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Abstract

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Paleozoic to modern marine ecological shift displayed in the northern Adriatic Sea

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ABSTRACT

One of the major changes in the history of life was the decline from abundant sedentary, suspension-feeding animals living on the seafloor during the Paleozoic to their relative scarcity afterward, while animal life within the sediment burgeoned after the end-Paleozoic extinction. In the northern Adriatic Sea there is a quantitative change from abundant exposed sedentary suspension feeders in eastern oligotrophic water to their virtual absence under western higher-nutrient waters, where prolific animal life occurs within sediments. This geographic gradient supports the hypothesis that an increase in neritic nutrients drove—and continues to drive—the Paleozoic to post-Paleozoic marine ecological transition.

Keywords: Phanerozoic, paleoecology, epibenthos, endobenthos, nutrients.

INTRODUCTION

The change from animals living predominantly on the soft-sediment surface of the seafloor (epibenthos) to being primarily buried within the sediment (endobenthos) is a pronounced and intriguing long-term ecological trend in the marine fossil record (Bambach, 1983). This transition generally corresponds with the change from statistically defined Paleozoic to modern marine taxonomic faunas (Sepkoski, 1981). Ordovician through Permian marine fossils (the Paleozoic fauna) are characterized by brachiopods, crinoids, ostracodes, cephalopods, anthozoans, stenolaemate bryozoans, and nearshore bivalves. The majority of these animals were epibenthic sedentary suspension feeders, though as the Paleozoic progressed the diversity and abundance of swimmers and sediment burrowers increased moderately. Many higher taxa that characterized the Paleozoic fauna were eliminated by, or never recovered appreciably, from the end-Paleozoic extinction (Sepkoski, 1981).

Post-Paleozoic modern faunal remains are dominated by bivalve and gastropod mollusks, along with teleost fish, malacostracan arthropods, polychaetes, and echinoids (Sepkoski, 1981). Diverse members of the modern fauna have vigorously exploited life within the sediment, including depths >1 m (Bambach, 1983), and endobenthic shelled species can reach densities of $>10^5$ live individuals per square meter (Ambrogi and Occhipinti Ambrogi, 1987). There has also been a proliferation of swimming, epibenthic, and endobenthic carnivores. In contrast with the increase in endobenthos and diverse carnivores, sedentary epibenthic suspension feeders declined significantly after the Paleozoic (Thayer, 1979, 1983), and in many environments are virtually or entirely absent.

Several hypotheses have been advanced to account for the change from the marine Paleozoic ecosystem rich in sedentary, suspension-feeding epibenthos to the modern endobenthos-rich ecosystem. These include (1) competitive displacement of the slow-growing, low-energy Paleozoic fauna by more rapidly growing, higher-energy members of the modern fauna (Vermeij, 1987); (2) increased bioturbation, i.e., sediment disturbance by animals living and probing within the sediment, potentially toppling and/or clogging the feeding mechanisms of epibenthic sedentary suspension feeders (Thayer, 1979, 1983); (3) increased predation of exposed sedentary animals leading to refuge seeking within sediments (Vermeij, 1987; Harper, 2003); and (4) change

from oligotrophic Paleozoic seas to more nutrient-rich post-Paleozoic seas, leading to greater availability of food resources on and within the sediments (Vermeij, 1987; Bambach, 1993, 1999).

Do ecological gradients in the Holocene provide any fundamental insight into the major marine ecological changes over tens to hundreds of millions of years? Abundant epibenthic sedentary suspension-feeding animals live in some areas of the northern Adriatic Sea (McKinney, 2003) but are completely absent in others (Ambrogi and Occhipinti Ambrogi, 1987). The gradient in epibenthic-endobenthic structure across this recently flooded region therefore relates to the question of Phanerozoic evolution of marine benthic ecosystems. The epicontinental Adriatic Sea, located on the narrow remnant of the subducting thin microplate Adria (Doglioni et al., 1994), is between Italy and the Balkan Peninsula. The entire northern portion is a low-gradient, flat-floored epeiric sea <18 k.y. old (Amorosi et al., 2003) with an average depth of ~ 35 m.

DATA

A unique set of more than 500 grab samples was taken in the 1920s–1930s across the sedimentary floor occupying the entire northern and middle Adriatic Sea (Vatova, 1935, 1949), from the Italian coast to the Balkan coast. At each station a sample was taken with a 0.2 m² Van Veen grab, and all benthic animal species in each sample were identified and their wet biomass determined. We used data from all 280 open-water stations in the northern Adriatic (Fig. 1C) to assess basic benthic ecosystem characteristics across the region (see GSA Data Repository Appendix DR1¹). Data from each station result in a data point in each part of Figure 1. For each species we determined character states (attributes) for three major life mode categories: (1) trophic type, i.e., suspension feeder, deposit feeder, detritus feeder, omnivore-grazer-herbivore, carnivore; (2) position relative to the sediment-water interface, i.e., epibenthic, endobenthic; and (3) mobility, i.e., sedentary, mobile nonbioturbator, bioturbator. Values for life mode attributes were coded for each species as wet biomass (0–500 g) for each station. Log-transformed wet biomass distribution and asso-

¹GSA Data Repository item 2006185, Appendix DR1, environmental characteristics and zoobenthos occurrence, is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

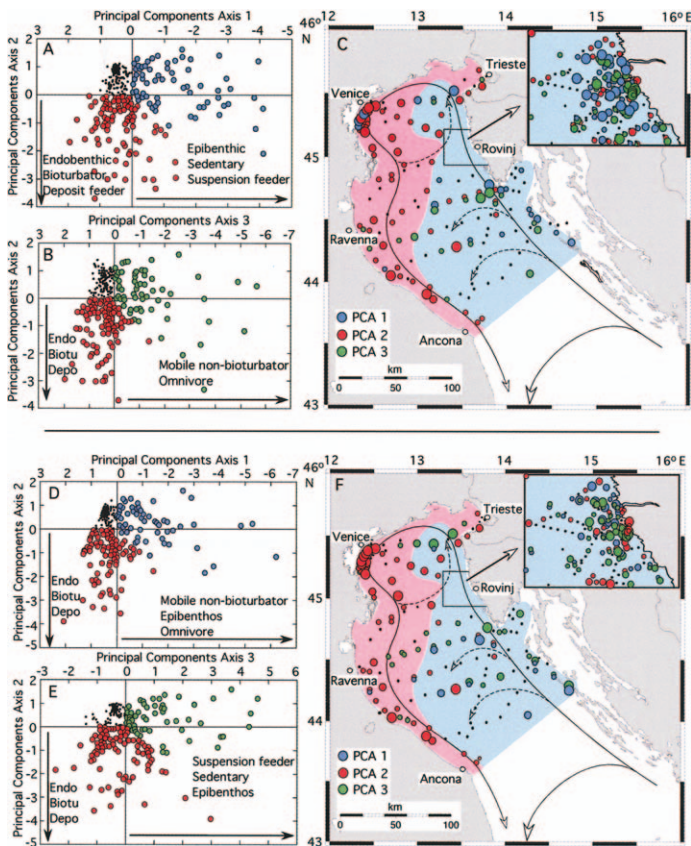


Figure 1. Rotated principal components axes (PCA) 1–3 for life mode attributes of zoobenthos from open-water northern Adriatic stations (Vatova, 1935, 1949) based on biomass of all species (A, B), and map (C) with sample stations and PCA affiliation, and similar figures (D–F) for results based only on mineralized species. In A–C, PCA 1 has high values for sedentary, epibenthic, and suspension feeder; PCA 2 has high values for bioturbator, endobenthos, and deposit feeder; and PCA 3 has high values for mobile nonbioturbator and omnivore. In D and E, PCA 1 has high values for mobile nonbioturbator, epibenthos, and omnivore; PCA 2 is same as in A–C; and PCA 3 has high values for sedentary, epibenthic, and suspension feeder. Small black dots represent samples with low biomass values and are not assigned to any PCA grouping; blue, red and green dots indicate samples with high absolute values along PCA 1, PCA 2, and PCA 3, respectively. Smallest colored dots indicate PCA values <1, intermediate size represents intermediate values, and largest dots denote values ≥ 2 . Average summer chlorophyll *a* concentration of $< 6 \mu\text{g L}^{-1}$ from 1948 to 1991 (Zavatarelli et al., 1998) is indicated by light blue shading and higher concentration is indicated by pink shading. Arrows on map indicate average annual major (solid arrows) and minor (dashed arrows) currents.

ciation of life habit attributes for all species and for the subset of species with mineralized skeletons (potential fossils) were analyzed using principal components analysis. For each sample locality, the log-transformed wet biomass for each life mode attribute was summed, resulting in a vector of 10 values, each value representing the relative importance of life mode attributes for that sample. The samples included a total of 330 species plus 16 indeterminate assignments within an order or family; 57% of determined species have mineralized skeletons.

Life Mode Attribute Distributions

Plots of rotated principal component axes (PCA) show two clear extensions along the respective axes if all species are included (Figs. 1A, 1B) and also if only mineralized species are included (Figs. 1D, 1E). On each graph, data points are assigned to one of two groups (color coded) based solely on their relative proximity to each axis.

TABLE 1. LOADINGS OF LIFE MODE CHARACTER STATES ON PRINCIPAL COMPONENTS AXES 1 THROUGH 3 (VARIMAX ROTATION) FOR ZOOBENTHOS

	All species			Mineralized species		
	PCA 1	PCA 2	PCA 3	PCA 1	PCA 2	PCA 3
Sedentary	-0.91*	-0.06	-0.22	-0.34	0.10	0.83*
Suspension feeder	-0.91*	-0.27	-0.12	-0.15	-0.32	0.87*
Epibenthos	-0.80*	-0.04	-0.54*	-0.77*	-0.04	0.59*
Bioturbator	-0.17	-0.94*	0.03	0.04	-0.96*	0.16
Endobenthos	-0.20	-0.93*	0.06	0.05	-0.95*	-0.14
Deposit feeder	0.05	-0.72*	-0.42	-0.47	-0.68*	-0.30
Mobile non-bioturbator	-0.34	-0.10	-0.85*	-0.92*	-0.07	0.14
Omnivore	-0.15	-0.00	-0.79*	-0.74*	0.02	0.19
Detritus feeder	-0.35	-0.21	-0.02	-0.09	-0.27	0.29
Carnivore	-0.27	-0.31	-0.11	-0.15	-0.34	0.18
<i>cumulative variance</i>	41%	60%	72%	36%	59%	71%

Note: Data from 280 stations in the open northern Adriatic Vatova (1935, 1949) based on biomass of all species and only species with mineralized skeletons. Characteristics most strongly correlated with each axis are highlighted in bold and an asterisk.

Sample localities with low biomass (upper left quadrant) are not differentiated by group and are indicated as small black dots.

The first three axes account for more than 70% of the variance among the samples (Table 1) for both analyses (all species and mineralized only). For all species (Figs. 1A, 1B), PCA 1 has high factor loading values for sedentary, epibenthic, and suspension feeder; PCA 2 has high values for bioturbator, endobenthos, and deposit feeder; and PCA 3 has high values for mobile nonbioturbator and omnivore (Table 1). For mineralized species only (Figs. 1D, 1E), PCA 2 remains unchanged but there is mixing of life habit attributes between PCA 1 and 3: PCA 1 has high factor loading values for mobile nonbioturbator, epibenthos, and omnivore; PCA 3 has high values for suspension feeder and sedentary and is moderately high for epibenthos (Table 1).

For all species (Fig. 1C) and for mineralized species (Fig. 1F), most samples with high absolute values for PCA 1 and PCA 3 occurred in the eastern part of the northern Adriatic, while those with high absolute values for PCA 2 occurred largely in the western part or adjacent to the harbor and fish factory of Rovinj, Croatia. Epibenthic sedentary suspension feeders and mobile epibenthic surface-feeding omnivores (grazers) are abundant across much of the northeastern Adriatic Sea but are largely absent in the northwestern Adriatic.

CORRELATIONS

Important environmental attributes that potentially vary geographically within the northern Adriatic Sea, and therefore might contribute to the distribution of communities characterized by endobenthos and communities rich in epibenthos, include sediment texture, sediment deposition rate, intensity of bioturbation, and nutrient availability.

Sediment Texture and Deposition Rate

Relatively fine sediments, largely silt-rich mud to medium sand (Pigorini, 1968; Jenkins et al., 2005), underlie most of the northern Adriatic. Coarser allochthonous sediments are largely restricted to the aprons immediately adjacent to rocky headlands or around the bases of steep-sided carbonate islands. Vatova (1935, 1949) briefly described sediments in each grab sample, using 5 basic size terms plus modifiers for a total of 26 descriptive combinations, which we placed into 11 relatively discrete size-graded (ϕ) groups.

Few individual life habit attributes correlate significantly with sediment grain size (Table 2). The strongest correlation for grain size is with epibenthos; less highly significant correlations are with sedentary, detritus feeder, and omnivore. These correlations between life habit attributes and sediment size (ϕ) are positive, indicating greater biomass with finer grain size.

If life habit attributes are combined, there are strong correlations

TABLE 2. PROBABILITIES (2-TAILED) FROM KENDALL'S TAU FOR THE CORRELATION OF INDIVIDUAL AND SELECTED COMBINATIONS OF LIFE MODE ATTRIBUTES WITH GRAIN SIZE (PHI) AND $\mu\text{G L}^{-1}$ CONCENTRATION OF CHLOROPHYLL *a* (ZAVATARELLI ET AL., 1998) IN THE SUMMER AND WINTER

	Grain size		Chlorophyll <i>a</i>			
			Summer		Winter	
	tau	<i>p</i>	tau	<i>p</i>	tau	<i>p</i>
Epibenthos	+ .12	.008	-.24	.000	-.14	.002
Endobenthos	+ .05	.064	+ .27	.000	+ .25	.000
Sedentary	+ .10	.023	-.01	.808	+ .02	.738
Mobile non-bioturbator	+ .07	.129	-.20	.000	-.11	.013
Bioturbator	+ .08	.072	+ .25	.000	+ .24	.000
Suspension feeder	+ .09	.052	+ .10	.040	+ .13	.002
Deposit feeder	+ .04	.404	+ .09	.060	+ .10	.023
Detritus feeder	+ .12	.023	+ .13	.016	+ .11	.023
Omnivore etc.	+ .12	.017	-.20	.000	-.16	.000
Carnivore	+ .06	.205	-.03	.471	+ .04	.333
Epibenthic and						
sedentary	+ .17	.001	-.22	.000	-.15	.002
mobile non-bioturbator	+ .08	.067	-.19	.000	-.10	.020
suspension feeder	+ .16	.001	-.26	.000	-.14	.002
omnivore	+ .05	.320	-.18	.001	-.13	.008
bioturbator	-.04	.486	+ .09	.092	+ .16	.002
Endobenthic and						
sedentary	-.13	.008	+ .10	.044	+ .14	.003
bioturbator	+ .09	.041	+ .24	.000	+ .23	.000
suspension feeder	-.03	.458	+ .32	.000	+ .27	.000
deposit feeder	+ .04	.347	+ .12	.010	+ .14	.001

Note: Grain size: n = 280.
Chlorophyll *a*: n = 272; 8 stations in and near the nutrient-enriched Rovinj harbor are omitted because they are not part of the open-water pattern documented by Zavatarelli et al.
p = .000 are all *p* < .0005.

(Table 2) between sediment phi and epibenthic sedentary, epibenthic suspension feeder, and endobenthic sedentary (i.e., animals that live within the sediment but inhabit one space that slowly expands to accommodate increased body size rather than habitually moving through the sediment). Weaker correlation occurs between sediment phi and endobenthic bioturbator. Among these correlations, only endobenthic sedentary is negative, i.e., correlates with larger grain size. All other life habit combinations with significant correlations are with smaller grain size, which was not the expectation for epibenthic sedentary organisms.

The Adriatic Sea occupies a sediment-starved basin, and most of the northern Adriatic seafloor consists of relict Pleistocene sand, locally covered by Holocene mud (Pigorini, 1968) at most a few centimeters thick (Colantoni et al., 1979). Otherwise the Holocene highstand system tract, developed within the past ~5500 yr, is almost nonexistent along the Croatian coast, confined to a coastal belt <10 km wide along the Italian coast north of the Po River mouth, and ~50 km wide south of the Po Delta (Correggiari et al., 1996; Frignani et al., 2005). The Po River is the primary sediment input into the Adriatic Sea. Although sedimentation rate is moderately high immediately at the Po River mouth (>2 g cm⁻² yr⁻¹), most of the narrow sedimentation belt receives <0.15 g cm⁻² yr⁻¹ (Frignani et al., 2005).

The narrow coastal belt of Holocene deposition in the northern Adriatic Sea does not correspond with the zone of transition from the region of predominantly endobenthic communities to that of epibenthos-rich communities. Even where sediment accumulation is most vigorous, near the mouth of the Po River, it is an order of magnitude less than the level that sedentary epibenthos tolerate on the Rhône Delta (Lagaaïj and Gautier, 1965). In addition, tidal currents can be sufficiently vigorous off the Croatian coast that sediment suspension during maximum tidal flow at 30–40 m depth reduces visibility at the seafloor to <1 m (A. Jaklin, 1998, personal commun.) where extensive living thickets of erect sedentary suspension feeders have baffled at

least 0.3 m thickness of fine sediment during the Holocene highstand (McKinney and Jaklin, 2001). Sedimentation rate is therefore insufficient to cause the east-west change from epibenthos-rich to endobenthic communities.

Nutrient Level

Overall cyclonic circulation within the Adriatic brings oligotrophic Aegean water through the Otranto Strait, little altered as it flows up the eastern coast, which then mixes with nutrient- and sediment-laden water of the Po and other northern rivers as it begins to flow along the Italian coast (Figs. 1C, 1F) and ultimately back out the Otranto Strait (Poulain, 2001). Better-developed cyclonic flow during winter produces a sharper gradient between the oligotrophic eastern water and eutrophic western water within the northern Adriatic (Krajcar, 2003), but the general pattern persists even during reduced summer circulation intensity.

Zavatarelli et al. (1998), on the basis of more than 5000 casts, compiled seasonal nutrient levels across the Adriatic Sea for 1948–1991. Vatova's sample sites from the 1920s–1930s were grouped into bins determined by 2 $\mu\text{g l}^{-1}$ chlorophyll *a* isograds for summer and winter 1948–1991 as given by Zavatarelli et al. (1998).

Northern Adriatic epibenthos-rich communities are located in oligotrophic water. In addition to epibenthos as a whole (Table 2), the attribute combinations epibenthic sedentary, epibenthic mobile nonbioturbating, epibenthic suspension feeding, and epibenthic omnivore correlate negatively with summer and winter chlorophyll *a* concentration, and each of these correlates more strongly with chlorophyll *a* concentration in summer, which is the primary growth period in the Adriatic.

Northern Adriatic endobenthos-dominated communities occur in mesotrophic and eutrophic waters. In addition to the individual life habit attributes endobenthos, bioturbator, suspension feeder, deposit feeder (winter), and detritus feeder (Table 2), summer and winter chlorophyll *a* concentrations in the overlying water correlate positively with the attribute combinations endobenthic sedentary and endobenthic deposit feeder and correlate very strongly with the attribute combinations endobenthic bioturbator and endobenthic suspension feeder.

Bioturbation-Induced Amensalism

Despite strongly opposed correlations with nutrient concentration, epibenthos does not correlate significantly with either abundance of endobenthos (*p* = 0.475) or with total bioturbators (*p* = 0.311). Within the northern Adriatic Sea, bioturbation has no obvious effect on presence or absence of sedentary epibenthos.

DISCUSSION

Within the northern Adriatic Sea, the Paleozoic-style epibenthic sedentary suspension-feeding-based ecosystem and its potential fossil residues are restricted to eastern oligotrophic water (Figs. 1C, 1F). In contrast, the modern-style endobenthos-based ecosystem is found in mesotrophic and eutrophic water in the west and locally in the nutrient-enriched Rovinj harbor in the east. This geographic distribution of ecological structure apparently is related to the greater energy requirements of actively burrowing animals that live within sediments and the lower energy requirements of sedentary suspension feeders (Bambach, 1993). The east-west change in ecological structure across the northern Adriatic occurs within higher taxa that are part of the modern fauna, so is dissociated from the high-level taxonomic change from the Paleozoic to modern faunas.

McMurdo Sound, Antarctica, also has opposite coasts bathed by oligotrophic and eutrophic water, with a similar partitioning between endobenthic communities in the higher-nutrient water and epibenthos-rich communities in the lower-nutrient water (Dayton and Oliver, 1977). Samples in McMurdo Sound were taken at depths (20–40 m)

similar to those across most of the northern Adriatic, and the range of epibenthic higher taxa in the oligotrophic water is similar to that in the oligotrophic waters of the northern Adriatic, including diverse epibenthic sedentary suspension feeders in oligotrophic water. Biomass is on average approximately seven times more abundant under eutrophic water of McMurdo Sound, just as in the Adriatic total biomass of samples is positively correlated with winter chlorophyll *a* ($p = 0.005$; for summer chlorophyll *a*, $p = 0.058$). In neither case can the contrasts be strongly influenced by depth gradients.

The east-west benthic ecological contrast seen in the northern Adriatic is generated by river-borne nutrients flushed into the Adriatic between Trieste and Ravenna. This is consistent with the hypothesis that the profound change in the shallow-marine benthic ecosystem has been driven by the two-phase late Paleozoic and Cretaceous proliferation and diversification of tracheophytes on land; the tracheophytes have progressively released more nutrients into a shallow marine halo around land masses (Bambach, 1999).

In contrast with oligotrophic tropical shallow seas, predation pressure on exposed animals on the seafloor is low in the Adriatic Sea (McKinney, 2003; Kelley, 2006). While the absence of abundant exposed animals on tropical shallow seafloors appears to be due to intense predation pressure (Vermeij, 1987), a predation gradient cannot explain the east-west change in the benthos of the northern Adriatic (Table 2). Instead, the low intensity of predation in the Adriatic Sea as a whole appears to be a background condition that allows epibenthos to flourish in the eastern oligotrophic water.

Bryozoans are epibenthic suspension feeders and with few exceptions are sedentary. Mesozoic and Cenozoic bryozoan limestones are composed of the accumulated skeletal residue of colonies that flourished locally on the shallow seafloor. Such limestones are common in the shallow-marine record, but in contrast with Paleozoic bryozoan limestones, those deposited since the Paleozoic have formed almost exclusively outside the predation-intense tropics (Taylor and Allison, 1998). The absence of appreciable land-derived sediments in such clean limestones suggests that they were formed in low-nutrient oceanic water beyond the influence of a land-derived nutrient-rich halo, and that Paleozoic-style benthic ecosystems can reappear where the ambient marine environment approaches that of the Paleozoic, despite being based largely on higher taxa that characterize the modern fauna. The Paleozoic to modern benthic ecosystem transition thus appears to be incomplete.

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REFERENCES CITED

Ambrogì, R., and Occhipinti Ambrogì, A., 1987, Temporal variations of secondary production in the marine bivalve *Spisula subtruncata* off the Po River Delta (Italy): Estuarine, Coastal and Shelf Science, v. 25, p. 369–379.

Amorosi, A., Cantineo, M.C., Colalongo, M.L., Pasini, G., Sarti, G., and Vaianni, S.C., 2003, Facies architecture and latest Pleistocene–Holocene depositional history of the Po Delta (Comacchio area), Italy: Journal of Geology, v. 111, p. 39–56, doi: 10.1086/344577.

Bambach, R.K., 1983, Ecospace utilization and guilds in marine communities through the Phanerozoic, in Tevesz, M.J.S., and McCall, P.M., eds., Biotic interactions in recent and fossil benthic communities: New York, Plenum, p. 719–746.

Bambach, R.K., 1993, Seafood through time: Changes in biomass, energetics,

and productivity in the marine ecosystem: Paleobiology, v. 19, p. 372–397.

Bambach, R.K., 1999, Energetics in the global marine fauna: A connection between terrestrial diversification and change in the marine biosphere: Geobios, v. 32, p. 131–144, doi: 10.1016/S0016-6995(99)80025-4.

Colantoni, P., Galignani, P., and Lenaz, R., 1979, Late Pleistocene and Holocene evolution of the North Adriatic continental shelf (Italy): Marine Geology, v. 33, p. M41–M50, doi: 10.1016/0025-3227(79)90130-0.

Correggiari, A., Roveri, M., and Trincardi, F., 1996, Late Pleistocene and Holocene evolution of the North Adriatic Sea: II Quaternario, v. 9, p. 697–704.

Dayton, P.K., and Oliver, J.S., 1977, Antarctic soft-bottom benthos in oligotrophic and eutrophic environments: Science, v. 197, p. 55–58.

Doglionni, C., Mongelli, F., and Pieri, P., 1994, The Puglia uplift (SE Italy): An anomaly in the foreland of the Apenninic subduction due to buckling of a thick continental lithosphere: Tectonics, v. 13, p. 1309–1321, doi: 10.1029/94TC01501.

Frignani, M., Langone, L., Ravaoli, M., Sorgente, D., Alvisi, F., and Albertazzi, S., 2005, Fine-sediment mass balance in the western Adriatic continental shelf over a century time scale: Marine Geology, v. 222–223, p. 113–133, doi: 10.1016/j.margeo.2005.06.016.

Harper, E.M., 2003, The Mesozoic marine revolution, in Kelley, P.H., et al., eds., Predator-prey interactions in the fossil record: New York, Kluwer Academic/Plenum, p. 433–455.

Jenkins, C., Trincardi, F., Hatchett, L., Niedoroda, A., Goff, J., Signell, R., and McKinney, K., 2005, Il fondo marino Adriatico: http://instaar.colorado.edu/~jenkinsc/dbseabed/adr_gis/ (December 2005).

Kelley, P.H., 2006, Low frequency of drilling predation in the northwest Adriatic: Cretaceous rather than Paleozoic analog: Geological Society of America Abstracts with Programs, v. 38, no. 3, p. 22.

Krajcar, V., 2003, Climatology of geostrophic currents in the northern Adriatic: Geofizika, v. 20, p. 105–114.

Lagaaij, R., and Gautier, Y.V., 1965, Bryozoan assemblages from marine sediments of the Rhône delta, France: Micropaleontology, v. 11, p. 39–58.

McKinney, F.K., 2003, Preservation potential and paleoecological significance of epibenthic suspension feeder-dominated benthic communities (northern Adriatic Sea): Palaios, v. 18, p. 47–62.

McKinney, F.K., and Jaklin, A., 2001, Sediment accumulation in a shallow-water meadow carpeted by a small erect bryozoan: Sedimentary Geology, v. 145, p. 397–410, doi: 10.1016/S0037-0738(01)00156-7.

Pigorini, B., 1968, Sources and dispersion of recent sediments of the Adriatic Sea: Marine Geology, v. 6, p. 187–229, doi: 10.1016/0025-3227(68)90031-5.

Poulain, P.-M., 2001, Adriatic Sea surface circulation as derived from drifter data between 1990 and 1999: Journal of Marine Systems, v. 29, p. 3–32, doi: 10.1016/S0924-7963(01)00007-0.

Sepkoski, J.J., Jr., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36–53.

Taylor, P.D., and Allison, P.A., 1998, Bryozoan carbonates through time and space: Geology, v. 26, p. 459–462, doi: 10.1130/0091-7613(1998)026<0459:BCTTAS>2.3.CO;2.

Thayer, C.W., 1979, Biological bulldozers and the evolution of marine benthic communities: Science, v. 203, p. 458–461.

Thayer, C.W., 1983, Sediment-mediated biological disturbance and the evolution of marine benthos, in Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: New York, Plenum, p. 479–625.

Vatova, A., 1935, Ricerche preliminari sulle biocenosi del Golfo di Rovigno: Thalassia, v. 2, p. 1–30.

Vatova, A., 1949, La fauna bentonica dell'alto e medio Adriatico: Nova Thalassia, v. 1, no. 3, p. 1–110.

Vermeij, G.J., 1987, Evolution and escalation: New Haven, Connecticut, Princeton University Press, 527 p.

Zavatarelli, M., Raicich, F., Bregant, D., Russo, A., and Artegiani, A., 1998, Climatological biogeochemical characteristics of the Adriatic Sea: Journal of Marine Systems, v. 18, p. 227–263, doi: 10.1016/S0924-7963(98)00014-1.