Oxygen and evolutionary patterns in the sea: Onshore/offshore trends and recent recruitment of deep-sea faunas

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ABSTRACT   Over the last 15 years a striking pattern of diversification has been documented in the fossil record of benthic marine invertebrates. Higher taxa (orders) tend to originate onshore, diversify offshore, and retreat into deep-water environments. Previous studies attribute this macro-evolutionary pattern to a variety of causes, foremost among them the role of nearshore disturbance in providing opportunities for the evolution of novel forms accorded ordinal rank. Our analysis of the post-Paleozoic record of ordinal first appearances indicates that the onshore preference of ordinal origination occurred only in the Mesozoic prior to the Turonian stage of the Cretaceous, a period characterized by relatively frequent anoxic/dysoxic bottom conditions in deeper marine environments. Later, in the Cretaceous and Cenozoic, ordinal origination of benthic organisms did not occur exclusively, or even preferentially, in onshore environments. This change in environmental pattern of ordinal origination roughly correlates with Late Cretaceous: (*i*) decline in anoxia/dysoxia in offshore benthic environments; (*ii*) extinction of faunas associated with dysoxic conditions; (*iii*) increase in bioturbation with the expansion of deep burrowing forms into offshore environments; and (*iv*) offshore expansion of bryozoan diversity. We also advance a separate argument that the Cenomanian/Turonian and latest Paleocene global events eliminated much of the deep-water benthos. This requires a more recent origin of modern vent and deep-sea faunas, from shallower water refugia, than the Paleozoic or early Mesozoic origin of these faunas suggested by other workers.

An onshore to offshore evolutionary pattern is evident in benthic marine invertebrate clades of the Paleozoic (1, 2) and post-Paleozoic (3–7) age. Ordinal rank taxa are observed to originate onshore, diversify offshore, and eventually relinquish nearshore habitat. This pattern has been attributed to a number of factors (5), the most clearly articulated of which invokes higher disturbance in shallow marine environments as a mechanism that eliminates niche incumbents, permitting the evolution of novel attributes subsequently recognized as new, ordinal rank, higher taxa (8). Expansion across the shelf to deeper offshore habitats then accompanies diversification of the clade (3–6). Explanations advanced for the subsequent offshore retreat of taxonomic groups include the evolution of new predators (9) and more effective competitors (10) in the nearshore environment. Thus, the nearshore is thought of as a source of evolutionary novelty resulting from disturbance, and subsidiary aspects of the pattern, such as offshore retreat, are thought of as responses to ecological interaction associated with the appearance of evolutionary novelty in the nearshore.

In this paper we argue (*i*) that a component of the post-Paleozoic onshore/offshore evolutionary pattern (3–7) resulted from the preferential influence of anoxic/dysoxic bottom conditions (a/dbc) on offshore faunas; (*ii*) that a/dbc were prevalent in the offshore in the Mesozoic before the Late Cretaceous and declined thereafter; and (*iii*) as a consequence of this quantitative change in a/dbc over time, the influence of a/dbc on evolutionary patterns can be subjected to a simple statistical test using the data of Jablonski and Bottjer (6). This statistical argument is a first-order analysis at a coarse scale of temporal resolution. More refined studies may be possible with the assembly of additional data.

Anoxia/Dysoxia and the Fossil Record

A variety of factors expanded the influence of a/dbc in offshore sedimentary environments in the Mesozoic beyond those observed in the Cenozoic. Anoxia is associated with transgression (11). First-order sea level rose from the Permo/Triassic to the Cenomanian increasing the proportion of transgressive and highstand facies in this part of the record. Tectonic factors in the Mesozoic generated a suite of intracratonic and oceanic basins with limited deep-water connection to the open ocean and frequent anoxic conditions (11). These basins include rift related features, such as the North Sea in Europe, and foreland basins, such as the Western Interior Seaway of North America. Furthermore, in the Mesozoic, large portions of the Atlantic and Tethys had limited deep-water connection to other ocean basins. Much of the Mesozoic fossil record derives from such basinal or adjacent settings.

Greenhouse conditions in the Mesozoic also greatly enhanced a/dbc and its biotic impact. Isotopic data suggest that Mesozoic bottom waters were on the order of 10–15°C warmer than mid and bottom waters today (12). As a consequence of the reduced solubility of gases in water with increasing temperature, this temperature difference would reduce the oxygen carrying capacity of bottom water by 15–20%. More importantly, increased bacterial metabolic rates result in a twofold increase in oxygen uptake of sediment for each 5°C increase in temperature, resulting in a four- to eightfold higher oxygen demand at the sediment–water interface under greenhouse conditions (13). Furthermore, metabolic oxygen requirements of benthic animals would also rise by ≈twofold for a 10°C increase in temperature (14). Thus, given a similar temporal sequence of organic carbon inputs, first principles support more intense and more volatile fluctuation in a/dbc under Mesozoic greenhouse conditions, and indicate that biotic responses to similar reductions in oxygen would have been greater. In addition, the reduced temperature gradient in the Mesozoic seas implies a much reduced density difference between surface and bottom waters. In this context, upwelling

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and consequent surface water productivity and organic carbon delivery to the bottom could be generated from much weaker thermohaline and dynamic forcing than are required in the modern ocean (15).

Mesozoic marine rocks record a/dbc on a wide range of temporal and spatial scales from global events to laterally extensive alternating carbon-rich and bioturbated beds indicative of fluctuating oxygenation of the sediment–water interface. The largest scale global and regional events are summarized in Fig. 1. Anoxic events of global extent have been documented for the Permo-Triassic, Toarcian (18), Lower Aptian (19), Lower and Upper Albian, and Cenomanian/Turonian (Cen/Tur) (20). Supporting evidence includes organic carbon preservation in stratigraphic sections and deep-sea drill cores distributed around the world, as well as global shifts in carbon isotopes thought to reflect the rate of organic carbon burial (20). Isotopic shifts suggest additional large events in the Valanginian stage (21) of the Lower Cretaceous,

as well as in the Triassic (22, 23). Additional significant events of regional extent are evident in the upper Jurassic (24). Subsidiary peaks in anoxia of more modest geographic scale precede and succeed anoxic events of global scale (18).

From the Aptian through the Cenomanian stages of the Cretaceous deep-sea drill cores document anoxic/dysoxic conditions that fluctuated in intensity, but were substantial in the deeper portions of the Atlantic basin (25). Thus, the global anoxic events of the mid-Cretaceous can be viewed as lateral expansions into shallower water environments of more continuous basinal a/dbc. Similarly, in anoxic events of regional scale, such as the late Jurassic (Kimmeridge) of Europe, reduced oxygen conditions expanded outwards from graben or other basinal settings in shelves or epieric seas (24). Thus, Mesozoic anoxia/dysoxia tended to influence outer shelf, slope, and basinal habitats more frequently, and for longer durations, than the major regional and global episodes recorded across the shelves (11, 24, 25) (Fig. 1). These offshore facies are the deepest water environments regularly sampled in the post-Paleozoic fossil record. Deep bathyal and abyssal sediments are not exposed on land, except in the most tectonically active settings, limiting sampling of these offshore paleoenvironments to deep-sea drill core, which does not generally recover macrofossils.

Carbon-rich deposits were widespread in epieric seas in the Coniacian and Santonian (23). However, these later Cretaceous a/dbc are not evident in the deep-sea deposits. Apparently, such conditions were confined to shelf environments (26). The latest Paleocene event seems to be a temporal outlier of short duration that, although global, only affected the deep sea. This event is not associated with expansion of a/dbc to outer shelf settings (27). For the purposes of this analysis we define a first-order epoch of a/dbc influence in offshore waters extending from the Permo-Triassic through the Cen/Tur. We place this endpoint to anoxia at the Cen/Tur boundary on the basis of (*i*) Cenomanian highstand and transition from first-order transgression to first-order regression, (*ii*) the transition to an oxygenated state in the deep Atlantic basin (25, 26), and (*iii*) the judgment of Tyson and Pierson (11), who observed that the frequency and anoxic dysoxic events were high before, and substantially lower after, the Cen/Tur. Others might wish to place a change to a more oxygenated world after the Coniacian or Santonian (22). We note that our analysis is robust to such changes in definition of the duration of an epoch of increased a/dbc. In addition, we are aware that there is higher order structure to the benthic oxygenation record in the sea and this structure is likely to have biological implications beyond the scope of this analysis.

Synchronous anoxic events of global significance that influenced the water column have received considerable attention (20, 22) (Fig. 1). We argue that these extreme events represent transient end members of a suite of processes operating on a variety of temporal and spatial scales that frequently reduced oxygen concentration at the sediment–water interface in offshore settings in the Mesozoic prior to the Late Cretaceous, and that these frequent a/dbc were important in generating the onshore/offshore patterns observed in the fossil record of benthic organisms. To understand the processes influencing the temporal and spatial structure of oxygenation at the sediment–water interface in the Mesozoic and its implications for the fossil record, we revisit the processes that influence oxygenation in the limited anoxic/dysoxic regions of Quaternary seas where modern oceanic processes can be more directly related to the production of anoxic/dysoxic sediments.

In the Mediterranean Sea, productivity fluctuates as a consequence of Milankovitch band (precessional) forcing. The causal chain involves increased monsoonal circulation, increased riverine input, and increased nutrient supply in the surface waters, resulting in a/dbc and the preservation of carbon-rich sapropels correlated with the precession cycle

	STAGE	AGE	ANOXIC/DYSOXIC EVENTS		OFFSHORE BIOTA	ONSHORE BIOTA
CENOZOIC	Quat	1.6				Oph
	Pllo	5.2				Oph
	Mlo3	10.4				Oph
	Mlo2	16.3			Oph	Oph
	Mlo1	23.3				Oph
	Oll2	29.3				Oph
	Oll1	35.4			30 N	Oph
	Eoc3	38.6				30 Oph
	Eoc2	50.0			Oph	30 Oph
	Eoc1	56.5			30 Oph	30 Oph
	Pal2	60.5	G,I		Oph	30 Oph
	Pal1	65.0				30 Oph
CRETACEOUS	Maa	74.0			30 Oph	30 Oph
	Cmp	83.0			10 Oph	10 Oph
	San	86.6	R		10 Oph	10 Oph
	Con	88.5	R			2 Oph
	Tur	90.4				2 Oph
	Cen	97.0	GI		N	2 Oph
	Alb	112.0	GI,GI			1
	Apt	124.5	G,I		0	1
	Bar	132.0	R+		N	1 Oph
	Hau	135.0			1 N	1
	Vlg	140.5	R,I		0	1 Oph
	Ber	145.5				1 Oph
JURASSIC	Tth	152.1			0	1 Oph
	Klm	154.7	R+		N	
	Oxf	157.1				Oph
	Clv	161.3	R			Oph
	Bth	166.1				Oph
	Baj	173.5				Oph
	Aal	178.0				
	Toa	187.0	G,I			
	Plb	194.5	RI		N	Oph
	Sln	203.5	R		N	N
	Het	208.0				N
TRIAS	Rht	210.0				
	Nor	223.0	R?			
	Crn	235.0	R,I			
	Tr2	241.0			N	N
	Tr1	245.0	G?			

FIG. 1. Post-Paleozoic anoxic events and biologic responses. Time (in millions of years) at the base of listed stages and epochs (16) occupies the vertical axis. The event column indicates the stages containing major anoxic events: G, global events; R, regional events; and I, events supported by carbon isotope ratio excursions. A schematic representation of major anoxic events appears in the adjacent column. Lines across the column indicate global events. Events that tended to affect deeper water or basinal events are on the left of the column. The presence of frequent anoxia in the deep Atlantic from the Aptian through Cenomanian is indicated by blocking out the left-hand side of the column. Biotic events include the presence of *Ophiomorpha*, a deep-burrowing trace fossil form in onshore and offshore habitats, indicated by *Oph*. Sampled intervals lacking *Ophiomorpha* are indicated by *N* (17). Note that *Ophiomorpha* occurs in all but one of the sampled offshore intervals after the Cen/Tur boundary and none before this boundary. Cheilostome diversity in onshore and offshore facies is noted by a numerical value [after Bottjer and Jablonski (3)].

(28). There is further sub-Milankovitch structure within these sapropels, indicating higher frequency fluctuations in a/dbc (29). In the Indian Ocean (30) and the Benguala current (31) there are similar climatically driven Milankovitch frequency fluctuations in upwelling and delivery of organic matter to the bottom. In the Santa Barbara Basin, detailed observation reveals greater fine-scale fluctuation in organic delivery to the bottom; these include (*i*) Heinrich events that repeat at 10^3–10^4 year intervals (32) and (*ii*) individual shell beds of *Macoma* indicating opportunistic settlement events of a few years duration and thought to have a millennial scale repeat time (33). Seasonal to decadal fluctuations in diatom deposition have been observed in laminated sediments in the Gulf of California (34). Recent interpretations of such research suggest that a/dcd are driven largely by fluctuations of productivity at the surface, rather than changes in bottom-water oxygenation (35), and have complex structure over short to intermediate time scales, 10^0–10^6 years, resulting from fluctuations in delivery of organic matter to the bottom (28–34). Examination of Mesozoic sections suggests that a/dbc in the Mesozoic had a similar complex, partially Milankovitch related, temporal structure (36, 37).

Modern anoxic events are often ephemeral in the stratigraphic record. Anoxic episodes of short duration exterminate benthic fauna, but subsequent physical and biological reworking erases the evidence after just a few years (38). Thus, in the stratigraphic record, those a/dbc events and associated faunas are only likely to be recognized where low oxygen conditions persisted for long periods of time, preventing reworking of the deposit by bioturbation. In addition, because dysaerobic conditions strongly influence the biota, complete or long-term anoxia is not required before biological effects are observed (39). Thus, reductions in oxygen that are ephemeral in a geological sense nevertheless have profound biological effects. Consequently, the biological impact of a/dbc is likely to be much more extensive than suggested by a narrow interpretation of the stratigraphic record.

Modern anoxic/dysoxic episodes demonstrate that particular taxa, primarily polychaetes and bivalve molluscs, preferentially survive dysoxic conditions and opportunistically recolonize sediments after anoxic extermination of faunas (11, 39). Thus, fluctuations in a/dbc are not likely to result in complete elimination of fossils from the stratigraphic column. Fossils, including bottom dwellers, may even be abundant, but are likely to be dominated by opportunistic species that can rapidly recolonize these offshore settings or resist dysoxic conditions. This interpretation is supported by the recent work of Sageman and Bina (40), who analyzed the community structure of proximal well-oxygenated and more distal offshore frequently dysoxic facies in the Cenomanian of the Western Interior Seaway. Using large sample sizes and an information statistic approach they found that oxygenated shelf environments had high diversity benthic faunas with large numbers of rare species such that diversity increased with increases in sample size. In contrast, offshore interbedded carbon-rich facies were dominated by one, or a few, opportunistic species and had truncated diversity distributions such that there was no increase in diversity associated with the recovery of rare species with increasing sample size. Thus, a/dbc appears to have a much stronger effect on the diversity structure of communities than on the presence/absence or abundance of fossils *per se*. A similar relationship between diversity structure and a/dbc has also been documented in the Paleozoic (41) and in the Aalenian (42) and Kimmeridgean (43) stages of the Jurassic. Thus, diversity of a/dbc effected offshore settings is low; however, this diversity will be much more efficiently and completely sampled by the incomplete and nonquantitative sampling typical of fossil collections.

In addition to the diversity structure discussed above, factors involving preservation and lineage continuity may lead to
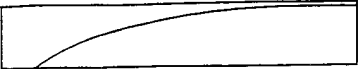
apparent diversity in offshore deposits that is not biologically real in terms of standing diversity, and is positively biased relative to the fossil record of nearshore habitats. Faunas of varying diversity may have colonized Mesozoic outer shelf and basinal environments during intermittent episodes of oxygenation. However, these faunas likely came from, and were present more continuously in, environments closer to shore. In addition, fossil preservation, even of disarticulated or poorly mineralized forms, is often excellent in offshore settings, especially when bioturbation is reduced by a/dbc. In nearshore and better oxygenated settings poorly mineralized and easily disarticulated fossils are destroyed by physical and biological reworking. This results in a relative bias in preservation operating against the nearshore habitats (6). Consequently, the fossil record of the nearshore may not record lineages that are continuously present, and offshore deposits affected by a/dbc may record lineages that are only present intermittently. Thus, one would expect substantially higher average or "standing" diversity in nearshore settings and that this difference in diversity should be partially masked by the nature and sampling of the fossil record. In addition, nonspecialized epifaunal or shallow infaunal deposit feeders dominate the suite of opportunistic species associated with a/dbc (41); other benthic invertebrate guilds such as deep burrowers or filter feeders are rarely present. Thus, given a/dbc, only a limited subset of niches and clades are likely to be available to diversify.

From these observations one would predict that evolution of ordinal-level evolutionary novelty in offshore settings intermittently affected by a/dbc taxa would be limited by the low diversity suite of opportunistic species that inhabit these environments and by the time *averaged* absence of diversity due to intermittency. Thus, one would expect a much reduced rate of generation of evolutionary novelty in offshore sedimentary environments during periods of frequent a/dbc than when offshore, outer shelf, slope, and basinal waters were more continuously oxygenated.

Hypothesis Test

Jablonski and Bottjer (6) compiled the most comprehensive data pertaining to onshore/offshore patterns evident in the Mesozoic and Cenozoic. These data consist of the time and environment of the first appearance of ordinal level taxa along an environmental energy gradient determined from sedimentary features and illustrated schematically as a suite of shelf environments from the nearshore to the slope (Fig. 2). Division of these data into an onshore and an offshore component, and a pre Cen/Tur, anoxic "treatment," and post-Cen/Tur oxygenated treatment permits a first-order test of the influence of a/dbc on the environmental pattern of ordinal origination. The null model is that there is no difference in the onshore/offshore pattern of ordinal origination before and after the Cen/Tur. Using a χ^2, as well as Fisher's exact test, we find that we can reject the null model at the 0.001 level (Fig. 2). Thus, there is a highly significant statistical relationship between the time period when anoxia was frequent, before the Cen/Tur, and the onshore origination of higher taxa. After the Cen/Tur there is no onshore preference in origination. Over 70% of post-Paleozoic ordinal originations occur before the Cen/Tur (Fig. 2). Thus, the "anoxia/dysoxia argument" may explain the general observation of onshore origination of ordinal rank taxa observed by Jablonski and Bottjer.

This statistical result is robust to minor changes involving the assumptions of the analysis. Some might argue that the boundary between times when a/dbc was prevalent should be extended to after the Coniacian and Santonian. Inclusion of these stages still yields results significant at the 95% level. One could argue that the Triassic record was poor relative to the later portion of the record, yet elimination of the bottom part of the record through the middle Jurassic still yields a signif-

FIG. 2. Contingency table based on the time and environment of first occurrence of ordinal rank groups of benthic macroinvertebrates. The series of environments, nearshore, inner-, middle-, and outer shelf, as well as the slope and basin, follows the interpretation of Jablonski and Bottjer (6). However, this figure is distinct in that stage names are included in the timescale simplifying comparison of geologic information with the record of first appearances. In addition, this figure treats the well-preserved and poorly preserved orders in a single graph. The symbolism of a continental shelf, repeated here, should not be taken literally. Jablonski and Bottjer (6) assessed environments using a sedimentological criteria. For example, storm wave base divides the middle from the outer shelf. Given this sedimentological basis the data are not constrained to continental shelves, but include data from epieric seas as well. Taxa that appeared simultaneously in two environments are placed in an intermediate position on the onshore/offshore environmental gradient and italicized. A vertical double line separates an onshore and an offshore region, and a horizontal double line separates an older, pre-Cen/Tur anoxic/dysoxic treatment, from a younger, oxic treatment. These divisions result in a two-by-two contingency table. Large open numerals indicate the number of ordinal originations in each of the four cells of the table. Column, row, and table totals appear around the margin in boldface type. Results of the analysis are highly significant using both a χ^2 and Fisher exact test ($\chi^2 P < 0.001$; Fisher exact test $P = 0.00017$). These statistical results are robust to minor shifts in position of the breaks in time and environment used to construct the contingency table. (Underlined numbers are well-preserved orders: 1, Encrinida; 2, Isocrinida; 3, Scleractinia; 4, Millericrinida; 5, Lychniscosida; 6, Phymosomatoida; 7, Pedinoida; 8, Hemicidaroida; 9, Pygasteroida; 10, Holectypoida; 11, Cyrtocrinida; 12, Microstomata; 13, Salenoida; 14, Disasteroida; 15, Cassiduloida; 16, Milliporina; 17, Cheilostomata; 18, Holasteroida; 19, Spatangoida; 20, Temnopleuroida; 21, Neogastropoda; 22, Helioporacea; 23, Bourgueticrinida; 24 Stylasterina; 25, Clpeasteroida; 26, Oligopygoida; and 27. Poorly preserved orders are: 1, Tricherasteropsida; 2, Forcipilatida; 3, Comatulida; 4, Notomyoida; 5, Valvatida; 6, Velatida; 7, Paxillocida; 8, Anaspidea; 9, Micropygoida; 10, Echinothuroida; 11, Diadematoida; 12, Spinulosida; 13, Sacoglossa; 14, Notaspidoidea; 15, Brisingida; and 16, Stolonifera) (6, 7).

icant result. One could argue that origination of orders determined to have a poor preservation potential should be given less weight than well-preserved taxa. Yet if these taxa are given one-fifth the weight of the well-preserved taxa the result still exceeds the 95% significance criterion. We placed the onshore/offshore break between the outer and middle shelf, in part because storm wave base is a reasonable marker for the upper mixed layer of the ocean, and in part because there is a break in the data at this point. However, placement of the onshore/offshore boundary at the inner/middle shelf still yields significant results. Jablonski and Bottjer (6) documented that first appearances of orders with poor preservation potential are further offshore than first appearances of well-preserved taxa. However, despite this bias toward offshore preservation of delicate fossils, no taxon with poor preservation potential has a first appearance in the offshore before the Cen/Tur. In addition, one could argue that our result is a consequence of a bias introduced by the shift in first-order sea level curve from transgressive to regressive. However, transgressive sequences should preferentially preserve deep water, rather than nearshore facies, so again this bias would be counter to our result. One might also argue that other factors besides a/dbc led to a poorer sampling of faunas from offshore environments. However, the sampling controls employed by Jablonski and Bottjer (6) mitigate this argument, and ancillary data support an anoxia/dysoxia causal interpretation.

Causality

Several lines of evidence document a Late Cretaceous transition from an a/dbc-influenced biota in offshore waters to a more trophically diverse fauna. Mesozoic organic rich "anoxic/dysoxic" sediments often contain a depauperate fauna dominated by nektonic organisms, usually including ammonites and a benthic fauna dominated by "flat" or "paper" clams such as, *Monotis* in the Triassic, *Posidonia* and *Buchia* in the Jurassic, and inoceramids in the Cretaceous. Fischer and Bottjer (44) refer to this dark shale associated fauna as a "lost biotope," no longer occupied because of increased oxygenation of the sea. It is a matter of some debate as to whether these clams were chemosymbiotic, taking more direct advantage of a redox gradient in the benthic boundary layer, or whether they were opportunists, capable of settling rapidly during brief periods of oxygenation (45).

Infaunal animals are particularly limited by low oxygen concentration, and depth of burrowing is closely correlated with oxygenation of the water column and sediment (11, 38, 40). *Ophiomorpha*, a distinctive pellet-lined deep-burrow form, expanded into offshore environments in the Late Cretaceous (Fig. 1), a pattern consistent with biological response to an increase in oxygenation after the Cen/Tur. The loss of inoceramids in the fossil record was associated with increased bioturbation and linked to a reorganization of oceanic circulation that resulted in cooler, better oxygenated bottom waters (46, 47).

In addition to the loss of a/dbc associated fauna, and an increase in burrowing and bioturbation, one might expect an increased presence offshore of organisms that did not conform to the vagile opportunistic deposit feeders that dominate dysoxia-associated benthic faunas (39–41). Bryozoans ought to be particularly sensitive to a/dbc because of their sessile filter-feeding mode of life. Data on cheilostomes indicate a rapid diversification across the shelf from onshore to offshore in the Late Cretaceous (3) (Fig. 1). Cyclostomes similarly diversified across the shelf in the Late Cretaceous (48). However, they show diversity peaks that extend offshore in the Hauterivian and in the Middle Jurassic. There is less evidence of a/dbc in the Late Valanginian and Hauterivian than for other stages of the Early Cretaceous, and the sole pre-Cenomanian offshore ordinal origination in the Jablonski–

Bottjer (6) data set is also in the Hauterivian. Similarly, cyclostomes diversified across the shelf in the Middle Jurassic after the Toarcian anoxic event, but that diversity disappears before the increased anoxia of the Late Jurassic. Thus, cyclostomes may be responding to the second-order structure in the anoxia data, a point consistent with our argument, but in need of further investigation. Nonetheless, bryozoan diversification across the shelves correlates with, and appears to have responded to, increasing oxygenation in offshore waters.

Of the three components of the onshore/offshore pattern, onshore origination appears to be correlated with, and causally related to, a/dbc offshore; diversification across the shelf may relate to release from offshore a/dbc either in episodes of increased anoxia or after the Cen/Tur, and retreat into deeper water may be a passive result of increased oxygenation offshore. Offshore retreat involves relinquishing nearshore components of the taxon's distribution. It may only be possible for many taxa when the offshore environment is continuously well oxygenated. Thus, shifting oxygenation could play a permissive role in offshore retreat in response to physical and biological factors preferentially influencing the nearshore environment, in the Cenozoic record, such as increased sea level fluctuation, predation pressure, and competition (10, 11).

Anoxic Events and the Age of the Modern Deep-Sea Fauna

Well-oxygenated bottoms in the deep sea support a more diverse and heterogeneous fauna than had been anticipated a decade or two ago (49). In addition, concentrations of biological activity dependent on bacterial chemautotrophy have been discovered at redox boundaries associated with hot vent (50), cold seeps (51), and the oxygen minimum zones (52). The deep sea has long been thought of as a refuge for Paleozoic forms of life, such as stalked crinoids and monoplacophorans, and deep-sea vent taxa are thought to have inhabited deep-vent environments since the Paleozoic or Early Mesozoic (50, 53, 54). However, all benthic marine invertebrates require oxygen. Thus, the most recent anoxic events to affect the deep sea on a global scale, the Cen/Tur and latest Paleocene, presented severe temporal and spatial constraints on the continuous occupation of deep-sea habitat by both typical marine benthos and vent faunas.

Near the Cen/Tur, organic carbon-rich sediments in shelf sediments, as well as in deep-sea core data from the Atlantic and tropical Pacific, attest to the global nature of the event (18–22). Only cores with extremely slow sedimentation rates in the center of the Pacific gyres, where reoxidation of an organic deposit would be expected, fail to document organic-rich sediments. As mentioned previously, there are only a few sections of Mesozoic and Cenozoic material available for study. Thus, most work on the Cen/Tur extinction event describes the progressive extinction of molluscs and microfaunas with expansion of anoxia up from a minimum zone into epieric sea environments (55, 56). The deep-ocean macrobenthos is poorly sampled in the accessible fossil record. However, a recent study of upper bathyal sediments from Hokkaido documents a 0.2–0.5 million year period of dysoxia punctuated by two anoxia spikes associated with benthic foram extinction (57). Given that this record is from a western ocean boundary not noted for upwelling and oxygen minima, this record of anoxia and extinction, in combination with the global distribution of organic carbon-rich sediments, provides strong support for the thesis of deep-water extinction near the Cen/Tur. Core records for the latest Paleocene document a dramatic 72% benthic foram extinction coincident with an isotopic anomaly interpreted as a warming of bottom waters that resulted in anoxia (29). This extinction was global, but almost exclusively deep sea in its distribution (58).

Given the nature of the Cen/Tur and latest Paleocene events and their effect on benthic forams, a proportion of which were

resistant to dysoxic conditions, it seem that all, or virtually all, of the deep marine habitat must have been uninhabitable for both normal marine invertebrate faunas and vent faunas. Thus, the deep-sea and vent faunas are likely to have been eliminated from these deep-water bathyal and abyssal habitats and most likely entered the deep sea after these events in the Late Cretaceous and early Tertiary. If vent faunas could not have persisted at bathyal and abyssal depths in the sea during the Cen/Tur and latest Paleocene where did they persist? First, the expansion of an oxygen minimum zone during these large anoxic events would expand the range of redox boundary environments available in shallower waters where the oxygen minimum zones impinge on the bottom. In addition, high spreading rates and off-ridge volcanism during the Cretaceous led to subaerial exposure of a suite of now submerged volcanogenic land masses in the Pacific (59). It seems likely that this volcanic activity may have generated vent habitats in shallow water that could have served as refuges for vent faunas in times of deep-water anoxia. Vent faunas in the eastern Pacific are much more diverse than in the Atlantic (52). This diversity difference may be due, in part, to the presence of shallow-water vent refugia in the Pacific, but not in the Atlantic, during times of deep-water anoxia.

Shallow water refugia may also have accommodated normal deep-sea faunas during times of deep-water anoxia. Although stalked crinoids and monoplacophorans, icons of deep-sea living fossils, were originally recovered from considerable depth, they have subsequently been found in substantially shallower water. The stalked crinoid *Metacrinus* lives in as little as 100 m of water in Suruga Bay, Japan (60), and monoplacophorans live at less than 200 m depth in the Antarctic, off southern California, and in the Mediterranean (61). Thus, deep-marine vent and seep forms may have taken advantage of expanded redox gradients in shallow water in times of reduced oxygenation in the sea, and normal marine faunas may have retreated to nearshore portions of their ranges.

Conclusions

Our argument pertaining to onshore/offshore evolutionary pattern in the fossil record is supported by statistical assessment of ordinal–origination data (Fig. 2), and ancillary information on the environmental distribution through time of aspects of bioturbation, and the extinction of faunas associated with a/dbc, as well as by patterns of diversification of Bryozoa. This combination of evidence suggests a causal relationship between anoxic/dysoxic conditions before the Late Cretaceous in Mesozoic seas and the onshore/offshore patterns of evolution observed in the fossil record. The data appear to speak particularly strongly to the onshore ordinal–origination component of the pattern, as the preponderance of such origination occurs onshore during times when a/dbc offshore was prevalent or frequent (Fig. 2). Observations of diversification of higher taxa across shelves may be a consequence of release of anoxic conditions, although this response may occur primarily in those taxa most susceptible to reduced oxygenation (1–5, 9). The retreat into offshore waters may be driven by other factors (9, 10) in the onshore environment, but might have only been possible when offshore benthic habitats were more continuously oxygenated. These last two points require further testing in a more refined stratigraphic context than this first-order analysis. Our analysis also raises the possibility that modern deep-sea faunas, both at vents and in the oxygenated realm, did not evolve *in situ* for long periods of time but colonized the deep-sea habitat after the last major disruptions of these habitats by anoxic events in the Cen/Tur and latest Paleocene.

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