



Crossing The Ecological Divide: Paleozoic To Modern Marine Ecosystem In The Adriatic Sea

By: **Frank K. McKinney, Steven J. Hageman,** and Andrej Jaklin

Abstract

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Crossing the Ecological Divide: Paleozoic to Modern Marine Ecosystem in the Adriatic Sea

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ABSTRACT

The northern Adriatic Sea supports both typical modern marine benthic associations of animals that live within the sediment and other associations with a Paleozoic ecological aspect, rich in sedentary animals that live exposed on the sea floor. Site-specific information on sediment grain size, deposition rate, currents, nutrient availability, and life habits of animals in the local associations are compared to test several hypotheses about the transition from the Paleozoic to the modern ecosystem. By far the strongest correlations of life habit attributes is with nutrient concentration, supporting the hypothesis that increased nutrient concentration in the sea was important in the change from Paleozoic to modern marine benthic ecology.

INTRODUCTION

Profound change in marine ecosystems took place during the Mesozoic. The sedentary, suspension-feeding animals living *on top* of the sea floor (epibenthos), prevalent in Paleozoic marine ecosystems gave way to animals living *in* the sediment (endobenthos e.g., clams) and mobile carnivores (e.g., crabs, snails). The change in dominant life habits is sufficiently striking to be apparent to fossil collectors and thoughtful historical geology students, and it has been well documented by paleobiologists (e.g., Bambach, 1983; Sepkoski, 1981). The change is not purely a result of which animals made it through the massive end-Permian extinction. Extinction survivors include some brachiopods, crinoids, sponges, and bryozoans that are sedentary epibenthic suspension feeders. Collectively, these survivors with Paleozoic life habits have dwindled in importance in the sea while other survivors thrived, evolving morphologically and behaviorally into efficient predators (primarily epibenthic), and invaded endobenthic habitats, thus developing into the modern fauna (Sepkoski, 1981).

What caused the profound change from the sedentary, epibenthic suspension feeding communities of the Paleozoic to the endobenthic/carnivore-dominated modern communities? Recent syntheses (McKinney and Hageman, 2006; McKinney, 2007) group the hypotheses explaining the change into four groups that are not mutually exclusive: 1) clogging and tipping of sedentary epibenthic suspension-feeders by sediment-disturbing animals (Thayer, 1979, 1983); 2) displacement of low-energy Paleozoic taxa by the more rapidly growing, higher-energy modern fauna (Vermeij, 1987); 3) increased predation intensity at the sediment-water

interface so that life is safer within the sediment (Vermeij, 1987); and 4) an increase from oligotrophic (low-nutrient) Paleozoic seas to more nutrient-rich conditions, with greater accumulation of food resources on and within the sea floor (Vermeij, 1987; Bambach, 1993, 1999).

These hypotheses were proposed twenty years ago, soon after the major changes in benthic marine communities were delineated. The hypotheses are difficult to test and since then, paleoecologists and evolutionary paleobiologists have changed focus; there have been few attempts to test the cause or causes of the most fundamental change in marine ecosystems during the Phanerozoic.

Here we test the hypotheses by using distributional patterns observable in the present to elucidate the processes recorded in the past. The shallow northern Adriatic Sea (Figure 1B) has a flat sedimentary floor averaging only 35 m deep yet includes local associations that have a Paleozoic ecological structure and others that have a modern structure. Adriatic oceanography has been intensely studied, and the benthos of the northern Adriatic is well known. This work provides a uniformitarian test for the four hypotheses listed above, comparing the distribution of benthic life habits within the northern Adriatic relative to a range of oceanographic variables.

OCEANOGRAPHIC CONTEXT

Oligotrophic water enters the Adriatic Sea from the Mediterranean through the Otranto Strait (Figure 1A) and then follows an overall cyclonic path with secondary cyclonic gyres in the southern, middle, and intermittently in the northern Adriatic (Artegiani et al., 1997). It is supplemented by fresh water along the way, 80% of which is added along the Italian coast, including water from the Po River (30% of the total), the single largest source (Raicich, 1994).

The northern Adriatic is so shallow that cyclonic flow is less vigorous there than elsewhere in the Sea. It is best developed during winter when low air temperatures and frequent windstorms eliminate the previous summer's density stratification so that both the western freshwater stream and northeastern windstorms enhance the basin-wide cyclonic pressure. In contrast, during the summer a variable combination of high discharge of the Po, high temperatures, and greatly diminished winds result in surface ponding of low density water that inhibits and sometimes almost stops cyclonic flow.

Terrigenous nutrients and sediment (70% silt; Colantoni et al., 1979) are introduced into the Adriatic Sea primarily by Po River. Only a small proportion of the Po's sediment load remains in its delta, the

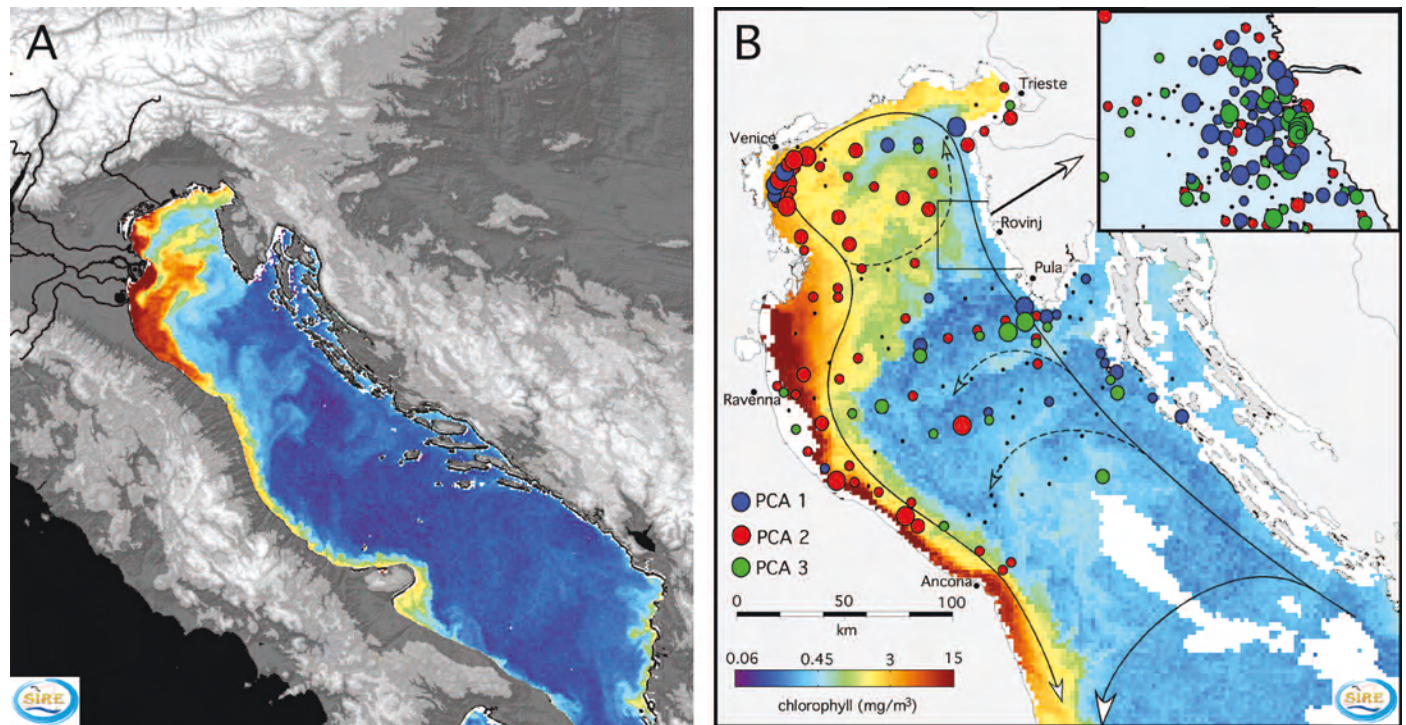


Figure 1. Chlorophyll *a* distribution in the Adriatic Sea. **A)** The entire Adriatic Sea on 14 August 2001. Counterclockwise circulation brings low-nutrient water (dark blue) through the Otranto Strait and up the Balkan coast, where nutrient input is virtually nil from the carbonates of the Dinarides. Nutrients - derived largely from the Apennines and the western Italian Alps - pour into the Adriatic from the Po and other rivers at the northwestern end of the Sea, and the basin-wide current system carries the nutrient-enriched water southward along the Italian coast; **B)** distribution of Vatova stations plotted on chlorophyll *a* map of the northern Adriatic for 16 February 2001.

bulk being swept southward (Cattaneo et al., 2003; Frignani et al., 2005) to accumulate in a relatively narrow band along the Italian coast. Most of the northern Adriatic is floored by Pleistocene carbonate sand that was partially reworked into overstepping parasequences during the Holocene transgression (Trincardi et al., 1994). Aside from coarse debris aprons at the base of carbonate escarpments and some local cemented sands, northern Adriatic sediments are fine-grained, largely silt-rich muds to medium sand (Jenkins et al., 2005).

Primary nutrients (N, P, Si) introduced by the Po River substantially exceed the mass of each transported up from the Mediterranean (Degobbi and Gilmartin, 1990). Lesser contributions from other Italian rivers combine with nutrients from the Po to result in about twice the mass of each of the primary nutrients being flushed out of the northern Adriatic southward along the Italian coast than stream northward along the Balkan coast, despite the loss of nutrients into sediments.

There is a permanent east to west increase in nutrients and chlorophyll *a* in the northern Adriatic Sea. Chlorophyll *a* measures the abundance of phytoplankton that are primary consumers, tracking nutrient availability. The east to west gradients in concentration are

steeper and on average farther west during the winter when cyclonic circulation and communication with the rest of the Adriatic are stronger.

LIFE MODE CHARACTERIZATION OF LOCAL BENTHOS

Aristotle Vatova (1935, 1949) took Van Veen grab samples at several hundred stations in the middle and northern Adriatic, and for each sample he determined wet biomass of each animal species present. The 280 samples in the northern Adriatic included a total of 330 species plus 16 indeterminate assignments within an order or family; over half the species had mineralized skeletons. Polychaetes, bivalves, crustaceans, and snails comprise 82% of the species, typifying a modern fauna. Ophiuroids and crinoids were the only descendants of the Paleozoic fauna and comprised only 2% of the species.

Life mode of each species in Vatova's samples was determined. Life mode attributes and their various states scored were 1) *trophic type*: suspension feeder, deposit feeder, detritus feeder, carnivore, omnivore-grazer-herbivore; 2) *position relative to the sediment-water interface*: epibenthic, endobenthic; and 3) *mobility*:

sedentary, mobile non-bioturbator, bioturbator.

Biomass values in Vatova's samples were log-transformed and analyzed using Principal Components Analysis. Principal Components Analysis is a method of combining variables through a weighting scheme into new dimensions. Thus variables with high values for coefficients of a combination (see examples in next paragraph) display the greatest degree of variation in the system. Localities with large values for biomass in a combination will plot high on an axis.

Three axes (PCAs) accounted for over 70% of the variance among samples. "Modern" attributes of bioturbator, endobenthos, and deposit feeder loaded on PCA 2, characterizing northwestern Adriatic sample stations (Figure 1 red dots). The "Paleozoic" attributes of sedentary, epibenthic, suspension feeder, and of epibenthic, mobile non-bioturbator, and omnivore loaded on PCA 1 and 3 respectively, characterizing northeastern sample stations (Figure 1B blue & green dots; Figure 2).

These results based on Vatova's systematic samples do not even include the most startlingly Paleozoic-appearing associations offshore of Rovinj, Croatia (Figure 2D, E). Samples located in these bryozoan tangles

were entered on Vatova's (1935) map of stations but were not included in either the discussion or tables of data. Quite possibly they were so rich in densely intergrown, firmly attached species that they could not be accommodated in Vatova's careful counts and biomass determinations.

LIFE MODES AND ENVIRONMENTAL VARIABLES

Sedimentation rate, sediment type, and nutrient environment are available for each of the northern Adriatic stations, along with distribution of biomass of carnivores and of bioturbators. Each of these is relevant to hypotheses for the Paleozoic to modern ecological change.

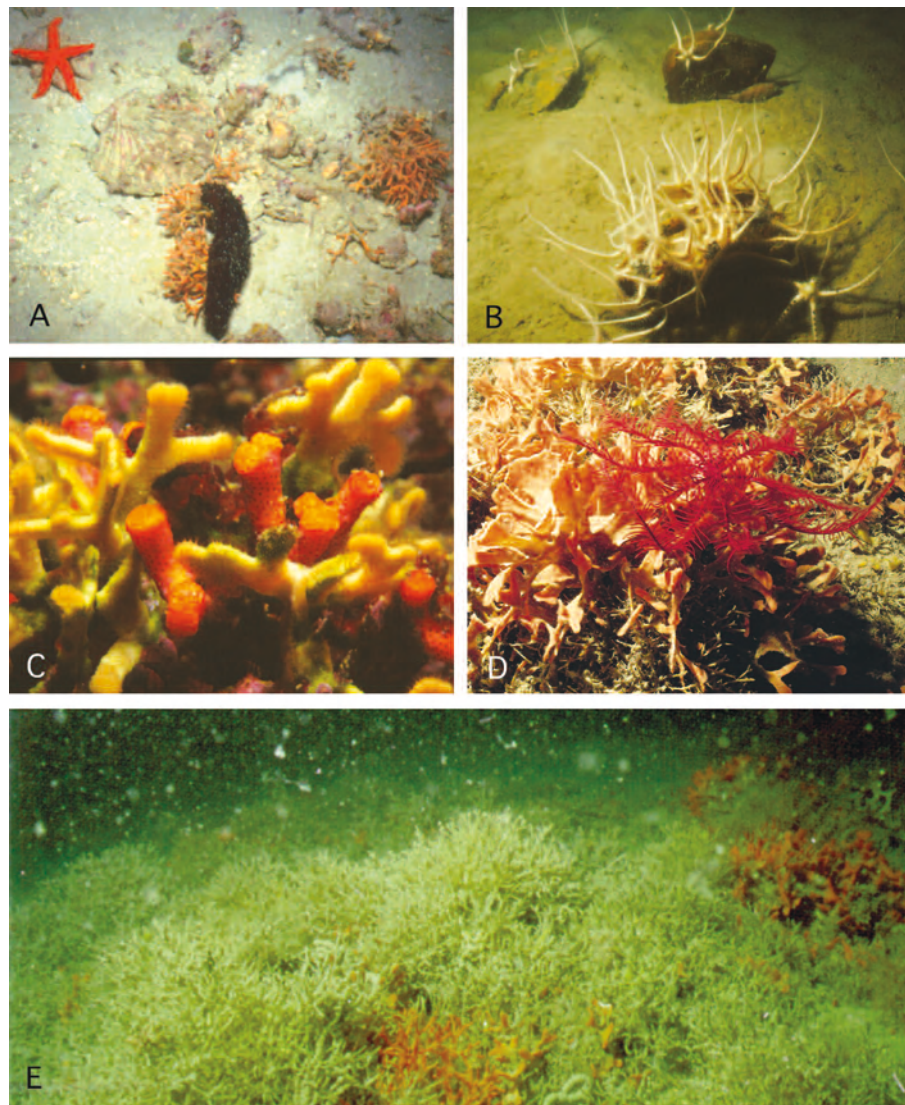
Variables with little regional influence

Sediment flux is considered detrimental to suspension feeders and is generated by sediment accumulation or by resuspension due to water motion or bioturbation (Rhoads and Young, 1970). Sixty-six of Vatova's stations were within the Italian coastal band of measurable sedimentation, spanning accumulation rates of 0.01-0.75 g cm⁻² yr⁻¹. None of the life habit attribute states is significantly correlated with sediment accumulation rate (Table 1), which suggests that these rates are too low to have a major effect on the distribution of life modes across the area. Bioturbators occur in 275 of the 280 benthic samples characterized. They do not correlate significantly with epibenthos as a whole ($p = 0.311$) or with sedentary epibenthos ($p = 0.714$), and there is no significant difference in endobenthic biomass between samples with and samples lacking sedentary epibenthos (McKinney, 2007).

Predation intensity is low in the northern Adriatic, similar to that of high latitudes rather than the more predation-intense tropical shallow waters (McKinney, 2007). Most predators that are present have relatively low impact; very few are shell-crushing, shell-drilling, high energy predators that originated during the Mesozoic Marine Revolution. Shell-drilling intensity along the northwestern, Italian coast is more similar to normal Cretaceous drilling intensity than to the more highly escalated Cenozoic intensity (Kelley, 2006). There is no evidence for a lateral gradient in overall predation intensity (see below). Predation is not a sufficient cause for the west to east increase in epibenthos.

Variables with pronounced influence

Sediment texture is an important aspect of the benthic environment and correlates with



Adriatic epibenthos near Rovinj, Istrian coast of Croatia. A) typical epibenthos of the sedimentary plain, both mobile (starfish, holothurian) and sedentary (bryozoans, tunicates, and diverse encrusting animals on the shell of a dead bivalve); B) suspension-feeding ophiuroids, Ophiothrix fragilis, exhibiting the common behavior of using a local topographic high (here the projecting portions of the semi-endobenthic bivalve Atrina pectinata) to gain elevation in the water column; C) intergrowth of the erect rigidly calcified bryozoans Myriapora truncata (red) and Schizotheca serratimargo (orange); D) the crinoid, Antedon mediterranea, using a colony of the bryozoan Pentapora fascialis as an ersatz stem, much as done by the ophiuroids on the cover and in the illustration above; E) meadow of the articulated erect bryozoan Cellaria salicornioides with scattered colonies of the bryozoan P. fascialis, during a marine snow event; white blobs in the water are mucilage generated by diatoms. Widths of view in A and B are about 40-50 cm in the foreground, in C about 9 cm, in D about 25 cm, and in E 1-1.5 m.

some life mode attributes (Table 1). Only sedentary endobenthos correlates with an increase in grain size, apparently due to endobenthic tube-dwelling polychaetes' preference for sandy sediment. All the other significant ($p < 0.05$) correlations with grain size are with finer grain size, including sedentary and suspension-feeding epibenthos. Finer grain sizes are more common in the west than the

east (Jenkins et al., 2005), so the absence of sedentary and suspension-feeding epibenthos in the west is not due to lack of availability of preferred substrate.

Remarkably, almost every individual life mode attribute state and critical combination of states correlates significantly with both summer and winter chlorophyll *a* distribution in the northern Adriatic Sea (Table 1). The

Table 1. Correlation of biomass of life mode attribute states and of position (endobenthos, epibenthos) in combination with associated critical attribute states. Note that “Paleozoic fauna” is negatively correlated with increase in productivity as indicated by chlorophyll *a*, whereas the biomass of “Modern fauna” increases with higher productivity. Correlations here and in the text are determined by Kendall's tau. Sign (positive, negative) is given for correlations $p \leq 0.05$. Biomass and grain size (approximated to phi by FKM) data are from Vatova (1935, 1949), deposition rate is from Frignani et al. (2005), and chlorophyll *a* data are from Zavatarelli et al., 1998. Deposition rate ranges from 0.01-0.75 g cm² yr⁻¹, grouped into 5 bins; phi ranges from -1.5 to 9, grouped into 11 bins; chlorophyll *a* ranges from 0- >3.5 µg l⁻¹, grouped into 13 bins.

		Deposition Rate	Grain size (phi)	Chlorophyll <i>a</i>	
				Summer	Winter
M	Endobenthos	.789	.064	+0.000	+0.000
O	Bioturbator	.828	.072	+0.000	+0.000
D	Deposit feeder	.487	.404	.060	+0.023
E	Endobenthic sedentary	.399	-.008	+0.044	+0.003
R	Endobenthic bioturbator	.666	+0.041	+0.000	+0.000
N	Endobenthic suspension feeder	.686	.458	+0.000	+0.000
	Endobenthic deposit feeder	.350	.347	+0.010	+0.001
	Detritus feeder	.429	+0.023	+0.016	+0.023
	Carnivore	.884	.205	.471	.333
P	Suspension feeder	.998	.052	+0.040	+0.002
A	Epibenthos	.893	+0.008	-0.000	-0.002
L	Sedentary	.621	+0.023	.808	.738
E	Mobile non-bioturbator	.572	.129	-0.000	-.013
O	Omnivore etc.	.913	+0.017	-0.000	-0.000
Z	Epibenthic sedentary	.124	+0.001	-0.000	-0.002
O	Epibenthic mobile non-bioturbator	.994	.067	-0.000	-.020
I	Epibenthic suspension feeder	.313	+0.001	-0.000	-0.002
C	Epibenthic omnivore etc.	.229	.320	-0.001	-.008

exceptions are for sedentary and carnivore, and summer correlation with deposit feeder. The poor correlation of carnivores with chlorophyll *a* reflects the essentially uniform predation intensity across the northern Adriatic, and the poor correlation of sedentary with chlorophyll *a* is due to “sedentary” including stationary endobenthos as well as attached epibenthos, so the sedentary condition does not sort out exclusively to epibenthos.

Highly significant *positive* correlations ($p < 0.01$) with chlorophyll *a* characterize all but three of the attribute states of PCA 2 and combinations of *endobenthos* with other importantly associated states (Table 1), and only one correlation is non-significant. The positive correlations indicate that life modes that characterize the modern marine ecosystem are dominant in nutrient-rich regions of the northern Adriatic.

Highly significant *negative* correlations with chlorophyll *a* characterize all but five of the attribute states of PCA 1 and 3 and combinations of *epibenthos* with other importantly associated states (Table 1). The patterns for sedentary and for suspension feeder are complicated by the abundance of endobenthic suspension feeders that live in stationary burrows. The negative correlations of all the other

attribute states and combinations indicate that life modes that characterized the Paleozoic marine ecosystem occur in nutrient-poor regions of the northern Adriatic.

WIDER IMPLICATIONS

Endobenthos and epibenthos alike are comprised of modern fauna taxa in the northern Adriatic. Therefore the marine benthic ecosystem that characterized the Paleozoic could have been carried on after the Paleozoic by the modern fauna. This is one of the most important paleontological insights from the northern Adriatic benthos.

As discussed above, the range of predation intensity and of sediment texture and flux, including flux generated by bioturbation, does not appear to have a major influence on the regional pattern of endobenthic versus epibenthos-rich associations in the northern Adriatic. The northern Adriatic offers no systematic support for the hypothesis that bioturbation caused the decline of the Paleozoic ecosystem. The basin-wide condition of low predation intensity means that the northern Adriatic in isolation does not provide an adequate test of predation as a cause of the change from Paleozoic to modern benthic ecology.

The environmental context that clearly determines the distribution of Paleozoic versus

modern ecosystem structure in the northern Adriatic is nutrient availability as reflected in chlorophyll *a* content of the water. This gives strong support to the hypothesis (Vermeij, 1987; elaborated by Bambach, 1993, 1999) that increased nutrient concentration in shallow marine water was critical in the change from Paleozoic to modern marine ecosystem organization.

Sedentary suspension-feeding epibenthic associations exist today in some areas in the shallow Antarctic (Dayton and Oliver, 1977; Gili et al., 2006) and also at bathyal and abyssal depths, all of which are characterized by both low nutrient levels and low predation intensity, as in the northeastern Adriatic. In contrast, shallow waters where either nutrient-rich water and/or high predation occur have an endobenthos-rich modern ecosystem (McKinney, 2007). The latitudinal distribution of bryozoan-rich limestones (Taylor and Allison, 1998) and some studies of Cenozoic benthos across ecological gradients (Lukasik et al., 2000; Tomasovych, 2006) see the same pattern. It appears that “Paleozoic” ecosystems composed of animals of the modern fauna reappear regularly if an appropriate environment of low nutrient levels and low predation intensity occurs.

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