

MOLLUSK SPECIES AT A PLIOCENE SHELF WHALE FALL (ORCIANO PISANO, TUSCANY)

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ABSTRACT

The recovery of an intact, 10 m long fossil baleen whale from the Pliocene of Tuscany (Italy) offers the first opportunity to study the paleoecology of a fully developed, natural whale-fall community at outer shelf depth. Quantitative data on mollusk species from the whale fall have been compared with data from the sediments below and around the bones, representing the fauna living in the muddy bottom before and during the sinking of the carcass, but at a distance from it. Although the bulk of the fauna associated with the fossil bones is dominated by the same heterotrophs as found in the surrounding community, whale-fall samples are distinguishable primarily by the presence of chemosymbiotic bivalves and a greater species richness of carnivores and parasites. Large lucinid clams (*Megaxinus incrassatus*) and very rare small mussels (*Idas* sp.) testify to the occurrence of a sulphophilic stage, but specialized, chemosymbiotic vesicomyid clams common at deep-sea whale falls are absent. The Orciano whale-fall community is at the threshold between the nutrient-poor deep sea and the shallow-water shelf, where communities are shaped around photosynthetic trophic pathways and chemosymbiotic specialists are excluded by competition.

INTRODUCTION

Since their first discovery in the deep sea, whale falls have attracted scientists for the exceptional fauna they host, largely based on chemoautotrophic pathways fuelled by lipid-rich whale skeletons (Smith et al., 1989; Bennett et al., 1994). Time series studies of natural and implanted deep-sea whale falls indicate that bathyal carcasses pass through four stages of ecological succession: mobile-scavenger, enrichment-opportunist, sulphophilic, and lastly reef stage (Smith et al., 2002 and references therein). An experimental study has yielded evidence of the fourth stage (Fujiwara et al., 2007), while the third, sulphophilic stage has been found on very old carcasses (Smith and Baco, 2003). Successional stages involve species turnover and changes in faunal mobility and trophic structure, with temporal overlaps in the onset of characteristic species from different stages. For these reasons, diversity in whale-bone faunal communities varies with successional stages, with the sulphophilic stage harboring the greatest number of species (Smith and Baco, 2003).

While research programs concentrate on the deep sea, remarkably little is known about ecosystem response to whale falls at shallow depth, where the flux of organic carbon to the bottom is already high and constant and a different degree, if not type, of resource exploitation is expected. Natural shelf occurrences are probably rare, due to refloating of carcasses by decay gas (Allison et al., 1991; Smith, 2006); however, artificially sunken carcasses show the presence of obligate whale-fall taxa even at shallow depth (Dahlgren et al., 2006). Paleontological reports of fossil whale-fall communities range from the Paleogene (Goedert et al., 1995; Nesbitt, 2005; Kiel and Goedert 2006; Kiel, 2008) to the early Neogene (Amano and Little, 2005;

Pyenson and Haasl, 2007) and are similarly unbalanced towards deep sea paleosettings.

Fossil whales are not rare in the Mediterranean Pliocene and their taphonomy was approached in the early days of paleontology (e.g., Cortesi, 1819). No quantitative study of the associated biota had been undertaken, however, until the recent finding of a whole and articulated skeleton of a large mysticete in the Pliocene of Tuscany, with a mollusk fauna testifying to the sulphophilic stage (Dominici et al., 2009). This is a particularly interesting find since it enables the study of a whale-fall community at shelf depth.

In the present paper the distribution of mollusk abundances and the trophic structure of the Orciano fossil community are discussed at the species level and compared with the background fauna. Species-level comparisons allow us to interpret the paleoecology at a finer resolution on uniformitarian grounds since many Pliocene species are still alive. Moreover, new samples were analyzed with respect to the previous family-level study (Dominici et al., 2009), allowing the discovery of new chemosymbiotic forms. Mollusk species from sediments in contact with whale bones have been compared with assemblages from the sediments below and around the whale fall, in order to reconstruct the paleoenvironmental conditions before and during the presence of the carcass on the sea floor. The results are discussed in terms of faunal adaptations to exploit whale carcasses at shelf depths where competition is keen.

GENERAL SETTING

Geology

The fossil whale was found at Orciano Pisano, in Southern Tuscany, a locality known for its rich marine vertebrate fauna including fishes, cetaceans, pinnipeds, and chelonids (Bianucci and Landini, 2005). Orciano is located in the Fine Basin (Fig. 1), on the Tyrrhenian side of the northern Apennines, a structure filled by 1000 m of mostly marine Tortonian–Pleistocene deposits. The depositional environment rapidly shifts from deltaic to bathyal depths at the start of the Pliocene (Carnevale et al., 2008 and references therein), at the onset of deposition of gray-blue marls. The skeleton was found in the middle part of the regressive deposits overlaying the gray-blue marls, within silty fine-grained sandstones marking the regression to shelf depths. Planktonic foraminifers and fossil nannoplankton indicate that the age of the whale fall ranges from the upper Piacenzian to the lower Gelasian (3.19–2.82 Ma) (Dominici et al., 2009).

Taphonomy

The fossil is a 10 m long rorqual-like mysticete, lying on its ventral side. As described in Dominici et al. (2009), the bones maintain their original relative position, are only slightly displaced and the skull is heavily worn. Cervical bones are cemented to the neurocranium, thoracic vertebrae are lacking, and costae are symmetrical around the vertebral column, preserving a large part of their cortical layer. Arm

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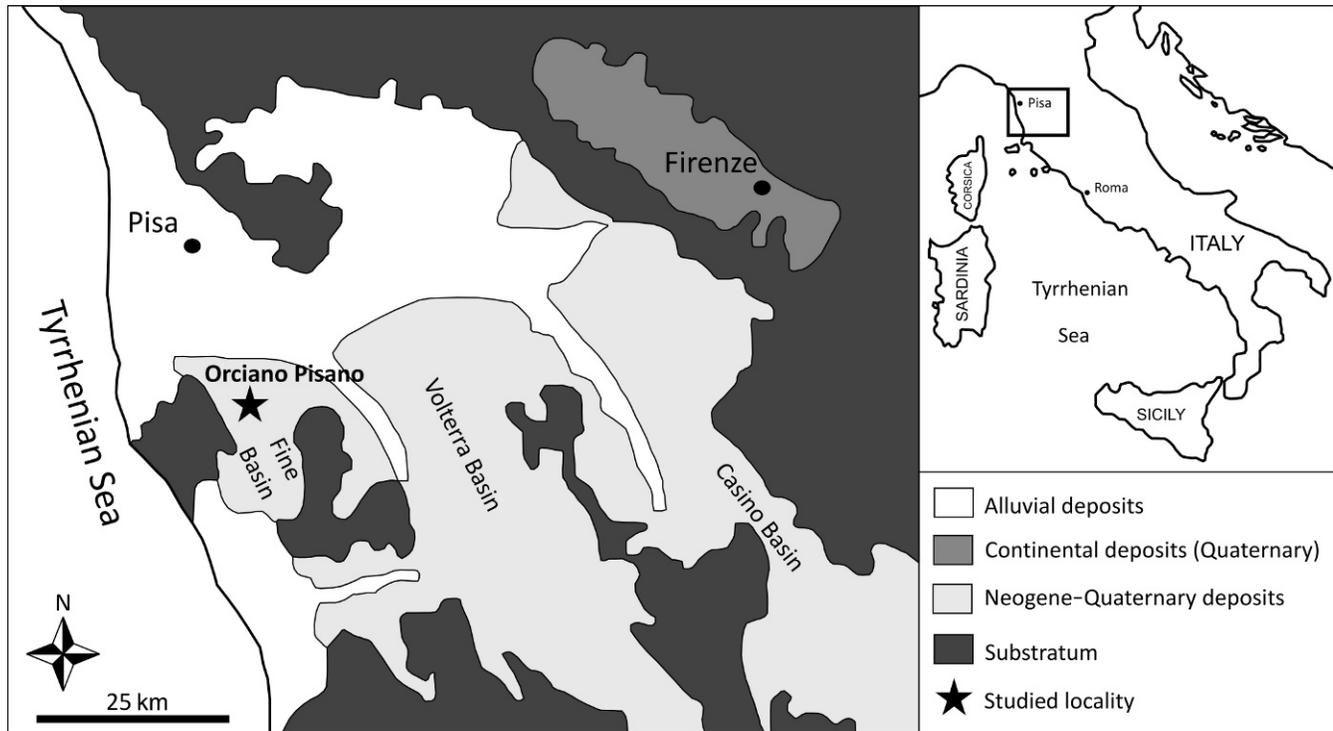


FIGURE 1—Location of the study area at Orciano Pisano, Italy and schematic geological map (modified after Carnevale et al., 2008).

bones are articulated, but corroded, whereas only a few phalanges have been recovered. Possibly all caudal vertebrae are present, but they lack dorsal processes and are frequently cemented to one another in the lowermost part. The cortical bone layer is corroded, exposing a fragile spongy bone tissue, which is more apparent approaching the chest region.

MATERIALS AND METHODS

Stratigraphy

The local succession is formed by the following units, from bottom to top (Fig. 2): (1) bioturbated gray-colored siltstones (50 cm thick) with a sparse macrofauna; (2) a 4–5 cm thick, densely packed *Archimediella spirata* shell pavement (*Turritella* bed in the sense of Allmon, 1988) that is regularly continuous in the whole area. In this unit bivalves are typically articulated and *Archimediella* shells are empty or partially filled with clay. Fragments of fossil wood are abundant and ≤ 15 cm long; remains of marine vertebrates are abundant (sharks, teleosts, marine mammals, and chelonids); (3) massive silty fine-grained sandstones, >1 m thick, with a sparse to loosely packed macrofauna. Adults of the highly mobile, epifaunal *Amusium cristatum* and other bivalves (e.g., *Anadara diluvii*, *Corbula gibba*, and *Tellina planata*) are in life position. *Archimediella spirata*, *Aporrhais uttingeriana uttingeriana*, spatangoid echinoderms, trace fossils (*Ophiomorpha* and *Thalassinoides*) and vegetal debris are abundant throughout the outcrop. The whale was lying in unit 3 ~20 cm above the *Archimediella* bed and parallel to it.

Sampling and Analytical Methods

A total of 17 bulk samples can be subdivided in four groups depending on their relative position with respect to the whale bones; these *a priori* groups are used for between-sample comparisons. The first group (whale-fall community: wfc) is represented by the seven samples representative of the whale-fall fauna (OP1–OP7) collected above the bones and positioned on a grid of 1-m-sized squares (Fig. 3).

Ten additional samples were collected from the background sediments (Fig. 2, Table 1): four from unit 1 (below wfc; OP8–OP11), three from the *Archimediella* bed (*Archimediella* bed; OP12–OP14), and three from unit 3 at 1–2 m from the closest bone (lateral wfc; OP15–OP17). The data set includes 12 samples used in a previous study (Dominici et al., 2009) and five new collections. All samples range from 0.5–1 liters and were wet sieved through a 1 mm screen; the residue was sorted under a binocular microscope for all recognizable biogenic components. The latter includes mollusks, polychaetes, echinoids, decapods, and fishes. Mollusks were determined at the species level, using the collection at the Museo di Storia Naturale di Firenze and many papers and monographs on Pliocene Italian mollusks, and used for quantitative comparisons. Bivalve number was counted as the highest number of right or left valves and half of the remaining, the latter roughly corresponding to the number of unmatched valves. Gastropods were equated to the number of apices. Each unit was scoured for large-sized species, which are likely to be underrepresented in bulk samples, and a species was added as present to the data matrix where appropriate.

The data set, including 2449 specimens belonging to 97 mollusk species (see Supplementary Data¹), forms the basis for a multivariate comparison and for trophic structure analysis. For multivariate elaboration, species occurring in only one sample were removed, resulting in a data set with 62 species and 2409 specimens (98.4% of the original specimens). Abundances were standardized and square-root transformed to de-emphasize the influence of most abundant taxa.

A similarity percentage analysis (SIMPER; Clarke and Warwick, 1994) was performed to determine which species were responsible for similarity within groups of samples. Those species for which the ratio of mean similarity to standard deviation of similarity is >1 typify the sample group and were listed in the comparison. Then a matrix of square-root transformed data was obtained based on the Bray-Curtis similarity coefficient, one of the most widely used in ecological studies (Bray and Curtis, 1957; Clarke and Warwick, 1994). Analysis of similarity (ANOSIM) was carried out to test the degree of differences

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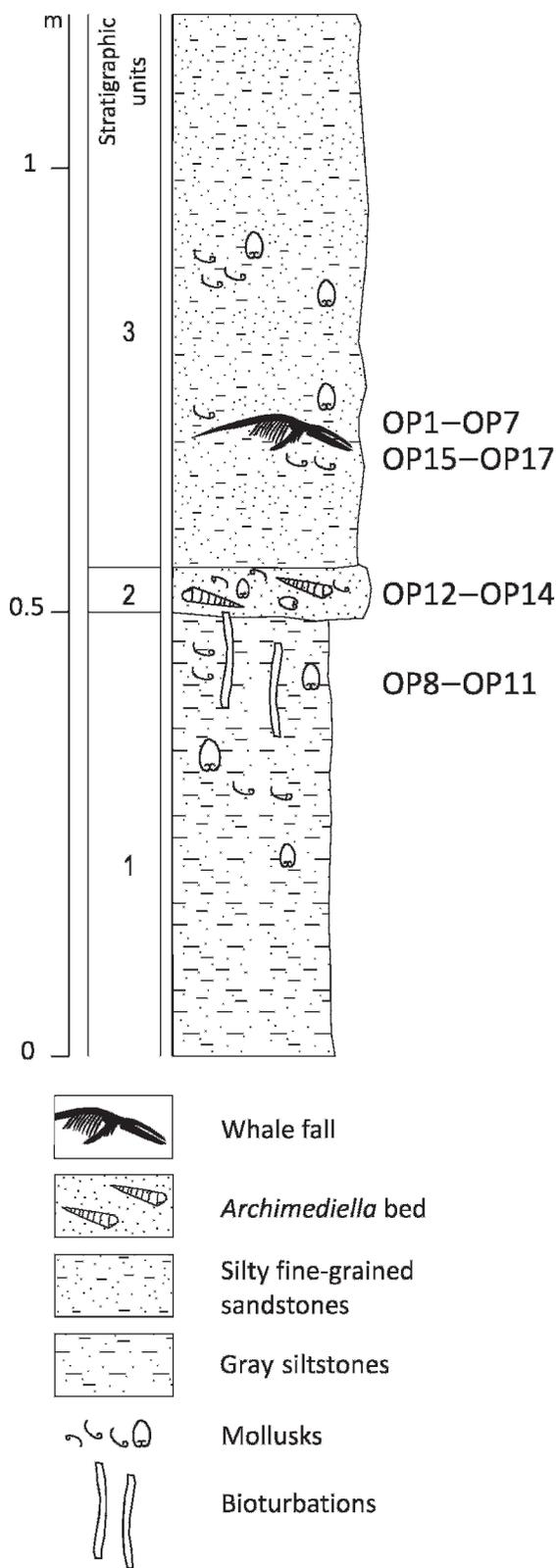


FIGURE 2—Studied Pliocene section subdivided into three stratigraphic units (unit 1, unit 2, unit 3). Sample locations are marked by OP.

between *a priori* groups of samples considering stratigraphic and taphonomic information. The important result of the pair-wise tests of the ANOSIM analysis is the pair-wise R-values; these give an absolute measure of separation between the groups, on a scale of zero

(indistinguishable) to one (all similarities within groups < any similarity between groups). With R-values >0.75, groups are well separated; with R-values >0.5, groups are overlapping but clearly different. With R-values >0.25, groups strongly overlap and with R-values <0.25, groups are barely separable.

Using nonmetric multidimensional scaling (NMDS; Clarke and Warwick, 1994), a map of the samples was produced wherein points that plot close together represent samples that are very similar in taxonomic composition. All statistical analyses were performed with the software PRIMER (Clarke and Warwick, 1994), except for ANOSIM, which was performed with PAST (Hammer et al., 2001).

The whole data set (n = 2449), subdivided into the *a priori* groups, was used for trophic analysis by considering trophism of modern mollusk genera or families. Seven trophic categories are distinguished consistently following the Molluscan Life Habits Databases (Todd, 2000), using abbreviations appropriate for the present study: suspension feeders (SU), deposit feeders (DE), predatory carnivores, including scavengers (CP), browsing carnivores (CB), herbivores (HE), parasites (PA), and chemosymbiotic forms (CH). Comparisons were expressed through percent of number of specimens (n, abundance) and number of species (S, richness) for each category.

RESULTS

Paleocommunity Structure

The full dataset includes 42 species of gastropods, 50 bivalves, 5 scaphopods, bony fishes, sharks, and rays (*Carcharhinus sp.*, *Hexanchus griseus*, *Raja cf. clavata*), decapods, barnacles, regular and irregular echinoids, serpulids (*Ditrupa cornea* and others), and foraminifers. The quantitatively important species of the mollusk dataset, contributing at least 1% to the total assemblage, are all represented in the four groups of samples, with minor exceptions. Species rank changes among the four *a priori* groups (Fig. 4). The most abundant species is the bivalve *Corbula gibba*, dominant in wfc, below-wfc, and lateral-wfc samples, with a mean abundance of 39%–41%. The turritellid *Archimediella spirata* largely predominates in the *Archimediella* bed group (average 31%), being rare in wfc and lateral-wfc groups (average 1%) (Fig. 4). SIMPER analysis shows that *Archimediella* bed samples have the highest similarity, with an average value of 70%, followed by wfc (67%), and below-wfc samples (62%). The most heterogeneous group is the lateral wfc, with an average similarity of 57% (Table 2). Characteristic species within each group of samples are mainly shared among all groups, with the exception of *Natica* sp. and *Hiatella rugosa*,

TABLE 1—Basic data for the studied samples.

Stratigraphic unit	Group of samples	Sample number	Volume (liter)	Number of individuals	Number of species
Unit 3	wfc	OP1	1.1	257	37
		OP2	1.1	228	41
		OP3	0.5.1	241	41
		OP4	0.5.1	116	27
		OP5	0.5.1	150	34
		OP6	0.5.1	204	29
		OP7	0.5.1	72	25
Unit 1	below wfc	OP8	0.5.1	56	22
		OP9	0.5.1	61	20
		OP10	0.5.1	92	24
		OP11	0.5.1	61	18
Unit 2	<i>Archimediella</i> bed	OP12	0.5.1	282	43
		OP13	0.5.1	172	27
		OP14	0.5.1	188	30
Unit 3	lateral wfc	OP15	0.5.1	54	22
		OP16	0.5.1	75	22
		OP17	1.1	140	28
		All samples	12.1	2449	97

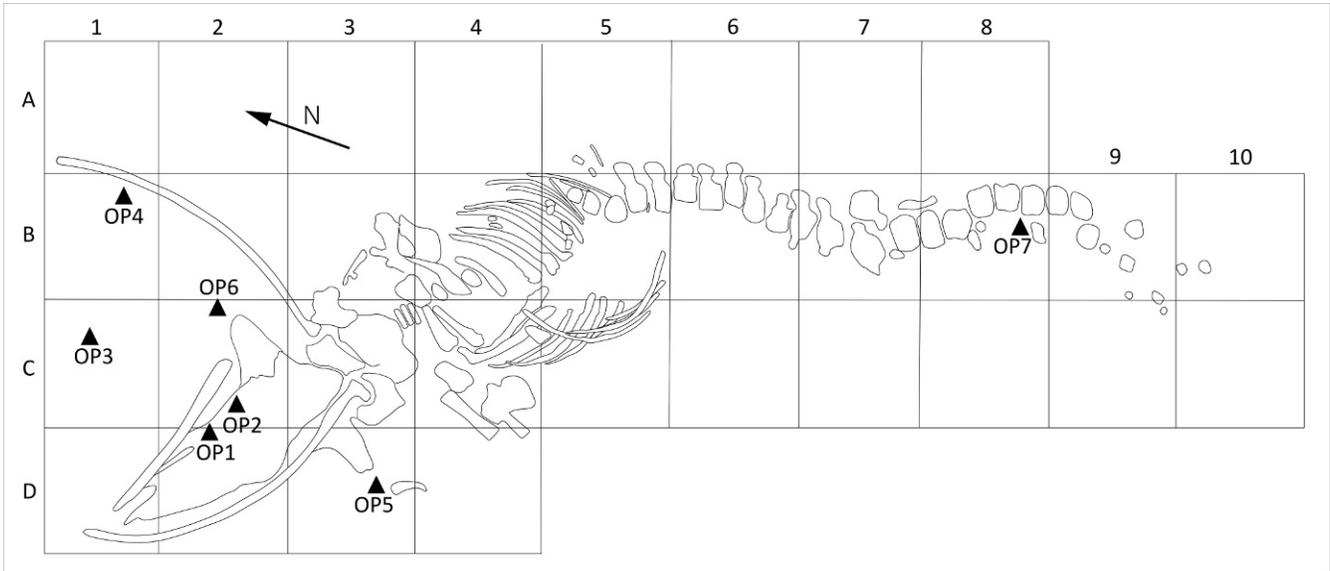


FIGURE 3—Plane view of the Orciano Pisano whale skeleton on a grid of 1 m squares. Triangles indicate the position of whale-fall samples (OP1–OP7).

characteristic of the *Archimediella*-bed and lateral-wfc groups, respectively, and the mytilid *Modiolula phaseolina* and the lucinid *Megaxinus incrassatus*, only typical of the whale fall. *Megaxinus incrassatus* is found exclusively in whale-fall samples, whereas *Modiolula phaseolina* abundance is statistically significant there with respect to the other settings (Kruskal-Wallis test: $p = 0.006$).

ANOSIM points out that the largest difference is observed between whale-fall and *Archimediella*-bed samples, the two groups being well separated ($R = 0.81$) and the statistical difference highly significant ($p = 0.0078$). Whale-fall samples overlap but are still distinguishable from below-wfc samples ($R = 0.66$; $p = 0.0033$). Whale-fall samples record the smallest difference when compared with samples from surrounding sediments of the same unit, a difference that is clear ($R = 0.56$), but statistically less significant ($p = 0.0402$), due to the small size of lateral-

wfc samples (Table 1). Even lower is the statistical significance when comparing lateral wfc with all other groups. Finally, a strong overlap is encountered between below-wfc and *Archimediella*-bed samples (Table 3).

NMDS allows us to visualize compositional differences between samples and their *a priori* groups. This underlines that there is no overlap between groups and a slightly larger distance between wfc samples and below-wfc or *Archimediella*-bed samples (Fig. 5). The three lateral-wfc samples appear scattered, consistent with their small size, which is too small for statistically meaningful comparisons. On the other hand, wfc and *Archimediella*-bed samples form tight clusters, depending on their inner similarities and sufficiently large sample size for comparisons. Samples with <80 specimens tend to be more scattered, whereas samples with ≥ 100 specimens tend to plot closer

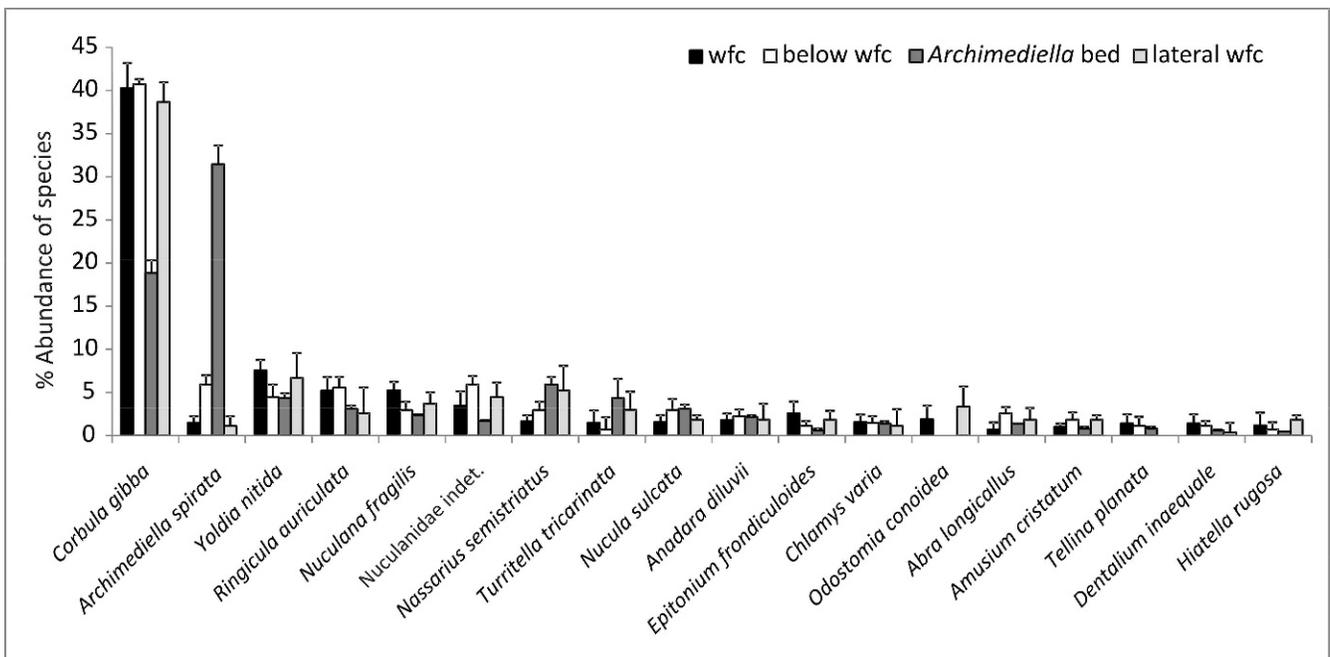


FIGURE 4—Percentage abundances in each of the four *a priori* groups of the quantitatively important species ($>1\%$) in the total data set. Mean percentage abundances shown with the upper limit of 95% confidence intervals; wfc = whale-fall community.

TABLE 2—Characteristic species of each group of samples, calculated for standardized data set and square-root transformed abundances using similarity percentage analysis (SIMPER, Clarke and Warwick, 1994). Underlined species are characteristic taxa not shared among the four groups.

Species	Average abundance	Average similarity	Sim/SD	Contrib. %
wfc samples				
Average similarity: 67.30				
<i>Corbula gibba</i>	39.95	13.20	9.19	19.62
<i>Yoldia nitida</i>	8.03	5.58	6.49	8.29
<i>Nuculana fragilis</i>	5.41	4.74	10.73	7.04
<i>Ringicula auriculata</i>	5.10	3.92	5.47	5.83
<u><i>Modiolula phaseolina</i></u>	1.58	2.54	6.27	3.78
<i>Anadara diluvii</i>	1.95	2.54	6.02	3.77
<i>Nassarius semistriatus</i>	1.75	2.48	4.20	3.68
Nuculanidae indet.	3.14	2.34	1.41	3.48
<u><i>Megaxinus incrassatus</i></u>	1.71	2.19	3.73	3.26
<i>Archimediella spirata</i>	1.77	2.18	2.66	3.23
<i>Epitonium frondiculoides</i>	2.74	2.09	1.42	3.11
<i>Amusium cristatum</i>	1.18	2.03	9.27	3.02
<i>Nucula sulcata</i>	1.68	1.95	1.47	2.90
<i>Chlamys varia</i>	1.82	1.88	1.48	2.79
<i>Dentalium inaequale</i>	1.23	1.58	1.52	2.35
<i>Limea strigilata</i>	1.14	1.54	1.37	2.29
<i>Anomia ephippium</i>	0.78	1.28	1.51	1.90
<i>Aporrhais uttingeriana</i>	1.25	1.24	1.25	1.84
<i>uttingeriana</i>				
below-wfc samples				
Average similarity: 61.97				
<i>Corbula gibba</i>	43.04	16.81	19.15	27.13
Nuculanidae indet.	5.93	6.02	41.60	9.72
<i>Archimediella spirata</i>	5.88	5.71	7.85	9.22
<i>Ringicula auriculata</i>	5.42	4.96	3.32	8.00
<i>Abra longicallus</i>	2.58	3.75	7.21	6.05
<i>Nuculana fragilis</i>	2.93	3.73	5.43	6.01
Archimediella-bed samples				
Average similarity: 70.45				
<i>Archimediella spirata</i>	32.35	12.41	37.34	17.62
<i>Corbula gibba</i>	19.48	9.29	14.94	13.18
<i>Nassarius semistriatus</i>	5.81	5.10	22.00	7.24
<i>Yoldia nitida</i>	4.83	3.93	7.63	5.58
<i>Ringicula auriculata</i>	3.18	3.62	6.94	5.15
<i>Nuculana fragilis</i>	2.40	3.44	23.57	4.88
<i>Nucula sulcata</i>	3.13	3.41	3.76	4.83
<i>Anadara diluvii</i>	2.26	3.06	69.92	4.34
Nuculanidae indet.	1.86	2.73	4.56	3.88
<i>Abra longicallus</i>	1.49	2.58	7.63	3.66
<i>Chlamys varia</i>	1.36	2.40	21.43	3.41
<i>Chlamys pesfelis</i>	1.11	2.38	28.32	3.38
<u><i>Natica sp.</i></u>	1.35	2.14	6.28	3.04
<i>Chlamys glabra cf. flexuosa</i>	1.77	2.10	7.75	2.99
<i>Aporrhais uttingeriana</i>	1.22	2.08	3.91	2.96
<i>uttingeriana</i>				
<i>Dentalium sexangulum</i>	0.87	1.72	2.88	2.45
<i>Dentalium inaequale</i>	0.62	1.69	22.39	2.41
lateral-wfc samples				
Average similarity: 56.68				
<i>Corbula gibba</i>	41.08	14.79	9.41	26.10
<i>Yoldia nitida</i>	5.55	4.17	3.19	7.35
Nuculanidae indet.	4.11	4.10	3.45	7.23
<i>Nassarius semistriatus</i>	4.17	3.61	10.01	6.37
<i>Nuculana fragilis</i>	4.17	3.46	3.66	6.10
<i>Limea strigilata</i>	2.64	3.34	4.32	5.90
<i>Amusium cristatum</i>	2.01	3.11	8.33	5.49
<i>Epitonium frondiculoides</i>	1.80	3.04	13.01	5.36
<i>Nucula sulcata</i>	2.19	2.90	33.85	5.11
<u><i>Hiatella rugosa</i></u>	2.40	2.78	2.20	4.90

together. Multivariate analyses overall show that mollusk assemblages living by the whale carcass are different from those that lived on the same bottom before the fall of the carcass. Even samples collected at a distance from the bones, but within the same unit, appear different.

Trophic Analysis

Trophic structure was analyzed after grouping individual samples into the four *a priori* groups (Fig. 6). Suspension feeders dominate in both richness (40%–50%) and abundance (56%–66%) in all groups. In below-wfc, lateral-wfc, and wfc groups, *Corbula gibba* is the most important suspension feeder, whereas the *Archimediella* bed is dominated by the turrnellids *A. spirata* and *Turritella tricarinata*. Other common suspension feeders in common among all samples are the pectinids, *Chlamys varia* and *Amusium cristatum*, and the arcid *Anadara diluvii*. The whale-fall assemblage shows a significantly higher abundance of the mussel *Modiolula phaseolina*. The second most important group is the deposit feeders ($S = 20.0\%–25.5\%$; $n = 17.0\%–24.3\%$), particularly nuculids and nuculanids (*Yoldia nitida*, *Nuculana fragilis*, *Nucula sulcata*, and Nuculanidae indet.) followed by the Tellinoidea (*Abra longicallus*, *Tellina planata*) and scaphopods. Abundance data are comparable for carnivores and scavengers, while whale-fall samples show a greater species richness. Ringiculids (*Ringicula auriculata*, *R. ventricosa*) and nassarids (*Nassarius semistriatus*) are the most common, the former feeding mainly on small copepods (Fretter, 1960) and the latter being secondarily an active predator on polychaetes and small crustaceans (Britton and Morton, 1994). Naticids (*Euspira helicina*, *Natica sp.*) are quite common, feeding mainly on bivalves and crustaceans (Taylor, 1980). Parasites are represented mainly by the ectoparasite pyramidellids in all assemblages, with a higher diversity in whale-fall samples. The browsing carnivores, i.e., predators which feed on sedentary and typically clonal animals without killing them, are poorly represented overall. This category includes the epitonids (*Epitonium frondiculoides*, *E. granulatum*) and the trochids (*Calliostoma granulatum*). Chemosymbiotic bivalves occur only in wfc and *Archimediella*-bed samples, with a low overall diversity. They are significantly more abundant in wfc samples and are represented by the lucinid *Megaxinus incrassatus*, followed by the lucinid *Myrtea spinifera*, and then by two specimens of the previously unreported bathymodioline mytilid, *Idas sp.* (Fig. 7). All the *Megaxinus incrassatus* specimens found associated with whale bones are 3.5–5.5 cm wide and juveniles are absent. In the *Archimediella*-bed samples, chemosymbiotic bivalves are represented exclusively by *Myrtea spinifera*. Herbivores are rare in all samples and rarest in the whale fall.

DISCUSSION

General Paleoenvironment

The mollusk species studied are generally indicative of a marine outer-shelf setting, as previously demonstrated by a family-level study (Dominici et al., 2009). The predominance of suspension feeders is consistent with the general composition of benthic communities at shelf depths, whereas the high diversity and abundance of deposit feeders is typical of the deeper parts of the shelf (Rhoads, 1974). The high frequency of *Corbula gibba*, a small infaunal species inhabiting soft bottoms, is indicative of stressed conditions, either through high turbidity or low oxygen values (Hrs-Brenko, 2006 and references therein). The dominance of turrnellids in the *Archimediella* bed is consistent with a high level of particulate organic matter usually associated with coastal upwelling (Allmon, 1988), but the abundance of fossil wood suggests instead that nutrients were of fluvial origin. The hypothesis of meso- or eutrophic conditions in the Fine Basin during the Pliocene is in accordance with modern conditions in the Ligurian Sea, facing the study region. Here, high-nutrient contents occur in both

TABLE 3—Results of ANOSIM (analysis of similarity) among the four identified groups of samples. Statistical decisions are based on R-values, which give an absolute measure of the separation of the groups; s = significant, ns = not significant.

Group of samples	R	Description (based on R-values)	p	Statistical decision
total	0.5569	groups overlapping but clearly different	<0.0001	s
wfc v below wfc	0.6614	groups overlapping but clearly different	0.0033	s
wfc v <i>Archimediella</i> bed	0.8135	groups well separated	0.0078	s
wfc v lateral wfc	0.5556	groups overlapping but clearly different	0.0402	s
below wfc v <i>Archimediella</i> bed	0.3333	groups strongly overlap	0.0857	s
below wfc v lateral wfc	0.2593	groups strongly overlap	0.117	ns
<i>Archimediella</i> bed v lateral wfc	0.6667	groups overlapping but clearly different	0.1015	ns

coastal areas and offshore. Modern coastal upwelling and high productivity in the Ligurian Sea sustain an abundant and diverse cetacean fauna (Notarbartolo Di Sciarra et al., 2008), conditions that would explain the general abundance and diversity of marine vertebrates at Orciano Pisano.

Whale-Fall Ecological Succession

Due to time averaging, fossil assemblages generally do not allow the positive subdivision of stages within an ecological succession (Miller, 1986). The following discussion is to be taken therefore as a hint to possible ecological pathways within a shallow-water whale fall, relying on both observed fossil data and known modern examples.

Chondrichthyes that might have scavenged the carcass include, in addition to *Prionace glauca* and *Carcharodon carcharias* (Dominici et al., 2009), the sharks *Carcharhinus* sp., *Hexanchus griseus*, and rays (*Raja* sp.). Greater richness of predatory gastropods in whale-fall samples with respect to our other samples suggests a general high quantity of prey species and trophic niches that could interest more than one stage of ecological succession. The predatory gastropods, together with decapods and echinoids (the latter are not considered in the quantitative analysis), give a clue to the later parts of the scavenger stage (e.g., amphipods and copepods are the small scavengers responsible for the ultimate flesh consumption; Smith, 2006). Carnivorous mollusks could also have been preying on species of the enrichment-opportunistic stage, one chiefly characterized by polychaetes (Smith et al., 2002; Dahlgren et al., 2004; Goffredi et al., 2004). Whether or not whale-fall polychaetes can be a food source for species such as *Natica tigrina*, *Ringicula auriculata*, or *Nassarius semistriatus* is

presently unknown. High diversity of parasites, dominated by pyramidellids, could also indicate the opportunistic stage through their possible hosts, such as polychaetes, gastropods, and bivalves (Robertson and Mau-Lastovicka, 1979). Smith and Baco (2003) report a great abundance of the pyramidellid *Eulimella lomana* from a recent California whale-fall community during the sulphophilic stage, which also suggests that pyramidellids belong to the third successional stage.

The sulphophilic stage, fuelled by the anaerobic breakdown of bone lipids, is well represented by the lucinid *Megaxinus incrassatus* and the occurrence of the mytilid *Idas* sp. Finally, even though suspension feeders are not more abundant in whale-fall samples with respect to the background fauna, field data confirm the presence of many suspension feeders in life position directly in contact with the bones, including the pectinid *Amusium cristatum* and the arcid *Anadara diluvium*. These taxa suggest the occurrence of the reef stage, commonly recognized at shelf depths (Dominici et al., 2009).

Smith et al. (2002) hypothesized that the ecological succession at lower latitudes and shallower depths proceeds more quickly than in

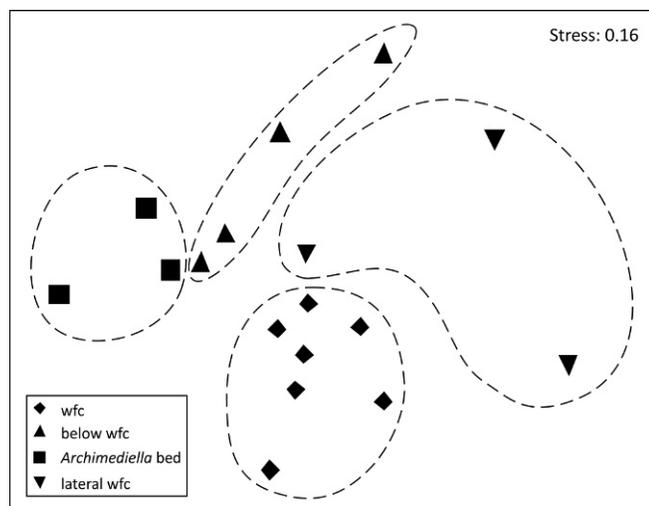


FIGURE 5—Multidimensional scaling ordination of samples belonging to the four identified *a priori* groups; wfc = whale-fall community.

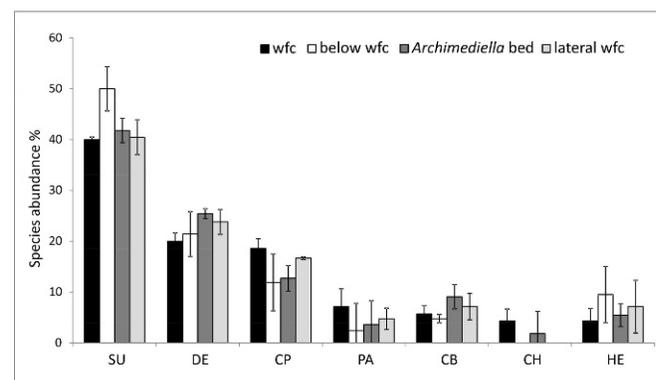
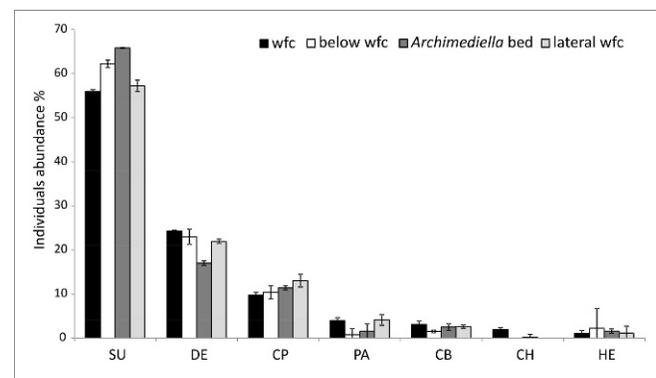


FIGURE 6—Trophic analysis expressed through percent of number of individuals (abundance) and number of species (richness). Trophic categories: suspension feeders (SU), deposit feeders (DE), predatory carnivores, including scavengers (CP), parasites (PA), browsing carnivores (CB), chemosymbiotic forms (CH) and herbivores (HE). Data shown with 95% confidence intervals; wfc = whale-fall community.

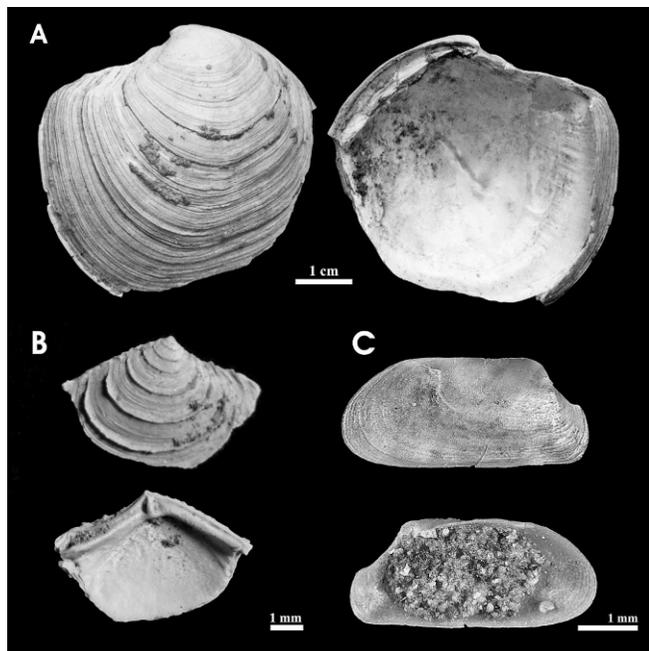


FIGURE 7—Chemosynthetic bivalves from the Pliocene whale fall at Orciano Pisano. A) *Megaxinus incrassatus*. B) *Myrtea spinifera*. C) *Idas* sp.

deep-water whale falls. In Japan, whale-fall successional stages at shallow depths suggest that the higher water temperature enhances bacterial activity on and in the carcass, shortening the duration of the sulphophilic stage (Fujiwara et al., 2007). In accordance with this hypothesis, the absence of juveniles among the paleopopulation of *M. incrassatus* suggests the presence of a single cohort.

Shallow-Water Whale Falls

Paleoecology and trophic analysis allow us to understand the effect of an episodic introduction of a large organic particle in the form of a whale carcass on the biota commonly inhabiting this area. The bulk of mollusk species found on the whale fall were already present at the site before the sinking of the carcass. The only meaningful difference concerns the introduction of two chemosymbiotic species, *Megaxinus incrassatus* and *Idas* sp., which are directly related to the whale carcass, the second with negligible abundance. These species allow us to recognize the final stages of ecological succession typical of whale falls, but with a completely different overall composition compared to deep-water analogues. Mollusk species at outer-shelf depths were thus tolerant of high organic and presumably low oxygen content around the carcass, and the study area may have experienced a generally high nutrient flux and eutrophic conditions. As a consequence, the outer-shelf species studied largely outcompeted whale-fall specialists of the sulphophilic stage, notwithstanding the fact that the Orciano whale fall could still be reached by the larvae of deep water, chemosymbiotic bivalves.

The paleoenvironmental distribution of the diagnostic, but extinct, bivalve *Megaxinus incrassatus* is not sufficiently known to understand its specificity to geologically ephemeral reducing habitats. It is also important to consider that lucinids are more generalist than deep-water vesicomyids and bathymodiolinids, and they occupy a broad range of reducing habitats from deep- to shallow-water settings (Taylor and Glover, 2006, and references therein).

In the Mediterranean Neogene, *Idas* has been previously found only at a deep-water wood fall (Bertolaso and Palazzi, 1993). Modern distributions of the genus include species (*I. simpsoni*, *I. ghisotti*, and *I. dalmasi*) found associated with sunken wood and whale carcasses at

depths of 170–430 m in the western Mediterranean (Warén and Carrozza, 1990; Warén, 1991; Bolotin et al., 2005). *Idas modiolaeformis* appears to be relatively ubiquitous in cold-seep communities of the deep eastern Mediterranean (Olu-Le Roy et al., 2004). These data confirm an outer-shelf setting at Orciano and the shallower limit of distribution of the genus *Idas*. Molecular studies single out the genus as a distinct clade in the mussel subfamily Bathymodiolinae, with putative origins in shallow water, and emphasize that *Idas* has the ability to live on various organic substrates (Jones et al., 2006; Lorion et al., 2009). This interpretation supports the stepping-stone hypothesis which assumes that carcasses of whales (and Mesozoic marine reptiles before them) facilitated the dispersal of chemosynthetic-based communities down the continental slope and into deep-sea vent and seep habitats (Smith et al., 1989; Distel et al., 2000; Kaim et al., 2008). In this scenario, outer-shelf settings such as Orciano Pisano would have a character intermediate between deep and shallow bottoms and would be sufficiently isolated from similar habitats to reduce competition for space and resources to a minimum and favor speciation within small populations of coastal-dwelling species like the mussels. Outer-shelf conditions are the most common place for the development of peripheral isolates of shallow-water species (Mayr, 1963; Frey, 1993), such as the suspension-feeding ancestors of bathymodiolins (Jones et al., 2006). These populations, therefore, would have experienced sufficiently high competition so as to suffer high selection pressure.

CONCLUSIONS

The species-level comparison of the mollusk assemblages sampled from fine-grained sediments at Orciano Pisano, some of which represent the community that lived around the carcass of a large whale, suggests that the localized reducing habitat had an intermediate character with respect to similar environments found in shallow and deep settings. In coastal bottoms, the sulphophilic stage has never been encountered, whereas in bathyal bottoms it is always one of the end stages of ecological succession.

The Orciano Pisano whale-fall community is recognizable thanks to the presence of the two chemosymbiotic bivalves *Megaxinus incrassatus* and *Idas* sp. The first is abundant, the second very rare, but both are suggestive of the sulphophilic stage of ecological succession. Although whale skeletons sunken at shelf depths are not unusual in the Neogene Mediterranean record, this is the first case of a fully developed whale-fall community at shelf depths and the first overall in the Mediterranean Sea. Other aspects of the whale-fall mollusk community, however, make it impossible to statistically recognize this community from the one living at this depth in more normal conditions. High organic content at the whale fall is largely exploited by shelf species already tolerant of dysoxic conditions.

Whale-fall deposits can serve as important sites to test the hypothesis that very large organic particles, such as whale carcasses, served as evolutionary stepping stones between marine environments. Whale falls in outer-shelf settings, as in the Orciano example, would be relatively isolated from shallow counterparts and be ideal sites for speciation within small populations commonly inhabiting coastal areas.

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