

ENERGETICS IN THE GLOBAL MARINE FAUNA: A CONNECTION BETWEEN TERRESTRIAL DIVERSIFICATION AND CHANGE IN THE MARINE BIOSPHERE

RICHARD K. BAMBACH

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ABSTRACT - The invasion of the land started in the Ordovician and continued into the Carboniferous. The peak of diversification rate and increase in biomass of terrestrial vegetation occurred during the Devonian. However, no permanent increase in marine diversity occurred at that time. Instead, a plateau of fluctuating but non-trending diversity extended for 200 million years from the later Ordovician to the beginning of the Late Permian. A second major increase in terrestrial productivity occurred with the diversification of the angiosperms. This began in the Cretaceous and continued into the Cenozoic. Although marine diversity also increased during the Mesozoic and Cenozoic, no permanent offset in diversification rate occurred during this interval. Instead, marine diversity increased nearly continuously through the Jurassic, Cretaceous, and Cenozoic at the same exponential rate of growth established early in the Mesozoic. Despite the lack of a clear signal of change in marine diversity associated with either interval of terrestrial plant diversification, patterns of turnover in the marine fauna during the Devonian and the Cretaceous suggest that these were times of increasing productivity in the oceans. In the Devonian, replacement in dominant orders of many taxa are consonant with the idea of increased food supplies and greater energetics in the fauna (energetics refers to the combination of biomass, general physical activity, metabolic rates, and the concomitant need for a level of food consumption sufficient for the support of metabolic needs). The possible linkage of increased marine productivity and increased energetics in the marine fauna is particularly clear in the turnover in dominance at the top of the food chain. During the Devonian, relatively sluggish, low metabolic rate predators were replaced by generally more active taxa with greater overall energy needs. Nautiloids, eurypterids, and asteroids decreased in diversity as ammonoids, malacostracans, and jawed fishes increased. Likewise, many changes that can be ascribed to increasing availability of food supplies in the oceans began in the Cretaceous. Not only was there a major increase in the diversity of phytoplankton, but the teleost fish and brachyuran crabs both exploded in diversity, predatory boring by gastropods increased, and deposit feeding echinoids become important. These changes during the Cretaceous fit a model of changing energetics in which (a) there was more primary productivity in the oceans, (b) sufficient biomass of prey became available to support a variety of specialized predators, and (c) enough organic detritus regularly accumulated in the sediment to support an increase in deposit feeding organisms. Because of the coincidence in timing of these changes with intervals of terrestrial diversification, it is possible that they were triggered (or fueled) by increased nutrient input from increasing productivity on land. Although increase in marine diversity is one possible consequence of intervals of terrestrial diversification, this did not seem to take place, either in the Devonian or the Cretaceous. A second logical consequence, however, increase in the energetics of the marine fauna, does match the timing of terrestrial diversification. Increases in terrestrial productivity and biomass would have increased the supply of organic detritus and dissolved organic materials to the oceans, as well as possibly increasing the supply of inorganic nutrients because of increased weathering rates as a result of increased organic acids and organic materials in soils. Both the Devonian "precursor to the Mesozoic marine revolution" and the concentration in the Cretaceous of the start of many of the changes associated with the Mesozoic marine revolution itself may have been supported by increases in diversity and biomass on land.

KEYWORDS: TERRESTRIAL DIVERSIFICATION, MARINE DIVERSITY, ENERGETICS, PRODUCTIVITY.

RÉSUMÉ - La conquête des continents débuta à l'Ordovicien et se poursuivit jusqu'au Carbonifère. Le pic du taux de diversification et l'accroissement de la biomasse de la végétation terrestre se produisirent pendant le Dévonien. Néanmoins, aucune augmentation permanente de la diversité marine n'eut lieu à ce moment. Au contraire, c'est un plateau de diversité fluctuante mais sans tendance qui dura 200 millions d'années, de l'Ordovicien terminal jusqu'au début du Permien supérieur. Un second accroissement majeur de la productivité terrestre se produisit avec la diversification des angiospermes, commençant au Crétacé et se continuant durant le Cénozoïque. Quoique la diversité marine s'accrut aussi durant le Mésozoïque et le Cénozoïque, aucune augmentation permanente du taux de diversification ne se réalisa durant cette période. Au lieu de cela, la diversité marine s'accrut presque continuellement durant le Jurassique, le Crétacé et le Cénozoïque au même taux exponentiel de croissance établi tôt au Mésozoïque. Malgré l'absence d'un signal clair de changement de la diversité marine associée à chaque moment de diversification des plantes terrestres, des patrons de remplacement dans la faune marine durant le Dévonien et le Crétacé suggèrent des périodes de productivité croissante dans les océans. Au Dévonien le remplacement des ordres dominants de beaucoup

de taxons s'accorde avec l'idée d'apports croissants de nourriture et de plus grande énergie dans les faunes (énergie réfère à la combinaison de la biomasse, de l'activité physique générale, des taux de métabolisme et de la nécessité concomitante d'un niveau suffisant d'utilisation de nourriture pour les besoins métaboliques). La relation possible d'une productivité marine accrue et d'une énergie augmentée dans la faune marine est particulièrement nette dans le renouvellement de la dominance au sommet de la chaîne alimentaire. Au cours du Dévonien, des prédateurs relativement peu actifs, à faible métabolisme ont été remplacés par des taxons généralement plus actifs avec de plus grands besoins surtout énergétiques. La diversité des nautiloïdes, des euryptérides et des astéroïdes diminua alors que celle des ammonoïdes, des malacostracés et des poissons augmenta. De même, beaucoup de changements attribuables à la disponibilité croissante d'apports de nourriture dans les océans ont débuté au Crétacé. Non seulement il y eut un accroissement de la diversité du phytoplancton mais celle des poissons téléostéens et des crabes brachyours explosa. La prédation perforante par les gastropodes augmenta et les échinoides dépositivores devinrent importants. Ces modifications au cours du Crétacé s'accordent avec un modèle de changement énergétique dans lequel: a) il y avait davantage de productivité primaire dans les océans, b) une biomasse suffisante de proies devenait disponible pour permettre une variété de prédateurs spécialisés et, c) une quantité suffisante de débris organiques s'accumulait dans les sédiments pour permettre un accroissement des organismes dépositivores. En raison de la coïncidence du rythme de ces changements avec les moments de diversification continentale, il est possible qu'ils aient été provoqués (ou entretenus) par un augmentation de nutriments liée à une productivité croissante sur terre. Bien que l'accroissement de la diversité marine soit une conséquence possible des diversifications terrestres, cela ne semble pas s'être produit à une autre époque que le Dévonien ou le Crétacé. Cependant, une seconde conséquence logique, l'accroissement de l'énergie des faunes marines, correspond aux rythmes des diversifications continentales. Les amplifications de la productivité terrestre et des biomasses auraient augmenté l'apport de débris et de matériaux organiques dissous dans les océans, ainsi que celui de nutriments inorganiques provenant des taux d'altération accrus par l'augmentation des acides organiques et des matériaux organiques dans les sols. Tant les phénomènes du Dévonien, "précurseur de la révolution marine mésozoïque", que la concentration au Crétacé du début de beaucoup des changements, associés avec la révolution marine elle-même, peuvent avoir été renforcés par les accroissements de la diversité de la biomasse terrestre.

MOTS-CLÉS: DIVERSITÉS TERRESTRE ET MARINE, ÉNERGIE, PRODUCTIVITÉ.

INTRODUCTION

MARINE DIVERSITY THROUGH TIME

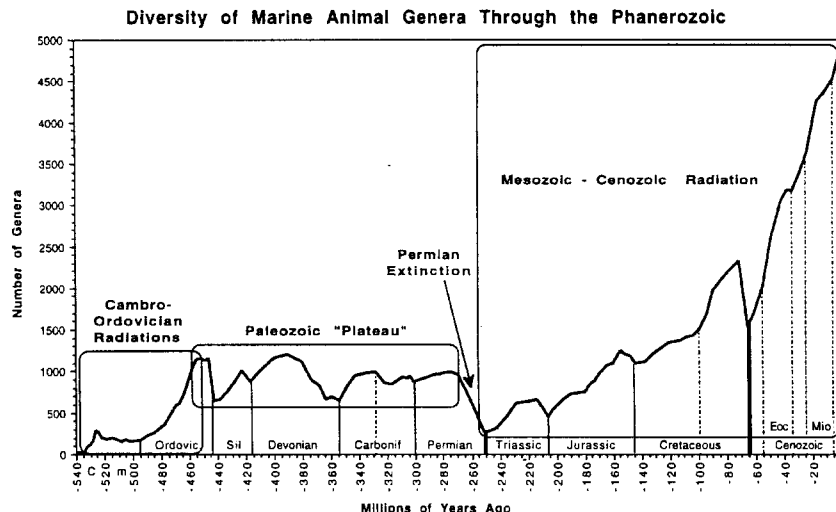
The accepted pattern of marine diversity through the Phanerozoic was established in 1981 (Sepkoski et al.) and is best known from the often reproduced summary figure (Sepkoski 1981) derived from Jack Sepkoski's compilation of stratigraphic ranges of families of marine organisms (Sepkoski 1982). Marine diversity rose sharply in the Early Cambrian, leveled off in the Middle and Late Cambrian, increased further during the Early and Middle Ordovician and leveled off again in the Late Ordovician. Despite the fluctuations caused by the Ashgillian (Late Ordovician) and Mid to Late Devonian extinction events and the recoveries of diversity following them, marine diversity only fluctuated, but did not trend either up or down, during the last 200 million years of the Paleozoic, from the Late Ordovician through the Mid Permian. Following the sharp end-Permian decrease in diversity, the most severe extinction of the Phanerozoic, marine diversity increased continuously through the Mesozoic and Cenozoic, interrupted only briefly by the end-Triassic and end-Cretaceous mass extinctions. Updated work at the family level by Sepkoski (1992, 1993) and Benton (1993, 1995) continues to show essentially the same pattern. The principal differences from the pattern established in 1981 are higher levels of diversity in the Cambrian and the later Mesozoic and Cenozoic, products of more intense recent

study of the Cambrian and of recent taxonomic revisions for the Cenozoic.

Although it has been suggested that decay in the quality of the geologic record may bias the apparent history of diversity (Raup 1976), Ronov et al. (1980) and Gregor (1985) have shown that, although the total amount of preserved sediment decreases with time, the amount preserved on continental platforms remains relatively unaffected. Most of the loss of the sedimentary record is in oceanic basins and on the margins of continental blocks. Since most of the fossil record comes from continental platforms, the loss of record does not strongly affect compilations of fossil diversity.

A new compilation derived from the unpublished database of the stratigraphic ranges of 35,872 marine animal genera compiled by J.J. Sepkoski, Jr. permits analysis of the diversity histories of many taxa. The pattern of overall marine diversity at the level of genera (Fig. 1) matches that established using families (as noted by Sepkoski 1997), again corroborating the general pattern of marine diversity through the Phanerozoic. Figure 1 uses the number of genera crossing from one interval to the next to show diversity, not the total number of genera in each interval, which is standard in most illustrations. Because of a variety of biases, total diversity in an interval does not represent actual standing diversity. Because originations accumulate over time, the opportunity to accumulate genera varies with the length of an interval. Total diversi-

FIGURE 1 - Diversity of genera of marine animals through the Phanerozoic. Data are number of genera crossing from one time interval (a hybrid of stages, substages, and, in a few cases, combined stages) to the next. The temporal resolution of that data averages about 5 million years per interval. The four major phases of diversity history are also labeled and outlined. *Diversité générique des animaux marins durant le Phanérozoïque. Les données sont les nombres de genres d'un intervalle de temps (étages, sous-étages et, dans quelques cas, étages combinés) au suivant. La résolution temporelle des données correspond à environ 5 millions d'années par intervalle. Les quatre phases majeures de l'histoire de la diversité sont aussi signalées et soulignées.*



ty for a long interval will include all the genera originating in the interval, whereas there is less time to add genera in a short interval. Monographic and lagerstätten effects, which are produced by reporting many taxa not recorded elsewhere in the fossil record, also increase the number of reported genera in particularly well sampled intervals. Finally, the total number of genera existing in an interval is not an accurate estimate of standing diversity because the only way to reach that diversity would be for all originations to occur before any extinctions took place in the interval. However, the number of genera extending from one time to the next (the number of genera crossing the boundary between two intervals) is an approximation of standing diversity. The number of genera crossing from one interval to the next can be calculated easily by subtracting the number of genera ending their range in the older interval from the total in that interval. The remainder is the number of genera passing on into the next interval. In tabulating the number of genera in each interval use is made of the "range through" concept, thus accounting for taxa that must have been present even though sampling has been incomplete and avoiding the problem of "Lazarus taxa" and artifactually high extinction. The change between the number of genera entering an interval and leaving that interval provides a robust evaluation of the change in diversity during that time independent of the intensity of study or vagaries of completeness of the geologic record associated with individual intervals. Therefore, the analyses in this study have been based on the numbers of genera known to cross interval boundaries.

Changes in diversity of genera through the Phanerozoic (Fig. 1) fall into the same four intervals noted above for the pattern of diversity of families. (1) The Cambrian and Ordovician diversifications occupy a complex interval in which two successive phases of diversification, separated by a short plateau in

diversity, establish the general level of diversity that persists through the rest of the Paleozoic. (2) The "Paleozoic Plateau" of marine diversity lasts from the Caradoc through the early Late Permian (through the Wordian in the Guadalupian Stage). Although two of the great mass extinctions and their subsequent recoveries occur during this interval, no trend to either increase or decrease world marine diversity occurs during this 200 million year time span. (3) The Permian Extinction reduces the total diversity of genera by over 70%. One effect of the end-Permian extinction is the change from the non-trending "Paleozoic Plateau" to continuous increase of diversity throughout the Mesozoic and Cenozoic. (4) The last 250 million years have seen continuous increase in diversity, interrupted only by the end-Triassic and end-Cretaceous mass extinctions. The result has been a quadrupling of marine diversity as measured by data on genera.

An interesting pattern emerges in comparing the diversity of families with the diversity of genera that may suggest something about the difficulty to determine quantitative degree of diversity change at the species level. The diversity of families increased by a factor of two or three times between the Paleozoic average and the late Cenozoic, but the diversity of genera has increased by a factor of four or slightly more. The increased quantitative change at the lower taxonomic level suggests that species diversity may have increased even more, possibly by as much as five or six times, although Valentine's (1970) early estimate of a ten-fold increase is probably too high. This rather conservative conclusion is also supported because the "pull of the Recent" is greater for lower taxa (Raup 1979). There may not be a significantly greater increase in species as compared to genera, just as the increase in genera is probably artifactually greater than for families. Also, Bambach (1990) showed that the paleobiogeographic argument of Valentine et al.

(1978) for an order of magnitude increase in species diversity from increased provinciality also overestimates the amount of increase, and Rosenzweig (1995: 282-283) also argued from theoretical grounds that changes in provinciality will not greatly affect global species diversity. Diversity changes of genera may be somewhat damped, compared to species, as diversity change of families appears less volatile than for genera, but the general patterns are similar, not widely different.

TWO CRITICAL INTERVALS FOR CONNECTING TERRESTRIAL EVENTS TO THE MARINE REALM

I want to focus on two intervals for the main part of this paper: (1) the mid-Paleozoic, with emphasis on the Devonian and (2) the Jurassic to Recent, with emphasis on the Cretaceous. These are the two times when diversity and biomass of vegetation on land increased dramatically. If change in the terrestrial biosphere has had a major influence on the marine realm, these are the two times when that influence should be most likely to be detectable.

The middle Paleozoic is when life invaded the land. Kenrick & Crane (1997) showed that although some terrestrialization began in the mid-Ordovician, the diversification of tracheophytes did not begin until the Silurian and the radiation of the four major lineages of larger land plants was concentrated in the Devonian. Likewise, the angiosperms entered the fossil record in the Early Cretaceous, increased in both diversity and abundance in the Late Cretaceous (Crane & Lidgard 1990), but did not achieve their modern dominance of abundance until sometime in the Cenozoic (Wing & Boucher 1998), making this a protracted transition.

Animals are consumers (heterotrophs). The base of the food chain for marine animals comes from algal production (including phytoplankton), bacteria, and organic detritus. Although much marine production is supported by dissolved and recycled nutrients in the marine ecosystem, the regular input of nutrients from the land both replenishes materials lost by sedimentation and adds new nutrients to the marine flux (Falkowski et al. 1998; Butler 1998; Jickells 1998; Duarte & Agusti 1998; Field et al. 1998). Both organic detritus and dissolved organics from the land enhance coastal productivity. Organic acids and root penetration increase rates of weathering and enhance the flux of inorganic nutrients to the oceans as well. Therefore, it is reasonable to expect some influence on life in the oceans from changes in terrestrial productivity.

The signal of the influence of organic matter from the land on the marine biosphere is the "halo" of high productivity ringing the ocean basins in the coastal waters and continental shelves, with pro-

ductivities comparable to the upwelling zones where nutrients are recycled from deep water. This can be seen in maps of primary productivity in the oceans such as those published in Berger (1989), Falkowski et al. (1998), and Field et al. (1998). Prior to the invasion of the land and the diversification of land plants, the nutrient supply from runoff from the land would have been much less than today. The times when diversity and biomass increased on land should be the times when supply of nutrients and food to the oceans changed the most. The thesis of this paper is that these times of diversity and biomass increase on land are the times when we should expect to see the largest response in the marine fauna. The main questions are: is there a detectable effect and what is it?

THE PALEOZOIC PLATEAU AND THE DEVONIAN

CHANGE ON LAND, DID IT INFLUENCE MARINE DIVERSITY?

Land plants had evolved by the Early Devonian, but they were still all quite small. However, by the Early Carboniferous every major plant lineage had evolved tree-size individuals and biomass, as well as diversity, had increased dramatically on land. This is documented in a variety of studies. Chaloner & Sheerin (1979) demonstrated that the maximum diameters of plant stems increased continuously during the Devonian. A number of large-size taxa had evolved by the Late Devonian. Algeo & Scheckler (1998) provide convincing evidence that the depth of root penetration increased significantly during the Devonian. This increased the depth and rate of weathering, developed modern soil systems, and is good evidence that productivity and total biomass on land increased markedly during the Devonian. Berner (1998) has modeled change in CO₂ abundance through the Phanerozoic. The dramatic plunge in atmospheric abundance of CO₂ during the Devonian and Early Carboniferous marks the shift of carbon into plant biomass, including buried organic matter, at that time.

Yet with all this change in plant diversity and biomass on land, marine diversity fluctuated, but did not increase, during the middle Paleozoic. The fluctuations were two major extinction events during the Paleozoic Plateau, with diversity recovering to near previous levels each time. But diversity per se was not affected by the mid-Paleozoic increase in biomass on land. A linear regression of diversity data against time from the Caradoc to the Leonardian is nearly level and, in fact, declines slightly. No obvious long term effect on diversity of the marine fauna correlates with the increase of terrestrial biomass during this interval.

PATTERNS OF DECREASE AND INCREASE: FAUNAL TURNOVER IN THE DEVONIAN

The phenomenon associated with change in marine diversity in the mid-Paleozoic that has most attracted our attention is the series of extinction events during the later Devonian (McGhee 1996). For example, the reef ecosystem collapsed. Stromatopora went extinct, tabulate corals declined and never recovered much diversity, and the Rugosa were decimated, although they did recover considerable diversity in the Carboniferous. Other groups suffered diversity loss as well. For example, trilobite diversity dropped precipitously in the Middle Devonian, and only one order, the proetids, survived into the later Paleozoic. 287 genera recorded in these four groups combined pass from the Emsian to the Eifelian but only 57 were left to go from the Frasnian into the Famennian (Note: as with all other reports of numbers of genera in this paper, the data are the number of genera I counted for the given subset of taxa as listed in Sepkoski's unpublished compilation on the stratigraphic ranges of marine animal genera). At the Viséan/Serpukhovian boundary, despite the recovery of the Rugosa, these four groups still only totaled 94 recorded genera, one-third of their combined diversity at the end of the Early Devonian.

But not all taxa decreased in diversity during the Devonian. The foraminifera increased, tripling in recorded diversity from the Early Devonian to the Early Carboniferous. Gastropods increased in recorded diversity by 38% between the mid-Silurian and the Early Carboniferous and bivalve diversity increased as well. Among passive suspension-feeders, recorded crinoid diversity increased by more than 50% from the Silurian to the Early Carboniferous. The extinction events in the later Devonian did affect lineages such as these briefly, but their recovery led to higher recorded diversity in every case. The four groups combined increased in diversity from 193 recorded genera at the Wenlock/Ludlow boundary in the Silurian to 378 recorded genera at the Viséan/Serpukhovian boundary in the Carboniferous, an increase of 96%. Therefore, one must differentiate between changes as responses to relatively brief events and long term changes, which mark permanent alteration of the biosphere.

When the taxa that permanently decline in diversity during the Devonian are compared with the taxa that show an overall increase in diversity it becomes clear that the Devonian is a time of faunal *turnover*. Total marine diversity changed little, but during the Devonian the diversity of many taxa changed markedly compared to either preceding or following intervals.

The pattern of faunal turnover or replacement in diversity dominance is often only clear at the ordi-

nal, rather than class, level. For example, the Stenolaemata did not change diversity greatly through the whole interval. However, between the Late Ordovician and the Late Devonian two of the four diverse orders of stenolaemates decreased in recorded diversity (the Trepustomata and the Cryptostomata) whereas two other orders (the Cystoporata and Fenestrata) doubled in recorded diversity during the same interval and a switch in dominance between the two sets of taxa occurred during the Devonian.

LOOKING AT THE TOP OF THE FOOD CHAIN: PREDATORS IN THE DEVONIAN

If change in biomass on land does influence the oceans, the top of the food chain, which is sensitive to perturbations throughout the food chain, may be the place where a response will be clearly expressed. Predators should be sensitive to changes in prey abundance. An increase in nutrients from the land could be responsible for generating a greater biomass of potential prey in the oceans, either as an increase in total numbers of prey or increased size (biomass) of individual prey organisms. An increase in either could permit an increase in consumers high in the food chain.

Evaluating predator diversity is difficult because some predator groups are rare and some, such as eunicid polychetes and conodonts in the Paleozoic, present taphonomic problems. Also, in groups such as the corals it is not clear how many of the extinct Paleozoic forms were passive predators and how many were suspension feeders. We do not know if any Paleozoic corals were hermatypic, either, and supported largely by photosymbionts. Interestingly, the recorded diversity of each of these groups (eunicid polychetes, conodonts, and anthozoans) does not change much throughout the middle Paleozoic. The anthozoa average about 60 to 80 genera crossing each interval boundary in the Silurian and average the same in the Carboniferous. The anthozoa do have a peak of recorded diversity during the Devonian (at about 120 recorded genera), but this is also when coral reef development in Canada, New York, and Australia was at its Paleozoic maximum. The eunicimorph polychetes, recognizable from scolecodonts, maintain a recorded diversity of about 20 genera crossing most interval boundaries from the Late Ordovician through the Middle Devonian and a recorded diversity of about 15 genera crossing interval boundaries during the Carboniferous. Likewise, the conodonts also maintain an average of about 15 recorded genera crossing interval boundaries from the Silurian through the Carboniferous. Because of uncertainties about the taphonomy and predatory activity of these groups, they were not analyzed, but their relatively unchanging diversity would not have altered the general

conclusions reached below about patterns of diversity among predators during the middle Paleozoic.

I chose to examine six major groups of predators, each with robust hard parts and each containing larger size representatives: the nautiloids, ammonoids, eurypterids, malacostracans, asteroids, and jawed fishes. A second reason, besides the combination of their preservation potential and relatively unambiguous status as predators, for choosing these groups is that three of the groups can be regarded as likely to have been relatively "low energy" groups with lower metabolic rates and, in some cases, sluggish life habits. The other three are "high energy" groups with comparatively high metabolic rates and more active life habits. These two sets of predator groups provide a contrast in energetics (energetics refers to the combination of biomass, general physical activity, metabolic rates, and the concomitant need for a level of food consumption sufficient for the support of metabolic needs) of the predators in the mid-Paleozoic fauna and, presumably, a contrast in the average amount of food required.

The "low energy" groups are the nautiloids, eurypterids, and asteroids. The "high energy" groups are the ammonoids, malacostracans, and jawed fishes. There is little controversy in regarding asteroids as low in energetics in contrast to jawed fish. Although nautiloids and ammonoids are both cephalopod molluscan groups, the contrast between the low energetics of living *Nautilus* (Redmond 1987; Boutillier et al. 1996) and the phylogenetically closest living relatives of ammonoids (Engeser 1990, 1996; Jacobs & Landman 1993), the squids, makes it reasonable to speculate that the nautiloids and ammonoids did have contrasting energetics. Likewise, the physiological studies of many living chelicerates (*Limulus*, scorpions, etc.) regularly report low metabolic rates compared to most malacostracan crustaceans. For example, Hamen (1980) notes that *Limulus* blood has a carrying capacity for oxygen little above that of plain water and less than one-third the average for crustaceans. Also, low metabolic rates are emphasized as characteristic of scorpions as a group (Polis 1990). Again, while admittedly speculative, it seems reasonable to suggest that if the living relatives of an extinct group seem to share generally low energetics, the extinct group, in this case the eurypterids, was possibly also characterized by low energetics.

The proportion of diversity of the whole fauna comprising the six chosen predator groups was fairly low (between six and nine percent of all recorded genera) during the mid-Paleozoic. But there is a remarkable replacement of dominance in these six predator groups (Fig. 2). Nautiloids, eurypterids, and asteroids - the likely "low energy" groups -

declined markedly in diversity during the Devonian and ammonoids, malacostracans, and jawed fishes - the "high energy" groups - diversified. The increase in predation resistant skeletal characteristics in the Devonian documented by Signor & Brett (1984) as an indication of the "precursor to the Mesozoic marine revolution" demonstrates the effect the increase in predation intensity, possibly caused by a change in energetics of the predators, had on the rest of the marine fauna. This turnover in dominance of predators took place during the Late Silurian to Middle Devonian. The new dominance of "high energy" predators established in the Late Devonian persisted unchanged through the entire Carboniferous (Fig. 3).

Another example of increased energetics in predator guilds in the Devonian is a marked increase in drilling predation during the Devonian (Kowalewski et al. 1998). Although drilling appears to decrease again in the later Paleozoic, more evidence of drilling during that time exists than was tabulated by Kowalewski et al. For instance, in the Permian alone Simões & Kowalewski (1998) report drill holes from Brazil and Cooper & Grant (1971-1976) illustrate a variety of drilled brachiopods from west Texas. Apparently the drilling mode of predation persisted consistently through the later Paleozoic, even if not at the level of the Devonian. The investment of energy in drilling is considerable; unfortunately the drilling animals are undetermined in the Paleozoic, so the producers of drill holes remain cryptic and their diversity can not be determined.

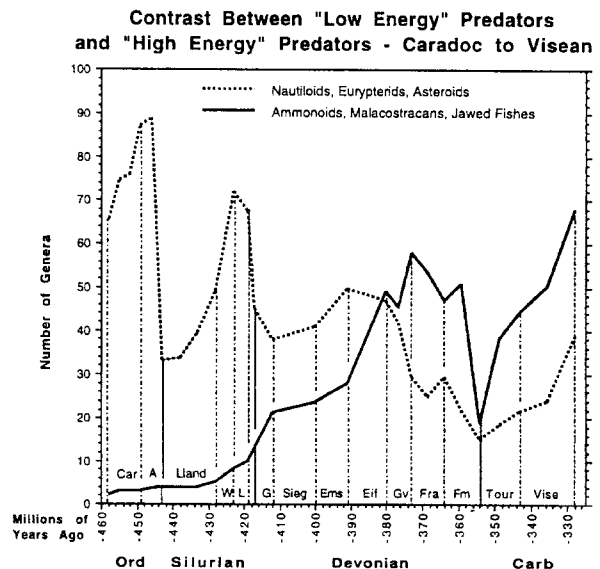
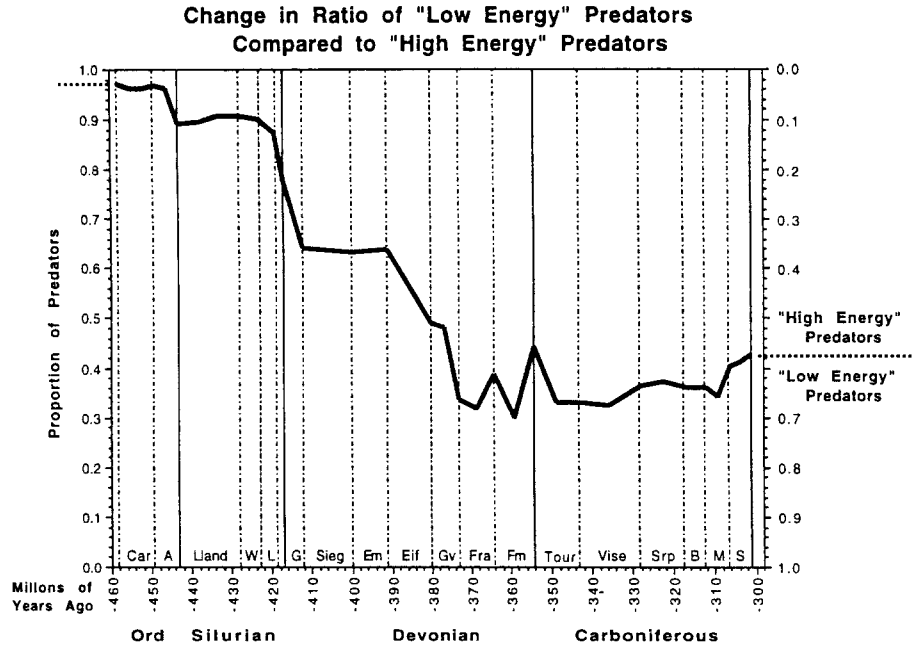


FIGURE 2 - Replacement in dominance of "low energy" predators (nautiloids, eurypterids, and asteroids) by "high energy" predators (ammonoids, malacostracans, and jawed fishes) during the Devonian. Remplacement de la dominance des prédateurs à "faible énergie" (nautiloïdes, euryptérides et astéroïdes) par des prédateurs à "haute énergie" (ammonoïdes, malacostracés et poissons) au cours du Dévonien.

FIGURE 3 - Changing balance of "low" and "high" energy predators, based on numbers of genera. Note relative stability in Late Ordovician and Silurian, change from the Pridolian through Givetian, and relative stability at the new "energetic" ratio from the Frasnian through the Carboniferous despite fluctuations in total overall diversity. *Changement d'équilibre des prédateurs de "faible" et "forte" énergie basé sur les nombres de genres. Notez la stabilité relative à l'Ordovicien supérieur et au Silurien, le changement du Pridolien jusqu'au Givétien et la stabilité relative du nouveau rapport "énergétique" du Frasnien au Carbonifère en dépit des fluctuations de la diversité totale.*



The proportion of total diversity comprised of predators actually did increase somewhat, although not dramatically, in the Devonian. Before the Middle Devonian the average proportion of the total fauna made up of the six predator groups considered was about seven percent. From the Middle Devonian through the Carboniferous these six groups of predators made up nine percent of total diversity, an increase of two percent, a small but persistent increase. So, although the diversity of predators in the oceans only increased slightly, replacement of former dominant groups of predators with low energetics by predators with higher energetics characterizes the qualitative change that occurred in the Devonian, the interval when biomass on land and potential additional food supplies from land to the oceans also increased. The energetics of the marine fauna changed during the Devonian. I suggest that this was one of the effects of changing nutrient supply to the oceans.

AN EXAMPLE OF A RESPONSE OF NON-PREDATORS TO INCREASED ENERGETICS IN THE MARINE BIOSPHERE: THE BRACHIOPODS

The articulate brachiopods provide an excellent example of the relationship in a non-predator group between increased energetics in the marine ecosystem and faunal turnover in the Devonian. The class as a group has a peak of diversity in the Devonian. In the Early Carboniferous brachiopod diversity was lower than the Devonian peak, but approximately the same as it had been in the Late Ordovician. But this pattern masks a clear faunal replacement at the ordinal level related to decline in orders and suborders that were less disturbance and predator resistant and an increase in orders and suborders

that were more disturbance and predator resistant (Fig. 4).

Three orders, the orthids, pentamerids and atrypids, declined in diversity, starting in the late part of the Early Devonian. These orders generally lacked mantle reversal in development (Williams & Rowell 1965), leading to a weaker, less protected pedicle. Pedicle base musculature and insertion could not develop in the varied and complex manners possible with mantle reversal. Also, the pentamerids were free-lying on the sea-floor as adults and vulnerable to disturbance. These features made these three orders relatively vulnerable to disturbance and predation. Three orders, the rhynchonellids, spiriferids, and terebratulids, increased in diversity in the Late Silurian and Early Devonian and reached and maintained an even higher diversity in the Carboniferous despite suffering in the extinctions of the later Devonian. All three of these orders had mantle reversal in development (Williams & Rowell 1965), which permitted more robust internal attachment and musculature for the pedicle as well as the secretion of protective plates associated with the pedicle opening. Such features made these groups less vulnerable to predation and disturbance. The last order of articulates, the Strophomenida, has a diversity pattern very similar to the class as a whole - an Early to Mid Devonian peak of diversity with Carboniferous diversity similar to that of the Late Ordovician. However, the Strophomenida comprise three suborders with very different capabilities for resisting disturbance (Rudwick 1970). The Strophomenidina commonly lacked a pedicle and lay free on the sea-floor. The Chonetidina had spines on the strophic

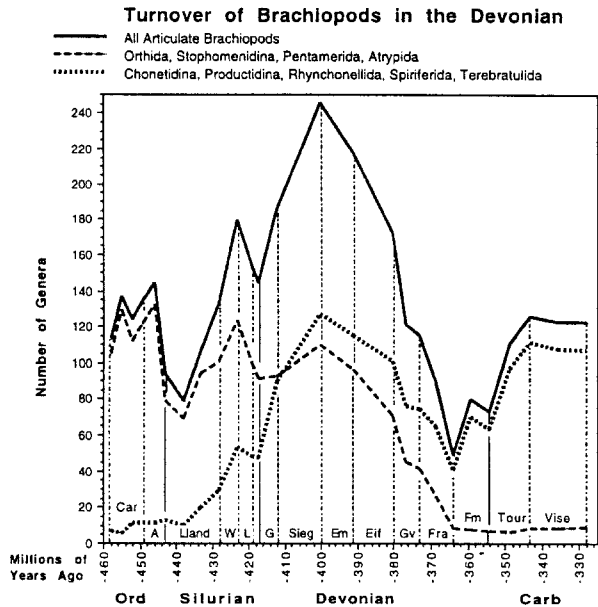


FIGURE 4 - Turnover of dominance in articulate brachiopods in the Devonian. Disturbance and predation sensitive groups (orthids, pentamerids, atrypids, and the Strophomenidina) decline and disturbance and predation resistant groups (rhynchonellids, spiriferids, terebratulids and the Chonetidina and Productidina) increase. The peak in total brachiopod diversity is an overlap when both groups are relatively diverse. *Modification de la dominance chez les brachiopodes articulés au Dévonien. Les groupes sensibles aux perturbations et aux prédateurs (orthides, pentamérides, atrypides et Strophomenidina) déclinent et les groupes résistants à ces phénomènes (rhynchonellides, spiriférides, térébratulides, Chonetidina et Productidina) s'accroissent. Le pic de diversité totale des brachiopodes correspond au recouvrement des deux groupes lorsqu'ils sont relativement diversifiés.*

hinge margin that aided in maintaining life position and also served a sensory function, and the Productidina had spines covering the pedicle valve surface that virtually "rooted" the shell in the sediment. Some had spines that grew around objects and held the shell firmly in place. Spines are also a protective device (Signor & Brett 1984; Vermeij 1987). The diversity of the Strophomenidina, the suborder most vulnerable to disturbance and predation, collapsed during the Middle and Late Devonian and never recovered, whereas the diversity of the Chonetidina and Productidina increased during the Devonian.

When the disturbance and predation resistant groups are compared as a unit to the less robustly attached and protected groups of articulate brachiopods, it is clear that the Devonian is a time of faunal turnover (Fig. 4). The dominance replacement in the articulate brachiopods is consistent with the transition to a fauna of greater energetics in which successful organisms commonly needed to cope with frequent biological disturbance. The peak of articulate brachiopod diversity in the late Early Devonian is simply the time when the transition in dominant groups occurred. The more predation and

disturbance resistant groups had reached high diversity and the more vulnerable groups had not yet waned. It would be interesting to compile relative abundance data, too, to determine whether abundance changes were taking place at this time, too. It may be that the abundance of the radiating suborders lagged behind their diversity increase, as Wing & Boucher (1998) document for the angiosperm radiation during the Cretaceous, or it may be that the waning taxa lost abundance before a significant loss of diversity occurred. Boucot (1975) has argued that the peak of brachiopod diversity in the Early Devonian reflects the time of maximum provinciality. The two maxima may coincide, but because the peak of diversity also coincides with changes in ordinal dominance, and the orders are not responding to biogeographic changes, high provinciality is probably not responsible for the peak, just as Rosenzweig (1995) has argued that global diversity is not strongly tied to provinciality.

THE MESOZOIC-CENOZOIC RADIATION AND THE CRETACEOUS

THE RISE OF THE ANGIOSPERMS, A SECOND INCREASE IN TERRESTRIAL PRODUCTIVITY AND BIOMASS

The middle of the Cretaceous is when angiosperms began to increase noticeably in diversity and abundance. Crane & Lidgard (1990) documented this for both angiosperm megafossils and palynomorphs. The diversity of angiosperm megafossils rose from a maximum of 20% of the flora in the Aptian to as much as 80% by the Cenomanian. Angiosperm pollen increased from a maximum of 30% of the palynoflora in the Albion to as much as 80% in the Cenomanian. The increase began earlier in low latitudes, as documented for pollen, but typified all latitudes by the midpoint of the Cretaceous. Although the data of Crane & Lidgard support the contention that angiosperm abundance increased during the Late Cretaceous, Wing & Boucher (1998) have shown that even after the diversity of angiosperms had increased the abundance of angiosperms is still relatively low, compared to gymnosperms, in many Late Cretaceous floras. Wing & Boucher agree with Crane & Lidgard that angiosperms first became quantitatively dominant in low latitudes. During the Cretaceous, however, they only dominated disturbed environments in mid latitudes. Their early success was probably in their ability to rapidly invade disturbed areas with low vegetation. Wing and Boucher also argue that the fast growth and high rate of resource use probably aided their success in lower latitudes. Because half the earth's surface is between 30° north and 30° south latitude, the expansion of angiosperms did contribute significantly to an increase in biomass

on land, although the angiosperms in the Cretaceous “still lacked the biomass dominance of global vegetation and range of ecological strategies that they achieved during the Cenozoic” (Wing & Boucher 1998: 415). Any influence of increased biomass on land from the angiosperm radiation would have begun in the Cretaceous but continued to develop in the Cenozoic.

MARINE DIVERSITY: MESOZOIC AND CENOZOIC

The diversity of genera in the marine fauna increased nearly continuously during the Mesozoic and Cenozoic (Fig. 5A). Although the rate of diversity increase changed during the Cretaceous and early Cenozoic, a simple exponential curve fitted to the entire Mesozoic and Cenozoic correlates diversity to time with an r^2 value of 0.95, suggesting that there is little statistical reason to view the Cretaceous as a time when diversity change is significantly different from that at any other time over the last 200 million years. As with the Paleozoic Plateau, no major change in the pattern of overall marine diversity seems to occur when diversification and biomass increased on land.

But total diversity is a composite, summing data from many different individual groups. Therefore, the general upward trend of overall diversity in the Mesozoic and Cenozoic masks a variety of other individual patterns. For example, the foraminifera show continuous increase, interrupted only by the great end-Cretaceous mass extinction. However, the modern corals diversify rapidly in the Middle Jurassic and then fluctuate, but do not increase, in diversity after that. In contrast, the diversity of the articulate brachiopods drifts downward through the Mesozoic into the early Cenozoic.

PREDATOR RADIATIONS DURING THE CRETACEOUS

Since we are looking for the effects on life in the oceans of another postulated increase in biomass and diversity of plant life on land, it is reasonable to look again at predators, the top of the food chain, where marine life would be most sensitive to change in food supplies. Both predator and prey groups increase in diversity from the Jurassic to now. Vermeij (1977) pointed out that the effects of predators on preserved shells increased markedly in the Mesozoic, indicating an increase in predation intensity which Vermeij named “the Mesozoic marine revolution.” Let’s look more closely at this pattern.

The prosobranch gastropods include both herbivores and carnivores. The Archaeogastropoda, which are predominantly herbivores and detritivores, do not increase at all in diversity until the Cenozoic and then they diversify at a lower rate

than either the Mesogastropoda or Neogastropoda. The Mesogastropoda, which include some drilling predators such as *Polynices* among a variety of trophic types, maintain a steady level of diversity through the Jurassic but begin an accelerating increase in diversity in the Cretaceous. The Neogastropoda, which are exclusively carnivorous, jump up in diversity first in the Late Cretaceous (from eight recorded genera entering the Cenomanian to 93 entering the Maastrichtian) and they continue to increase rapidly in diversity throughout the Cenozoic. The non-crab malacostracans, which include a variety of trophic types, increase in diversity slowly but continuously from the Jurassic onward. The true crabs (brachyurans), which are predators and often use their varied claws to specialize on particular types of prey, first diversify noticeably in the middle of the Cretaceous (doubling from eight to 17 recorded genera between the Aptian/Albian and Albian/Cenomanian boundaries) and undergo a striking radiation in the early Cenozoic (increasing from 15 to 62 recorded genera between the Paleocene/Eocene boundary and the middle of the Middle Eocene). Among the cartilaginous fishes both the rays (Batoidea), shell crushing carnivores, and the active true sharks (Galeomorpha), the highest level of the food pyramid, diversify rapidly in the middle of the Cretaceous (increasing from 11 recorded genera at the Aptian/Albian boundary to 28 at the Cenomanian/Turonian boundary), whereas the dogfishes and their relatives (Squalomorpha) diversify more slowly (five recorded genera at the Aptian/Albian boundary and still five at the Cenomanian/Turonian boundary, although they reach 13 recorded genera by the Campanian/Maastrichtian boundary). The teleosts, the modern bony fish, which include many predators as well as other trophic types, first diversify in the Late Cretaceous and then expand rapidly in diversity throughout the Cenozoic. The vast majority of tetrapods that have re-invaded the oceans are predators. Although there were important marine reptiles in the Triassic and Jurassic, they underwent an explosive radiation in the Late Cretaceous, prior to the end Cretaceous extinction (seven recorded genera cross the Albian/Cenomanian boundary and 32 cross the Campanian/Maastrichtian boundary). Interestingly, the Cenozoic radiation of marine mammals reached, but did not exceed, the diversity of genera attained by marine reptiles in the Late Cretaceous.

Although there is no major overall change in the pattern of diversification during the Cretaceous, the diversity of all the major predator groups does increase sharply during this time, with the greatest change in the mid to late Cretaceous, and predator groups continue diversifying at a higher rate than non-predators during the Cenozoic. This is reflected

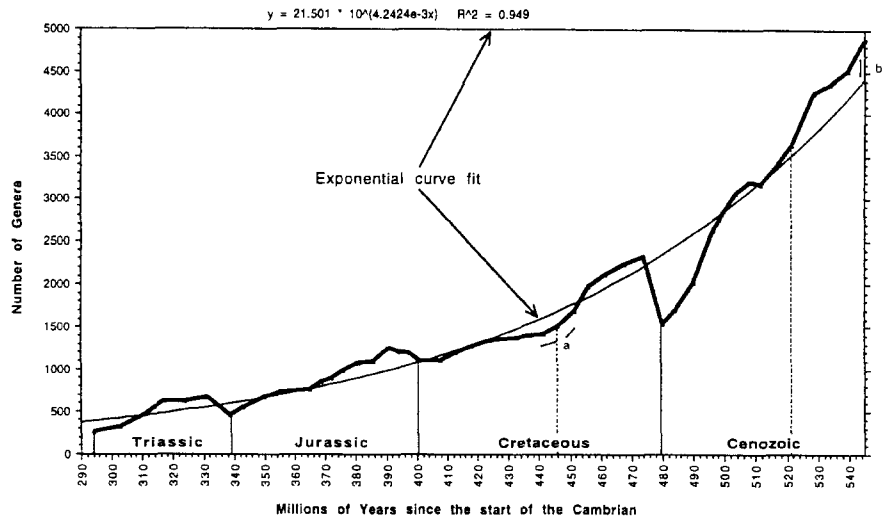
FIGURE 5 - **5A.** Diversity of marine animal genera in the Mesozoic and Cenozoic. An exponential curve fit has been added (which has an r^2 of 0.95!). The small letter a marks the inflection in diversity increase at the transition into the Late Cretaceous. The small letter b marks the difference between the exponential curve fit and the diversity that develops by the late Cenozoic. Late Cretaceous and Cenozoic diversification appears to "outrun" the modeled exponential growth. **5B.** The same data as 5A except that the low diversities of the intervals following the end-Cretaceous extinction are omitted. Now the exponential curve fit to the data follows that data path very closely. It appears that post-Paleozoic diversity change is purely exponential and the apparent "outrun" in the later Cenozoic in Figure 5A (letter b) is an artifact of curve fitting influenced by the low diversity data following the end-Cretaceous extinction. **5A.** *Diversité des genres d'animaux marins au Mésozoïque et au Cénozoïque. Un ajustement de la courbe exponentielle a été ajouté (avec $r^2 = 0,95!$). La lettre "a" marque l'inflexion de l'accroissement de la diversité à la transition du Crétacé supérieur. La lettre "b" marque la différence entre l'ajustement de la courbe exponentielle et la diversité qui se produit au Cénozoïque supérieur. La diversification du Crétacé supérieur et du Cénozoïque semblent "dépasser" la croissance exponentielle modélisée. **5B.** Mêmes données que 5A mais les faibles diversités des intervalles suivant l'extinction fini-crétacée sont omises. Maintenant l'ajustement de la courbe exponentielle suit très précisément la courbe des données. Il apparaît que le changement de la diversité post-paléozoïque est nettement exponentiel et que le "dépassement" apparent au Cénozoïque terminal de la figure 5A (lettre b) est un artifice de l'ajustage de la courbe influencée par les données de faible diversité suivant l'extinction fini-crétacée.*

in the changing proportion of total marine animal diversity made up of predators (Fig. 6). During the Jurassic and most of the Early Cretaceous the proportion of predators averaged nine percent of the total fauna, the same as it had during the Late Devonian and Carboniferous. During the Late Cretaceous and Paleocene it jumped to an average of 12 percent and rose to average over 20 percent for the rest of the Cenozoic. This is almost certainly represents increasing specialization of predators on particular target prey and prey combinations and is not a result of a decrease in the ratio of the number of prey per individual predator. A further increase in nutrient supply from the land, driven by the rise of the highly productive angiosperms, could have permitted an increase in the numerical abundance (biomass) of prey of all sorts, providing ade-

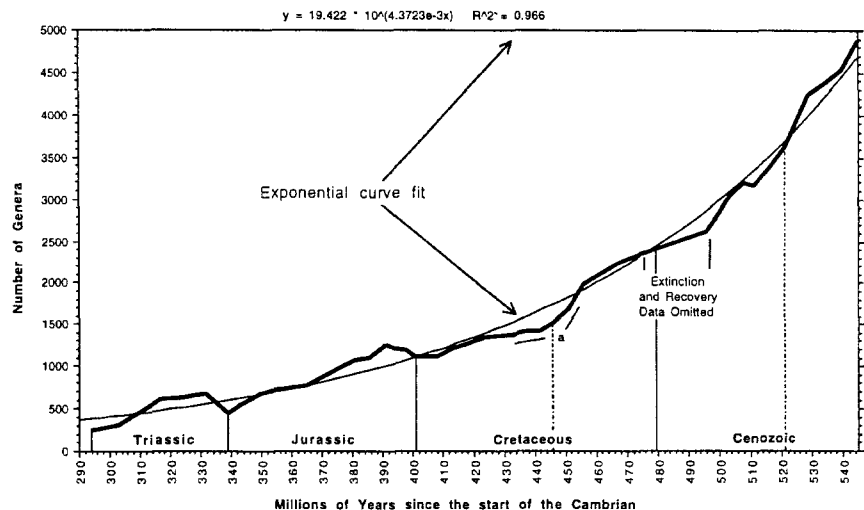
quate numbers to support specialization of predators on particular prey, thus opening the way to a co-evolution of a higher diversity of predators.

In discussing changes in the pelagic realm during the Mesozoic and Cenozoic, Fischer & Arthur (1977) argued that predators were be influenced by changes in oceanic conditions, but they claimed predators increased during times of "decreased fertility and productivity in the open ocean." Their analysis emphasized a speculative 32 million year periodicity of "polytaxic" and oligotaxic" episodes. Their database was only for the pelagic realm and, unlike more recently compiled global databases, showed no particular secular trends. Fischer and Arthur's suggested pattern does not match with the global and temporal scale of analysis used here, but may relate to the fluctuations within the long-term glo-

A. Diversity of Marine Animal Genera through the Mesozoic and Cenozoic



B. Diversity of Marine Animal Genera through the Mesozoic and Cenozoic Omitting the Cretaceous Extinction and Recovery



bal pattern (such as the variations around the exponential curve fit to diversity with the unusual low values following the end-Cretaceous extinction removed (Fig. 5B).

OTHER LINKAGES TO INCREASED MARINE PRODUCTIVITY IN THE CRETACEOUS

Other diversity data also fits with these postulated changes in marine food supplies. For example, the suspension feeding bryozoa increase diversity sharply in the Late Cretaceous (from 71 recorded genera at the Albian/Cenomanian boundary to 238 recorded genera at the Campanian/ Maastrichtian boundary), suggesting that supplies of food in suspension may have increased (but, as noted above for angiosperm diversity versus abundance, see McKinney et al. (1998) for another compelling analysis suggesting the need for quantitative abundance data as well as diversity data for making a complete analysis of the nature of faunal transitions). The two primary reasons for adopting an infaunal mode of life are deposit-feeding and protection from predators. The regular echinoids, which are epifaunal, radiated in the Jurassic and then remained fairly constant in diversity (rising from 10 to 33 recorded genera during the Jurassic, but with no more than 35 genera recorded crossing the Oligocene/Miocene boundary in the mid Cenozoic). However, infaunal irregular echinoids, both those that retained the lantern and those that lost all mouthparts, diversified in the Cretaceous (rising from 10 recorded genera at the Jurassic/ Cretaceous boundary to 77 at the Campanian/ Maastrichtian boundary). Deposit-feeding may have increased during the Cretaceous when marine productivity, driven by more nutrient runoff from the land, increased and more food was buried in the sediment. We have already seen that an increase in predation pressure would have accompanied the radiation of predators during and after the Cretaceous. Similarly, although there is only modest increase in diversity of attached epifaunal bivalves (who live exposed directly to predators), with 204 genera recorded at the Campanian/Maastrichtian boundary in the Late Cretaceous and 229 genera at the Miocene/Pliocene boundary in the later Cenozoic, infaunal forms (both deposit-feeders and suspension-feeders), which are concealed in the sediment from direct observation by predators, skyrocket in diversity during the Cenozoic (from 197 recorded genera at the Campanian/Maastrichtian boundary in the Late Cretaceous to 531 at the Miocene/ Pliocene boundary in the later Cenozoic).

A major increase in average size and biomass of individuals of most marine organisms occurred between the Paleozoic and Cenozoic and I argued (Bambach 1993) that this may have resulted from increased nutrient supplies to the oceans. Recently,

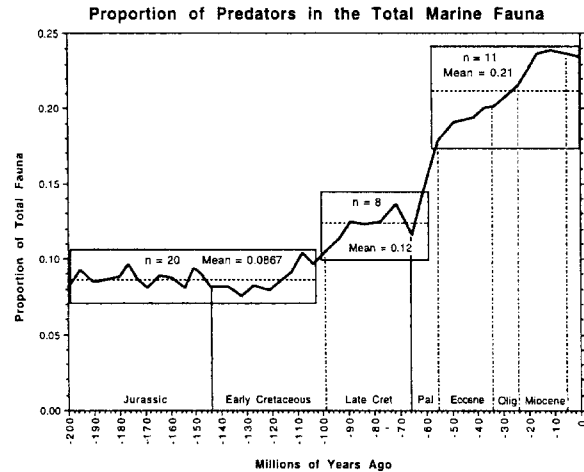


FIGURE 6 - The proportion of total diversity of marine animal genera composed of predators from the Jurassic to the Plio-Pleistocene. The estimate of predator diversity is conservative, comprising all cenogastropods, cephalopods, chondrichthyans, reptiles and mammals, but only 1/3 of the mesogastropods, 1/3 of the teleosts, and 1/2 of the malacostracans. *Proportion de diversité totale des genres d'animaux marins composée de prédateurs du Jurassique au Plio-Pleistocène. L'estimation de la diversité des prédateurs comprend tous les cénogastropodes, céphalopodes, chondrichthyens, reptiles et mammifères mais seulement 1/3 des mésogastropodes, 1/3 des téléostéens et la moitié des malacostracés.*

Kidwell & Brenchley (1996) have shown that shell beds increased in thickness in the Mesozoic, implying that the changes in biomass in the Mesozoic may also include an increase in total number of organisms, an increase I could not advocate with confidence in 1993. A final piece of evidence supporting the idea that nutrient availability in the oceans increased in the Cretaceous comes from the classic work of Tappan & Loeblich (1973). Preserved diversity of phytoplankton more than doubled between the Early and Late Cretaceous. Apparently primary production in the oceans did increase during the Cretaceous.

Increase in marine diversification appears to be continuous through the Mesozoic and Cenozoic, and it closely approximates pure exponential increase (Fig. 5). However, an inflection in the rate of diversification is apparent in the mid Cretaceous (a in Fig. 5). This fits with the timing of increased food supply from the diversification of angiosperms and the increase in diversification of predators that appears to be concentrated in the Cretaceous. Although it appears in figure 5A that diversity increases faster than the exponential curve fit from the mid-Cretaceous on and that diversity consistently exceeds the value of the curve fit from the end of the Oligocene to now (b in fig. 5A), this is an artifact of fitting the single exponential function to data that include the lower diversities immediately after the end-Cretaceous extinction event. If these low diversity values are omitted from the analysis,

the exponential curve maps on the total diversity path very closely. It is as if the end-Cretaceous extinction had no long-lasting effect on total global marine diversity at all (see Sepkoski 1984 for a similar conclusion). Recovery from the end-Cretaceous extinction was complete by the Late Eocene and then diversity continued to rise at the same exponential rate set during the Mesozoic.

The radiation of predators and the expansion of infaunal forms, as well as the increase in diversity of phytoplankton, all begin in the Cretaceous when the increased influx of organic detritus and nutrients associated with the diversification of the angiosperms also started, and continued into the Cenozoic, just as the angiosperms continued to diversify and gain abundance dominance on land. Predators, prey, and producer taxa appear to respond together. These changes were shifts in importance of different life habits that can be tied to increased energetics in the biosphere, but were not associated with increases in total diversification rates.

CONCLUSIONS

The two times of increased diversity and biomass of plant life on land have little effect on the pattern of marine diversity as such, but major change in the energetics of the marine fauna occur during both episodes of diversification on land (Fig. 7). In the Paleozoic episode of faunal turnover, the replacement of low energy predators by high energy predators indicates that, although there was no permanent change in marine diversity, a qualitative change had occurred in the fauna. Some of the responses in non-predators, such as the increase in disturbance-resistant adaptations in brachiopods, also support the idea of an increase in energetics in the fauna as a whole. In the Paleozoic case, to support a change to predators with greater energetics, either a larger biomass of prey would have been needed to maintain approximately the same diversity and abundance of predators or populations of more energetic predators would have been smaller than the populations of the dominant low energy predators of the early Paleozoic. Further study, incorporating abundance data, will be needed to differentiate between these possibilities. The increase in food supplies associated with the Cretaceous and Cenozoic affected the already energetic global fauna by increasing productivity and prey abundance enough to permit an increase in specialization of predators, thus raising the proportion of diversity made up of predators. In effect this was a co-evolutionary expansion, a quantitative addition of biomass at most levels in the food chain, not a qualitative change in predator energetics alone, although one result was lengthened food chains.

Many of the adaptive changes in the marine biosphere discussed by Bambach (1983, 1985, 1993) are related to the increase in energetics of the marine fauna considered in this paper. These changes in energetics also permitted the escalation of intensity of biotic interactions documented at length by Vermeij (1987). The increases in nutrient supply to the oceans and the increased base of the food chain has not reduced diversity and, in the Mesozoic and Cenozoic, has contributed to the expansion of diversity. The diversity relations to oligotrophy and eutrophy postulated by Valentine (1971) do not hold on a global scale, possibly because sufficiently eutrophic conditions to affect diversity have not been achieved, at least on a long-term basis. However, I differ from Vermeij (1995) in believing that much of the increase in nutrient supply to the oceans and subsequent changes in the marine biosphere are primarily a consequence of biotic changes, especially those on land, and their influence on weathering and nutrient recycling, rather than being related to tectonic or volcanic changes. While it is true that tectonic and volcanic fluxes do change over time, my experience with paleogeographic reconstructions (Scotese et al. 1979; Bambach et al. 1980) suggests that no secular increases in purely physical (inorganic) processes have occurred in the Phanerozoic that alone could have permanently altered the nutrient and energetic structure of the biosphere.

For almost twenty years our overview of the history of the marine fauna has been governed by Sepkoski's (1981) designation of three evolutionary faunas. The groupings designated by Sepkoski were based strictly on diversity within classes. It is interesting that the two major changes in predation and energetics in the marine fauna documented in this paper both take place in the middle of spans of apparently homogeneous dominance by one or another of the evolutionary faunas as designated by Sepkoski, not at times of transition between the faunas. The changes documented here generally occurred within classes, but Sepkoski (1981) did extract two factors (his factors VI and VII) that relate to transitions in the mid-Paleozoic and between the Mesozoic and Cenozoic, the times studied in this paper. The effects on the marine fauna from changes in life on land took place by altering energetics and ecological responses, not overall diversity or diversity trends.

The surprising conclusion is that major increases in global organic productivity have had no apparent direct effect on total marine diversity. This means that the pattern of diversity increase at the global level is not directly related to this ecological parameter. Raup et al. (1973) pioneered in arguing that appropriate null models of diversity change be created against which causal controls could be tested. For instance, one of my students, Matt Powell,

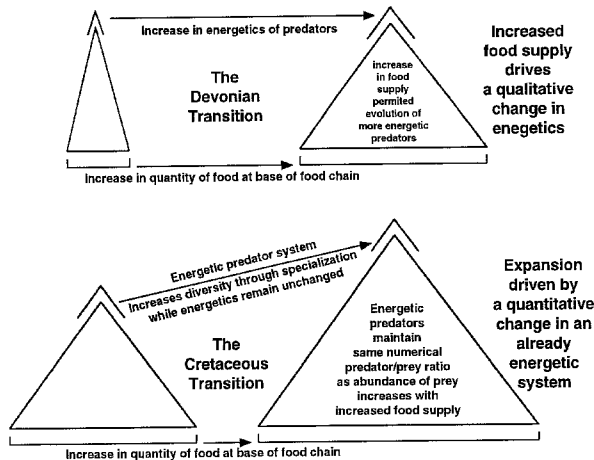


FIGURE 7 - Diagram illustrating the difference between the apparent Devonian increase in energetics (a qualitative increase, but with no significant diversity change) and the Cretaceous increase in diversity and biomass (a quantitative expansion, but with little change in organism energetics). Areas of the triangles represent total marine animal biomass. Widths of the bases of the triangles represent the input of quantity of food at the base of the biomass pyramid. Heights of the triangles represent diversity at the top of the food chain. The angle at the apex of the pyramids represents the average energetics of the dominant predators (less energetics for the more acute angles, greater energetics for the more obtuse). In the Devonian case the base of the food chain expands but diversity at the top does not change much, although there is an increase in the energetics of the predator system. In the Cretaceous case the expanded base of the food chain permits increased diversity at the top of the food chain but the predators do not increase individual energy requirements. In this case there is simply diversity and abundance increase throughout the fauna. *Diagramme illustrant la différence entre l'accroissement apparent en énergie au Dévonien (un accroissement qualitatif mais sans changement significatif de la diversité) et l'accroissement de la diversité et de la biomasse au Crétacé (une expansion quantitative mais avec peu de changements en énergie des organismes). Les surfaces des triangles représentent la biomasse animale marine totale. Les largeurs des bases des triangles représentent l'apport de quantité de nourriture à la base de la pyramide de la biomasse. Les hauteurs des triangles représentent la diversité de la chaîne trophique. L'angle au sommet des pyramides représente l'énergie moyenne des prédateurs dominants (énergie moindre pour les angles les plus aigus, énergie plus grande pour les plus obtus). Dans le cas du Dévonien, la base de la chaîne trophique s'agrandit mais la diversité au sommet ne change guère quoique qu'il y ait un accroissement de l'énergie dans le système des prédateurs. Dans le cas du Crétacé, la base étendue de la chaîne trophique permet une diversité accrue au sommet de la chaîne mais les prédateurs n'augmentent pas leurs besoins en énergie individuelle. Dans ce cas, il y a simplement accroissement de la diversité et de l'abondance au sein de la faune.*

has done a time-series analysis that suggests the diversity history of marine genera is indistinguishable from a random walk (unpublished personal communication 1999). Because no relationship between global diversity and productivity increase was found in my analysis, it does not mean that no connection exists between productivity and the changes in the fauna during the Devonian and starting in the Cretaceous, only that other factors

than total diversity are relevant. The co-ordination of change in both predator and prey taxa and in plant productivity during the Devonian and starting in the Cretaceous, plus the fact that each relates to energetics in the biosphere and that similar response patterns occur in both instances, suggest that these are not simply stochastic events coincidentally occurring at the same time. But the ultimate test of the hypotheses put forth in this paper will come from abundance data, combined with diversity analysis. We will need to expand the available database in paleontology to permit successful resolution of these questions.

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R.K. BAMBACH

Department of Geological Sciences
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061-0420, U. S. A.
e-mail: bambachr@vt.edu