

### 4.3 Implications for deep-sea productivity

By delivering organic matter and stimulating chemosynthetic and heterotrophic microbial processes, whale falls enhance local productivity and support complex food webs in the deep sea (Treude et al., 2009; Smith et al., 2015). The enrichment of carbon, sulfur, nitrogen, and phosphorus at whale-fall sites fosters biodiversity and evolutionary innovation, while also linking surface and deep-sea biogeochemical cycles (Goffredi et al., 2008; Treude et al., 2009; Smith et al., 2015; Sheehy et al., 2022). These processes underscore the importance of whale falls as drivers of ecosystem function and productivity in the deep ocean.

## 5 Specialized Fauna of Whale Falls

### 5.1 Adaptations of deep-sea species to whale fall habitats

Deep-sea species colonizing whale falls have evolved a suite of adaptations to exploit the rich but ephemeral resources provided by decomposing whale carcasses. Notable adaptations include tolerance to high concentrations of sulfide and other toxic compounds, rapid colonization abilities, and specialized feeding strategies. For example, bone-eating worms of the genus *Osedax* possess root-like tissues that penetrate bones to extract nutrients, relying on symbiotic bacteria for digestion (Smith et al., 2015; Shimabukuro et al., 2019; Georgieva et al., 2023). Other annelids, such as dorvilleids and hesionids, display trophic niche partitioning and physiological tolerance to the chemically challenging conditions of whale falls, promoting high species diversity and reducing competition (Shimabukuro et al., 2019; Georgieva et al., 2023). These adaptations enable deep-sea fauna to thrive in the unique, resource-rich microhabitats created by whale falls (Smith et al., 2015; Shimabukuro et al., 2019; Georgieva et al., 2023).

### 5.2 Endemic species and evolutionary implications

Whale falls are hotspots for endemic and newly discovered species. Many taxa found at whale falls, including annelids, mollusks, and crustaceans, are new to science or rarely observed elsewhere (Smith et al., 2015; Sumida et al., 2016; Shimabukuro et al., 2019; Georgieva et al., 2023). The high diversity and endemism, particularly among annelids such as *Osedax* and *Sirsoe*, suggest that whale falls have driven adaptive radiation and speciation (Smith et al., 2015; Shimabukuro et al., 2019; Georgieva et al., 2023). Molecular and paleoecological evidence indicates that whale falls have acted as evolutionary stepping stones, facilitating the dispersal and diversification of chemosynthetic fauna between isolated deep-sea habitats like hydrothermal vents and cold seeps (Smith et al., 2015; Sumida et al., 2016; Shimabukuro et al., 2019). This evolutionary connectivity underscores the importance of whale falls in shaping deep-sea biodiversity patterns (Smith et al., 2015; Sumida et al., 2016; Shimabukuro et al., 2019).

### 5.3 Symbiotic relationships between bacteria and invertebrates

Symbiosis is a defining feature of whale-fall communities. Many invertebrates, such as *Osedax* worms and bathymodiolin mussels, harbor chemosynthetic bacteria that enable them to utilize the organic and inorganic compounds released during whale decomposition (Lorion et al., 2009; Verna et al., 2010; Smith et al., 2015). *Osedax* worms, for instance, rely on endosymbiotic bacteria within their root tissues to digest bone-derived organic matter (Verna et al., 2010; Georgieva et al., 2023). Bathymodiolin mussels found on whale falls also maintain specific associations with thioautotrophic bacteria, which are closely related to those found in vent and seep environments (Lorion et al., 2009). These symbiotic relationships are often horizontally transmitted and display high diversity, allowing hosts to adapt to varying substrates and environmental conditions (Lorion et al., 2009; Verna et al., 2010). Such partnerships are central to the success and ecological roles of specialized whale-fall fauna.

## 6 Human Impacts and Conservation Issues

### 6.1 Effects of whaling and reduced whale populations on whale fall frequency

Historical and industrial whaling have drastically reduced global whale populations, leading to a significant decline in the frequency of whale falls. This reduction diminishes the input of large organic matter to the deep sea, potentially impacting the unique communities and ecosystem functions that depend on these nutrient-rich oases (Ramirez-Llodra et al., 2011). The loss of whale falls may reduce habitat availability for specialized fauna and disrupt deep-sea nutrient cycling.