

Copyright © 2004, The Geological Society of America, Inc. (GSA). All rights reserved. Copyright not claimed on content prepared wholly by U.S. government employees within scope of their employment. Individual scientists are hereby granted permission, without fees or further requests to GSA, to use a single figure, a single table, and/or a brief paragraph of text in other subsequent works and to make unlimited photocopies for noncommercial use in classrooms to further education and science. For any other use, contact Copyright Permissions, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA, fax 303-357-1070, editing@geosociety.org; reference *Geology*, ISSN 0091-7613. GSA provides this and other forums for the presentation of diverse opinions and positions by scientists worldwide, regardless of their race, citizenship, gender, religion, or political viewpoint. Opinions presented in this publication do not reflect official positions of the Society.

Extinction of a fast-growing oyster and changing ocean circulation in Pliocene tropical America

Michael X. Kirby* Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093, USA
 Jeremy B.C. Jackson Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093, USA, and Center for Tropical Paleocology and Archaeology, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panamá

ABSTRACT

Ocean circulation changed profoundly in the late Cenozoic around tropical America as a result of constriction and final closure of the Central American seaway. In response, regional planktonic productivity is thought to have decreased in the Caribbean Sea. Previous studies have shown that shallow-marine communities reflect these changes by reorganizing from a suspension-feeder-dominated community to a more carbonate-rich, phototrophic-based community. Although changes in diversity, abundance, and body size of various shallow-marine invertebrates have previously been examined, no study has specifically used growth rate in suspension feeders to examine the effect that changes in ocean circulation may have had on shallow-marine communities. Here we show that a fast-growing oyster went extinct concurrently with changes in ocean circulation and planktonic productivity in the Pliocene. Faster-growing *Crassostrea cahobasensis* went extinct, whereas slower-growing *Crassostrea virginica* and *columbiensis* survived to the Holocene. Miocene–Pliocene *C. cahobasensis* grew 522% faster in shell carbonate and 251% faster in biomass relative to Quaternary *C. virginica* and *C. columbiensis*. Although differences in growth are due to proximate differences in environment, the disappearance of faster-growing *C. cahobasensis* from shallow-marine environments and the continued survival of slower-growing *C. virginica* and *C. columbiensis* in marginal-marine environments (e.g., estuaries, lagoons) is consistent with the view that concurrent changes in ocean circulation and declining primary production resulted in the restriction of *Crassostrea* to marginal-marine environments.

Keywords: Central American seaway, paleoproductivity, growth rate, oyster, *Crassostrea*.

INTRODUCTION

Shallow-marine communities around tropical America underwent significant change in the late Cenozoic (Coates et al., 1992). These changes include increased speciation and extinction of mollusks (Allmon, 1992; Allmon et al., 1993; Jackson et al., 1993, 1996, 1999), changes in the body size of various mollusks (Jackson et al., 1996; Roopnarine, 1996; Anderson, 2001), decrease in the abundance of suspension feeders and their predators (Todd et al., 2002), changes in coral diversity and reef structure (Budd et al., 1996; Collins et al., 1996), and the disappearance of some highly specialized molluscan symbioses (Vermeij, 1998). A regional decline in planktonic productivity related to changing ocean circulation associated with final closure of the Central American seaway has been implicated in these biotic changes (Woodring, 1966; Vermeij, 1978; Vermeij and Petuch, 1986; Allmon, 1992; Allmon et al., 1993; Jackson et al., 1993; Todd et al., 2002). Although open-ocean sediment cores from both the Pacific and Caribbean Basins show profound changes in ocean circulation resulting from constriction of the Central American seaway (Emiliani et al., 1972;

*Present address: Center for Tropical Paleocology and Archaeology, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panamá.

TABLE 1. LATE CENOZOIC *CRASSOSTREA* SPECIES FROM TROPICAL AMERICA

Species	Locality	Formation	Age
<i>C. columbiensis</i>	El Rompio, Panamá	–	Recent
<i>C. virginica</i>	Orinoco Delta, Venezuela	–	Recent
<i>C. virginica</i>	Saline Bay, Trinidad	–	Recent
<i>C. virginica</i>	Paraguaipoa, Venezuela	–	Recent
<i>C. virginica</i>	Colón, Panamá	–	Holocene
<i>C. virginica</i>	Gatun Locks, Panamá	Atlantic muck	late Pleistocene
<i>C. columbiensis</i>	Miraflores Locks, Panama	Pacific muck	Pleistocene
<i>C. virginica</i>	Falcon, Venezuela	Casa Ventura	Pleistocene
<i>C. virginica</i>	Barbados	Coral rock	Pleistocene
<i>C. virginica</i>	Panamá	–	Pleistocene
<i>C. virginica</i>	Limón, Costa Rica	Moin	Pleistocene
<i>C. virginica</i>	Trinidad	Talparo	early Pleistocene
<i>C. cahobasensis</i>	Rio Seco, Venezuela	Codore	Pliocene
<i>Crassostrea</i> aff. <i>C. virginica</i>	Trinidad	Springvale	Pliocene
<i>Crassostrea</i> aff. <i>C. virginica</i>	Araya Peninsula, Venezuela	Cubagua	Pliocene
<i>C. cahobasensis</i>	San Rafael, Nicaragua	El Salto	Pliocene
<i>Crassostrea</i> aff. <i>C. virginica</i>	Jamaica	August Town	Pliocene
<i>C. cahobasensis</i>	Monte Oscuro, Venezuela	Canjarao	early Pliocene
<i>C. cahobasensis</i>	Las Lomas, Venezuela	La Vela	late Miocene
<i>C. cahobasensis</i>	Quebrada La Vela, Venezuela	La Vela	late Miocene
<i>C. cahobasensis</i>	Araurima, Venezuela	Ojo de Agua	late Miocene
<i>C. cahobasensis</i>	Río Chico, Panamá	Tuira	late Miocene
<i>C. cahobasensis</i>	Tick Creek, Panamá	Gatun	late Miocene
<i>C. cahobasensis</i>	Madden Basin, Panamá	Alhajuela	Miocene

Keigwin, 1982; Haug and Tiedemann, 1998; Chaisson and Ravelo, 2000; Haug et al., 2001; Kameo, 2002), it is unclear how or to what extent these changes may have affected coastal communities. Here we examine changes in the growth rate of carbonate and biomass of *Crassostrea* oysters in order to see if these important suspension feeders reacted to changing ocean circulation and planktonic productivity in the late Cenozoic. *Crassostrea* mostly consumes phytoplankton through suspension feeding (Langdon and Newell, 1996) and should, therefore, have been sensitive to changes in planktonic productivity through time. Changes in phytoplanktonic food supply have been shown to affect the growth and survival of living *Crassostrea* (Brown and Hartwick, 1988; Lenihan et al., 1996; Lenihan, 1999). In addition, other environmental factors, such as temperature, salinity, and current velocity, are also known to affect growth of *Crassostrea*, as well as other mollusks (Remane and Schlieper, 1971; Lenihan et al., 1996; Lenihan, 1999).

METHODS

We examined 542 oyster shells from 24 localities in tropical America ranging in age from the Miocene to Holocene in collections at the Naturhistorisches Museum Basel and U.S. National Museum of Natural History (Table 1; Fig. 1). We recognize three species in these collections: (1) shallow-marine *Crassostrea cahobasensis* from Miocene and Pliocene localities in both the Caribbean and Pacific Basins, (2) marginal-marine *Crassostrea virginica* and *Crassostrea* aff. *C. virginica* from Pliocene–Holocene localities in the Caribbean, and (3) marginal-marine *Crassostrea columbiensis* from Pleistocene–Holocene localities in the Pacific (Woodring, 1982; Harry, 1985; Kirby, 2001). A collection of extant *C. columbiensis* was also assembled in October

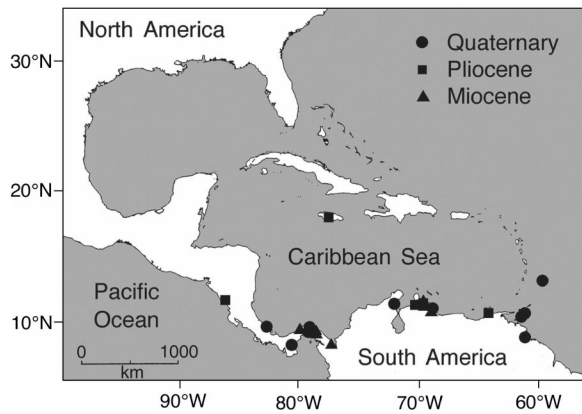


Figure 1. Map of tropical America showing localities of Miocene, Pliocene, and Quaternary *Crassostrea* species.

2002 from the Santa Maria estuary at El Rompío, Panamá. Stratigraphic age for each locality was derived from museum collections and from Woodring (1982), Dengo and Case (1990), and Collins and Coates (1999), and was updated to the most current time scale (Berggren et al., 1995). The carbonate mass (m_{carb} in g) produced per individual was calculated from measurements of shell height (H), length (L), and thickness (W) (all in cm) of the left valve multiplied by the shell density (ρ in g/cm^3):

$$m_{\text{carb}} = 2HLW \times (\rho). \quad (1)$$

Dial calipers were used to measure shell height at the longest dimension of the left valve, length was measured perpendicular to height, and thickness was measured at the ventral margin of the adductor muscle scar (Fig. 1 of Kirby, 2001). We used a conservative estimate for shell density that takes into account the differing percentage of lighter chalky deposits relative to the denser foliaceous layer contained in shells of *Crassostrea* (Palmer and Carriker, 1979). On the basis of estimates of the percentage of chalky deposits in Quaternary and Tertiary *Crassostrea* (Kirby, 2001), we used an average shell density of $2.35 \text{ g}/\text{cm}^3$ for *C. virginica* and *C. columbiensis* and $1.40 \text{ g}/\text{cm}^3$ for *C. cahobasensis*. These estimates are similar to those estimated for living *C. virginica* (Palmer and Carriker, 1979) and Miocene *C. gravitesta* (Chinzei, 1995), respectively. As a test of this method, the estimated mass of carbonate derived from 35 living *C. virginica* did not differ significantly from the measured mass of carbonate (paired t -test, $p = 0.0945$). Biomass was estimated from the cross-sectional area of the adductor muscle, which is used to oppose the spring-like ligament, thereby allowing the oyster to adduct both valves. The area of muscle insertion leaves behind a distinctive trace in each valve known as the muscle scar, which is easily identified in both fossil and modern shells. Estimates of total biomass were made in the absence of the actual soft tissue by first measuring the area of the muscle scar with a visual-analysis computer program (NIH Image 1.62) from a scanned image of each muscle scar. Biomass was then estimated by using the relationship between muscle scar area (A , in cm^2) and dry biomass (m_{bio} in g) measured in 34 living *C. virginica*:

$$m_{\text{bio}} = 0.011611 + 0.8089A \quad (p < 0.0001; R^2 = 0.61). \quad (2)$$

We estimated the life span of individual oysters by counting the number of annually formed, skeletal growth increments in each left valve (Kirby et al., 1998; Kirby, 2000, 2001). Growth rates of carbonate and biomass were calculated from these shell measurements and estimated life spans. We used Kruskal-Wallis and Mann-Whitney U -tests to test

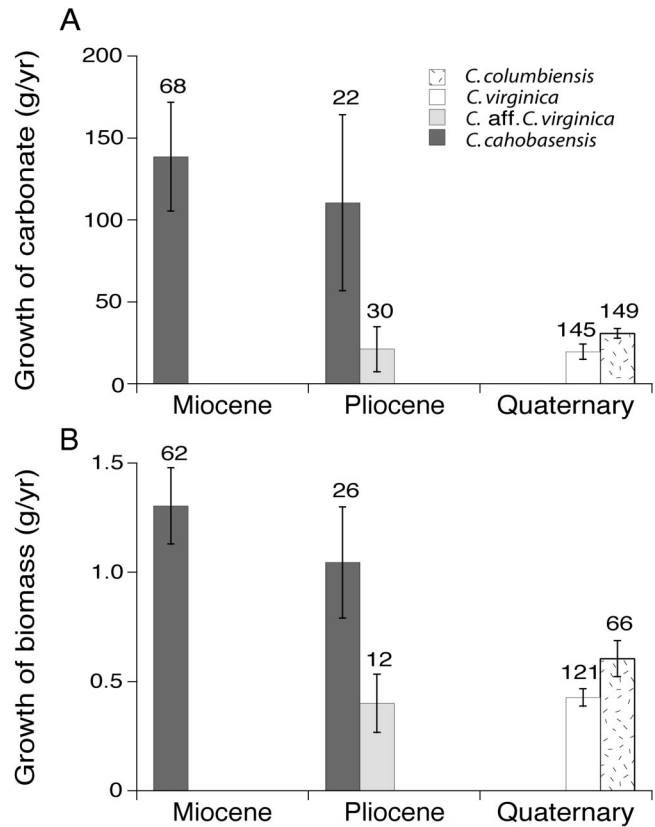


Figure 2. Histogram comparing mean growth rate of (A) carbonate and (B) biomass in Miocene, Pliocene, and Quaternary *Crassostrea* species in tropical America. Vertical error bars represent 95% confidence intervals.

whether growth rate and life span differed significantly between species (Sokal and Rohlf, 1995).

RESULTS

The data show a significant difference in both growth of shell carbonate and biomass between all species of *Crassostrea* examined in this study ($p < 0.0001$; Fig. 2). Both Miocene and Pliocene *C. cahobasensis* grew faster than Quaternary *C. virginica* and *C. columbiensis* ($p < 0.0001$). Pliocene *C. cahobasensis* grew slower than Miocene *C. cahobasensis*, but this difference is not significant ($p > 0.15$). Pliocene *Crassostrea* aff. *C. virginica* grew significantly slower than Pliocene *C. cahobasensis* ($p < 0.0045$), whereas Pliocene *Crassostrea* aff. *C. virginica* and Quaternary *C. virginica* had similar growth rates ($p > 0.19$). Life span was not significantly different between time intervals ($p = 0.8862$). These patterns of growth are clear when mean carbonate and biomass are plotted as a function of life span (Fig. 3). Miocene to Pliocene *C. cahobasensis* grew faster after 1–2 yr of life relative to *C. virginica* and *C. columbiensis*.

DISCUSSION

Crassostrea oysters have lived in one of two environments during the Cenozoic (Kirby, 2000, 2001). Species have either inhabited marginal-marine environments (brackish, hypersaline, intertidal), which are unfavorable to their marine predators (Galtsoff, 1964; Carriker and Van Zandt, 1972; O'Beirn et al., 1996; White and Wilson, 1996) or, alternatively, they have inhabited shallow, fully marine environments where they survived marine predation by growing thicker shells that offered protection against predators (Kirby, 2001). Today, *Crassostrea* species only inhabit marginal environments (Harry, 1985), but during the Tertiary, various species also inhabited fully marine environments where they grew very large body sizes (Stenzel, 1971;

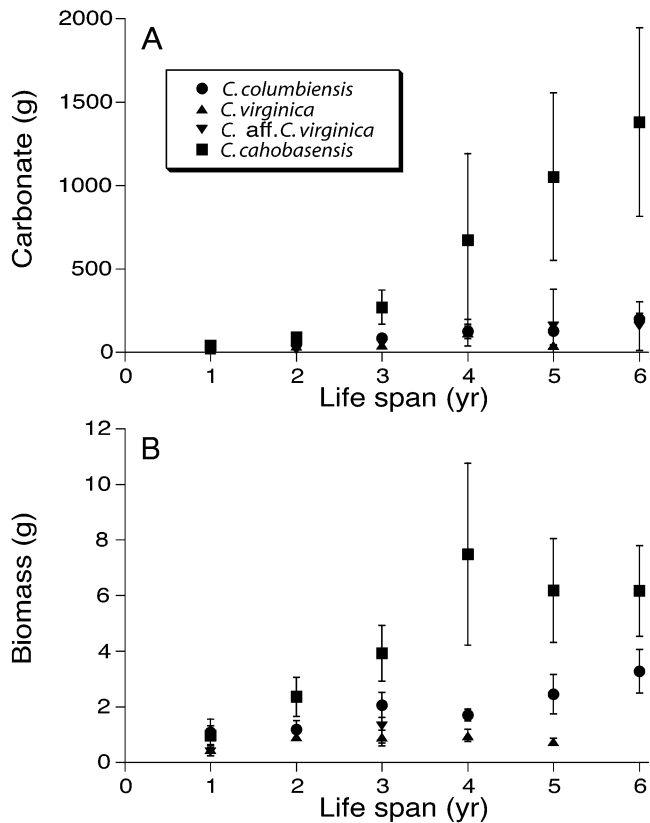


Figure 3. Scatter plot comparing mean (A) carbonate and (B) biomass as function of life span for Miocene, Pliocene, and Quaternary *Crassostrea* species in tropical America. Vertical error bars represent 95% confidence intervals.

Kirby, 2001). *Crassostrea cahobasensis* represents one of these large, fully marine species (Woodring, 1982). The stratigraphic distribution of *Crassostrea* species examined in this study indicates that *C. cahobasensis* disappeared in the Pliocene, whereas marginal-marine *C. virginica* survived in the Caribbean and *C. columbiensis* survived in the Pacific. The youngest occurrence of *C. cahobasensis* found in this study was in Pliocene deposits from Venezuela and Nicaragua; the oldest occurrence of *Crassostrea* aff. *C. virginica* was in the Miocene–Pliocene August Town Formation of Jamaica, and the oldest occurrence of *C. virginica* was in Pleistocene sediments of the Limón Basin, Costa Rica. There are two alternative explanations for this pattern. Either *C. virginica* and *C. columbiensis* descended from *C. cahobasensis*, or alternatively, *C. cahobasensis* went extinct at the end of the Pliocene, and *C. virginica* and *C. columbiensis* were already present or had invaded from elsewhere. Given the broad biogeographic distribution of both *C. virginica* and *C. columbiensis* (Gulf of St. Lawrence to Brazil and Gulf of California to Chile, respectively; Carriker and Gaffney, 1996), as well as reports of both species from pre-Quaternary localities (early Miocene *C. virginica* in Delaware and New Jersey [Lawrence, 1995]; Pliocene *C. columbiensis* in California [Moore, 1987]), we find the first alternative unlikely. It is more plausible that *C. virginica* and *C. columbiensis* descended from an estuarine species in the late Tertiary either in tropical America or elsewhere. Their marginal-marine habitat provided these species refuge from fully marine predation, whereas larger and faster-growing *C. cahobasensis* went extinct in the Pliocene. Differences in growth rate between *C. cahobasensis* and *C. virginica*–*C. columbiensis* are most likely due to proximate differences in environment, as marginal-marine environments vary more in temperature, salinity, and productivity, all of which affect growth rate, relative to fully marine environments.

Our results showing (1) the extinction of a fast-growing oyster

from shallow-marine environments and (2) the continued survival of slower-growing oysters in marginal environments are consistent with previous studies that examined body size of tropical American bivalves in the late Cenozoic. Roopnarine (1996) reported the extinction of all large-bodied (>35 mm) species of chionine bivalves after the early to middle Pliocene in the southern Caribbean Sea (Atlantic Gatunian province). Anderson (2001) showed a significant decrease in body size of Caribbean corbulid bivalves after the Miocene. Our data are also consistent with studies that looked at broad changes in molluscan life habits and trophic composition through the late Cenozoic of tropical America. Todd et al. (2002) noted a significant decline in the relative abundance of bivalve suspension feeders between the Miocene and early Pliocene, as well as between the early Pliocene and late Pliocene–Quaternary.

These patterns of smaller, fewer, and slower-growing suspension feeders may relate to regional changes in ocean circulation resulting from constriction of the Central American seaway. Changes in ocean circulation almost certainly affected environmental factors that can influence growth in suspension feeders, particularly changes in temperature, salinity, and planktonic productivity. In our study, the extinction of *C. cahobasensis* may reflect the major constriction of the Central American seaway between 4.7 and 4.2 Ma. This time frame is based on the increasing surface-water salinity in the Caribbean (Keigwin, 1982; Haug et al., 2001), an increasing temperature gradient in the Pacific (Chaisson and Ravelo, 2000), increases in carbonate sand deposits and $\delta^{13}\text{C}$ values of epibenthic foraminifera in the Caribbean (Haug and Tiedemann, 1998), and cessation of vast diatom-mat assemblages in the eastern equatorial Pacific (Kemp and Baldauf, 1993). Although these deep-marine records were derived from open-ocean settings, a corresponding change in shallow-marine benthic foraminifera and corals indicates that changes in ocean circulation also affected nearshore environments during this interval (Collins et al., 1996).

Alternatively, the extinction of *C. cahobasensis* may have occurred during the end-Pliocene reorganization of shallow-marine communities that occurred ~1 m.y. after final closure of the Central American seaway (Allmon et al., 1993; Budd et al., 1996; Jackson et al., 1993, 1996, 1999). Stratigraphic resolution, however, is not fine enough to resolve when in the Pliocene *C. cahobasensis* went extinct. The Pliocene units that contain *C. cahobasensis* include the Chiguaje Member of the Codore Formation, the Turupia Member of the Canjarao Formation, and the El Salto Formation; the first two are from the Falcon Basin of Venezuela, and the last is from San Rafael, Nicaragua. As all of these formations are poorly dated, only detailed biostratigraphic analysis will resolve this issue. For now, however, we may infer that the extinction of fast-growing, shallow-marine *Crassostrea* in the Caribbean coincided with regional changes in ocean circulation and productivity during the Pliocene, whether resulting from the earlier constriction of the Central American seaway at 4.7–4.2 Ma (Haug and Tiedemann, 1998; Haug et al., 2001) or from the seaway's final closure in the late Pliocene ca. 3.1–2.8 Ma (Coates and Obando, 1996).

CONCLUSION

Our study is the first to quantify growth rate of carbonate and biomass in a shallow-marine suspension feeder in order to examine how suspension feeders may have responded to changing ocean circulation and productivity in Pliocene tropical America. We control for life span as a factor when comparing body-size data by examining skeletal growth increments that formed annually. A new technique for estimating biomass in fossil bivalves allows our study to show differences in growth of soft tissue in suspension-feeding oysters during this interval. Extinction of fast-growing *C. cahobasensis* from shallow-marine environments and the continued survival of slower-growing species of this genus (*C. virginica* and *columbiensis*) in marginal-marine environments are consistent with the view that changes in ocean circulation and productivity had an effect on these suspension feeders.

This study demonstrates that using both body size and life span to estimate growth rate can allow us to infer how benthic suspension feeders have responded to changes in their environment that affect growth.

ACKNOWLEDGMENTS

We thank W. Blow, R. Cooke, P. Franceschi, A. Heitz, P. Jung, A. O'Dea, R. Panchaud, F. Rodriguez, F.C. de Sierra, J. Villa, T. Waller, F. Wiedenmayer, and the Autoridad del Canal de Panamá for assistance. Funded by a National Science Foundation Earth Sciences Postdoctoral Research Fellowship to Kirby.

REFERENCES CITED

- Allmon, W.D., 1992, Role of temperature and nutrients in extinction of turrilline gastropods: Cenozoic of the northwestern Atlantic and northeastern Pacific: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 92, p. 41–54.
- Allmon, W.D., Rosenberg, G., Portell, R.W., and Schindler, K.S., 1993, Diversity of Atlantic Coastal Plain mollusks since the Pliocene: *Science*, v. 260, p. 1626–1629.
- Anderson, L.C., 2001, Temporal and geographic size trends in Neogene Corbulidae (Bivalvia) of tropical America: Using environmental sensitivity to decipher causes of morphologic trends: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 166, p. 101–120.
- Berggren, W.A., Kent, D.V., Swisher, C.C., and Aubry, M.-P., 1995, A revised Cenozoic geochronology and chronostratigraphy, in Berggren, W.A., et al., eds., *Geochronology, time scales, and global stratigraphic correlation: SEPM (Society for Sedimentary Geology) Special Publication 54*, p. 129–212.
- Brown, J.R., and Hartwick, E.B., 1988, Influences of temperature, salinity and available food upon suspended culture of the Pacific oyster, *Crassostrea gigas*: I. Absolute and allometric growth: *Aquaculture*, v. 70, p. 231–251.
- Budd, A.F., Johnson, K.G., and Stemann, T.A., 1996, Plio–Pleistocene turnover and extinctions in the Caribbean reef-coral fauna, in Jackson, J.B.C., et al., eds., *Evolution and environment in tropical America*: Chicago, Illinois, University of Chicago Press, p. 168–204.
- Carriker, M.R., and Gaffney, P.M., 1996, A catalogue of selected species of living oysters (Ostreacea) of the world, in Kennedy, V.S., et al., eds., *The eastern oyster Crassostrea virginica*: College Park, University of Maryland, Maryland Sea Grant College, p. 1–18.
- Carriker, M.R., and Van Zandt, D., 1972, Predatory behavior of a shell-boring muricid gastropod, in Winn, H.E., and Olla, B.L., eds., *Behavior of marine animals: Current perspectives in research*: New York, Plenum Press, p. 157–244.
- Chaisson, W.P., and Ravelo, A.C., 2000, Pliocene development of the east-west hydrographic gradient in the equatorial Pacific: *Paleoceanography*, v. 15, p. 497–505.
- Chinzei, K., 1995, Adaptive significance of the lightweight shell structure in soft bottom oysters: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 195, p. 217–227.
- Coates, A.G., and Obando, J.A., 1996, The geologic evolution of the Central American isthmus, in Jackson, J.B.C., et al., eds., *Evolution and environment in tropical America*: Chicago, Illinois, University of Chicago Press, p. 21–56.
- Coates, A.G., Jackson, J.B.C., Collins, L.S., Cronin, T.M., Dowsett, H.J., Bybell, L.M., Jung, P., and Obando, J.A., 1992, Closure of the Isthmus of Panama: The near-shore marine record of Costa Rica and western Panama: *Geological Society of America Bulletin*, v. 104, p. 814–828.
- Collins, L.S., and Coates, A.G., 1999, A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama: *Bulletins of American Paleontology*, v. 357, 351 p.
- Collins, L.S., Budd, A.F., and Coates, A.G., 1996, Earliest evolution associated with closure of the tropical American seaway: *National Academy of Sciences Proceedings*, v. 93, p. 6069–6072.
- Dengo, G., and Case, J.E., 1990, *The Caribbean region*: Boulder, Colorado, Geological Society of America, *Geology of North America*, v. H, 528 p.
- Emiliani, C., Gartner, S., and Lidz, B., 1972, Neogene sedimentation on the Blake Plateau and the emergence of the Central American isthmus: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 11, p. 1–10.
- Galtsoff, P.S., 1964, The American oyster *Crassostrea virginica* Gmelin: *Fish and Wildlife Service Fishery Bulletin*, v. 64, 480 p.
- Harry, H.W., 1985, Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae): *Veliger*, v. 28, p. 121–158.
- Haug, G.H., and Tiedemann, R., 1998, Effect of the formation of the isthmus of Panama on Atlantic Ocean thermohaline circulation: *Nature*, v. 393, p. 673–676.
- Haug, G.H., Tiedemann, R., Zahn, R., and Ravelo, A.C., 2001, Role of Panama uplift on oceanic freshwater balance: *Geology*, v. 29, p. 207–210.
- Jackson, J.B.C., Jung, P., Coates, A.G., and Collins, L.S., 1993, Diversity and

extinction of tropical American mollusks and emergence of the Isthmus of Panama: *Science*, v. 260, p. 1624–1626.

- Jackson, J.B.C., Jung, P., and Fortunato, H., 1996, *Paciphilia revisited: Transisthmian evolution of the Strombina group (Gastropoda: Columbellidae)*, in Jackson, J.B.C., et al., eds., *Evolution and environment in tropical America*: Chicago, Illinois, University of Chicago Press, p. 234–270.
- Jackson, J.B.C., Todd, J.A., Fortunato, H., and Jung, P., 1999, Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America: *Bulletins of American Paleontology*, v. 357, p. 193–230.
- Kameo, K., 2002, Late Pliocene Caribbean surface water dynamics and climatic changes based on calcareous nannofossil records: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 179, p. 211–226.
- Keigwin, L., 1982, Isotopic paleoceanography of the Caribbean and east Pacific: Role of Panama uplift in late Neogene time: *Science*, v. 217, p. 350–352.
- Kemp, A.E.S., and Baldauf, J.G., 1993, Vast Neogene laminated diatom mat deposits from the eastern equatorial Pacific Ocean: *Nature*, v. 362, p. 141–144.
- Kirby, M.X., 2000, Paleoeological differences between Tertiary and Quaternary *Crassostrea* oysters, as revealed by stable isotope sclerochronology: *Palaios*, v. 15, p. 132–141.
- Kirby, M.X., 2001, Differences in growth rate and environment between Tertiary and Quaternary *Crassostrea* oysters: *Paleobiology*, v. 27, p. 84–103.
- Kirby, M.X., Soniat, T.M., and Spero, H.J., 1998, Stable isotope sclerochronology of Pleistocene and Recent oyster shells (*Crassostrea virginica*): *Palaios*, v. 13, p. 560–569.
- Langdon, C.J., and Newell, R.I.E., 1996, Digestion and nutrition in larvae and adults, in Kennedy, V.S., et al., eds., *The eastern oyster: Crassostrea virginica*: College Park, University of Maryland, Maryland Sea Grant College, p. 231–269.
- Lawrence, D.R., 1995, Diagnosis of the genus *Crassostrea* (Bivalvia, Ostreidae): *Malacologia*, v. 36, p. 185–202.
- Lenihan, H.S., 1999, Physical-biological coupling on oyster reefs: How habitat structure influences individual performance: *Ecological Monographs*, v. 69, p. 251–275.
- Lenihan, H.S., Peterson, C.H., and Allen, J.M., 1996, Does flow speed also have a direct effect on growth of active suspension-feeders: An experimental test on oysters: *Limnology and Oceanography*, v. 41, p. 1359–1366.
- Moore, E.J., 1987, Tertiary marine pelecypods of California and Baja California: Plicatulidae to Ostreidae: U.S. Geological Survey Professional Paper 1228c.
- O'Beirn, F.X., Walker, R.L., and Heffernan, P.B., 1996, Enhancement of subtidal eastern oyster, *Crassostrea virginica* (Gmelin, 1791), recruitment using mesh bag enclosures: *Journal of Shellfish Research*, v. 15, p. 313–318.
- Palmer, R.E., and Carriker, M.R., 1979, Effects of cultural conditions on morphology of the shell of the oyster *Crassostrea virginica*: *National Shellfisheries Association Proceedings*, v. 69, p. 58–72.
- Remane, A., and Schlieper, C., 1971, *Biology of brackish water*: New York, Wiley, 372 p.
- Roopnarine, P.D., 1996, Systematics, biogeography and extinction of chionine bivalves (Bivalvia, Veneridae) in tropical America—Early Oligocene–recent: *Malacologia*, v. 38, p. 103–142.
- Sokal, R.R., and Rohlf, F.J., 1995, *Biometry*: New York, W.H. Freeman, 887 p.
- Stenzel, H.B., 1971, *Oysters*, in Moore, R.C., ed., *Treatise on invertebrate paleontology, Part N, Mollusca 6, Volume 3*: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. N953–N1224.
- Todd, J.A., Jackson, J.B.C., Johnson, K.G., Fortunato, H.M., Heitz, A., Alvarez, M., and Jung, P., 2002, The ecology of extinction: Molluscan feeding and faunal turnover in the Caribbean Neogene: *Royal Society of London Proceedings, ser. B*, v. 269, p. 571–577.
- Vermeij, G.J., 1978, *Biogeography and adaptation: Patterns of marine life*: Cambridge, Massachusetts, Harvard University Press, 332 p.
- Vermeij, G.J., 1998, *Sabia* on shells: A specialized Pacific-type commensalism in the Caribbean Neogene: *Journal of Paleontology*, v. 72, p. 465–472.
- Vermeij, G.J., and Petuch, E.J., 1986, Differential extinction in tropical American molluscs: Endemism, architecture, and the Panama land bridge: *Malacologia*, v. 27, p. 29–41.
- White, M.E., and Wilson, E.A., 1996, Predators, pests, and competitors, in Kennedy, V.S., et al., eds., *The eastern oyster: Crassostrea virginica*: College Park, University of Maryland, Maryland Sea Grant College, p. 559–579.
- Woodring, W.P., 1966, The Panama land bridge as a sea barrier: *American Philosophical Society Proceedings*, v. 110, p. 425–433.
- Woodring, W.P., 1982, *Geology and paleontology of Canal Zone and adjoining parts of Panama*: U.S. Geological Survey Professional Paper 306F, 759 p.

Manuscript received 26 July 2004

Revised manuscript received 17 August 2004

Manuscript accepted 31 August 2004

Printed in USA