bremer Marine Park.

ID	DIVE	DATE	LAT (DDEG)	LON (DDEG)	DEPTH (M)	OBSERVATION	TAXONOMY	NOTES	FIGURE REFERENCES
1	S0315	January 2, 2020	-34.74	119.66	1531	Whale skull	<i>Mesoplodon layardii</i>		Fig. 2
2	S0323	2/13/2020	-34.75	119.62	952	Caudal vertebra		Broken during sampling	Fig. 3 A,B
3	S0323	2/13/2020	-34.76	119.63	1041	Central part of rostrum	Ziphiidae		Fig. 3C and D
4	S0323	2/13/2020	-34.76	119.63	1040	Central part of rostrum			
5	S0323	2/13/2020	-34.76	119.63	1045	Skull	<i>Mesoplodon grayi</i>		Fig. 3 E,F
6	S0323	2/13/2020	-34.76	119.63	1110	Several vertebrae	<i>Mesoplodon?</i>		Fig. 3 I,J,K
7	S0323	2/13/2020	-34.76	119.63	1115	Bone			Fig. 3 G,H
8	S0323	2/13/2020	-34.76	119.64	1120	Skull and jaw bones	<i>Mesoplodon hectori</i>		Fig. 3 L,M,N

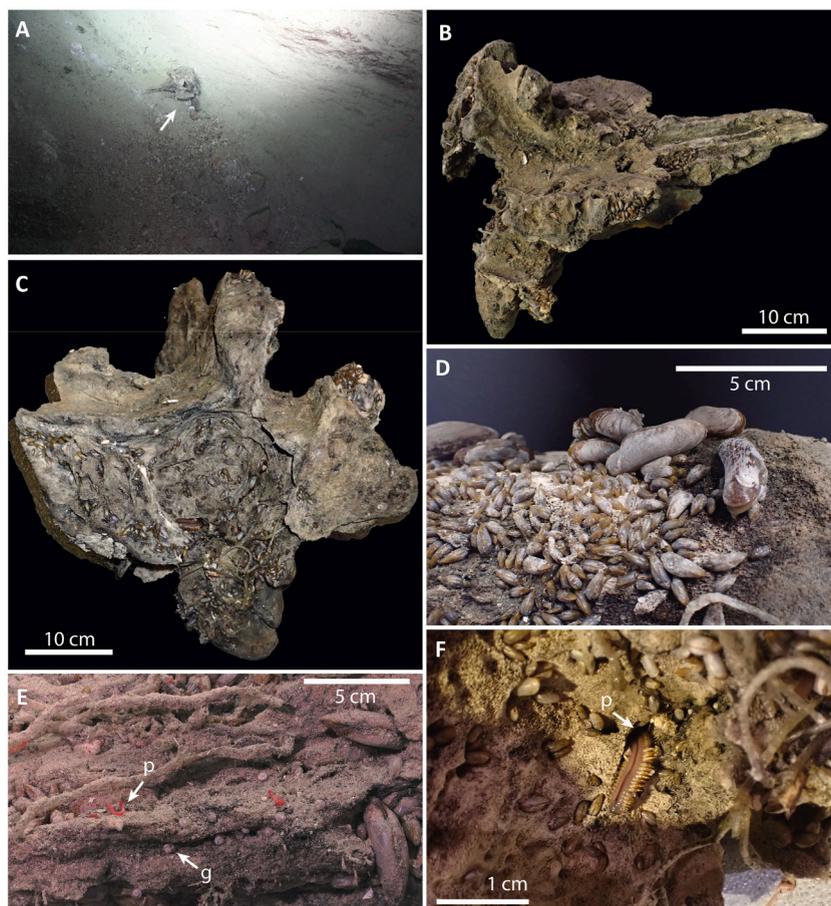


Fig. 2. Whale fall at dive 315, Hood Canyon, depth 1530 m. (A) location of the skull of a ziphiid whale (arrow), provisionally assigned to *Mesoplodon layardii*, at the foot of a Tertiary-age chalk escarpment. Note abundant shell hash and debris in the foreground; (B–C) ex situ detail of the same skull showing clusters of bathymodioline mussels and the occurrence of chaetopterid polychaete tubes; (D) detail showing dense “*Adipicola*” bathymodiolins at different growth stages; (E) detail of a section of the skull colonized by skeneimorph gastropods (g), living polychaetes (p) and chaetopterid polychaete tubes; (F) the polychaete *Eunoe* crawling out of a cavity, small bathymodiolins nested in cavities, and chaetopterid polychaete tubes.

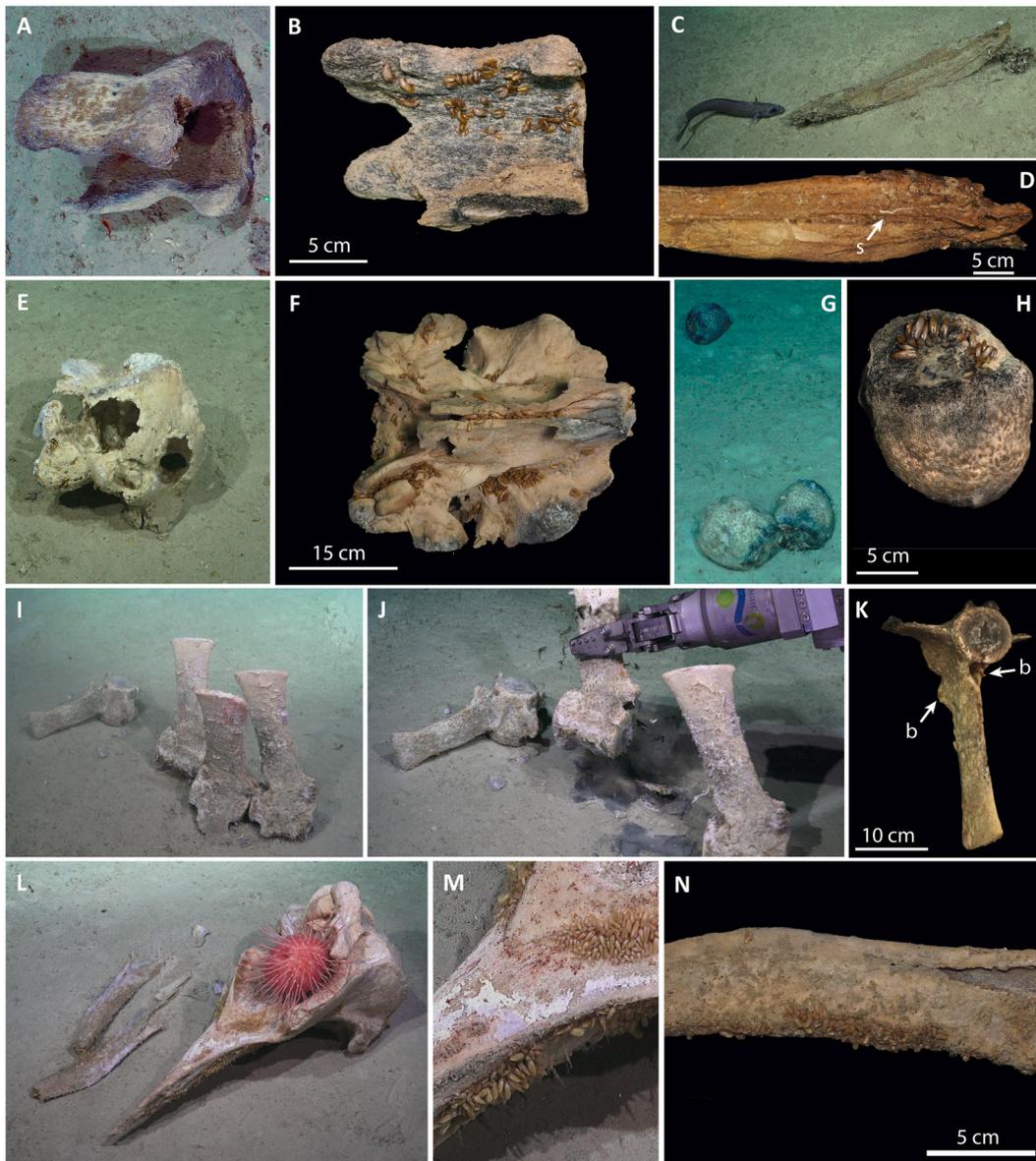


Fig. 3. Whale bone falls at dive 323. (A) caudal vertebra on the seafloor at ~952 m; (B); fragmented part of the same specimen after collection, showing colonization by bathymodiolineae mussels; (C) rostral bones of a Ziphiidae species on the seafloor at ~1040 m; (D) same rostral bones after collection showing the bone at the “reef stage” of decomposition, and encrusted by non-chemosymbiotic fauna such as serpulids (s); (E) in situ skull of *Mesoplodon grayi* at ~1044 m; (F) ex situ skull of *M. grayi* (ventral view) same as in E), showing the presence of bathymodiolineae bivalves; (G) caudal vertebrae of provisionally-identified ziphiid spread at ca. ~115 m; (H) detail of one caudal vertebra after collection showing a cluster of bathymodiolineae; (I) the most complete sequence of bones (vertebrae, possibly *Mesoplodon*) which was recorded at ~1109 m; (J) recovery of one vertebrae with ROV *SuBastian*'s robotic arm causing seepage of sulphidic compounds (black swirls); (K) the same sample on board revealed some bathymodiolineae (b) colonizing its surface; (L) skull and disarticulated lower jaws of *Mesoplodon hectori* at ~1120 m, with an echinoid on the skull; (M) detail of the previous image showing dense clusters of small bathymodiolineae; (N) one of the two lower jaws recovered on board appeared colonized by a row of small bathymodiolineae.

2. Material and methods

The data and material discussed in this study were obtained during Cruise FK200126 (26 January-26 February 2020) aboard the Schmidt Ocean Institute's research vessel *Falkor*. Video and still images, together with samples from the seafloor, were collected using the ROV *SuBastian*.

Multibeam bathymetry was acquired using *Falkor*'s Kongsberg EM 302 and 710 sonar systems. Oceanographic data and water samples were collected with a Rosette system equipped with a Seabird SBE 911plus CTD and associated SBE 43 dissolved oxygen sensor

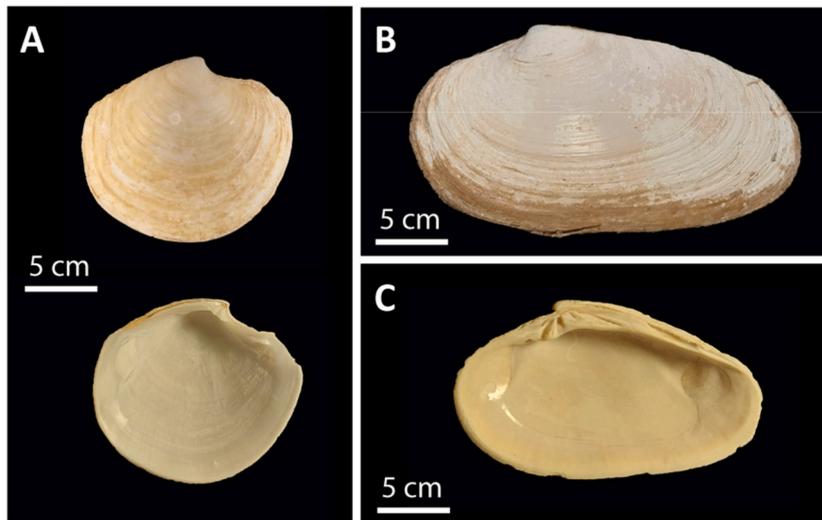


Fig. 4. Chemosymbiotic bivalves found alive in the reducing sediment beneath the ziphiid skull at 1530 m, dive 315: (A) *Lucinoma* sp.; (B–C) *Calyptogena* sp., valves that belonged to two different individuals.

and Wet Labs ECO- FLNTU fluorescence sensor. Water column parameters measured in-situ included temperature (T), conductivity (salinity: S), dissolved oxygen (DO), and pressure (depth). Further cruise operational details can be found in Trotter et al. 25.

Bones were carefully recovered from the seafloor using *SuBastian's* hydraulic arms (Table 1). At station 315, after the removal of the large bone, the underlying sediments and shells were collected using scoops and vacuum devices manipulated by the robotic arms. Once onboard, the bone material was immediately inspected for associated fauna; a full photographic record was obtained together with a detailed description of the samples. Living organisms were removed and stored in ethanol for biomolecular analyses, with an aliquot selected for more detailed inspection by stereo microscopy and macrophotography. Due to the strong odour from the release of hydrogen sulphide, the skeletons were frozen and kept in sealed containers onboard, then archived post-cruise at the Western Australian Museum in Perth.

While onboard, the sediment was washed with freshwater through a 0.5 mm mesh sieve. The resulting fraction was examined for live fauna, which were handpicked for initial identification and photographic documentation prior to fixing in ethanol. The remaining skeletal fraction was dried in an oven at 40 °C, then inspected to provide an initial taxonomic assessment prior to storage. The sediment fractions are currently archived at the ISMAR-CNR, Bologna, repository.

3. Results

3.1. Bone remains

The whalebone material described in this study (Figs. 2 and 3; Table 1) consists of three almost complete skulls, several vertebrae, and two mandibles and one rostrum.

One skull was collected from the Hood Canyon during ROV dive 315 (1530 m), which has been identified as a beaked whale in the family Ziphiidae (Fig. 2A). The skull is ascribed to *Mesoplodon layardii* (Gray, 1865), the most common ziphiid in these waters 32. The beaked whale skull appeared very porous, cracked, and friable in places. The skull surfaces that were not in direct contact with the underlying sediment were densely colonised by hundreds of mussels at various growth stages (Fig. 2B–D). Based on shell resemblance, the mussels were provisionally ascribed to *Adipicola* Dautzenberg, 1927 a chemosymbiotic bathymodiolineae 33. These “*Adipicola*” s.l. resemble *A. pacifica* Dall et al., 1938, and *Terua osseocola* Dell, 1987, the latter being a bathyal species previously reported with organic remains found offshore New Zealand 30. The skull was also intensely colonised by chaetopterid polychaetes (possibly *Phyllochaetopterus*), either as a carpet of soft tubes attached to the bone, or as isolated individuals settled within cavities in the bone (Fig. 2C–E,F). We observed numerous specimens of amphipods belonging to at least three different species, including *Seba* sp., and *Leptamphopus*?, which were very active on and within holes in degraded areas of the bones. Finally, we collected a still unclassified skeneimorph gastropod. Background macro- (2 mm–20 mm) and megabenthic (>20 mm) species comprised large predatory polychaetes (*Eunoe* sp. and Eunicidae) crawling inside a cavity in the bone (Fig. 2 F).

The other two skulls, found at dive site 323, were attributed to *Mesoplodon grayi* von Haast, 1876, and *M. hectori* (Gray, 1871), and the five vertebrae, two mandibles and one rostrum likely belong to the Ziphiidae, possibly *Mesoplodon* (Fig. 3). These skeletal remains were scattered at various sites along the ROV track, more often as isolated findings but in one case as a series of four adjacent vertebrae (Fig. 3 I). Although the skull (*M. hectori*) was not collected, we sampled a skull (*M. grayi*), vertebrae and other bones at this station, which were colonised by “*Adipicola*” mussels (Fig. 3B–D,F,H,K,M,N). The background macro- and megabenthos included a sea urchin nestled in the concave part of the skull (Fig. 3 L), mobile shrimp *Eualus* and *Nematocarcinus*, and polychaetes *Mellicephala* and *Nothria*

on or around the bones. One jaw represented older remains, which hosted sessile organisms including both live and dead barnacles of *Gibbosaverruca*, and empty tubes of Serpulidae.

All skulls and bones lacked obvious flesh, with the community typology indicating that most of the whale bones observed in the Hood Canyon are presently in the sulfophilic stage of decomposition^{34–36}, the penultimate phase of becoming a simple substrate for non-chemotrophic communities (reef stage). One rostrum appeared to be in this more advanced reef stage, acting as substrate for cemented serpulid polychaetes and barnacles (Fig. 3C).

The apparent absence of the boneworm *Osedax* at the study sites is somewhat surprising. This siboglinid annelid has been consistently recorded as an inhabitant of organic falls on the seafloor³⁷ since the Mesozoic³⁸. *Osedax* plays a crucial role in fostering the exploitation of whalebones by other chemosymbiotic fauna and scavengers¹⁷. Hence, its absence where dissolved oxygen levels seem suitable to *Osedax*²⁵ is notable, with more extensive studies required to ascertain whether this is a site-specific or regional anomaly.

3.2. Sediments

Removal of one of the skulls (*M. layardii*) exposed the underlying sediment (dive 315). It was comprised of a muddy-sandy shell hash, highly enriched in molluscan shell remains and other skeletal biosomes and fragments, below which appeared to be reducing conditions. These reducing sediments were inhabited by a few living specimens of chemosymbiotic bivalves (Fig. 4), namely a lucinid (*Lucinoma* sp., Fig. 4A) and a vesicomid (*Calyptogena* sp., Fig. 4B and C).

The coarse fraction contains abundant non-chemosymbiotic skeletal components, predominantly benthic molluscs (*Acesta* sp., *Fusitriton oregonensis*, *Sassia remensa*, various protobranchs, gastropods, scaphopods, etc), bryozoans, brachiopods, echinoids, serpulids, scleractinians, large foraminifers (e.g., *Pyrgo*), as well as planktic (pteropods) and pelagic (*Janthina*) molluscs. Infauna collected around these remains revealed a diverse crustacean assemblage including seven species of amphipod (including *Leptamphropus*, *Seba*, Lysianassidae, Oedicerotidae, Phoxocephalidae, Stenothoidae), two Isopods (Munnidae, Gnathiidae), one tanaid (Parataniadae), and one leptostracan (*Nebalia*). Amphipods are common inhabitants of whale falls, particularly Lysianassoidea^{11,39}, many as scavengers/predators (e.g., *Leptamphropus*, *Stenothoe*) or microbial grazers (e.g., *Seba*) attracted to the nutrient-rich environment of the whale fall.

We also identified some shells of chemosymbiotic bivalves^{40–44}, which include at least 1 large solemyid (*Acharax*), 3 species of Thyasiridae, 3 species of Lucinidae, and 2 species of Vesicomidae. Limpet shells are also present, some of which are possibly associated with organic fall habitats (see Refs. 7,44–46). An in-depth taxonomic examination is beyond the scope of the present study but will be undertaken in future assessments by specialists.

Finally, the sediments display an unusual abundance of miliolid foraminifer tests, especially *Pyrgo* spp., a phenomenon observed elsewhere in association with hydrocarbon seeps, such as the Strait of Sicily in the Mediterranean Sea (47 and unpublished data) and the Bay of Bengal in the Indian Ocean, the latter accompanied by anomalous δ^{13} compositions⁴⁸.

4. Discussion

The paleontological record of fossil whale fall communities dates back to the Paleogene and most commonly since the Miocene^{49–53}. It should also be recognised that specialized communities associated with large carcasses decomposing on the seafloor occurred much earlier, when large marine reptiles dominated the Mesozoic oceans^{38,54}. Therefore, organic falls of large aquatic animals have provided an important and widespread energy source, essential for supporting specialized chemosynthetic habitats in the ocean, since Mesozoic times.

Kiel and Goedert⁵⁵ raised an interesting point that early cetaceans, being smaller, contained fewer lipids, the breakdown of which would eventually trigger the chemosynthetic processes essential to these specialized communities. Consequently, those authors proposed that early whale fall communities shared more traits with vent faunas than Miocene–modern whale falls. However, Pyenson and Haas⁵¹ noted that, regardless of the size, the richness in oils in mysticete skeletons was the main controller that forms modern whale fall communities, consistent with our findings in the Hood Canyon.

It has been proposed that, within the general scheme of the evolution and biogeography of vent-type taxa, whale falls could represent “stepping stones” for specialized chemosynthetic and chemosymbiotic organisms like those associated with geologically-older hydrothermal vents and hydrocarbon seeps^{3,56–58}. Kiel^{59,60} lends support to this view, including whale-falls within its biogeographic network, while Smith et al.⁵⁷ deem that whale fall communities are still too poorly described to reach a definitive conclusion. Acknowledging these limitations, our case-study contributes new, albeit preliminary, faunal data and a novel geographic location to this on-going debate.

Besides these evolutionary debates, it has been argued that the human-driven decline of cetaceans during the 19th and 20th centuries would also have had detrimental effects on the populations of associated fauna and their distribution^{61,62}. This theory has not gained general consensus⁶³ but it has attracted attention from the environmental humanities⁶⁴.

It is evident from our case study that isolated carcasses dispersed on the sea floor provide an opportunity for local chemosymbiotic invertebrates to utilise this food source. Bathymodiolinae mussels, the dominant chemosymbiotic metazoan observed on the whale bones in the canyon, are among the most common colonizers of past and present organic fall habitats^{49,65–71}. While many chemosymbiotic taxa (e.g., some bivalves) have developed strategies to enhance their dispersal in the water mass to track these energy sources, and hence are widely distributed^{72–75}, this is not always the case³¹. The latter scenario would thus promote greater endemicity, as observed at some whale fall sites³¹.

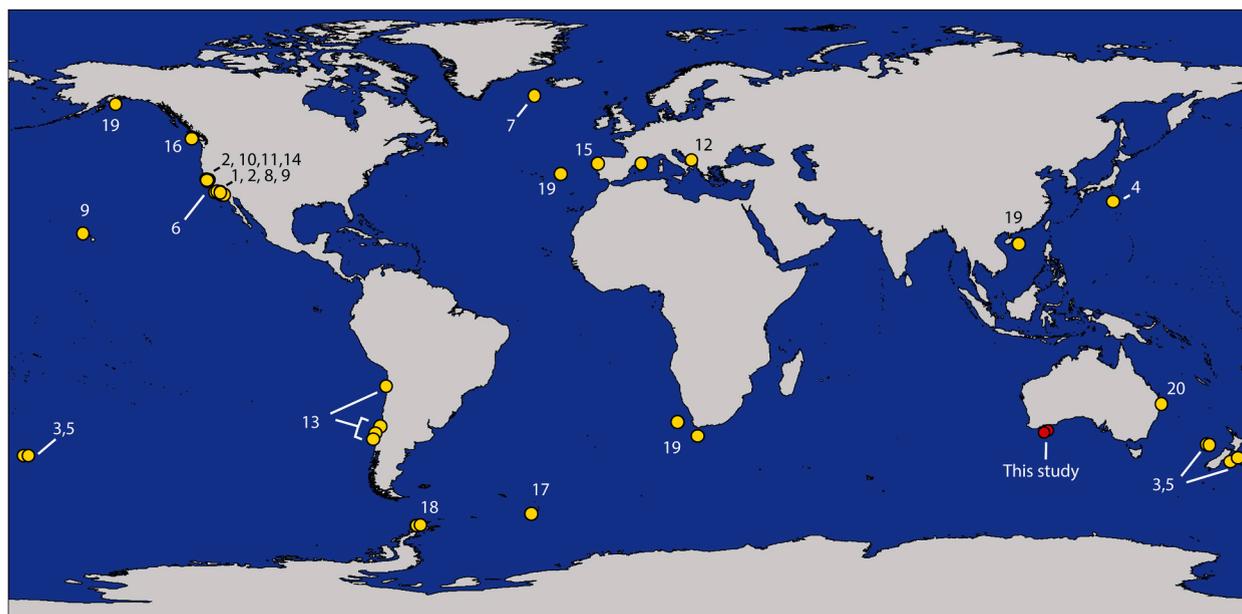


Fig. 5. Map showing natural whale falls with associated chemosynthetic and chemosymbiotic communities recorded in the literature, together with new locations discussed in text (modified from Li et al., 2022). Yellow dots refer to literature records, and red dots to sites described in this study. 1: Smith, 1989; 2: McLean, 1992; 3: Bennett et al., 1994; 4: Dell, 1994; 5: Marshal, 1994; 6: Wada et al., 1994; 7: Warén, 1996; 8: Smith & Baco, 2003; 9: Dahlgren et al., 2004; 10: Goffredi et al., 2004; 11: Rouse et al., 2004; 12: Bolotin et al., 2005; 13: Milessi et al., 2005; 14: Braby et al., 2007; 15: Pelorce & Poutiers, 2009; 16: Lundsten et al., 2010; 17: Amon et al., 2013; 18: Glover et al., 2013; 19: Digitalized from Li et al., 2022; 20: Georgieva et al., 2023. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Ziphiids are mid-sized odontocetes (4.5–10 m) and elusive animals that normally live in deep waters⁷⁶, so their life habits are less well known compared to larger whales and many of the dolphins. While we could not determine the cause of death of the ziphiid discovered in the Hood Canyon, documented causes of ziphiid mortality in southwestern Australian waters have been linked to net entanglements and predation by killer whales^{28,77}. Skeletal remains of beaked whales on the sea bottom are known at some locations, such as offshore South Africa⁷⁸, but are not otherwise commonly reported. Therefore, our samples represent a rare case of ziphiid skeletal remains on the sea floor that have been examined in-situ. The lack of articulated bones, together with their occurrence at the foot of a canyon wall at dive site 315, suggest that the carcass was subject to post-mortem dismemberment and downslope transport.

It is likely that some flesh was present on the *M. layardii* skull when it settled on the sea floor at dive site 315. This is inferred from the high organic enrichment of the sediments in direct contact, or immediately adjacent, to the skull. In fact, this whale fall promoted the development of sulphate-reducing and methanogenic bacterial-archaea consortia, which resulted in chemosynthetic habitats similar to cold seeps^{12,16,79}. These habitats are limited in their areal extent, depending also on the size of the decaying carcass and the type and quantity of lipids⁹, but could exceed the area covered by the whale fall (Bull's eye), and the increase in carbon could be up to 3.5% with respect to adjacent sediments⁸⁰. The “bull's eye” at the ziphiid remains (dive 315) appeared to be almost limited to the sediment beneath the skull. The total diversity of chemosymbiotic bivalves at this site is, however, quite high and is interpreted as representing different stages in carcass consumption and exploitation of the associated reducing sediments over time.

In a biogeographic context, our study helps fill the large distributional gap in known whale fall sites. Li et al.⁸¹ (Fig. 1) recently summarised all available evidence of whale falls at a global scale, including carcasses relocated to deeper water for scientific observations. Their review reveals an absence of data from the Indian Ocean and Southern Ocean Australian waters (Fig. 5), thus the data presented by Trotter et al. [25] and this paper contribute the first datum within this large and underexplored region.

5. Conclusion

We provide the first direct evidence of the occurrence of deep-sea whale fall communities inhabiting the continental margin of southwestern Australia, where high concentrations and a large variety of both seasonally transient and resident odontocete and mysticete cetaceans occur.

Our discovery includes beaked whales, the first documented case of a whale fall community feeding off an elusive member of the odontocete family Ziphiidae. The whale fall community represents a sulfophilic stage of carcass and skeleton consumption, which is comprised of chemosymbiotic bathymodiolineae bivalves (“*Adipicola*” s.l.) and associated skeneimorph gastropods, polychaetes, and amphipods. A single occurrence represents the reef stage.

It is highly probable that many other whale fall communities at varied ecological stages of exploitation by chemosynthetic and chemosymbiotic faunas also occur along the southwestern and western Australian margins, from shelf to abyssal environments. Their

importance to deep-sea ecosystems highlights the need to systematically examine these habitats using advanced marine technologies, such as remotely operated and autonomous underwater vehicles. Within the still scant documentation of deep-sea whale falls in the world's ocean, this study represents the first record for the Indian-Austral Southern Ocean region.

CRediT authorship contribution statement

Marco Taviani: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Paolo Montagna:** Supervision, Investigation, Data curation. **Andrew M. Hosie:** Writing – review & editing, Investigation, Data curation. **Giorgio Castellan:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Catherine Kemper:** Writing – review & editing, Identification of cetacean material. **Federica Foglini:** Investigation, Data curation. **Malcolm McCulloch:** Writing – review & editing, Investigation, Data curation. **Julie Trotter:** Writing – review & editing, Resources, Project administration, Funding acquisition.

Declaration of competing interest

Marco Taviani reports financial support was provided by Institute of Marine Sciences, National Research Council CNR-ISMAR (Italy). Paolo Montagna reports financial support was provided by Institute of Polar Sciences, National Research Council CNR-ISP (Italy). Julie Trotter reports financial support was provided by Australian Research Council and The University of Western Australia. Malcolm McCulloch reports financial support was provided by Australian Research Council and The University of Western Australia. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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