Using the Succession Rates of Deep-water Zombie Worms (*Osedax Sp.)* to Determine Post Whale-Fall Intervals

Introduction

Since their 2002 discovery on a 2893m, bathymetric whale fall in the Monterey Submarine Canyon, California, Zombie worms (*Osedax sp.)* have garnished plenty of research. While whale fall can provide a nutrient rich, organic resource in deep-sea, oligotrophic environments, it is difficult to determine the length of time the whale has been on the sea floor, hence the need for determining a post whale fall interval (PWFI).

Whale fall can attract a diverse and abundant succession of organisms that can consume and inhabit the whale fall from a few months to decades. These faunal assemblages arrive to exploit the new food source in successional stages that are predictable, based on the lifestyle requirements of the organism (Alfaro-Lucas et al., 2017). The whale fall is consumed by groups of feeding generalists and specialists. While the flesh of the whale is eaten by mobile scavengers (generalists), such as the Hagfish (family Myxinidae) and Sleeper sharks (family Somniosidae), the bones of the whale are consumed by specialists, like the bone-eating Zombie worm (*Osedax sp.*) (Amon et al., 2013; Lundsten et al., 2010; Smith et al., 2014). *Osedax*, a sessile polychaete worm, have a rapid dispersal and colonization tactic. While it was first considered a whale only specialist, research by Jones et al., (2008) and Rouse et al., (2018), discovered that Osedax will colonize a wide variety of vertebrate bones. Research by Braby et al., (2007), has revealed that they can infiltrate a new set of bones in as little as two months. Due to their interesting biology, *Osedax* have received much scientific interest. They have been recovered from bathymetric ranges of 30 meters (m) to over 3000m, in almost every ocean worldwide (Braby et al., 2007; Grover et al., 2003).

Osedax is a genus of marine worms that have the ability to exploit the nutritional content of bones via ramifying root structures (Figure 2. B). They are of the phylum annelid, but lack the segmentation. They reside in the class Polychaeta, order Sabellida, and family Siboglinidae. To date, under the genus of *Osedax*, there are 34 described species (Rouse et al., 2018). Each different species has a specific size, shape, and bore depth (Alfaro-Lucas et al., 2017). All female *Osedax* species contain heterotrophic bacteria (Oceanospirillales), in their root systems (Miyamoto et al., 2013; Rouse et al., 2004). The *Osedax* root epithelium is capable of absorbing the whalebone collagen and lipids, via their heterotrophic bacteria, which metabolize the compounds and provide nutrients to the *Osedax* (Rouse et al., 2004; Smith et al., 2003). *Osedax* roots have the ability to secrete acid by a derived calcium hydration of CO_2 created by aerobic metabolism. The catalyzed hydration is strong enough to dissolve the hydroxyapatite lattice of the bone's matrix, and make the nutrients within accessible (Weigel, 2015). The *Osedax* use their feathery palps (plumes) for absorbing dissolved oxygen, which is indicative of aerobic metabolism (Figure 2.A, B). From the species currently described, the male *Osedax* are paedomorphic and live in the tube sheath of the females (Figure 2. D) (Rouse et al., 2004; Rouse et al., 2008).

The aim of this paper is to review current published research on the *Osedax* genus in general, and determine if the PWFI of deep-water (>1000 meters [m]) whale fall can be calculated by using the succession rates of Zombie worm settlement. The emphasis of research will be on the data publications related to the Monterey Submarine Bay, CA whale falls. This is due to the volume of research from initial discovery in 2002, to a newly released publication in February 2018, heralding the most described *Osedax* species recovered from one area. Research in Monterey Bay entailed studying six whale falls, one natural and five implanted at various depths. This review looks at the Osedax succession on the deep-water whale fall at 1018m (2004 deployment), 1820m (2006 deployment), and 2893m (approximately 2001). Determining the PWFI is important for a couple of reasons. *Osedax* may be the linchpin engineer to a more diverse sea floor. The more we know about what drives deep-sea diversity, the better equipped we are to address human impacts that can alter, stunt or cause trophic failures in a realm we have barely begun to understand.

Methods

Since the 1987 whale fall, a 20m baleen whale in the Santa Catalina Basin was discovered by oceanographer Dr. Craig R. Smith, and the subsequent discovery of the *Osedax* in 2002, research on successional faunal assembles has produced abundant amounts of data. With the review of published research, an effort to discern the role of *Osedax* in establishing a PWFI (time the whale set down on the sea floor), was made. Published works reviewed covered topics that are pertinent to a PWFI, such as; whale taphonomy in the deep-sea, whale fall faunal assemblage successions, *Osedax* reproduction and succession, and environmental factors that can affect the PWFI calculations. Data on *Osedax* clades will also be touched on, in an effort to understanding the relationship, if any, between *Osedax* clades and their potential taphonomy and depth preferences.

Results

Whale taphonomy. The degree of skeletal disarticulation can vary greatly from the size of the whale to the different water bodies and depth. In some instances, the gas filled whale carcass will disarticulate at the surface and then bones with some flesh, sink to the sea floor. Other times, the whole whale is on the sea floor. It is proposed that the increase in hydrostatic pressure at depth is responsible for keeping the whale from floating up as it fills with decomposition gasses (Allison et al., 1991). *Osedax* settlement has a direct impact on the taphonomy of whale fall. Bones that have *Osedax* infiltration show a rapid degradation where as bones with sparse *Osedax* aggregations displayed a much slower break down (Braby et al., 2007; Smith et al., 2003). Amon et al., 2013 reports that bones with higher lipid densities have a wider range of faunal diversity. Research on clade relationships using Rouse et al's 2018 research did not reveal a strong association for any clade to have an affinity for a particular taphonomy stage. There seemed to be a slight correlation between the researched *Osedax* in clade I (*O. sigridae,* and *O. talkovici*) (Figure 1), for a succession arrival between 1 and 1.5 years (yr) (Table 4.). With only two species addressed, this may be more of a coincidence than a trend. There may also be a correlation between clades and their preferred depth ranges.

Affects on Succession Rate. It appears that some *Osedax* species have a preferred stage of whale taphonomy for settlement. *O. rubiplumus* and *O. frankpressi*, prefer freshly exposed bone, while *O. jabba* has the physiology to exploit buried bone. *Osedax* infestation can also vary by whalebone type. *Osedax. crouchi*, *O. nordenskjoeldi* and *O. rogersi* have shown a preference for bones with higher densities of lipids, such as the jaw bones and vertebrae from the thorax. The heavy, lipid filled bones of the vertebrae and caudal bones are the bones that show the most colonization. However, there are some species, such as *O.rubiplumus*, that will colonize any open bone, even a low lipid bone such as a rib, which the scavenger assemblage has exposed.

There seems to be a loose affinity for species in a particular clade to be able to inhabit a specific range of depths, but there is not enough data to support a firm clade affinity for depth preference or taphonomy arrival. The lack of data does not mean there is no connection, it will require more research.

Whale fall assemblage successions. There are four stages of faunal succession on whale fall. The first to arrive at the body are considered generalists, they will feed off any carcass. This is referred to as the mobile-scavenger stage (Smith et al., 2001). According to Smith et al., (2003), this stage can last months to years. Research at Monterey Bay has revealed that a large whale can be scavenged to bone within 18 months (mths). Aggregations of scavengers such as Hagfish, various invertebrates, Rat-tails (family Macrouridae) and Sleeper sharks consume the tissues at a rate of 40–60 kilogram per day^{-1} (kg/d). Any exposed bones can also be colonized by *Osedax* at this time. The next phase is called an enrichment opportunist stage that can also last months to years (Smith et al., 2001; Smith et al., 2003). The sediments around the carcass that have been organically enriched by the decaying whale are then colonized by opportunistic polychaetes and crustaceans. Smith et al., (2003) reports the feeding assemblages can be as dense as 40000 meter ^{2} (m). The next to last stage is the sulfophilic stage, where bacteria anaerobically break down the fats in the bones, which are about 4% to 6% of the body weight. The mats created by the bacteria provide a food source for clams, limpets, and sea snails. This digestion stage can last over 50 years (Smith et al., 2003). The last stage is the reef phase. If there are any bones left on the sediments, they can be used by sessile fauna, such as tubeworms and other filter feeders as a base.

Affects on Succession Rate. The most advantageous timeframe for *Osedax* to settle on whale fall would be after the mobile scavengers were done tearing at the carcass soft tissues and any major movement of the carcass had decreased. Depending on the size of the whale, this could take months. The enrichment phase is the presumable point of colonization. However, *Osedax* can settle on a new set of bones in the time span of two months, even while the mobile scavengers are feeding. Any bone that is exposed can entice an early arriving *Osedax;* such is the case with *O. rubiplumus* and *O. frankpressi*. *O. rubiplumus* has been discovered on ribs that were exposed in as little as two months. *O. frankpressi* was the next successor in about four months. While, a body devoid of flesh would make a better settlement platform, it appears that any revealed bone is acceptable for certain species of *Osedax* settlement. The disarticulated and reef stage can also be advantageous for specific species of Zombie worm, such as *O. Jabba*, that prefer bones disarticulated from the body and under the sediment. *O. Jabba* has the particular physiology of an extended root base to be able to infiltrate buried bones.

Osedax reproduction and dispersion. All described *Osedax* demonstrate sexual dimorphism with vermiform females and paedomorphic males that inhabit the females' tube (Figure 1. D, E. G). It is proposed that sexual differentiation is determined environmentally by having a trochophore land on a settled female, that trochophore then becomes male (Figure 1. C) (Grover, et al., 2013; Miyamoto et al., 2013; Weigel, 2015). Settled females spawn eggs into their tubes, which are then fertilized by the inhabiting males. Some females incorporate a harem of males, up to 144 individuals and can spawn up to 355 eggs a day with near 100% fertility (Figure 1. F) (Rouse et al., 2008). The negatively buoyant oocytes are spawned into the water column and within 24 to 72 hours, they develop into swimming trochophores (Miyamoto et al., 2013; Rouse et al., 2008). The trochophores develop cilia and are active swimmers with a large dispersal range due to their attached yolk sacs. Rouse et al's (2008) research on five different species of *Osedax* revealed that *Osedax* could travel up to 16 days before settling. If the trochophores become infected with the heterotrophic bacteria they need for nutrient extraction, when they land on a bone and settle, they can develop rapidly. Upon settlement, females grow rapidly and start reproducing within 6 weeks (Miyamoto et al., 2013; Rouse et al., 2008). It is hypothesized that *Osedax* use whale falls as stepping-stones to extend their range across the sea floor. Little (2010) estimates that there are approximately 690,000 carcasses of large whales in one of the three stages of degradation and aggregation at any point in time. Along a migration route, this places the spacing between any two dead whales between 5 kilometers (km) and 12km.

Affects on Succession Rate. There is some question about how the ciliated trochophores find a decomposing whale to infest. It is possible that Zombie worm larvae can sense the decaying and diffusing organics from the whale carcass. With some motile ability, the trochophores swim toward the attractant and when the organic components reach a sensory threshold, the larvae settle. It should also be considered that not all the trochophores swim away from the present whale fall, but instead, settle immediately, where they have guaranteed heterotrophic bacterial infection, access to males and a ready food source. If whale fall are between 5km and 12km apart, going with the ocean currents and the extended travel times due to larval yolk sacs, this could allow the *Osedax* to propagate along the deep-sea floor, migrating from body to body.

Environmental Factors. The environmental factors that can affect determining an accurate PWFI using Zombie worm infestation could range from ocean water temperature fluctuations, salinity changes, currents and oxygen minimum zones (OMZ). Braby et al.'s, 2007 research determined that for their study subjects off the coast of California (Monterey Bay), the salinity and temperatures stayed fairly stable at depth and didn't affect *Osedax* infestation. The oxygen content had variability, depending on the location of their subject in an OMZ. Those whale falls located in an OMZ had lower diversity and the *Osedax* were delayed in arrival by about seven months, in comparison to *Osedax* succession in a non-OMZ (Braby et al., 2007). This research contends with those whale falls over 1000m and the OMZ along the California coast is at depths less than 1000m. Currents also could play a factor in succession rates by either sedimentation of the whale fall, or the trochophores drift patterns. In shallower waters, the currents were shown to turn bones over and bury them to the point that *Osedax* had a difficult time settling. Currents can also play a role in how far a trochophore can travel, either inhibiting their travel, or by carrying the larvae further and making more whale fall accessible (Braby et al., 2007).

Affects on Succession Rate. With the limited ability to swim against a current, it would be more advantageous for *Osedax* to travel with the current. There seems to be a correlation between prevailing continental shelf currents and a whale fall line along the California coast. *Osedax* swimming in a whale fall current would have a higher likelihood of a successful settle on one of the 690,000 whale carcasses. Especially since this area is also a known Gray Whale (*Eschrichtius robustus*) migration route.

Discussion

The use of *Osedax* to yield a PWFI in deep-water is subject to multiple factors and additional research on succession rates of each species is still needed. However, using current research, a presumed PWFI based on *Osedax* infestation of whale fall at Monterey Bay, CA, can be tentatively calculated, and graphed (Table 3.).

The taphonomy of whale fall plays a direct role in the settlement of some species and the whale fall need not be disarticulated or totally skeletonized for *Osedax* succession to start. Not only do some *Osedax* prefer particular bones for their lipid density, but *Osedax* colonization can also accelerate whale fall decomposition, possibly enticing a different succession of *Osedax* to colonize.

The four stages of faunal assemble on whale fall affect *Osedax* colonization by revealing the bone needed for settling. While the enrichment phase would appear to be the most advantageous time of trochophore settlement, the dispersal rate of *Osedax* has this species poised to exploit bone at most any phase. With the potential for whale fall present along the California coastline every 5km to 12km at any given state of faunal assemblage, locating a potential bone source may be more than plausible.

The Zombie worms' reproductive physiology lends them to be very prolific. With females spawning over 300 fertilized oocytes a day, the likelihood of a successful colonization increase. While it is highly unlikely that the ciliated trochophores have the capabilities to swim against an ocean current and track down whale fall, their yolk sac gives them the advantage of a larger dispersal range. Research on whether all trochophores leave the current whale fall, would be helpful in determining colonizing densities. It would seem reasonable that some trochophore would remain on or near the whale they were spawned on. They have a ready source of bone, males and the much needed heterotrophic bacterial. The deep-sea environment in the bathyal and abyssal zones are fairly stable, with little fluctuations in salinity and temperatures in the Monterey Bay area. Outside of this region, salinity and temperatures may play a role in regulating Zombie worm colonization and would require monitoring and inclusion is any research. An OMZ has definite implications on *Osedax* colonization, and has stalled successful infiltration by about 7 months. Any research of *Osedax* in a potential OMZ will need to include oxygen monitoring to see which species are more adversely affected by lower oxygen levels. Changing currents will also affect the swimming trochophores. The currents along the California continental shelf have been very advantageous to the diversity of *Osedax* in the area. The odds of finding a whale fall line with prevailing currents, within 5km to 12 km and have a trochophore be able to make it to a fall in 16 days, go up significantly on the California coast. Combined with the known Grey Whale (*E. robustus*), migration route, this whale corridor is an *Osedax* buffet line.

The PWFI displayed in Table 3. was calculated by taking into consideration what is known about each described *Osedax*, such as their taphonomy and bone preferences. Previous research conducted by prominent Zombie worm scientists, was cross-referenced with dates of whale fall deployment and *Osedax* specimen collection. Twenty species of *Osedax* in the Monterey Bay have been collected in depths of water over 1000m. Research by Lundsten et al., (2010), produced a table of all Zombie worms collected by date for over 67 months, in 6-month increments, starting in February of 2002 (Table 2.). A research publication by Rouse et al., (2018), revealed 14 new *Osedax* species to the Monterey Bay area. Table 1. represents the cumulative data, including the range of depths each *Osedax* species was recovered from. Rouse et al's (2018) data does not include the original collection date for new species. Any species that where collected below 1000m, but not on Lundstens dated list, was then cross-referenced with previous research geared toward that particular species. Most collection dates over the intervening 15 years were found in previous publications by Braby et al. 2007; Jones et al. 2008; Grover et al., 2013; Rouse et al. 2015 and Vrijenhoek et al. 2009.

The resulting data on each species, displayed in Table 3., reflects a combination of their preferred state of whale taphonomy, known collection depths, and how long they were observed inhabiting the whale fall. Some species, such as *O. bryani* (3yr marker), were only collected from one depth. It is presumed that they would also inhabit water above and below the collection depth and they were assigned a presume depth range based on research estimations and clade association. The red line across the presumed depth range denotes its depth when collected. The species *O. lonnyi* (5yr marker), have only been collected at the reef stage and at a depth of 2898m, but it is presumed that its range is broader. Those species that have only been collected once do not display a time line. Those species that were collected multiple times were given a time of inhabitation with an indication arrow. Their time line was stopped, once they were no longer collected. *O. rogersi* was collected once, at a taphonomy state of being nearly skeletonized, and at a depth of 1446m. Based on the depth range of other clade II *Osedax*, *O. rogersi* was given a conservative range of 633m to 1820m. There are multiple clade II species that inhabit depths up to 2898m and it could very well be likely that some of the Zombie worms that were encountered in more shallow depth can also move to deeper water.

The PWFI chart can be used in several ways. First, if the taphonomy state of the whale is known, then the Osedax that falls within the depth of the whale fall can be deduced. If deep-water Osedax is identified, but no whale fall is apparent, then looking at the reef stage and its colonizers is the place to start. If a researcher wishes to only study a particular Zombie worm (such as *O. sigridae*), then the whale fall should be deployed between 1700m and 3000m, and given an arrival time of about 1.2 yrs.

Conclusion

While the current research on *Osedax* is every growing with additional species being added, there is a lack of data on multiple aspects of Zombie worms. The first is in reference to how the trochophores find a whale fall and if they live longer in the ocean than in the lab. It is conceivable that the trochophores live longer in the ocean than the lab environment, by way of actively consume phytoplankton, which would extend their yolk reserves. This could also extend their dispersion range. There is also the question of how the trochophores know where the whale fall is and when to settle. Perhaps they have an undiscovered sensory system that leads them to the fall.

Additional research into potential clade affiliations in regards to preferred state of taphonomy and depth range would also be worth exploring. From all the research consumed, it seems that the biggest push was to get new organisms named and assigned a clade. Additional information about lifestyle preferences, especially a succession rate has not been thoroughly addressed. Osedax could very well exceed their assigned depths, and additional deployed whales between the depths of the original implanted whales will help fill in the lack of data. To date, only one publication has assigned dates of colonization on whale fall. Given the Zombie worms over all importance to the diversity of deep-water whale fall, increased research would not be misplaced. Whale fall colonized by *Osedax* support significantly distinct and more diversely abundant faunal assemblages. By producing new microhabitats and boosting biodiversity in deep-sea whale-fall communities, *Osedax* could be considered an ecosystem engineer of the sea floor.

As unusual and diverse as whale fall assemblages are proving to be, whaling during the 19^{th} and early 20^{th} century, has probably reduced the overall volume of whale fall. This can have dire consequences for the proliferation and diversity of whale fall specialists that live on the sea floor. It is estimated that 15 percent of whale fall specialist may disappear, and that about one-third of whale fall specialists may have already been decimated. With the continued decline in whale populations, the loss of whales will not be the only extinction, but it is likely that hundreds of deep-sea species that depend on whale fall to complete their life cycle will also go extinct (Vrijenhoek et al., 2008).

If there was ever needed another reason to “Save the Whales”, this is it, an obvious connection between deep-sea biodiversity and the population of cetaceans. Regardless of what the future holds, science will continue to pursue new discoveries between the ex-land lubber, leviathans above and their watery, bone yards below.

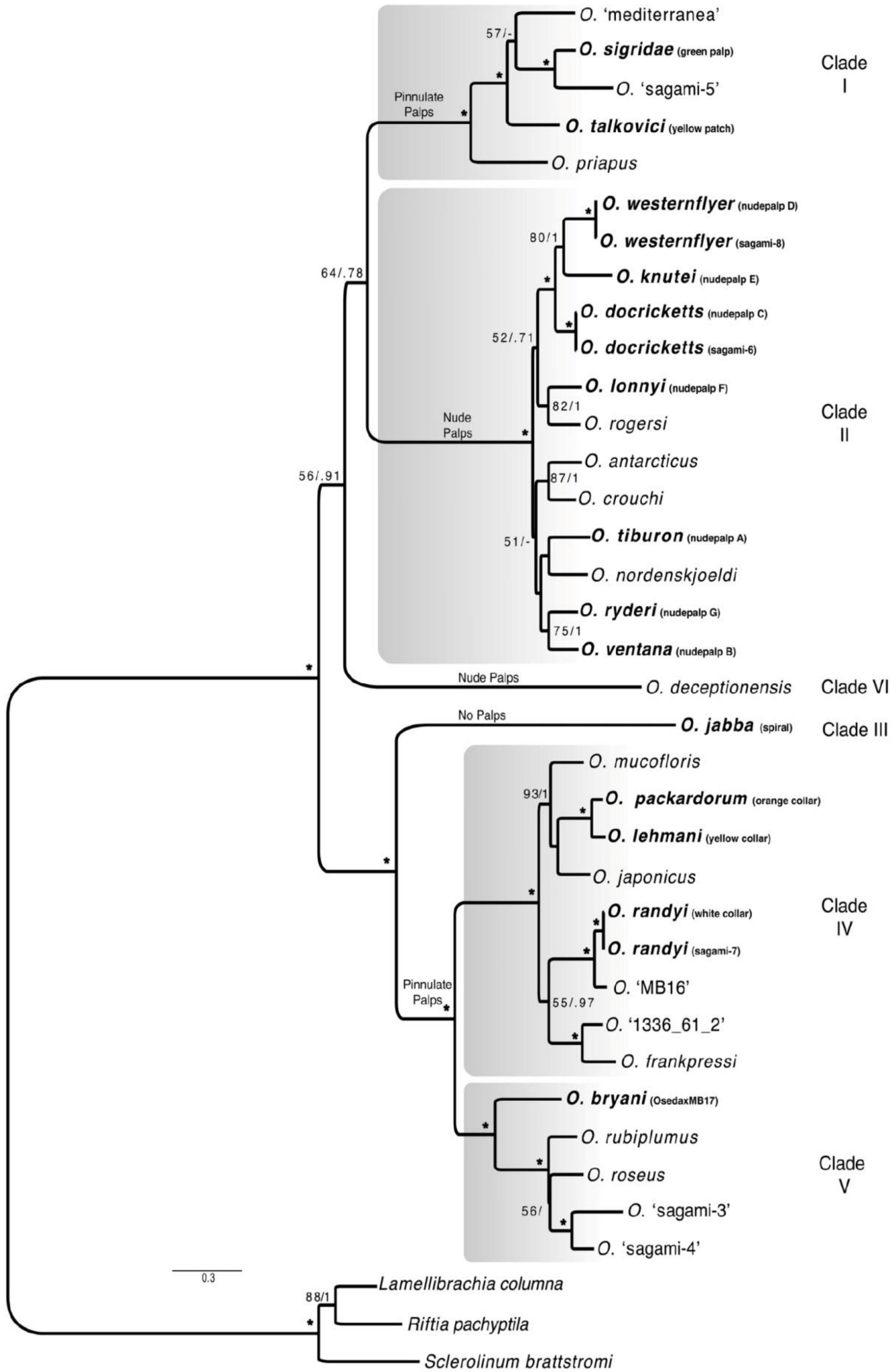

Figure 1. Osedax plylogenetic analyses. Osedax multi-gene phylogeny and tree topology based on 5 gene segments. Displayed in clade groups. Reprinted from Rouse et al., 2018. An inordinate fondness for Osedax (Siboglinidae: Annelida: Fourteen new species of bone worms from California.

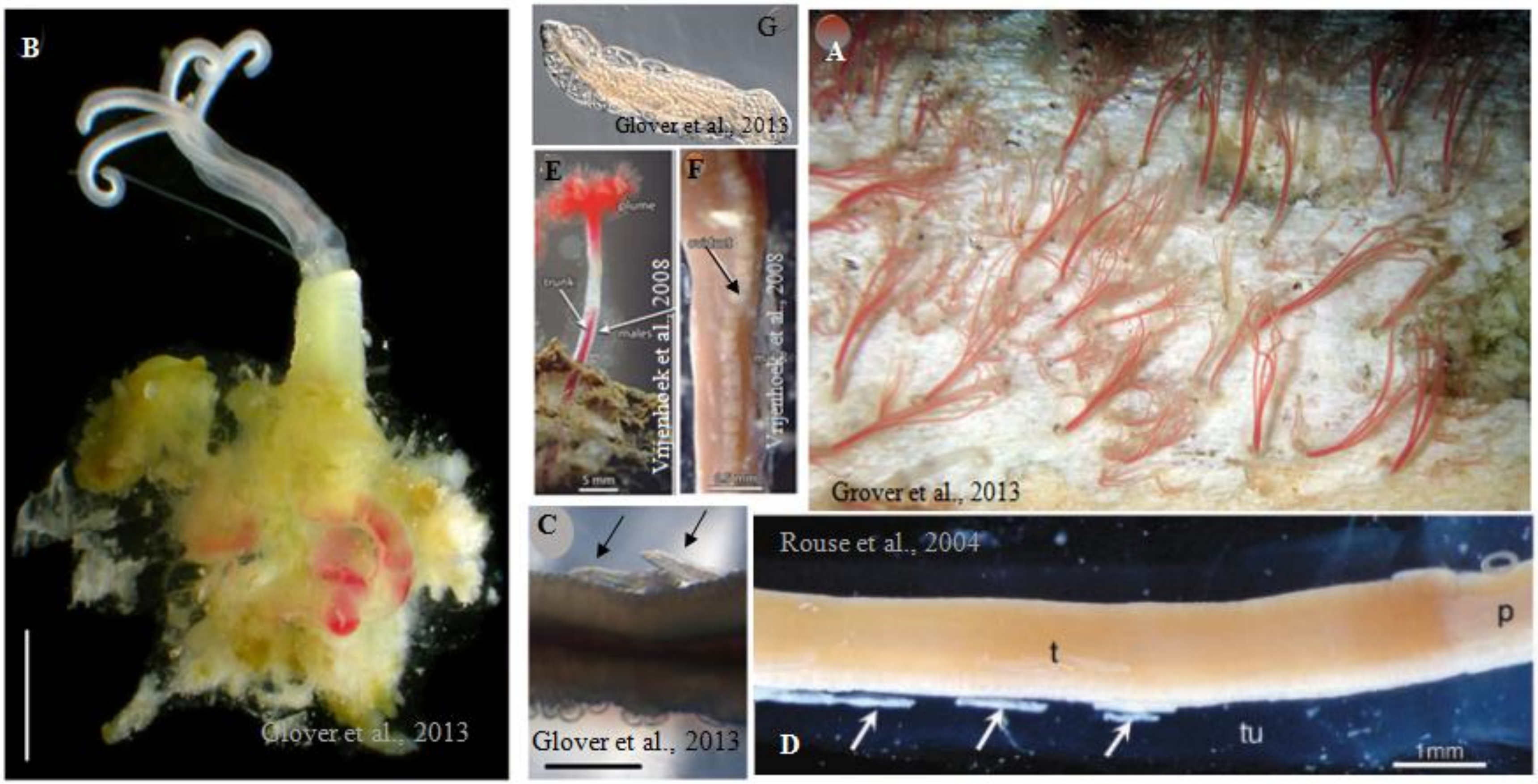

Figure 2. Specimens of *Osedax sp*. **A**. *Osedax rubiplumus*, emerging from bone after retrieved from the ocean floor. **B**. Whole *O. antarcticus* specimen, with palps, oviduct, trunk, and root after dissection from bone. **C**. Two dwarf *O. antarcticus* males attached to trunk (arrows). **D**. Dwarf male, *O. rubiplumus*, in tube of female. **E.** *O. rubiplumus*, adult female on dissected bone with plume. **F**. The anterior trunk of *O. rubiplumus*, female, showing a harem of males lying adjacent to her oviduct (arrow). **G**. Dwarf male, *O. antarcticus*, magnified. Adapted from: Glover et al., (2013), Bone-eating worms from the Antarctic: the contrasting fate of whale and wood remains on the Southern Ocean seafloor. Rouse et al., (2004), *Osedax*: Bone-Eating Marine Worms with Dwarf Males. Vrijenhoek et al., (2008), Bone-eating *Osedax* females and their 'harems' of dwarf males are recruited from a common larval pool

Table 1. Details of *Osedax* species locations, substrates, depths, vouchers, types and GenBank sequences. New species in bold.

Species	Substrate	Latitude	Longitude	Depth (m)	Other names	Vouchers or types	COI sequences
antarcticus	Whale	63°10.98'S	61°38.16'W	568-1446		(Glover *et al.* 2013)	e.g. KF444422
***bryani* n. sp.**	**Whale, cow**	**36°42.496'N**	**122°6.316'W**	**1820**	**'MB17'**	**SIO-BIC A4619 (Holotype)**	**JX280609 (Holotype), JX80610**
crouchi	Whale	63°10.98'S	61°38.16'W	1446		(Amon *et al.* 2014)	e.g. KJ598038
deceptionensis	Whale	62°59.33'S	30°33.45'W	10-156		(Taboada *et al.* 2015)	e.g. KF444428
***docricketts* n. sp.**	**Whale**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'nude-palp C'**	**SIO-BIC A1644 (Holotype)**	**FJ347625-6 (Holotype), EU267675-6**
	Whale	**35°05'N**	**139°13'E**		**Sagami-6**	(Pradillon *et al.* unpublished)	**FM998088-107; Some questionable, see text**
frankpressi		36°42.496'N	122°6.316'W	1820			
	Whale	36°36.606'N	122°26.122'W	2898		(Rouse *et al.* 2004)	e.g., AY586486, EU223312-16, FJ347606
***Jabba* n. sp.**	**Whale**	**36°36.606'N**	**122°26.122'W**	**2898**	**'spiral' 'sp.1 SBJ-2006'**	**SIO-BIC A1639, A7832 (Holotype), A7833, A7834, A7835, A7836, A7837, A7838, A7839**	**DQ996622 (A7833), DQ996623, DQ996624 (A1639), FJ347636-7 (A7834, A7835), FJ347638 (Holotype)**
japonicus	Whale	31°23.865'N	129°58.766'E	234		(Fujikura *et al.* 2006)	e.g. AB259569
***knutei* n. sp.**	**Whale, cow, teleost turkey**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'nude-palp E'**	**SIO-BIC A1646, A7812 (Holotype), A7813, A7814, A7815, A7816**	**FJ347632(A7814), J347634, FJ347634 (A1646), FJ347635 (Holotype), JF509952 (A7815), JF509952-55, MG262305, MG262306 (A7816)**
	Teleost	**36°36.606'N**	**122° 26.12'W**	**2898**			**MG262307**
***lehmani* n. sp.**	**Whale, cow**	**36°47.401'N**	**122° 53.235'W**	**389**	**'yellow collar'**	**SIO-BIC A1640, A7804 (Holotype), A7805, A7806, A7807, A7808**	**EU223320-31, EU223332 (A7807), EU223333-36, EU223337 (A7808), EU223338, DQ996629 (Holotype)**
					'sp. 3 SBJ-2006' 'sp. 4 SBJ-2006' 'orange collar' sic		**DQ996630-31 (A1640, A7806), DQ996632-38 As 'sp. 4 SBJ-2006 DQ996640, DQ996643 As orange collar EU267762**
***lonnyi* n. sp.**	**Whale**	**36°36.606'N**	**122° 26.12'W**	**2898**	**'nude-palp F'**	**SIO-BIC A1647**	**FJ347643** (Holotype)
mucofloris	Whale	58°53.1'N	11°06.4'E	125		(Glover *et al.* 2005)	AY827562-AY827568
	Cow	38°16.856'N	09°06.734'W	120		(Schander *et al.* 2010)	HM045512-13
nordenskjoeldi	Whale	63°10.98'S	61°38.16'W	1446		(Amon *et al.* 2014)	e.g. KJ598039
***packardorum* n. sp.**	**Whale**	**36°47.401'N**	**122° 53.235'W**	**389**	**'orange collar' 'sp. 4 SBJ-2006'**		EU267673-4, FJ347627 DQ996639, DQ996641, DQ996642
	Whale, cow	**36°48.178'N**	**121°59.677'W**	**633**		**SIO-BIC A7844**	FJ347628-29, FJ4311989-9, **FJ431200 (A7844),** FJ431202-204
	Whale	**36°46.308'N**	**122° 4.981'W**	**1018**		**SIO-BIC A1641 (Holotype), A7840, A7841, A7842, A7843**	**EU223339 (A7840), EU223340 (A7841), EU223341 (Holotype), EU223342 (A7843), EU223343 (A7842),** EU223344-46, EU223349-55
priapus	Elephant seal	36°48.178'N	121°59.677'W	633	'pinnnules' (some)	(Rouse *et al.* 2015)	FJ431196-7, FJ431201, FJ431205, KP119564-71
	Fur seal	36°36.307'N	122°9.240'W	873	'sp. 16'		GQ504740-1

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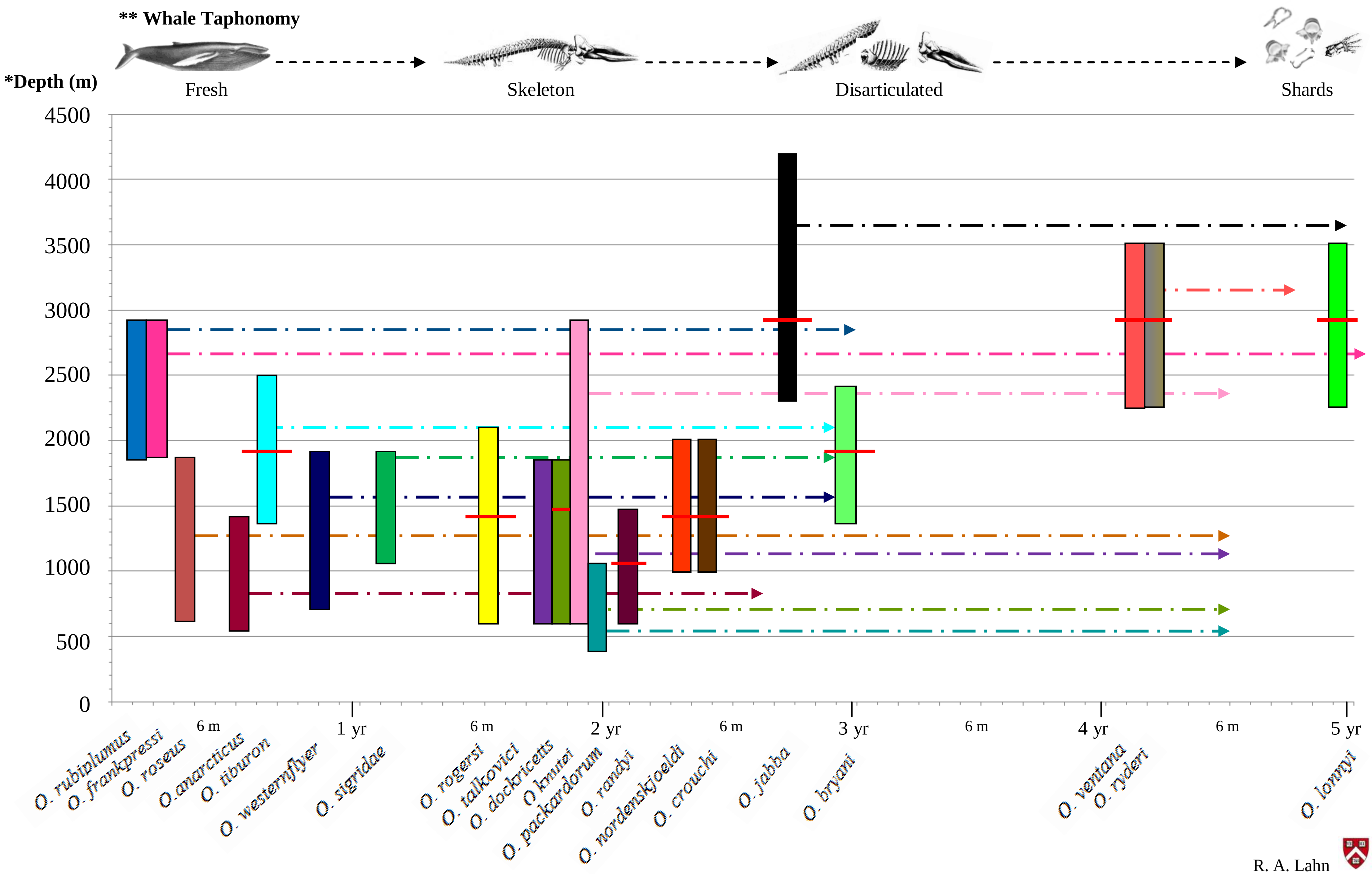
Table 1. (*Continued*). Reprinted from Rouse et al., (2018), An inordinate fondness for *Osedax* (Siboglinidae: Annelida): Fourteen new species of bone worms from California

Species	Substrate	Latitude	Longitude	Depth (m)	Other names	Vouchers or types	COI sequences
***randyi* n. sp.**	**Whale**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'white collar'**	**SIO-BIC A1648, A7845 (Holotype), A7846, A7847**	**FJ347610-11, FJ347612-14 (A7845, A7846, A7847), FJ347615 (Holotype)**
	Whale	**35°05'N**	**139°13'E**		**Sagami-7**	(Pradillon *et al.* unpublished)	**FM998108-9**
rogersi	Whale	59°41.671'S	28°21.089'W	1446		(Amon *et al.* 2014)	e.g. KJ598034
roseus	Whale	36°48.178'N	121°59.677'W	633	SBJ-2007a	(Rouse *et al.* 2008)	EU164760-73
	Whale, cow	36°46.308'N	122° 4.981'W	1018	sp.2 SBJ-2006		DQ996625-28, EU032471-84, EU164774,
	Whale	36°42.496'N	122°6.316'W	1820	'rosy'		KJ598034, JF509949, KJ598037, KJ598040 EU032469-70
	Whale	35° 04.897'N	139° 13.987'E		roseus (Japan)	(Paradillon *et al.* unpublished)	FM998064-077
rubiplumus	Whale, cow	36°42.496'N	122°6.316'W	1820		(Rouse *et al.* 2004)	EU852298-305, EU852431-88
	Whale	36°36.606'N	122°26.122'W	2898			EU852306-09, EU852420-30
	Whale	35° 04.897'N	139° 13.987'E		rubiplumus (Japan)	(Pradillon *et al.* unpublished)	FM998060-63
***ryderi* n. sp.**	**Whale, teleost, turtle**	**36°36.606'N**	**122°26.122'W**	**2898**	'nude-palp G', 'nude palp #20'	**SIO-BIC A4617 (Holotype), A4618 (Allotype)**	**KP119563 (Holotype), MG262308-09**
***sigridae* n. sp.**	**Whale, cow**	**36°42.496'N**	**122°6.316'W**	**1820**	**green palp**	**SIO-BIC A1650, A7809 (Holotype), A7810, A7811**	**FJ347639, FJ347640, FJ347641 (Holotype), FJ347642**
***talkovici* n. sp.**	**Whale, Elephant seal**	**36°48.178'N**	**121°59.677'W**	**633**	**'yellow patch' 'pinnules'**	**SIO-BIC A1649, A7822, A7823, A7824, A7825, A7826, A7827, A7828, A7829, A7830**	**FJ347620 (A7822), FJ347620 (A1649), FJ431196-97 (A7823, A7824), FJ431201 (A7825), FJ431205, (A7826), MG262311 (A7829), MG262310 (A7827)**
		36°46.308'N	**122° 4.981'W**	**1018**	**'yellow patch'**		**JF509950-51, FJ347616-18**
	Whale, cow					**No vouchers**	**MG262313 (Holotype), MG262312 (A7831)**
***tiburon* n. sp.**	**Whale, cow**	**36°42.496'N**	**122°6.316'W**	**1820**	**'nude-palp-A'**	**SIO-BIC A1642, A7817 (Holotype), A7818, A7819, A7820**	**FJ347622 (Holotype), FJ347623-24 (A7818, A7819), EU223356, EU223357 (A7820) EU223358-59 (A1642)**
***ventana* n. sp.**	**Cow**	**36°36.606'N**	**122°26.122'W**	**2898**	**'nude-palp-B'**	**SIO-BIC A1643 (Holotype)**	**EU236218**
***westernflyer* n. sp.**	**Whale**	**36°46.308'N**	**122° 4.981'W**	**1018**	**'nude-palp-D'**		**FJ347630**
	Whale, cow	**36°42.496'N**	**122°6.316'W**	**1820**		**SIO-BIC A1645 (Holotype), A7802, A7803**	**FJ347631, MG262303 (Holotype), MG262303 (A7802), MG262304 (A7803)**
	Whale	**35°05'N**	**139°13'E**	**925**	**Sagami-8**	(Pradillon *et al.* unpublished)	**FM998110**
1336_61_2	Whale	28° 31.119' S	41° 39.401' W	4204		(Sumida *et al.* 2016)	LC106303
MB16	Whale, cow	36°42.496'N	122°6.32'W	1820		(Salathé & Vrijenhoek 2012)	JX280611-13 (No vouchers)
mediterranea	Whale	41°40' 15' N	2°53' 23' E	53		(Taboada *et al.* 2015)	KT860548
Sagami-3	Whale	35°05'N	139°13'E	925		(Pradillon *et al.* unpublished)	FM998078-81
Sagami-4	Whale	35°05'N	139°13'E	925		(Pradillon *et al.* unpublished)	FM998082
Sagami-5	Whale	35°05'N	139°13'E	925		(Pradillon *et al.* unpublished)	FM998083-87

Table 2. Relative abundance of bone specialist *Osedax sp*. and two provannid gastropods in 6 month bins. Rare (+), moderately abundant (++), and dense (+++) populations were observed in ROV video footage. Reprinted from Lundsten et al., (2010), Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA.

Months since deployment	0–6	7–12	13–18	19–24	25–36	37–42	43–48	49–54	55–60	67+
Whale-382a										
Osedax 'yellow collar'		+	+							
Osedax 'orange collar'		+	++	+	+					
Whale-382p										
Osedax 'yellow collar'	+	+								
Whale-633										
Osedax roseus	+	++	++		+					
Osedax 'orange collar'		+	+							
Osedax 'yellow patch'		++	++		+					
Whale-1018										
Osedax roseus	+++	++	++	++	++	++		++		
Osedax 'orange collar'				+	+	+		+		
Osedax 'yellow patch'				+	+	+		+		
Osedax 'white collar'				+						
Osedax 'nude palp C'				+	+	+		+		
Osedax 'nude palp D'				+	+	+		+		
Osedax 'nude palp E'				+	+	+		+		
Osedax frankpressi			++	++	+					
Osedax roseus		+	+	+	+					
Osedax 'green palp'			+	+	+					
Osedax 'nude palp A'		+	+	+	+					
Osedax 'nude palp D'		+	+	+	+					
Rubyspira osteovora					+					
Whale-2898										
Osedax rubiplumus	+++	++								
Osedax frankpressi	+	+	++	++	++		++	++	++	+
Osedax 'spiral'					+		+		+	+
Osedax 'nude palp B'								+	+	
Osedax 'nude palp F'										+
Rubyspira osteovora					+	+++	+++	+++	+++	+++
Rubyspira goffrediae								+	+	+

Table 3. *Osedax* succession rates of 20 described deep-water species, illustrating known occupancy depth and preferred state of whale fall taphonomy.



R. A. Lahn

- recorded collection depth

*depth ranges are estimates based on published research and clade associations.

**whale taphonomy scale not wholly accurate; used for presentation purposes.

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