Life After Death:
A Characterization of Changing Whale-fall Communities

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Introduction

A whale carcass or "whale-fall" arriving at the sea floor provides a massive influx of energy to an otherwise food-limited environment. A 40-ton carcass may hold 2000 to 3000 kg of lipids in its skeleton alone, and represent 100 to 200 times the typical levels of organic carbon sinking annually to a hectare of seafloor.[1,2] Dynamic communities of benthic invertebrates and vertebrates harvest this energy. Some studies suggest that whale carcasses linger on the seafloor for decades, or even centuries[1,2], while others report much shorter decomposition times[7]. Whale-falls are also hypothesized to serve as "stepping stones" for the dispersal of vent and seep-dwelling organisms, bridging gaps between seep and vent habitats.[5,6] Other studies suggest the existence of "whale-fall specialists" that are specifically adapted to conditions at whale carcasses.[3,7]

These contradictory findings suggest high variation among whale-fall communities in terms of structure and development[4]. We hypothesize that the variation between studies is driven by differences in temperature, oxygenation, and sedimentation. This study characterizes community succession at several whale-fall sites that span a range of depths and physical conditions in the Monterey Bay and provide a unique opportunity to understand the factors influencing whale-fall communities.

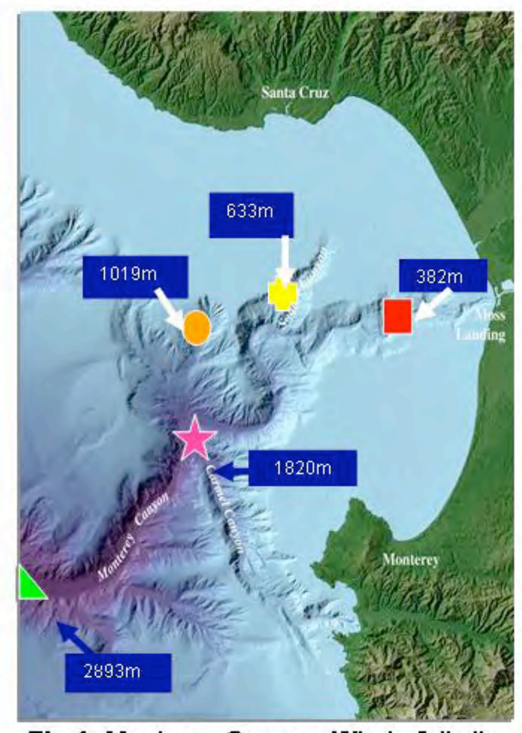


Fig 1. Monterey Canyon: Whale-fall site locations identified by depth.

Table 1. Whale-fall characteristics by site, adapted from Braby et al. (2007)

Whale Site	Whale 382p	Whale 382a	Whale 633	Whale 1019	Whale 1820	Whale 2893
Depth (m)	382	382	633	1019	1820	2893
Implanted/Natural	Implanted	Implanted	Implanted	Implanted	Implanted	Natural
Carcass Length (m)	6	8	10	17	10	10
Whale Species	Gray	Gray	Gray	Blue	Gray	Gray
Avg. Salinity (ppm)	34.05	34.18	34.24	34.44	34.42	34.53
Avg. Temperature (°C)	7.15	7.11	5.52	3.86	2.30	1.67
Avg. [O_2]	0.992	0.951	0.568	0.476	1.423	2.426
Deployment Date	7 Feb., 2007	10 April, 2005	11 April, 2007	5 Oct., 2005	20 March, 2006	Unknown
First monitored	4 June 2007	5 May 2005	17 Aug., 2007	10 Dec., 2004	23 May 2006	6 Feb., 2002
Number of visits	4	3	4	15	5	14
Total number of species observed*	24	47	50	58	48	81
Months at Bottom	10	13	27	39	21	~70

* Underestimates species richness, because some identifications are not to species level.

Materials and Methods

Study Sites

One natural and five implanted whale-falls form the basis of this study (Fig. 1). Whales were implanted by towing stranded carcasses out to sea using the R/V *Zephyr*, sinking them with iron train wheels.

All sites are located within the Monterey Canyon (Fig.1), however they span a wide range of physical, environmental conditions (Table 1.):
- Depths range from 382 m to 2893 m,
- Sites span the oxygen minimum zone,
- Environmental factors vary between sites (currents, sedimentation, whale-fall layout).
(Note: "Samples" are defined as biological communities at different whales at different time periods).

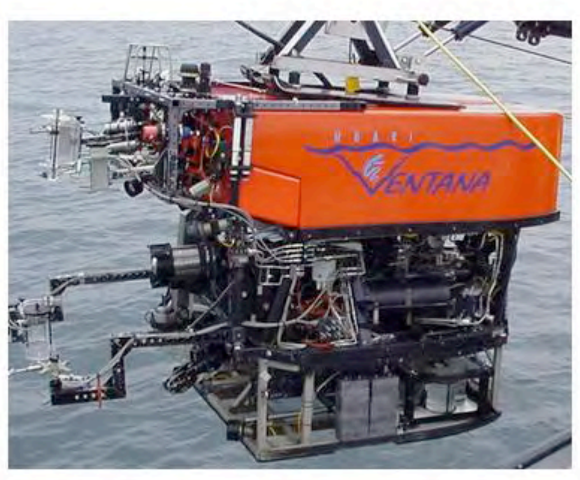


Fig 2. Remotely operated vehicle *Ventana* used to monitor whalefall sites

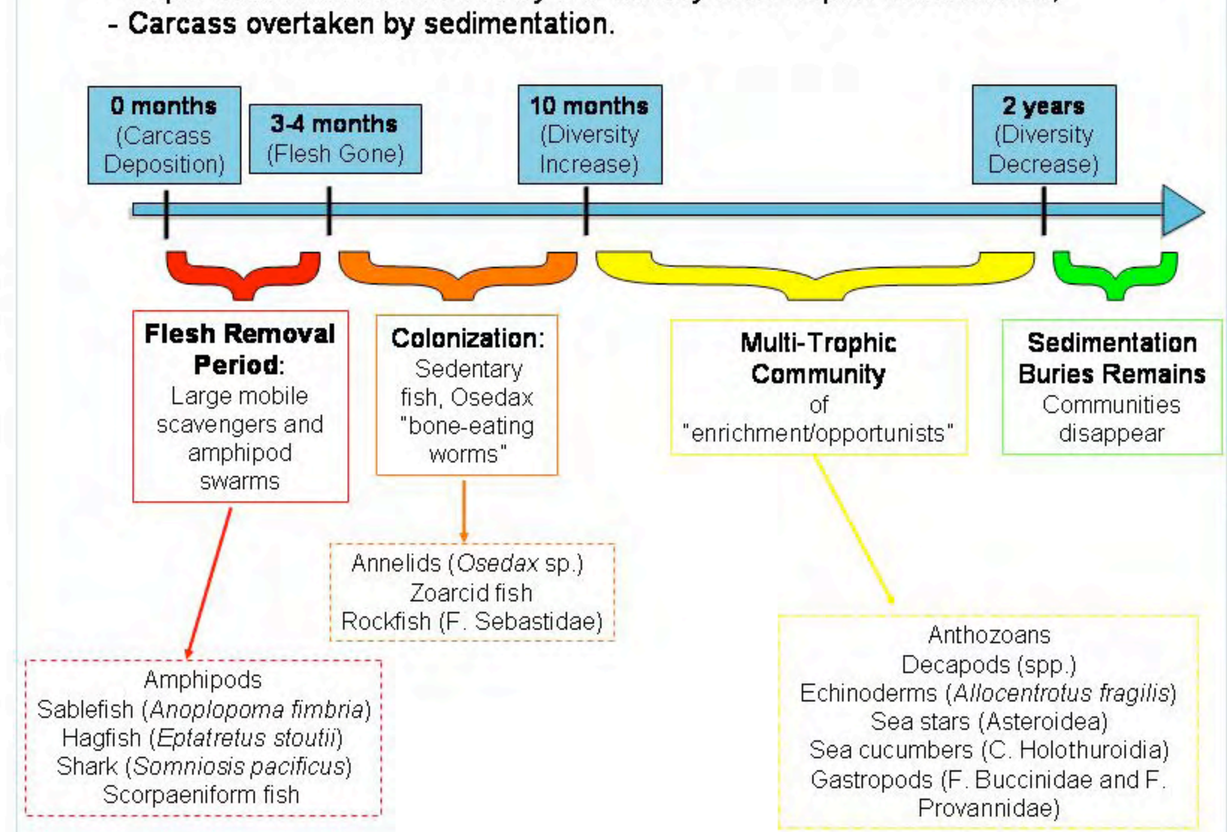
Data Collection

Sites were (and continue to be) monitored using MBARI's remotely operated vehicles, R.O.V *Tiburon* and R.O.V. *Ventana* (Fig. 2). Standard definition video footage, and physical conditions (depth, temperature, oxygen concentration, and salinity) are recorded throughout each dive.

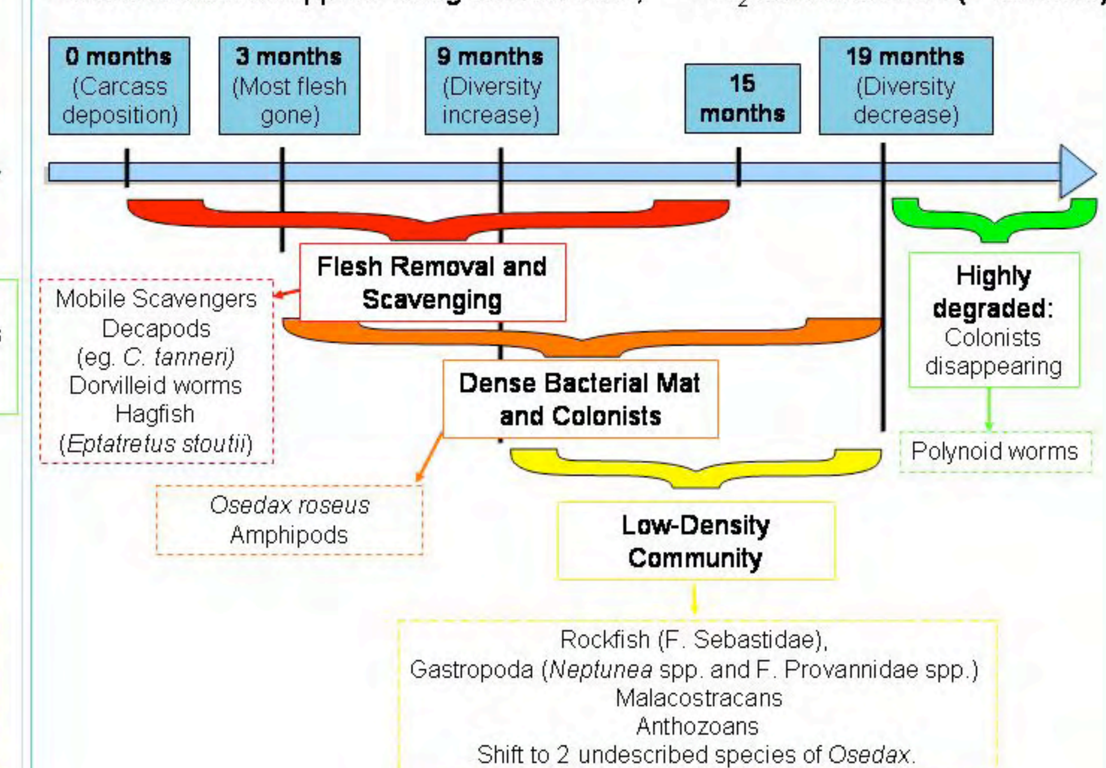
This study incorporates 175 hours of video footage from 45 dives. All footage was visually reviewed twice. MBARI Video Lab specialists cataloged major features in a preliminary review of the dive footage. A secondary analysis refined organism identifications and relative abundances. Organisms were identified to the lowest taxonomic category possible. Some organisms observed are currently undescribed.

Community Characterizations

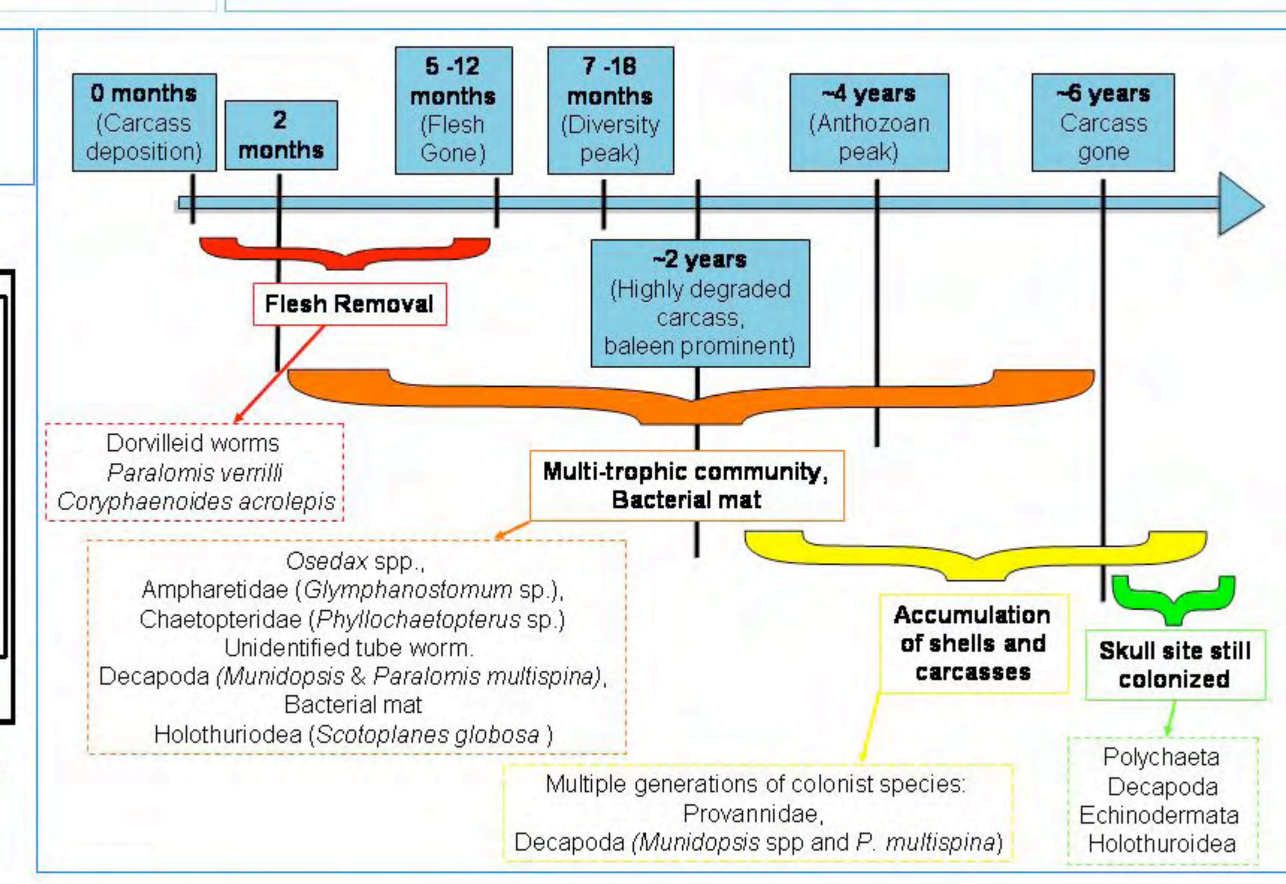
Shallow Sites (382 and 630 m):
- Rapid flesh removal followed by low-density multi-trophic communities,
- Carcass overtaken by sedimentation.



Intermediate Depth (1019 m):
- Low-density, high-turnover communities,
- Communities disappear along with carcass,
- Overlapping phases,
- O_2 minimum zone (< 0.5 ml/L)[8]



Deep Sites (1820 and 2893 m):
- Slow flesh consumption,
- Consistent community structure,
- Colonization outlasting carcass.



Results

Physical Characteristics

Across the range of depths studied, physical characteristics followed general trends (Fig. 3):
- Oxygen concentration decreased with increasing depth, reaching a minimum near 1000 m, and subsequently increased with increasing depth.
- Temperature decreased with increasing depth.
- Salinity increased slightly with increasing depth.

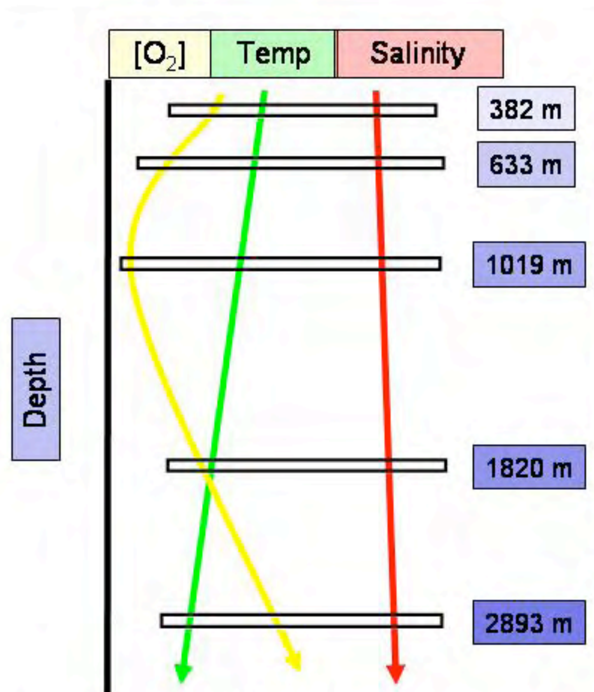


Figure 3. General trends in physical conditions over the range of depths.

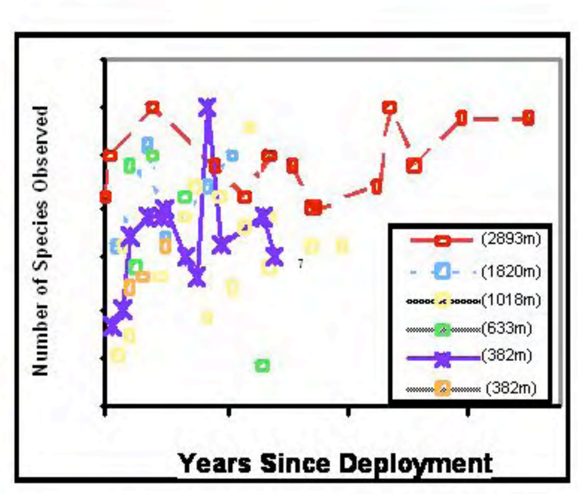


Figure 5. Community richness to nearest known taxon relative to months since deployment, at each whale.

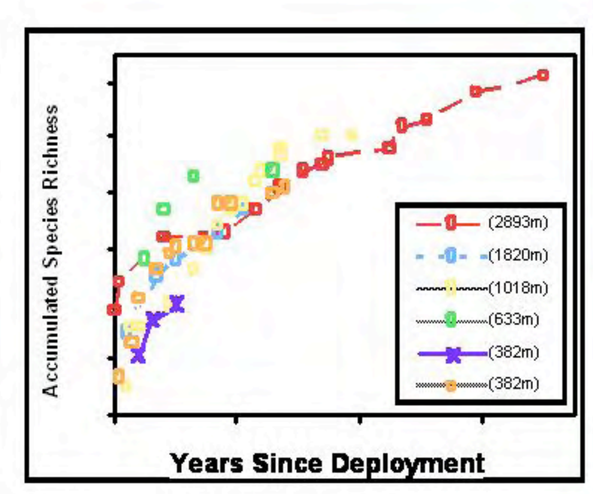


Figure 6. Species accumulation relative to years since deployment at each whale.

Statistical Analysis

An MDS plot reflecting biological community structure at various whales over time, based on Bray-Curtis similarities using presence/absence data, produces groupings (2D stress value: 0.19, Fig. 4.) which indicate that depth is an important factor.

The three shallower sites are pooled, showing high resemblance. Early dives (circled in yellow) for whale 382a lie apart, likely due to the very early visits at this site.

Species richness (Fig. 5) and accumulation (Fig. 6) were quantified relative to time since carcass deployment. Organisms which had not been observed initially, appeared at later visits.

PCA analysis illustrates the relationship between samples and the environmental factors recorded (Fig. 7). Axis "PC1". most closely tied to temperature and depth, accounts for 79.3% of the variation among samples. An additional 16.1% is accounted for on axis "PC2", roughly tied to O2 concentration.

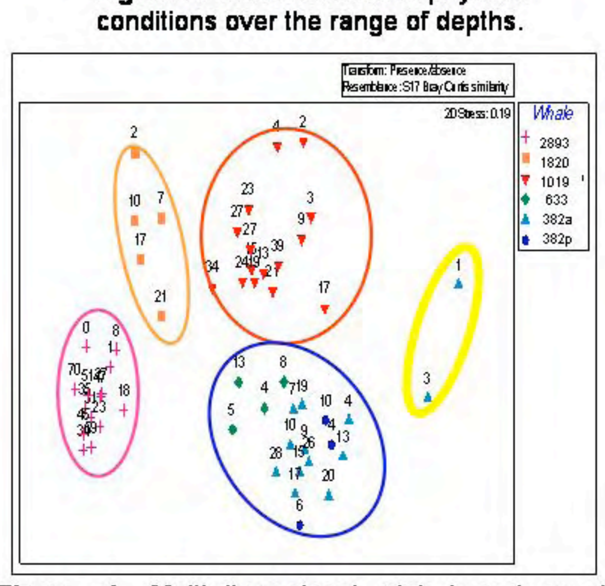


Figure 4. Multi-dimensional plot based on the presence/absence of species over time using a Bray-Curtis similarity index. Dives are identified by whale (symbols) and months post-deployment (numbers). Multi-site clustering occurred in for the shallow sites, which resemble each other more closely to each other than to the deep sites.

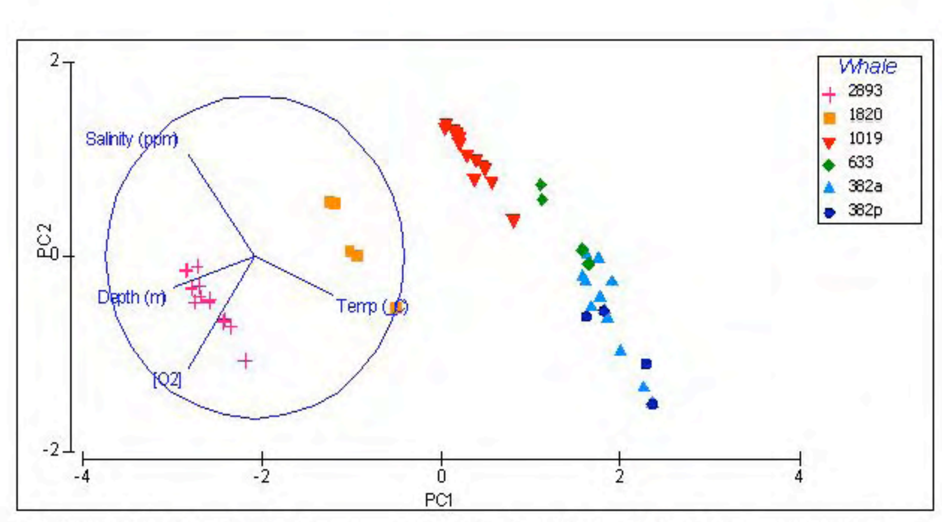


Figure 7. Principal Component Analysis (PCA) relating four measured environmental factors on samples collected at each site. Axis PC1 correlates most strongly with depth and temperature.

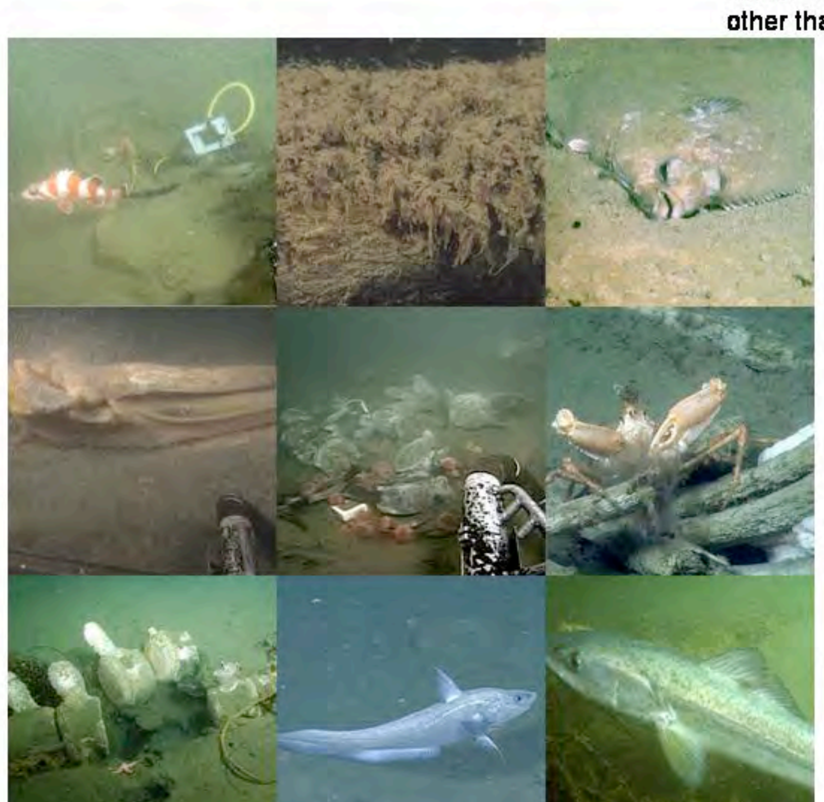


Fig 8. Shallow Site Composition (From left to right)
Top: Rockfish (F. Sebastidae); ***Osedax*** **sp.**; flatfish ***Microstomus pacificus***;
Center: Cloud of Amphipods feeding on skull; urchins ***Allocentrotus fragilis***; crab ***Chorilia longipes*** feeding;
Bottom: Whale vertebra and sea star; rattail fish ***Coryphaenoides*** sp.; sablefish ***Anoplopoma fimbria***.

Fig 9. Intermediate Site Composition (From left to right)
Top: Whale carcass at 3 months; crabs ***Chionoecetes tanneri***; eelpout ***Lycenchelys sp.***;
Center: Bacterial mat; flatfish ***M. pacificus*** and ***O. roseus***; seastar Asteroidea;
Bottom: Hagfish ***E. stoutii*** feeding on flesh; Fin, partially decayed; Osedax worms

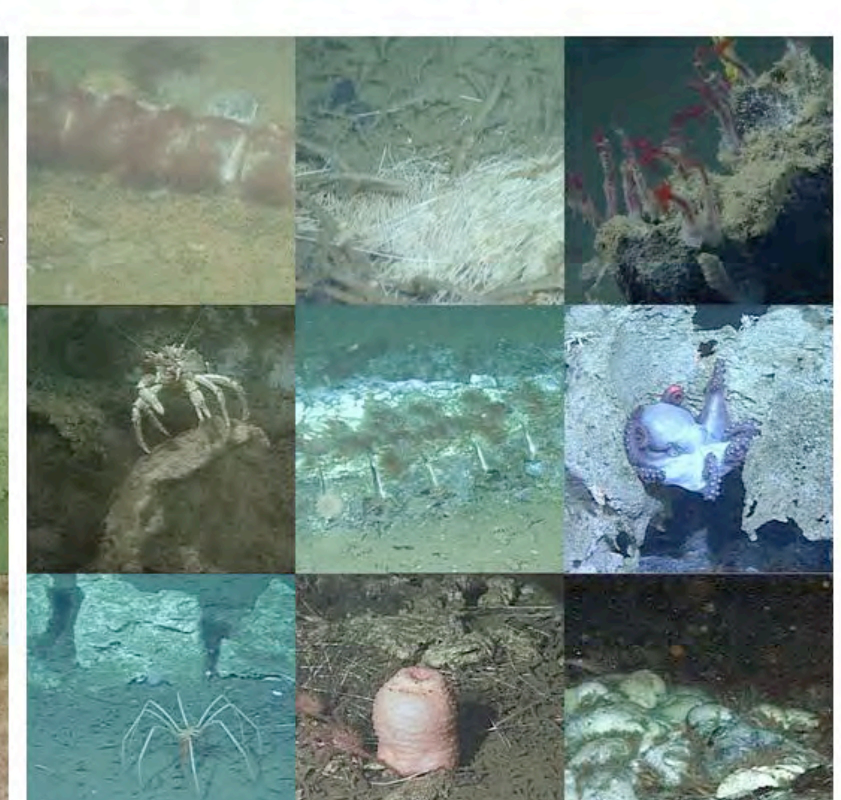


Fig 10. Deep Site Composition (From left to right)
Top: Thick ***Osedax*** mats ("Bone-eating" worms); Baleen with snails (gastropods); ***Osedax*** sp.;
Center: squat lobster ***Munidopsis*** sp.; Bacterial mat; flatfish ***M. pacificus*** and ***O. roseus***; octopus ***Benthoctopus*** sp.;
Bottom: sea spider (Pycnogonid); anemone; Whale intestines.

Discussion

The present study presents one of the broadest spectrum and longest-term data sets exploring whale-fall community development available. Based on this data, whale-fall communities:

1) Become established shortly after carcass deposition, and change composition significantly through multiple years of slow but steady whale-fall degradation.
2) Differ in composition and development over the range of physical conditions studied.
3) Resemble each other most closely at similar depths.
4) Increase in species richness with depth.

At sites 630 m and above, community composition is heavily influenced by temperature, and begins with a scavenger stage of eels, amphipods, and highly mobile scavenging fish. Flesh consumption was swift and complete, leaving bare bones within 4 months of deployment. A multi-trophic community of mainly "enrichment/opportunist" organisms followed[1]. When sulphophilic bacterial were present, they co-occurred with these enrichment/opportunists. Shallower sites experienced high sedimentation, causing the bones to become buried and inaccessible for colonization.

The site situated in the O_2 minimum zone at 1000 m differed from shallower and deeper sites. Flesh consumption was slower than at shallower sites, and a sulphophilic stage was more apparent in the form of a thick bacterial mat. Stages overlapped, and species showed high turnover (inconsistent presence) and low densities. The bones will soon be completely gone. At these sites it appears that the sulphophilic and scavenging stages may outlast the carcass. Any reduction in species diversity linked to limited oxygen was ambiguous.

Below ~2000 m, the rate of flesh removal seemed to slow with increasing depth, and the deepest whale-fall displayed the largest number of site-specific taxa. The longest lasting feature was the head, although all bones were densely colonized. Flesh consumption was accomplished by crabs and worms. Based on the rate of degradation of this carcass, an eventual reef stage of suspension and filter feeders (suggested by Smith and Baco[1]) seems unlikely. The bones will soon be completely gone, while sulphophilic and scavenging stages are outlasting the carcass.

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