

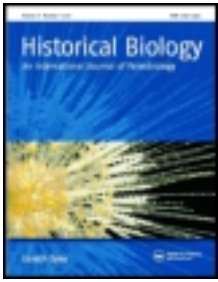
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Biogeography of recent marine bivalve molluscs and its implications for paleobiogeography and the geography of extinction: A progress report

Karl W. Flessa^a & David Jablonski^b

^a Department of Geosciences, University of Arizona, Tucson, Arizona, 85721, USA

^b Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois, 60637, USA

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BIOGEOGRAPHY OF RECENT MARINE BIVALVE MOLLUSCS AND ITS IMPLICATIONS FOR PALEOBIOGEOGRAPHY AND THE GEOGRAPHY OF EXTINCTION: A PROGRESS REPORT

KARL W. FLESSA*

Department of Geosciences, University of Arizona, Tucson, Arizona 85721 USA

DAVID JABLONSKI

*Department of the Geophysical Sciences, University of Chicago
Chicago, Illinois 60637 USA*

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The geographic distribution of Recent taxa is important in interpreting paleobiogeography and the fossil record of extinction. We examine the latitudinal diversity gradient in Recent marine bivalve molluscs and the effects of bivalve distributional patterns on the severity of model extinctions using a global biogeographic database for genera of Recent shallow (<200 m) marine bivalve molluscs. To date, we have collected information on genera and subgenera from 14 superfamilies: Arcoidea, Limopsoidea, Mytiloidea, Pterioidea, Pinnoidea, Pectinoidea, Trigonidea, Carditoidea, Cardioidea, Tridacnoidea, Solenoidea, Tellinoidea, Arcticoidea and Veneroidea. Although these superfamilies represent only 30% of all marine superfamilies, they include approximately 49% of the extant marine genera. We used recent monographs to disentangle many generic assignments, thus attaining uniformity of treatment at the generic level among 115 sites or regions.

The expected latitudinal diversity gradient is clearly seen in our data. Although high latitude faunas are consistently low in generic diversity, tropical bivalve faunas exhibit a wide range of diversities, mainly because of the relative impoverishment of Atlantic faunas and the low diversity of tropical island faunas relative to their continental shelf counterparts. Island faunas are dominated by cosmopolitans, underscoring the importance of dispersal in maintaining bivalve populations on oceanic islands.

We simulated extinction of bivalve faunas by “eliminating” genera restricted to particular latitudinal zones, oceans, continental shelves or oceanic islands. Because endemism at the generic level is low (despite today’s high global thermal gradient and wide dispersal of continents), extinctions comparable to the major mass extinctions of the past can be accomplished only through the annihilation of faunas in several latitudinal zones or oceans. Either today’s fauna is more cosmopolitan than those of the past (which is unlikely), or major mass extinctions required truly pervasive and profound environmental upheavals

KEY WORDS: Recent marine bivalve molluscs, biogeography, extinction.

INTRODUCTION

Analyses of the biogeography of living organisms have proven useful in understanding paleobiogeographic and paleogeographic patterns (e.g., Stehli *et al.*, 1967; Newton, 1988),

*To whom correspondence should be addressed.

changes in Phanerozoic diversity (e.g., Valentine, 1971; Flessa and Sepkoski, 1978), and temporal and spatial patterns of extinction (e.g., Raup, 1982; Jablonski and Flessa, 1986; Valentine and Jablonski, 1991). In this paper, we present some preliminary results based on our compilation of biogeographic data on Recent marine bivalve molluscs. Because our database is not yet complete, this paper should be viewed as a progress report rather than a definitive analysis.

We explore two aspects of the biogeography of Recent marine bivalve molluscs: the latitudinal diversity gradient and the effects of biogeographic distribution on the magnitude of extinction.

MATERIALS AND METHODS

We chose to examine marine bivalve molluscs because they are a diverse, well-studied and widely distributed group of marine organisms. They have not only left behind an excellent paleobiogeographic record in their own right, they are reasonable proxies for many other well-skeletonized groups. To date, we have collected information from the literature (see Appendix for complete list) on the species diversity and generic and subgeneric composition of shallow water (<200 m) marine bivalves from 14 superfamilies in each of 115 localities (Table 1). These fourteen superfamilies constitute 30 percent of the 41 extant superfamilies; the 607 genera (including subgenera) in these 14 superfamilies make up 49% of the 1247 marine genera in the class (our counts of genera and superfamilies are based on Vaught (1989)). Our present sample of the fauna includes genera from the two most diverse superfamilies – Veneroidea and Tellinoidea, as well as genera from superfamilies of intermediate and low diversity. Most major bivalve life habits are represented by the sampled superfamilies: infaunal siphonate suspension feeders, infaunal, non-siphonate suspension feeders, boring suspension feeders, siphonate deposit feeders, eipifaunal suspension feeders, and bysally attached suspension feeders. Only labial palp deposit feeders and those with chemotrophic symbionts are lacking. Even though we have not yet completed our compilation, our sample is a good one – it represents the taxonomic and ecological breadth of the class.

Table 1 Superfamilies considered in this study. Number of genera is based on counts of genera and subgenera in Vaught (1989).

<i>Superfamily</i>	<i>Number of genera</i>	<i>Superfamily</i>	<i>Number of genera</i>
Arcoidea	38	Carditoidea	46
Limopsoidae	24	Cardioidea	48
Mytiloidea	70	Tridacnoidea	4
Pterioidea	12	Solenoidea	15
Pinnoidea	6	Tellinoidea	127
Pectinoidea	54	Arcticoidea	10
Trigonoidea	1	Veneroidea	152

We have compiled faunal lists from all latitudinal zones, from each ocean and many marginal seas, and from continental shelves as well as oceanic islands (Table II); most of our 115 localities represent small regions rather than geographic points. Most of the faunal lists for these regions are derived from a single literature source, although a few represent syntheses from several sources (see Appendix). Although our coverage is geographically broad, the quality of coverage is inevitably uneven. While some regions

of the world's ocean are well-sampled and well-studied (e.g., the eastern Pacific, the North Atlantic, Japan), other regions (e.g., the Indian Ocean, the Atlantic coast of Africa north of South Africa) are not as well known.

In the course of these compilations, we also constructed a master list of valid species names and their correct generic assignments. This master list was assembled by the use of major recent monographs or systematic studies of particular taxa. Cross-checking each locality's species list with the master list of valid species names and generic assignments allowed us to improve the uniformity of taxonomic treatment at the generic level.

Taxonomic problems surely remain and can be resolved only through more systematic study. Two general problems affect our compilation. "Chauvinotypy" (Rosen, 1988, p. 447), or the tendency to erect invalid taxa in one's homeland, tends to artificially increase the diversity and endemism of local faunas. Iredale's studies of the Australian bivalve fauna (see his work cited under localities 27 and 28 in Appendix) are an example of this bias. An opposite effect is produced by "imperialistic taxonomy", the tendency to recognize taxa from one's home country in a distant region. This bias, perhaps exemplified by 19th century European malacologists, tends to result in less diverse, more cosmopolitan faunas. The relative effect of these opposing biases has yet to be assessed, and of course varies from locality to locality.

Following the construction of faunal lists for each locality, information on the species diversity of the genera in each of the localities was entered in a dBASE-compatible database file. Only 575 of the 607 genera listed in Vaught (1989) were actually encountered in our literature survey. The remainder are either deep-water forms, invalid genera, or rare and/or geographically restricted. The results reported in this paper were achieved through use of conventional dBASE-compatible query commands.

Faunal lists for each locality, master lists of valid species names and generic assignments, and dBASE files are available on request from the authors.

RESULTS AND DISCUSSION

The Latitudinal Diversity Gradient

The expected latitudinal diversity gradient is clearly detectable in our data at both the species and the generic level (Figures 1 & 2). The four most diverse (we use taxonomic richness as a measure of diversity) localities are the Philippines (512 species, 182 genera within our 14 superfamilies), Taiwan (463 species, 207 genera), North Queensland, Australia (439 species, 207 genera) and Japan's Wakayama Prefecture (421 species, 216 genera) – see Table 2. Although north of the tropics, Wakayama Prefecture is bathed in the warm waters of the Kuroshio Current, which originates in the tropics.

Note however, that not all tropical regions are characterized by high diversity bivalve faunas. Although poor sampling and limited study may be responsible for some low-diversity, low-latitude points (the Gulf of Kutch, Indian Ocean, for example), most of the apparently anomalous points represent either island faunas or the low-diversity (relative to the tropical Indo-Pacific) faunas of the tropical Atlantic (see Table 2).

Reduced diversity on islands, relative to mainlands, is typical of terrestrial floras and faunas (Brown and Gibson (1983) and Williamson (1988) provide good introductions to the vast literature on island biogeography). Our data show this pattern for marine bivalves on the margins of islands relative to bivalve faunas of the continental shelf. Such reduced diversity may result from both the smaller habitat area of the islands – the "area effect" – and the isolation of the islands from a source of immigration – the "distance effect" (see MacArthur and Wilson, 1967).

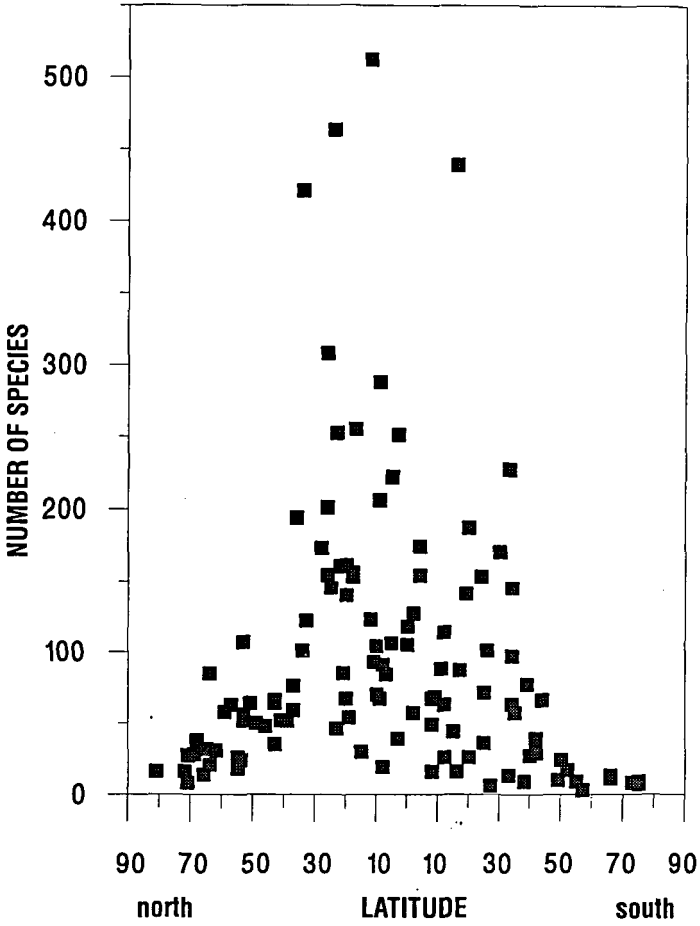


Figure 1 Species diversity of the marine bivalves sampled plotted against the latitude of the locality.

As species diversity increases with latitude, so does generic diversity (Figure 3). (Regression or correlation analysis is inappropriate here: the variables are not independent – the number of genera can never exceed the number of species in a locality). Figure 3 suggests that geographic gradients in generic diversity may serve as good proxies for gradients in species diversity, despite the uncertain evolutionary status of the genus (see Allmon, 1992 for a discussion of the meaning of the genus). These results corroborate and extend those of Campbell and Valentine (1977), who found that provincial distinctions also remain at genus and family levels. This is probably a general pattern: generic diversity patterns are reasonable proxies for those at the species level (e.g., gastropods, Campbell and Valentine, 1977; benthic algae, Jousten and van den Hoek, 1986)

Stehli *et al.* (1967) compiled data on the diversity of bivalve faunas from 36 localities throughout the globe and were also to discern the latitudinal diversity gradient. They also noted substantial “noise” in the data – variation attributed to differences in diversity

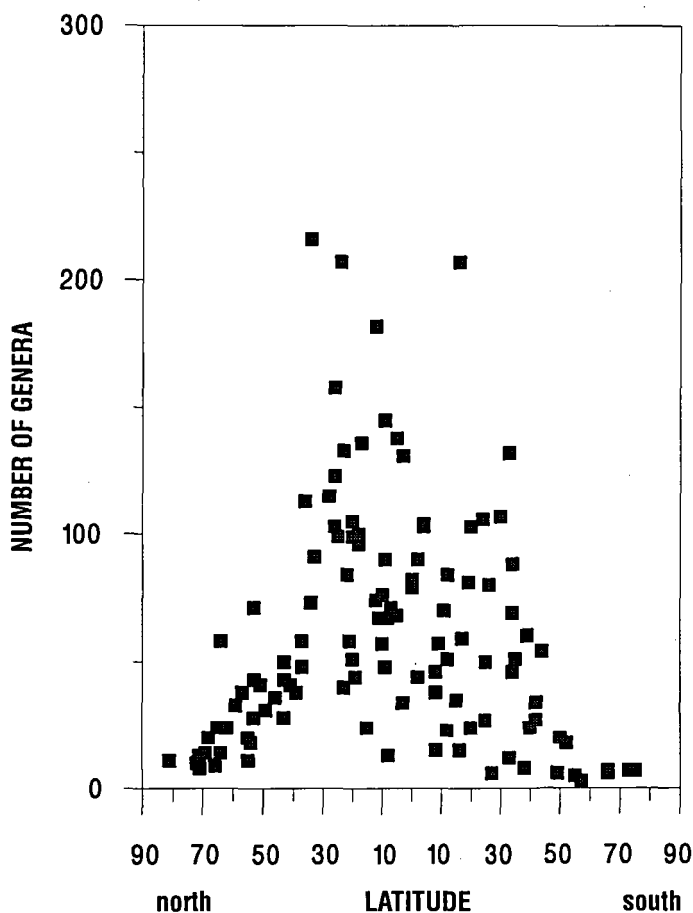


Figure 2 Generic diversity of the marine bivalves sampled plotted against the latitude of the locality.

between the tropical Indo-Pacific and the tropical Atlantic. Despite this regional variation, they were able to calculate spherical harmonic surfaces from their data and noted that such mathematically derived trend surfaces were good predictors of Recent latitudes. They suggested, therefore, that diversity gradients among fossil faunas could be used as paleogeographic indicators. Our data are still incomplete (34 superfamilies and 640 genera remain to be compiled) and a similar analysis would be premature. However, it is already clear that our datasets are quite different. Stehli *et al.*'s (1967) dataset is dominated by continental shelf faunas: of the 36 localities, only 2 (6%) are oceanic islands. Our dataset includes many more oceanic islands (32, or 28% of the total). As a result, our data (Figure 1 and 2) suggest that predicting latitude from fossil diversity alone would be problematic. Although oceanic islands are easily recognized in the Recent, the accretion of island terraces onto continental margins can make the discrimination of fossil island faunas from shelf faunas much more difficult.

Table 2 Number, name, approximate location, and species and generic (and subgeneric) diversity of sampled superfamilies for localities used in this study. Literature source for each locality is given in Appendix 1.

<i>Locality</i>	<i>Degrees latitude</i>	<i>Degrees longitude</i>	<i>Number of species</i>	<i>Number of genera</i>
PACIFIC OCEAN				
1. Nunivak Island, Alaska	60 N	166 W	38	20
2. Cook Inlet, Alaska	59 N	153 W	58	33
3. Sitka, Alaska	57 N	135 W	63	38
4. N. Vancouver Is., B.C.	51 N	128 W	64	41
5. Tillamook, Oregon	46 N	124 W	48	36
6. Eureka, California	41 N	125 W	52	41
7. Monterey, California	37 N	122 W	76	58
8. Los Angeles, Calif.	34 N	119 W	101	73
9. Bahia Magdalena, Mexico	25 N	112 W	145	99
10. Mazatlan, Mexico	23 N	107 W	252	133
11. Acapulco, Mexico	17 N	100 W	255	136
12. Pacific Panama	9 N	80 W	288	145
13. Pacific Columbia	3 N	79 W	251	131
14. Northern Peru	4 S	81 W	174	103
15. Southern Peru	12 S	77 W	26	23
16. Northern Chile	20 S	72 W	26	24
17. Central Chile	40 S	74 W	27	24
18. Southern Chile	50 S	75 W	24	20
19. Kamchatka, Siberia	53 N	162 E	52	28
20. E. Sakhalin Island, Siberia	49 N	144 E	50	31
21. Vladivostok, Siberia	43 N	133 E	64	43
22. Wakayama Prefect., Japan	34 N	133 E	421	216
23. Okinawa Is., Japan	26 N	128 E	308	158
24. Taiwan	24 N	121 E	463	207
25. South China Sea	22 N	114 E	160	84
26. Philippines	12 N	123 E	512	182
27. North Queensland, Australia	16 S	146 E	439	207
28. New South Wales, Australia	33 S	152 E	227	132
29. North Island, New Zealand	39 S	176 E	77	60
30. South Island, New Zealand	44 S	171 E	66	54
31. Galapagos Islands	0	91 W	105	82
32. Juan Fernandez Is.	33 S	80 W	13	12
33. Easter Island	27 S	109 W	6	6
34. Pitcairn Island	25 S	130 W	36	27
35. Hawaiian Islands	21 N	157 W	85	58
36. Fanning Island	3 N	159 W	39	34
37. Cook Islands	15 S	161 W	44	35
38. Chatham Islands	42 S	177 W	39	34
39. Funafuti Island	8 S	179 E	49	38
40. Fuji Islands	17 S	178 E	87	59
41. Enewetak Island	11 N	162 E	93	67
42. Macquarie Island	57 S	159 E	3	3
43. E. Caroline Islands	8 N	155 E	19	13
44. N. Marianas Islands	15 N	146 E	30	24
45. Belau & Yap Islands	8 N	135 E	91	67
INDIAN OCEAN				
46. Northwest Australia	19 S	120 E	141	81
47. Central W. Australia	25 S	112 E	71	50
48. Southwest Australia	34 S	115 E	63	46
49. South Australia	34 S	135 E	145	88
50. E. Andaman Sea	5 N	100 E	222	138
51. Sri Lanka	9 N	81 E	206	90

Table 2 (contd.)

Locality	Degrees latitude	Degrees longitude	Number of species	Number of genera
52. Gulf of Kutch	23 N	69 E	46	40
53. Oman	20 N	58 E	67	51
54. Persian Gulf	26 N	52 E	154	103
55. Red Sea	20 N	39 E	161	105
56. Kenya	4 S	40 E	154	104
57. S. Mozambique	24 S	33 E	153	106
58. S.E. South Africa	30 S	31 E	170	107
59. S. South Africa	34 S	25 E	97	69
60. Cocos-Keeling Is.	12 S	97 E	63	51
61. Chagos Islands	8 S	72 E	67	46
62. Kerguelen Islands	49 S	70 E	10	6
63. Mauritius Island	20 S	58 E	187	103
64. Aldabra Island	9 S	45 E	68	57
ATLANTIC OCEAN				
65. Norway	64 N	10 E	85	58
66. Iceland	65 N	18 W	32	24
67. Britain & Ireland	53 N	2 W	107	71
68. Baltic Sea	55 N	20 E	26	20
69. Belgium & Netherlands	53 N	5 E	56	43
70. S. Bay of Biscay	43 N	2 W	66	50
71. Southeast Spain	37 N	7 W	59	48
72. Mediterranean Sea	36 N	15 E	194	113
73. Mauritania - Liberia	12 N	15 W	123	74
74. Ivory Coast - Nigeria	5 N	0	106	68
75. Cameroon - Congo	0	8 E	118	79
76. Angola	11 S	12 E	88	70
77. East Greenland	64 N	35 W	21	14
78. Newfoundland-Labrador	54 N	58 W	24	18
79. Massachusetts - Gulf of St. Lawrence	43 N	65 W	35	28
80. North Carolina - Massachusetts	39 N	75 W	51	38
81. North Carolina - Georgia	33 N	80 W	122	91
82. Florida	26 N	82 W	201	123
83. Texas	28 N	96 W	173	115
84. Yucatan, Mexico	20 N	90 W	140	99
85. Atlantic Costa Rica	10 N	82 W	70	57
86. Atlantic Panama	9 N	80 W	67	48
87. Atlantic Columbia	10 N	75 W	104	76
88. Suriname	7 N	55 W	84	71
89. Maranhao, Brazil	2 S	44 W	127	90
90. Bahia, Brazil	12 S	38 W	114	84
91. Parana & Santa Catarina, Brazil	26 S	48 W	101	80
92. Uruguay	35 S	56 W	57	51
93. Golfo San Matias, Argentina	42 S	64 W	29	27
94. Faroe Islands	62 N	7 W	31	24
95. Cape Verde Islands	2 S	23 W	57	44
96. Grand Cayman Is.	19 N	81 W	54	46
97. Jamaica	18 N	77 W	153	96
98. Puerto Rico	18 N	66 W	156	100
99. Ascension Is.	8 S	15 W	16	15
100. St. Helena Is.	16 S	6 W	16	15
101. Tristan da Cunha	38 S	12 W	9	8
102. Falkland Islands	52 S	59 W	17	16
103. South Georgia Is.	55 S	37 W	9	5

Table 2 (contd.)

<i>Locality</i>	<i>Degrees latitude</i>	<i>Degrees longitude</i>	<i>Number of species</i>	<i>Number of genera</i>
ARCTIC OCEAN				
104. Beaufort Sea	71 N	140 W	27	13
105. Chukchi Sea	69 N	175 W	28	14
106. White Sea	66 N	40 E	14	9
107. Canadian Arctic Is.	72 N	95 W	17	10
108. Hudson Bay	55 N	85 W	18	11
109. Jan Mayen	71 N	9 W	8	8
110. Franz Josef Land	81 N	58 E	16	11
ANTARCTICA				
111. Weddell Sea	75 S	50 W	7	6
112. Bellingshausen Sea	73 S	80 W	8	7
113. Ross Sea	75 S	180 W	9	7
114. Davis Sea	66 S	95 E	13	7
115. Enderby Land	66 S	50 E	11	6

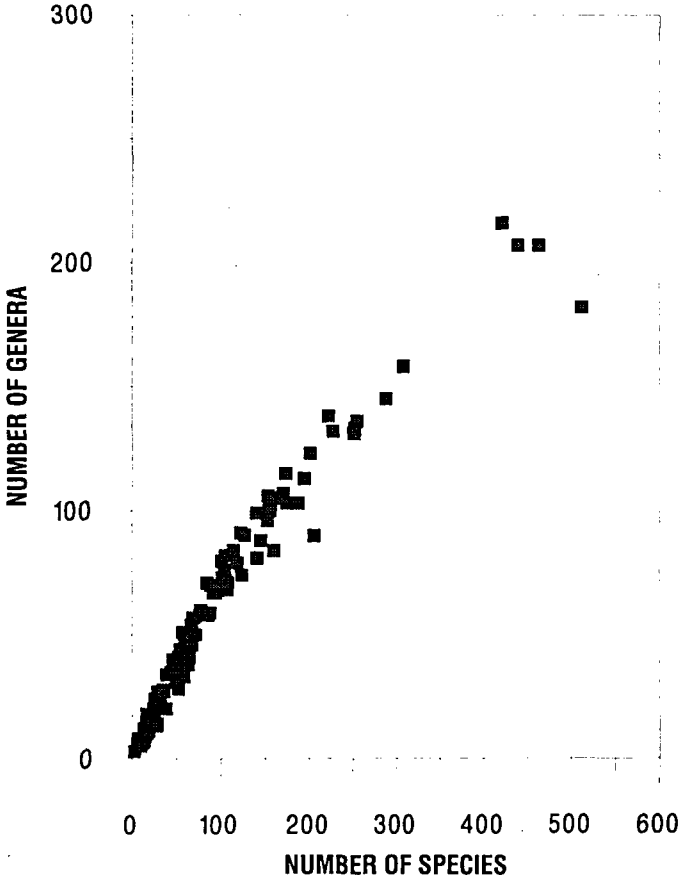


Figure 3 Number genera of plotted against the number of species in each locality.

Modelling Extinction

We can use the information on the biogeography of Recent bivalve molluscs to evaluate the levels of extinction apparent in the fossil record. For example, we can test the effects of eliminating genera confined to a given region or climatic zone. Our modelling strategy, which presumes that the causes of extinction act over a particular geographic area, is essentially the same as that of Raup (1982). Raup used information on the geographic distribution of families of terrestrial vertebrates and genera of marine corals and echinoids, and simulated extinction by eliminating all taxa in areas of varying size. This approach estimated the potential effects of bolide impacts and other point-source catastrophes because those families or genera confined to the affected area suffered global extinction while those also present elsewhere survived. Our simulations differ in using a sample of genera of marine bivalve molluscs and in focusing on specific geographic regions or geologic settings.

We present here the results of three sets of simulations: 1) extinctions confined to certain latitudinal zones; 2) extinctions confined to certain oceans; and 3) extinctions confined to either continental shelves or the shallow marine margins of oceanic islands. We used the querying commands in a dBASE-compatible program (Foxbase +) to identify genera present in the "target" region but nowhere else in the world. For example, some simple Foxbase commands allowed us to identify those genera present in the Atlantic Ocean localities but nowhere else in our database. Such genera would become globally extinct in a catastrophe whose effects were confined to the Atlantic Ocean. Genera also present elsewhere would survive the geographically restricted catastrophe.

The simulation results shown in Table 3 suggest that substantial levels of generic extinction of marine bivalve molluscs can be produced only through geographically extensive environmental changes. Even elimination of the entire Indo-Pacific fauna (at all latitudes) would result in the extinction of only slightly more than half the global

Table 3 Results of extinction simulations. The "percent of global sample" column is the percent of the 575 genera actually recorded in our database (not the 607 genera potentially present). The percent of global sample represents the level of global extinction that would result from the elimination of all bivalve genera in the particular region.

	<i>Number of genera confined to region</i>	<i>Percent of global sample</i>
<i>Latitudinal zone</i>		
Polar regions (>60°)	2	<1
High latitude ^a (>30°, <60°)	66	11
Low latitude ^a (<30°)	193	34
<i>Oceanic region</i>		
Indian Ocean	19	3
Atlantic Ocean	56	10
Low-latitude Atlantic	17	3
Pacific Ocean	130	23
Indo-Pacific Ocean	301	52
Low-latitude Indo-Pacific ^a	157	27
<i>Continental shelves and oceanic island margins</i>		
Continental shelves	275	48
Oceanic island margins	5	1

^a Because of the tropical affinities of its fauna, Japan's Wakayama Prefecture, at 34°N is included with low-latitude groups.

fauna. Clearly, the widespread distribution of Recent genera provides some protection from geographically restricted environmental catastrophes.

Our simulations assume that geographic distribution is the sole determinant of susceptibility to extinction. Reality is surely more complicated. Although the correlation between geographic range and geologic duration in bivalve molluscs is well-documented (Bretsky, 1973; Jackson, 1974; Hoffman and Szubzda-Studencka, 1982; Jablonski, 1986), other factors such as trophic group (Levinton 1974, Sheehan and Hansen (1986) or intrinsic population growth rates (Stanley, 1986, 1990) must surely play a role.

Furthermore, our modelling is based on the distribution of genera, not species. A genus may achieve a broad distribution because each of its constituent species is widely distributed, because its species have narrow, but non-overlapping geographic ranges, or by some combination. Our data do not reveal the cause of each genus' distribution. Nevertheless, it is clear that species must have distributions equal to or less than their genus. We expect, therefore, that species-level extinctions would be higher in each of the categories shown in Table 3. In any case, these considerations may be most important for background extinctions: Jablonski (1986) found that survivorship of end-Cretaceous molluscan genera was unrelated to the geographic range of constituent species.

Note also that oceanic island margin faunas include only five genera not found on mainland continental shelves. We have also noted low endemism at the species level in the bivalve faunas of oceanic island margins. This low endemism of marine island faunas is in sharp contrast to the typically high endemism of terrestrial island faunas and floras. Though requiring much more documentation and study, it appears that dispersal to and among island faunas may be very effective. This is also suggested by Scheltema's (1986) records of molluscan larvae in Pacific plankton tows.

Figure 4 shows the simulated extinctions in relation to actual levels of bivalve extinctions in the fossil record as calculated by Sepkoski (1990). Bivalve extinctions at the end-Cretaceous event are comparable to extinctions that would result from the elimination of all bivalve faunas from today's Indo-Pacific or from all of today's continental shelves. Bivalve extinctions at the Permo-Triassic (not shown on Figure 4) are similar in magnitude to those at the end of the Cretaceous, despite the higher overall extinction rate at the end of the Permian (Sepkoski, 1990). Late Triassic bivalve extinctions are similar in magnitude to those that would result from the annihilation of today's tropical (<30°) regions. The Cretaceous-Tertiary, Permo-Triassic and Late Triassic extinctions are three of the "big five" mass extinction events of the Phanerozoic. (The other two, the Late Ordovician and Late Devonian mass extinctions occurred before the extensive diversification of the class, and so we excluded them from comparison to our simulated extinctions). We do not suggest that the bivalve extinctions of the past were the result of the particular geographic scenarios modelled here. The comparisons shown in Figure 4 simply illustrate that geographically extensive environmental changes are required to produce the major mass extinctions of the fossil record. Lesser episodes of extinction, such as the Late Jurassic Tithonian event or the Early Jurassic Pliensbachian event (not shown on Figure 4 but estimated at about 10% by Sepkoski [1990]) are likely to be the result of regional environmental changes – as was suggested by Hallam (1986).

Our results are similar to those of Raup (1982) who found that affected areas exceeding half the Earth's surface area were required to produced extinctions similar to the mass extinctions of the fossil record. The results are also consistent with our previous analysis, on the family level and using fewer localities, of gastropods, bivalves, echinoderms, and scleractinian corals (Jablonski and Flessa, 1986).

An extinction comparable to the major mass extinctions of the Phanerozoic would require a near-global environmental catastrophe. Our model is rather severe, postulating the complete demise of all genera within the affected region. Given more realistic kill

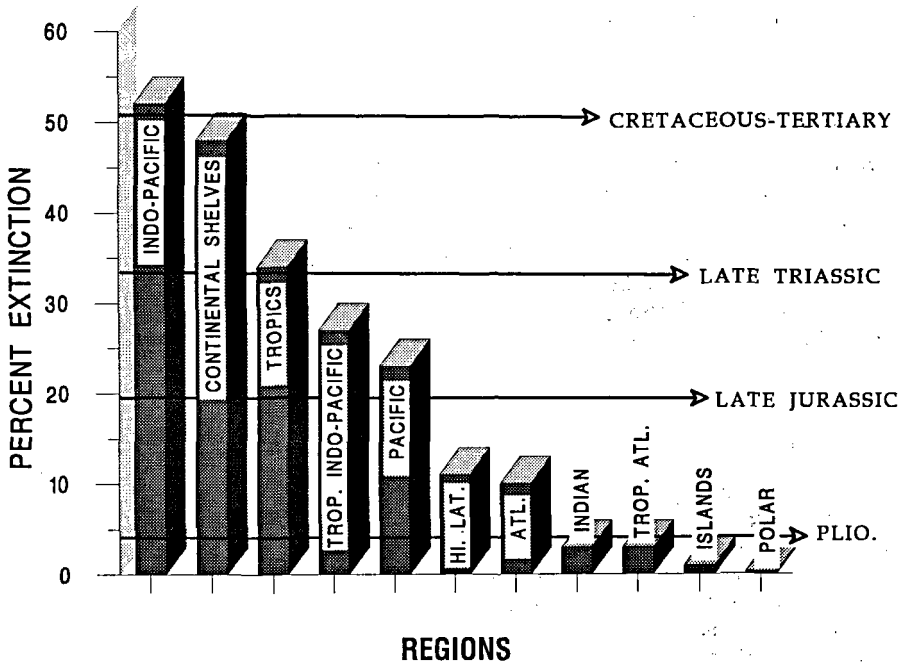


Figure 4 Comparison of modelled extinctions of Recent marine bivalve molluscs with levels of bivalve extinction in the fossil record. Estimates of fossil extinctions from Sepkoski (1990).

levels, an even greater geographic scope would be required to produce extinction intensities comparable to those of the mass extinctions in the fossil record.

This result is rather surprising, given the prevailing assumption that the high diversity of the late Cenozoic is at least partly a consequence of high provinciality imparted by steep pole-to-equator thermal gradients and the wide geographic dispersal of continents (Valentine and Moores, 1972; Valentine *et al.*, 1978; Signor, 1990). Mass extinctions in a less provincial world than today's would require an even greater geographic extent of environmental catastrophe than the most extreme event modelled here. Our models probably *underestimate* the geographic scope necessary for the production of major mass extinctions.

CONCLUSIONS

Latitudinal diversity gradients in our sample of Recent marine bivalve genera show that while high latitude localities are invariably of limited diversity, low-latitude sites are not always characterized by high diversity. This pattern results from the low diversity of many tropical island faunas and the low diversity of the tropical Atlantic faunas (when compared to the tropical Indo-Pacific).

Simulations show that extinctions comparable at the genus level to the major mass extinctions of the Phanerozoic must be nearly global in scope. End-Cretaceous or end-Permian magnitude extinctions on today's world would require the annihilation of the entire Indo-Pacific fauna or of all the continental shelf fauna. The broad geographic

range of Recent genera make them resistant to regional or even widespread environmental perturbations.

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APPENDIX 1.

Sources of information on sampled bivalve genera. This appendix does not list the many taxonomic papers that augmented the regional citations. Numbers correspond to localities listed in Table 1.

1 – 18. Eastern Pacific:

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Jablonski, D. and Valentine, J.W. 1990. From regional to total geographic ranges: Testing the relationship in Recent bivalves. *Paleobiology*, **16**: 126–142 (and references therein).

Skoglund, C. (1990) Additions to the Panamic Province bivalve (Mollusca) literature 1971 to 1990. *Festivus*, **22** (Supplement 2), 1–79.

19 – 21. Kamchatka, E. Sakhalin Island & Vladivostok, Siberia:

Scarlato, O.A. (1981) Bivalvia of the temperate latitudes of the western part of the Pacific Ocean [in Russian]. *Opredelites po faune SSSR*, **126**, 1–480.

22. Wakayama, Japan:

Habe, T. (1981) Editor. A catalogue of Molluscs of Wakayama Prefecture, the Province of Kii. I. Bivalvia, Scaphopoda and Cephalopoda. Based on the Kuroda's Manuscript. *Publications of the Seto Marine Biological Laboratory, Special Publication Series*, **7**(1), 1–301.

23. Okinawa Islands, Japan:

Kuroda, T. (1960) *A Catalogue of Molluscan Fauna of the Okinawa Islands*, Okinawa: University of Ryukyus, 106 p.

24. Taiwan:

Wu, Wen-Lung (1980) The list of Taiwan Bivalvia fauna. *Quarterly Journal of the Taiwan Museum*, **33** (Nos. 1 & 2), 55–208.

25. South China Sea:

Cai Yingya and Zhang Ziquian (1988) Molluscs in the Beinu Gulf. In *Proceedings in Marine Biology of the South China Sea*, edited by Xu Gongzhao and Brian Morton, pp. 121–142. Beijing: China Ocean Press.

26. Philippines:

Springsteen, F.J. and Leobrera, F.M. (1986) *Shells of the Philippines*, Manila: Carfel Seashell Museum, 377 p.

Sotto, F.B. and von Cosel, R. (1982) Some commercial bivalves of Cebu, Philippines. *The Philippine Scientist*, **19**, 43–101.

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27. North Queensland, Australia:

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- Shirley, J. (1911) Additions to the marine Mollusca of Queensland. *Proceedings of the Royal Society of Queensland*, **23**, 93–102.

28. New South Wales, Australia:

- Iredale, T. and McMichael, D.F. (1962) A reference list of the marine Mollusca of New South Wales, *The Australian Museum (Sydney), Memoir*, **11**, 1–109.
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29, 30 North & South Islands, New Zealand:

- Powell, A.W.B. (1979) *New Zealand Mollusca*. Auckland: Collins, 500p.
- Beu, A.G. and Maxwell, P.A. (1990) Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin*, **58**, 518 p.

31, 32. Galapagos & Juan Fernandez Islands:

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33. Easter Island:

- DiSalvo, L.H., Randall, J.E. and Cea, A. (1988) Ecological reconnaissance of the Easter Island sublittoral marine environment. *National Geographic Research*, **4**, 451–473.
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34. Pitcairn Island:

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35. Hawaiian Islands:

- Kay, E.A. (1979) *Hawaiian Marine Shells*. Honolulu: Bishop Museum Press, 652 p.

36. Fanning Island:

Kay, E.A. (1971) The littoral marine molluscs of Fanning Island. *Pacific Science*, **25**, 260–281.

Kay, E.A. and Switzer, M.F. (1974) Molluscan distribution patterns in Fanning Island lagoon and a comparison of the mollusks of the lagoon and the seaward reefs. *Pacific Science*, **28**, 275–295.

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Coles, J. (1981) A check-list of the molluscs of the Cook Islands (Mollusca). *Poiriera* **11**(1): 7–11; **11**(2): 17–21.

Paulay, G. (1987) Biology of Cook Island's Bivalves. Part 1: heterodont families. *Atoll Research Bulletin*, No. **298**, 1–31.

38. Chatham Islands:

Powell, A.W.B. (1979) *New Zealand Mollusca*. Auckland: Collins 500p.

39. Funafuti Island:

Hedley, C. (1899) The Mollusca. In *The Atoll of Funafuti, Ellice Group. Memoirs of the Australian Museum*, **3**, 397–510, 547–565.

40. Fiji Islands:

Gustav Paulay, University of Guam, personal communication.

41. Enewetak Island:

Kay, E.A. and Johnson, S. (1987) Mollusca of Enewetak Atoll. In *The Natural History of Enewetak Atoll, Vol. II. Biogeography and Systematics*, edited by D.M. Devaney, E.S. Reese, B.L. Burch and P. Helfrich, pp. 105–146. Washington, D.C.: Office of Scientific and Technical Information, U.S. Department of Energy, DOE/EV/00703-T1.

42. Macquarie Island:

Powell, A.W.B. (1960) Antarctic and subantarctic Mollusca. *Records of the Auckland Museum and Institute*, **5**, (nos. 3 & 4), 117–193.

Dell, R.K. (1964) Marine Mollusca from Macquarie and Heard Islands. *Records of the Dominion Museum*, **4**, (no. 20), 267–301.

43. East Caroline Islands:

Matsukuma, A. (1984) Intertidal bivalved molluscs collected from the eastern Caroline and Marshall Islands, western Pacific. *Proceedings of the Japanese Society of Systematic Zoology, Tokyo*, **27**, 1–34.

44. Northern Marianas Islands:

Vermeij, G.J., Kay, E.A. and Eldridge, L.G. (1983) Molluscs of the Northern Mariana Islands, with special reference to the selectivity of oceanic dispersal barriers. *Micronesia*, **19**, 27–55.

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Okutani, T. (1982) A list of marine mollusks collected from the Palau and Yap, western Caroline Islands, during June–July, 1980. *Proceedings of the Japanese Society of Systematic Zoology, Tokyo*, **23**, 12–35.

46. Northwest Australia:

- Kosuge, S. (1985) Noteworthy Mollusca from northwestern Australia (1) (Preliminary Report). *Bulletin of the Institute of Malacology Tokyo*, 2(3), 58–59.
- Wells, F.E. and Slack-Smith, S.M. (1986) Molluscs. In Faunal surveys of the Rowley Shoals, Scott Reef and Seringapatam Reef, edited by P.F. Berry. *Records of the Western Australia Museum, Supplement*, 25., 41–56.

47. Central Western Australia:

- Cotton, B. C. (1961) *South Australian Mollusca. Pelecypoda*. Adelaide: Handbook of the Flora and Fauna of South Australia. 363p.
- Wells, F.E. and Bryce, C.W. (1986) *Seashells of Western Australia*. Perth: Western Australia Museum, 207 p.

48. Southwest Australia:

- Cotton, B.C. (1961) *South Australian Mollusca. Pelecypoda*. Adelaide: Handbook of the Flora and Fauna of South Australia. 363p.
- Roberts, D. and Wells, F.E. (1980) The marine and estuarine molluscs of the Albany area of Western Australia. *Records of the Western Australia Museum*, 8(3), 335–357.
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49. South Australia:

- Cotton, B.C. (1961) *South Australian Mollusca. Pelecypoda*. Adelaide: Handbook of the Flora and Fauna of South Australia. 363p.

50. Eastern Andaman Sea:

- Tantanasiwong, R. (1979) A checklist of marine bivalves from Phuket Island, adjacent mainland and offshore islands, western peninsular Thailand. *Phuket Marine Biological Center, Phuket Thailand, Research Bulletin*, 27, 1–15.
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51. Sir Lanka:

- Kirtisinghe, P. (1978) *Sea Shells of Sri Lanka*, Rutland, Vermont: Charles E. Tuttle, 202p.
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52. Gulf of Kutch:

- Kundu, H.L. (1965) On the marine fauna of the Gulf of Kutch. *Bombay Natural History Society*, 62, 84–103, 211–236.

53. Oman:

Bosch, D. and Bosch, E., edited by Smythe, K. (1982) *Seashells of Oman*. London: Longman Group, 206p.

54. Persian Gulf:

Biggs, H.E.J. (1973) The marine Mollusca of the Trucial Coast, Persian Gulf. *Bulletin of the British Museum of Natural History (Zoology)*, **24**, 344–421.

Glazer, B.A., Glazer, D.T. and Smythe, K.R. (1984) The marine Mollusca of Kuwait, Arabian Gulf. *Journal of Conchology*, **31**, 311–330.

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Smythe, K.R. (1979) The marine Mollusca of the United Arab Emirates, Arabian Gulf. *Journal of Conchology*, **30**, 57–80.

55. Red Sea:

Kiseleva, G.A. (1971) On the species composition and ecology of Bivalvia in the Red Sea [in Russian]. In *Benthos of the Red Sea's Shelf*, edited by V.A. Vodyanitskii, pp. 216–232. Kiev: Naukova Dumka.

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Sharabati, D. (1984) *Red Sea Shells*. London: KPI, 127 p.

56. Kenya:

Solene Morris, British Museum (Natural History), personal communication,

57. Southern Mozambique:

Boshoff, P.H. (1965) Pelecypoda of Inhaca Island, Mozambique. *Memories do Instituto de Investigacao Cientifica de Mocambique Serie A (Ciencias Biologicas)*, 65–206.

58, 59. Southeastern and southern South Africa:

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Maes, V.O. (1967) The littoral marine molluscs of Cocos-Keeling Islands (Indian Ocean). *Proceedings of the Academy of Natural Sciences of Philadelphia*, **119**(4), 93–217.

61. Chagos Islands:

Sheppard, A.L.S. (1984) The molluscan fauna of Chagos (Indian Ocean) and an analysis of its broad distribution patterns. *Coral Reefs*, **3**, 43–50.

62. Kerguelen Islands:

Powell, A.W.B. (1960) Antarctic and subantarctic Mollusca. *Records of the Auckland Museum and Institute*, **5**(3 & 4), 117–193.

Dell, R.K. (1964) Marine mollusca from Macquarie and Heard Islands. *Records of the Dominion Museum*, 4(20), 267–301.

63. Mauritius Islands:

Viader, R. (1951) New or unrecorded shells from Mauritius and its dependencies. *The Mauritius Institute Bulletin*, 3(part 2), 127–155.

Michel, C. (1974) Notes on marine biology studies made in Mauritius. *The Mauritius Institute Bulletin*, 7(part 2), 215–266.

64. Aldabra Island:

J.D. Taylor, British Museum (Natural History), personal communication.

65. Norway:

Hoisaeter, T. (1986) An annotated check-list of marine molluscs of the Norwegian coast and adjacent waters. *Sarsia*, 71, 73–145.

Backeljau, T., de Meyer, M., Janssens, L., Liesse, H. and Proesmans, R. (1986) The bivalve molluscs of Varangerfjorden, northern Norway. *Fauna Norvegica, Series A* 7, 1–9.

66. Iceland:

Madsen, F.J. (1949) Marine Bivalvia. *The Zoology of Iceland*, 4 (part 63), 1–116.

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67. Britain and Ireland:

Smith, S.M. and Heppell, D. (1991) Checklist of British Marine Mollusca. *National Museums of Scotland Information Series*, 11, 1–114.

68. Baltic Sea:

Jagnow, B. and Gosselck, F. (1987) Bestimmungsschlüssel für die Gehäuschncken und Muscheln der Ostsee. *Mitteilungen aus dem Zoologisches Museum in Berlin*, 2, 191–268.

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Backeljau, T. (1986) Lijst van de Recente marine Mollusken van Belge. *Institut Royal des Sciences Naturelles de Belgique, Documents de Travail*, 29, 1–106.

Janssen, A.W. (1975) Systematische lijst van Nederlanse Recente en fossiele Mollusken. *Mededelingen van de Werkgroep voor Tertiare en Kwarttaire Geologie*, 12(4), 115–170.

Eisma, D. (1966) The distribution of benthic marine molluscs off the main Dutch coast. *Netherlands Journal of Sea Research*, 3, 107–163.

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Borja, A. (1983) Sistematica de los moluscos marinos de la Costa Vasca. *Sociedad Cultural "Insub", Publicacion*, 2, 1–96.

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71. Southeast Spain:

van Aartsen, J.J., Menkhorst, H.P.M.G. and Gittenberger, E. (1984) The marine Mollusca of the Bay of Algeciras, Spain, with general notes on *Mitrella*, *Marginellidae* and *Turridae*. *Basteria Supplement*, 2, 1–135.

72. Mediterranean Sea:

Sabelli, B., Giannuzzi-Savelli, R. and Bedulli, D. (1990) *Catalogo Annotato dei Molluschi Marini del Mediterraneo*, vol. 1. Bologna: Societa Italiana di Malacologia. Libreria Naturalistica Bolognese. 348 p.

73. Mauritania to Liberia:

Nickles, M. (1955) Scaphopodes et Lamellibranches recoltes dan l'Ouest Africain, *Scientific results of the Danish expedition to the coasts of tropical west Africa 1945-1946. Atlantide-Report*, **3**, 93-237.

Talavera, F.G. (1975) Moluscos de sedimentos de la plataforma continental de Mauritania. *Boletin del Instituto Espanol de Oceanografia*, **192**, 1-18.

74. Ivory Coast to Nigeria:

Nickles, M. (1955) Scaphopodes et Lamellibranches recoltes dan l'Ouest Africain, *Scientific results of the Danish expedition to the coasts of tropical west Africa 1945-1946. Atlantide-Report*, **3**, 93-237.

75. Cameroon to Congo:

Bernard, P.A. (1984) *Coquillages du Gabon*. Libreville: P.A. Bernard, 140 p.

von Cosel, R. (1989) Taxonomy of tropical West African bivalves. I. Four new species of eulamellibranchiate bivalves. *Bulletin du Museum National d'Histoire Naturelle, (Paris)*, 4th ser., **11** (Section A, no.2), 315-331.

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76. Angola:

Anonymous, 1975. Contribuicao ao conhecimentoda Malacofauna de Angola. Boletim do Instituto de Cienciea Biologicas e Geociencias. No. 10. Universidade Federal de Juiz de Fora.

Gofas, S., Afonso, J.P. and Brandao, M. (1984) *Conchas e Moluscos de Angola*. Universidade Agostinho Neto/Elf Aquitaine Angola, 139 p.

77. East Greenland:

Ockelmann, W.K. (1958) Marine Lamellibranchiata. The Zoology of East Greenland. *Meddelelser om Grønland*, **122**(4.: 1-257).

78. Newfoundland-Labrador:

Lubinsky, I. (1980) Marine bivalve molluscs of the Canadian central and eastern Arctic: Faunal composition and zoogeography. *Department of Fisheries and Oceans Bulletin*, **207**, 1-111.

Abbott, R.T. (1974) *American Seashells*, 2nd. ed. New York: Van Nostrand Reinhold, 663 p.

79-81. Massachusetts - Gulf of St. Lawrence; North Carolina - Massachusetts, Georgia - North Carolina:

Abbott, R.T. (1974) *American Seashells*, 2nd. ed. New York: Van Nostrand Reinhold, 663 p.

Franz, D.R. and Merrill, A.S. (1980) Molluscan distribution patterns on the continental shelf of the middle Atlantic Bight (Northwest Atlantic). *Malacologia*, **19**, 209-225.

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82. Florida:

Abbott, R.T. (1974) *American Seashells*, 2nd. ed. New York: Van Nostrand Reinhold, 663 p.

Perry, L.M. and Schwengel, L.M. (1955) *Marine Shells of the Western Coasts of Florida*. Ithaca, N.Y.: Paleontological Research Institute, 318p.

83. Texas:

Odé, H. (1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1982) Distribution and records of the marine Mollusca in the northwest Gulf of Mexico. A continuing monograph. *Texas Conchologist*, **11**, 27–32, 52–63, 84–98; **12**, 10–26, 40–56, 79–94, 108–126; **13**, 16–32, 52–68, 74–88, 106–107, 114–122; **14**, 10–11, 14–24, 44–52, 64–75, 92–104; **15**, 10–23, 45–56, 69–80, 92–112; **16**, 14–32, 44–52, 71–80, 98–103; **17**, 11–24, 48–52, 76–80; index **18**, 78–110.

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Vokes, H.E. and Vokes, E.H. (1983) Distribution of shallow-water marine mollusca, Yucatan Peninsula, Mexico. *Mesoamerican Ecology Institute Monograph 1, Middle American Research Institute, Publication*, **54**, 1–183.

85. Atlantic Costa Rica:

Robinson, D.G. and Montoya, M. (1988) Los moluscos marinos de la Costa Atlántica de Costa Rica. *Revista de Biología Tropical*, **35**(2), 375–400.

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Olsson, A.A. and McGinty, T.L. (1958) Recent marine molluscs from the Caribbean coasts of Panama with the description of some new genera and species. *Bulletins of American Paleontology*, **39**(177), 1–58.

87. Atlantic Columbia:

Diaz, J.M. and Goetting, K-J. (1988) Die Mollusken der Bahia de Nenguange (Karibik, Kolumbien) und ihre zoogeographischen Beziehungen. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie de Tiere*, **115**, 145–170.

88. Suriname:

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