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Case Study **Open Access**

Whale-Fall Ecosystems in the Deep Sea Ecological Succession, Biodiversity, and Biogeochemical Significance

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Abstract This study systematically analyzes the formation process and ecological succession stages of whale falls, including initial descent, mobile scavenger stage, enrichment opportunist stage, sulfophilic stage, and reef stage, elucidating their roles in maintaining deep-sea biodiversity and nutrient cycling. Key findings highlight that whale falls not only significantly enhance local productivity and species richness but also share ecological and evolutionary links with other deep-sea chemosynthetic environments such as hydrothermal vents and cold seeps, serving as “stepping stones” for species dispersal and adaptive radiation. The crucial functions of whale falls in biogeochemical processes, including carbon sequestration, sulfur cycling, and nitrogen and phosphorus cycling, are also emphasized. However, with the intensification of anthropogenic activities such as whaling, deep-sea mining, bottom trawling, and climate change, the frequency and ecological functions of whale falls are increasingly under threat.

Keywords Whale falls; Deep-sea ecosystems; Biodiversity; Nutrient cycling; Biogeochemistry

1 Introduction

Whale falls, the term for sunken whale carcasses and the ecosystems they create, represent unique and vital habitats in the deep-sea environment. These massive organic inputs deliver concentrated pulses of nutrients to the otherwise food-limited deep ocean, supporting a succession of specialized biological communities and driving significant ecological processes (Smith and Baco, 2003; Smith et al., 2015; Chen and Wang, 2020).

A whale fall is defined as the process and aftermath of a whale carcass descending to the ocean floor, where it forms a localized ecosystem rich in organic matter. These oases provide a substantial energy source for a diverse array of deep-sea organisms, including scavengers, chemosynthetic bacteria, and highly specialized fauna such as bone-eating worms and snails (Smith et al., 2015; Chen and Wang, 2020; Li et al., 2022). Whale falls are considered biodiversity hotspots, supporting thousands of individuals and dozens of species, many of which are new to science or exhibit evolutionary novelties (Smith et al., 2015; Sumida et al., 2016; Chen and Wang, 2020; Li et al., 2022).

The ecological significance of whale falls was first speculated upon in the 19th century, but it was not until the late 20th century that direct observations confirmed their role as unique deep-sea habitats. The discovery in 1989 of a chemoautotrophic community on a whale skeleton in the northeast Pacific marked a turning point, leading to a surge in research and the identification of similar communities in other ocean basins and even in the fossil record dating back 30 million years (Butman et al., 1995; Smith and Baco, 2003; Smith et al., 2015).

Studying whale falls is crucial for understanding deep-sea biodiversity and nutrient cycling. These carcasses act as stepping stones for the dispersal of chemosynthetic organisms, facilitate adaptive radiation, and contribute to the maintenance and connectivity of deep-sea ecosystems (Smith et al., 2015; Sumida et al., 2016; Shimabukuro et al., 2019). The decomposition of whale biomass drives complex successional stages, from scavenger-dominated to chemosynthetic communities, profoundly influencing carbon flux and biogeochemical cycles in the deep ocean (Goffredi et al., 2008; Smith et al., 2015; Chen and Wang, 2020; Amendola et al., 2021; Li et al., 2022).

This study aims to synthesize current knowledge on whale falls, focusing on their ecological roles, successional dynamics, and contributions to deep-sea biodiversity and nutrient cycling. By integrating findings from recent studies, the study seeks to highlight research advances, identify knowledge gaps, and underscore the importance of whale falls as natural laboratories for understanding the functioning and resilience of deep-sea ecosystems.

2 Formation and Stages of a Whale Fall: Succession in Deep-Sea Oases

2.1 Initial fall and physical breakdown

When a whale dies, its carcass sinks rapidly to the ocean floor, often reaching great depths. The descent and initial deposition are influenced by the whale's size, buoyancy, and decomposition gases. Upon arrival, the intact carcass provides a massive, localized input of organic matter to the deep-sea benthos, setting the stage for a series of ecological transformations (Danise et al., 2014; Smith et al., 2014; Bolstad et al., 2023).

2.2 Mobile scavenger stage

The first stage is dominated by large, mobile scavengers such as sharks, hagfish, amphipods, and zoarcid fish. These necrophagous species rapidly consume the soft tissues, often within months to a few years, leaving behind bones and lipid-rich remains. This stage is characterized by intense feeding activity and a sharp increase in local scavenger populations, which can be observed in both modern and fossil whale falls (Danise et al., 2014; Smith et al., 2014; Bolstad et al., 2023; Ibrahim et al., 2024; Serafini et al., 2024).

2.3 Enrichment opportunist stage

As soft tissues are depleted, the whale fall enters the enrichment opportunist stage. Here, the surrounding sediments and exposed bones become colonized by dense populations of opportunistic invertebrates, including polychaete worms (notably Osedax), amphipods, crustaceans, and mollusks. These organisms exploit the remaining organic matter and the enriched sediments, often forming dense assemblages that can persist for months to years (Danise et al., 2014; Smith et al., 2014; Silva et al., 2021; Bolstad et al., 2023; Ibrahim et al., 2024; Serafini et al., 2024).

2.4 Sulfophilic stage

The sulfophilic stage is marked by the anaerobic breakdown of bone lipids, producing hydrogen sulfide. This chemical energy supports chemosynthetic bacteria and a specialized community of symbiotic organisms, such as chemosymbiotic bivalves and sulfur-oxidizing bacteria. The sulfophilic stage can last decades, with the composition and abundance of fauna influenced by the geochemical environment and the amount of remaining organic substrate (Amon et al., 2013; Danise et al., 2014; Onishi et al., 2018; Onishi et al., 2020; Bolstad et al., 2023).

2.5 Reef stage (long-term habitat)

In the final reef stage, after most organic material is exhausted, the remaining bones serve as hard substrate for sessile suspension feeders, including barnacles, bryozoans, corals, and tube-dwelling polychaetes. This stage can persist for years, providing a long-term habitat and contributing to local biodiversity until the bones are buried or fully degraded (Danise et al., 2014; Ibrahim et al., 2024; Serafini et al., 2024).

These stages may overlap, and their duration and community composition can vary with depth, carcass size, and environmental conditions, but together they illustrate the remarkable role of whale falls as dynamic oases in the deep ocean.

3 Ecological Importance of Whale Falls in the Deep Ocean

3.1 Nutrient input in nutrient-poor deep-sea environments

Whale carcasses deliver massive pulses of labile organic matter to the deep-sea floor, a region typically starved of nutrients. This input sustains a succession of scavengers, opportunists, and chemosynthetic organisms, increasing local biomass and altering community structure for years or even decades (Butman et al., 1995; Smith and Baco, 2003; Hilário et al., 2015; Dasgupta et al., 2024). Even smaller mammal falls, such as cow or dolphin carcasses, enrich the seafloor and support diverse assemblages, though their impact is less extensive than that of whale falls

(Hilário et al., 2015; Dasgupta et al., 2024). The organic enrichment from whale falls is a key driver of productivity in otherwise food-limited deep-sea environments (Butman et al., 1995; Smith and Baco, 2003; Dasgupta et al., 2024).

3.2 Enhancement of local biodiversity and creation of ecological hotspots

Whale falls act as biodiversity hotspots, supporting unique assemblages of macrofauna, including generalist scavengers, chemosynthetic fauna, and bone-specialist species. Many species found at whale falls are new to science or rarely observed elsewhere, and the presence of ecosystem engineers like Osedax worms increases habitat complexity and microhabitat diversity (Lucas, 2015; Shimabukuro et al., 2019; Shimabukuro et al., 2022). Studies show that whale-fall communities are distinct from those in surrounding sediments, with higher species richness and evolutionary novelty (Danise et al., 2014; Hilário et al., 2015; Lucas, 2015; Shimabukuro et al., 2019; Shimabukuro et al., 2022). These communities can persist for years, and some taxa exhibit interbasin distributions, highlighting the global significance of whale falls for deep-sea biodiversity (Shimabukuro et al., 2019; Shimabukuro et al., 2022).

3.3 Connection with other chemosynthetic environments

Whale falls share ecological and evolutionary links with other deep-sea chemosynthetic environments, such as hydrothermal vents and cold seeps. Many whale-fall specialists, including chemosymbiotic bivalves and polychaetes, are closely related to or shared with vent and seep communities (Levin et al., 2007; Bernardino et al., 2012; Duperron et al., 2013; Shimabukuro et al., 2019; Avila et al., 2023). Whale falls may serve as “stepping stones” for the dispersal of chemosynthetic fauna, facilitating gene flow and connectivity among spatially isolated habitats (Bernardino et al., 2012; Hilário et al., 2015; Shimabukuro et al., 2019; Avila et al., 2023). The similarity in community structure and reliance on chemosynthetic production underscores the role of whale falls in the broader network of deep-sea reducing ecosystems (Levin et al., 2007; Bernardino et al., 2012; Duperron et al., 2013; Avila et al., 2023).

Whale falls thus represent essential oases in the deep ocean, driving nutrient cycling, supporting high biodiversity, and connecting the patchwork of chemosynthetic habitats across the seafloor.

4 Whale Falls and Biogeochemical Cycles in the Deep Ocean

4.1 Role in carbon sequestration

Whale falls represent a significant mechanism for transferring organic carbon from the surface to the deep ocean. When a whale carcass sinks, it delivers a concentrated pulse of organic carbon to the seafloor. A single large whale can provide an input of organic carbon equivalent to thousands of years of background sedimentation rates (Sheehy et al., 2022). While soft tissues are typically recycled into the food web within about two years, the bones—especially when deposited at depths greater than 1000 meters—can persist for over a century, effectively sequestering carbon and removing it from atmospheric exchange. Restoration of cetacean populations could thus enhance carbon sequestration through increased whale-fall events, contributing to climate change mitigation (Sheehy et al., 2022).

4.2 Influence on sulfur, nitrogen, and phosphorus cycles

Whale falls create localized zones of intense microbial activity, particularly sulfate reduction and methanogenesis, which drive the sulfur cycle in deep-sea sediments (Goffredi et al., 2008; Treude et al., 2009). Sulfate-reducing bacteria break down organic matter, producing hydrogen sulfide that supports chemosynthetic communities similar to those at hydrothermal vents and cold seeps (Treude et al., 2009). Methanogenic archaea also thrive, establishing active methane cycles beneath whale falls (Goffredi et al., 2008). Additionally, cetaceans contribute to nitrogen and phosphorus cycling through the "whale pump"—the vertical and horizontal transport of nutrients via feeding and excretion—which enhances nutrient availability for phytoplankton and supports primary productivity in nutrient-limited waters (Sheehy et al., 2022). This nutrient cycling is crucial for sustaining deep-sea and surface productivity, with estimates suggesting that cetacean-driven processes recycle substantial amounts of nitrogen annually (Sheehy et al., 2022).

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.

6.2 Potential consequences for deep-sea ecosystems

The decline in whale falls can lead to decreased biodiversity and loss of ecosystem services in the deep sea. Whale falls support unique assemblages and contribute to nutrient cycling, so their reduction may have cascading effects on deep-sea food webs and biogeochemical processes (Ramirez-Llodra et al., 2011; Armstrong et al., 2019). Additionally, the deep sea is already facing multiple anthropogenic pressures, including pollution, overfishing, and oil and gas extraction, which further threaten its biodiversity and resilience (Glover and Smith, 2003; Armstrong et al., 2019).

6.3 Deep-sea mining, trawling, and climate change threats

Emerging threats such as deep-sea mining and bottom trawling pose significant risks to deep-sea habitats. Mining activities can cause long-lasting and potentially irreversible damage through habitat destruction, sediment plumes, and pollution, directly impacting both whale falls and the broader deep-sea environment (Levin et al., 2020; Smith et al., 2020; Thompson et al., 2023). Bottom trawling disrupts sedimentary habitats and can reduce carbon sequestration capacity (Levin et al., 2020). Climate change compounds these threats by increasing ocean temperatures, acidification, and hypoxia, which can alter deep-sea community structure and reduce the resilience of ecosystems to other stressors (Ramirez-Llodra et al., 2011; Armstrong et al., 2019; Levin et al., 2020). The cumulative and synergistic effects of these activities are likely to intensify the vulnerability of deep-sea ecosystems, making effective management and conservation strategies increasingly urgent (Ramirez-Llodra et al., 2011; Armstrong et al., 2019; Levin et al., 2020; Smith et al., 2020).

The combined pressures of exploitation, pollution, and climate change highlight the urgent need for comprehensive conservation and management of deep-sea environments, including the protection of whale fall habitats.

7 Case Study: The Monterey Canyon Whale Fall

7.1 Background – discovery and placement of a gray whale carcass

In 2002, a well-preserved gray whale carcass, approximately 9-10 meters long and weighing about 20,000 kg, was discovered at a depth of 2891 meters in Monterey Canyon, California. This site, along with several experimentally implanted carcasses at varying depths, enabled researchers to systematically study whale-fall community development and ecological processes in the deep sea (Goffredi et al., 2004; Lundsten et al., 2010).

7.2 Observations – successional stages documented over several years

Long-term monitoring using remotely operated vehicles (ROVs) revealed that whale-fall communities in Monterey Canyon progress through distinct successional stages. Initial colonization by mobile scavengers (e.g., hagfish, amphipods) was followed by enrichment opportunists and, over time, the establishment of chemosynthetic and bone-specialist fauna. The rate and nature of succession were influenced by depth and environmental conditions, with carcass degradation occurring over sub-decadal timescales (Goffredi et al., 2004; Braby et al., 2007; Lundsten et al., 2010; McGann and Lundsten, 2019).

7.3 Key findings – new species discovery, microbial activity patterns, and food web complexity

The Monterey Canyon whale fall led to the discovery of several new species, including novel polychaetes such as Osedax bone-eating worms, with at least four new species described from the site (Goffredi et al., 2004; Braby et al., 2007). Microbial studies revealed a dynamic succession of methanogenic and sulfate-reducing archaea and bacteria, with methane cycling and elevated carbon concentrations extending up to 10 meters from the carcass (Goffredi et al., 2008; Hasegawa, 2009). The food web was found to be highly complex, involving background deep-sea taxa, opportunists, and chemosynthetic specialists, with Osedax worms acting as foundation species that regulate bone degradation and community succession (Goffredi et al., 2004; Braby et al., 2007; Goffredi et al., 2008; Lundsten et al., 2010).

7.4 Ecological insights – comparisons with other deep-sea chemosynthetic habitats

The Monterey Canyon whale fall shares key features with other chemosynthetic environments, such as hydrothermal vents and cold seeps, including the presence of chemosymbiotic invertebrates and similar microbial processes (e.g., sulfide and methane production) (Feldman et al., 1998; Braby et al., 2007; Goffredi et al., 2008; Smith et al., 2015). However, the majority of species at Monterey whale falls are background deep-sea taxa, with bone and seep specialists contributing less to overall richness than in some other regions (Lundsten et al., 2010; Smith et al., 2015). The site provides evidence that whale falls can serve as evolutionary stepping stones for vent and seep fauna, supporting the hypothesis of faunal connectivity among deep-sea chemosynthetic habitats (Feldman et al., 1998; Braby et al., 2007; Smith et al., 2015).

The Monterey Canyon whale fall case study highlights the ecological richness, successional dynamics, and evolutionary significance of whale falls as deep-sea oases and their role in connecting chemosynthetic ecosystems.

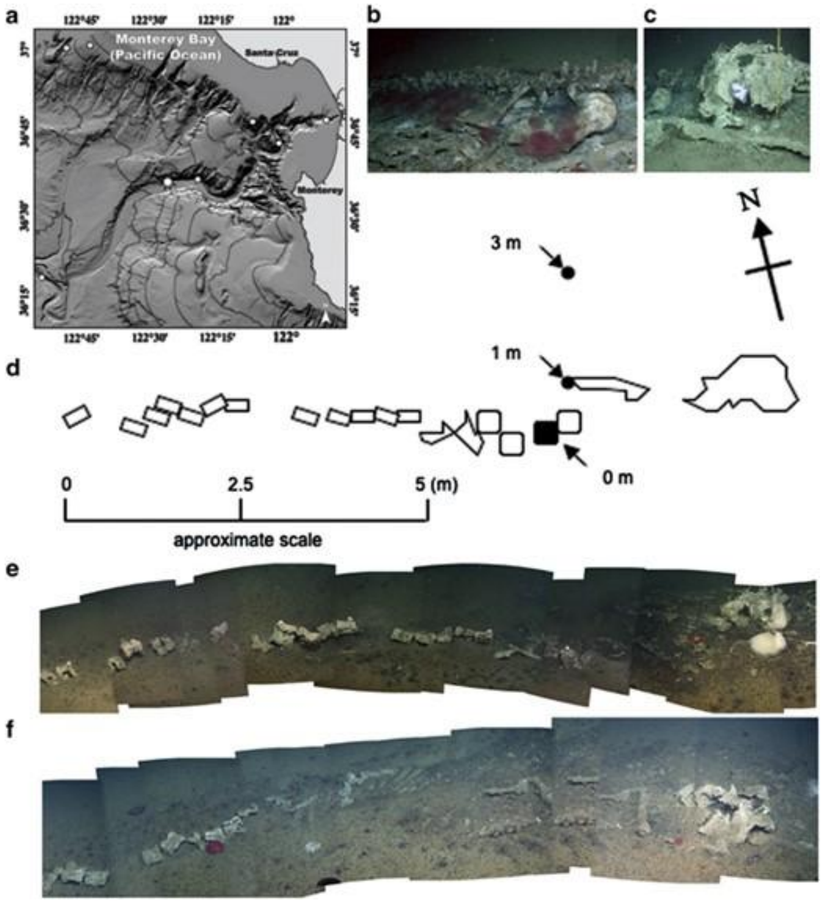

Figure 1(a) Shaded relief map of the continental margin off Monterey Bay showing the whale-fall location at 2891 m depth (large white star). Modified from Goffredi et al., 2004. (b, c, e, f) Photo mosaics of digital still images. (d) Schematic of the whale skeleton at 2893 m showing areas of sediment collections and sampling strategy. (b, c) At 33 months (dive no. T769, November 2004), (e) 45 months (dive no. T917, November 2005) and (f) 51 months (dive no. T991, May 2006) (Adopted from Goffredi et al., 2008)

8 Future Directions in Whale Fall Research

8.1 Gaps in current knowledge

Major gaps remain in the detailed understanding of microbial succession at whale falls. While the broad stages of faunal succession are established, the temporal and spatial dynamics of microbial communities—especially the interplay between sulfate-reducing, methanogenic, and sulfur-oxidizing microbes—are still poorly characterized, partly due to technical challenges in deep-sea sampling and monitoring (Smith et al., 2015; Moriya et al., 2016; Amendola et al., 2021). Additionally, the connectivity between whale falls and other chemosynthetic habitats (e.g., vents, seeps) is not fully resolved. While molecular and faunal evidence suggests whale falls act as evolutionary stepping stones and dispersal corridors for specialized taxa, the extent and mechanisms of this connectivity, particularly for meiofauna and microbes, require further study (Smith et al., 2014; Smith et al., 2015; Avila et al., 2023).

8.2 The role of artificial whale falls in research

Artificial whale falls - experimentally deployed carcasses or large mammal analogs—have become invaluable for studying ecological succession, microbial processes, and faunal colonization in controlled settings (Hilário et al., 2015; Moriya et al., 2016; Aguzzi et al., 2018; Silva et al., 2021). These experiments allow for high-frequency, long-term monitoring and manipulation, helping to overcome the rarity and unpredictability of natural whale falls. Artificial deployments have revealed new species, documented behavioral rhythms, and provided insights into the dispersal and adaptation of deep-sea organisms (Hilário et al., 2015; Aguzzi et al., 2018; Silva et al., 2021). Cow carcasses and whale bones in aquaria or shallow waters have also served as accessible models for testing hypotheses about community assembly and environmental influences (Hilário et al., 2015; Moriya et al., 2016).

8.3 Predicting whale fall distribution with whale migration data

Integrating whale migration and population data with oceanographic models offers a promising avenue for predicting the spatial and temporal distribution of whale falls. Such predictive frameworks could improve estimates of whale fall frequency, guide targeted exploration, and inform conservation strategies by identifying potential biodiversity hotspots and connectivity corridors (Smith et al., 2015). This approach is especially relevant as whale populations recover or shift in response to climate change and human impacts, potentially altering the distribution and ecological role of whale falls in the deep sea (Smith et al., 2015).

Addressing these gaps will deepen understanding of whale falls as dynamic, interconnected oases and their broader significance in deep-sea ecology and evolution.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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