is not only a natural consequence of the evolutionary branching process (*8*) but also is a result of ecological species packing (*9*). The simplest index of this change is the overall ratio of species to genera. For groups of organisms living today, this ratio has a minimum of about 4. The living representatives of the paleontologically significant groups of marine organisms have ratios of species to genera averaging about 12 (*9*).

Valentine estimated that average ratios of species to genera increased from about 6 in the middle Cambrian to 10 in the late Cretaceous; his estimate closest to the Permian is for the Late Carboniferous: 8.2 species per genus (*9*). For my analysis, I have chosen to use data for living echinoids because this group has a species/genus ratio of 4.03 and thus is a conservative choice as a proxy for true species-level Permian data. The extinction data in Table 1 for genera, families, and orders have been entered in Fig. 1 in order to estimate species extinctions. Sepkoski's family and order data yield identical species extinction values: 96 percent. The generic data yield 88 percent.

These results support the conclusion of Valentine *et al.* (*2*) that the percentage of species going extinct was high. My analysis goes further, however, by suggesting a mass extinction of truly dramatic proportions, possibly approaching (though of course not reaching) complete extinction of marine life.

Species extinction of 88 or 96 percent is so high that a search for logical errors or biases in the analysis is necessary. One problem might be that estimates of species extinctions are exaggerated because some families and orders were small (near extinction) in the late Permian (*1*), but this is largely accounted for when rarefaction is used: it is assumed that most taxa are small. It could be argued that the Permo-Triassic extinctions are taxonomic artifacts caused by the reluctance of some taxonomists to continue taxa over a major era boundary, but if this were the case, the terrestrial fossil record would show a comparably severe mass extinction. It could even be argued that normal species turnover is so rapid that extinction of nearly 100 percent during the Permian is to be expected even without a mass extinction. But the concern here is not with normal turnover covering the span of the Permian but with extraordinary turnover in the late Permian (mass extinction). Finally, it could be argued that the extinctions were actually selective [in spite of some evidence to the contrary (*10*)], so that some higher taxa had relative immunity to extinction. If so, the estimates of species extinction would have to be lowered because the rarefaction method assumes nonselective extinction. In a worst case, if all species in half the higher taxa were immune to extinction, the family data (Table 1) would predict a 76 percent decrease in standing diversity. Thus, although the 88 and 96 percent estimates from Fig. 1 may be on the high side, we are still left with a bottleneck at least as narrow as that computed from Valentine's data.

The magnitude of the extinction has evolutionary implications. In the Permian, the standing species diversity was at least 45,000 (*2*) and at most 240,000 (*11*). If only 4 percent survived, the marine biosphere would have been left with between 1,800 and 9,600 species. Under the circumstances, chance sampling effects would have influenced the composition of the surviving biota through an evolutionary founder effect analogous to the phenomenon observed when oceanic islands are populated by small numbers of chance migrants. In such cases, the colonizing group is not typical of the source group because of accidents of dispersal as well as true differences in dispersal ability. The compositional changes that followed the Permo-Triassic extinction (*12*) may have resulted to some degree from founder effects. It would be predicted that some of these changes should make sense ecologically and others not. And this is indeed the case. The critical problem remaining is to measure the importance (or presence) of selectivity in species extinction in order better to evaluate the rarefaction results.

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13. I thank L. G. Marshall, R. S. Lande, T. J. M. Schopf, J. J. Sepkoski, Jr., and S. M. Stanley for advice and assistance. Supported in part by NSF grant EAR 75-03870.

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Estuarine Influences on a Continental Shelf Plankton Community

Abstract. *On the southeastern U.S. continental shelf, phytoplankton primary production and the densities of zooplankton, fish eggs, and fish larvae peak simultaneously in late summer and early fall. Some community response to irregular storm events is observed. However, the gross plankton community dynamics on this shelf are dominated by couplings with the local estuaries and shallow nearshore zone.*

Although man may have a great impact on estuarine ecology and an interest in maintaining the natural productivity of continental shelf communities, little is known of the ecological couplings between estuaries and coastal waters. Our purpose in this report is to describe some of these couplings for the plankton community of the South Carolina and Georgia continental shelf. Community metabolic processes in the local estuaries

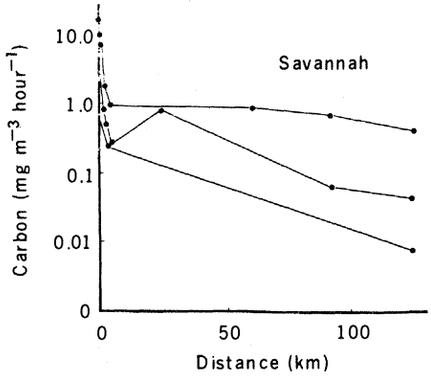

Fig. 1. An example of the seasonal changes in P_{max} along a transect at Savannah, Georgia (0 km is at the outermost sea buoy at the entrance to Wassaw Sound). From top to bottom the sampling months are November, August, and June. The rates vary up to 10 times between cruises and decrease going offshore. The pattern is similar for data collected along transects normal to the coast at Jacksonville, Florida; Sapelo Island, Georgia; and Charleston, South Carolina.

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strongly influence the plankton community on the continental shelf within 5 km of land (*1*). The seasonal pattern of the phytoplankton production is similar in each area; as the estuarine plankton are carried by the net oceanward flow into the nearshore zone, the improved light conditions lead to a greatly increased rate of phytoplankton production [90 versus 547 g of carbon per square meter per year (*1*, *2*)] and subsequent depletion of dissolved nutrients from the water column (*2*, *3*). In contrast, the rate of phytoplankton production is lower farther seaward on the broad, shallow continental shelf, which is bordered on the east by the Gulf Stream (*4*, *5*). This area is poor in nutrients (*6*), and the fish biomass is 10 percent of that of the northeastern U.S. continental shelf (*7*). It is of interest, therefore, to examine how wide this transition zone is and whether the coupling between estuary and nearshore coastal zone is in fact influencing the plankton community further out on the shelf.

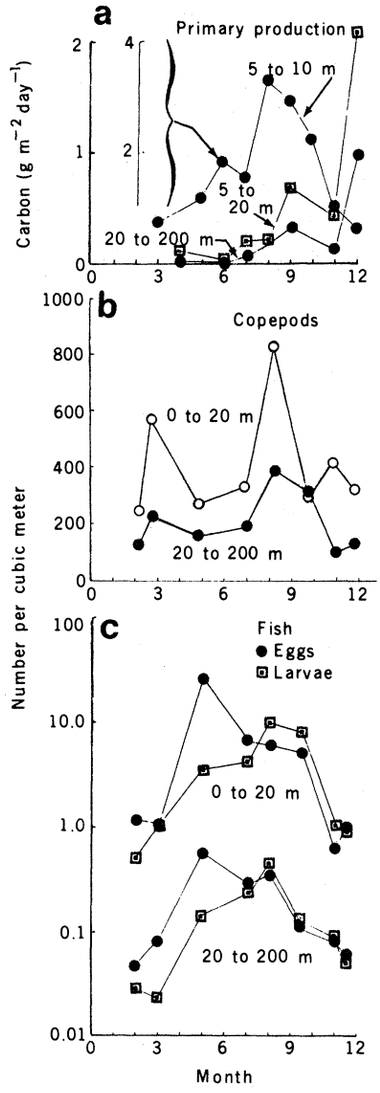

Fig. 2. Seasonal changes in the plankton community at different depth contours on the continental shelf. Primary production (a) is an average of 32 sites from Thomas's (*2*) study near the Altamaha River; data for the other two areas are a combination of results from this study and that of Haines and Dunstan (*4*, *18*). The densities of copepods (b) and of fish eggs and fish larvae (c) caught in a 0.5-μm plankton net are from the unanalyzed reports of the R.V. *Gill* cruises of 1953 through 1954. (*19*).

We determined the phytoplankton photosynthetic activity along four transects normal to the coast between Charleston, South Carolina, and Jacksonville, Florida (*8*). The maximum rate of primary production at full sunlight, P_{max} (in milligrams of carbon per cubic meter per hour), is directly correlated with the simulated in situ estimates of production per unit area (in milligrams of carbon per square meter per day) (*9*). We therefore assume that P_{max} is a good, although relative, index of actual in situ photosynthetic activity. The value of P_{max} dropped dramatically within 10 km of shore along all transects for each cruise (Fig. 1). The large changes observed in the nearshore zone on different cruises are reflected in the proportional changes in P_{max} across the shelf. In general, primary production in the shallow nearshore zone (depth, 0 to 20 m) is closely coupled with the rate of photosynthetic activity observed in deeper waters (20 to 200 m) (Fig. 2a). The transition zone between the two areas is only 5 km wide. Seasonal production per square meter in shallow and deeper portions of the shelf follow each other closely. The spatial pattern in community plankton respiration is similar (*10*). The exception is a large increase in phytoplankton production during the winter offshore and is attributable to storm conditions (*11*). This latter increase was not observed in the shallow zone, but there is a brief midwinter increase in the estuary (*1*, *12*). Otherwise, these data show evidence of seasonal patterns which peak coincidentally in the late summer and early fall.

Because zooplankton are able to quickly exploit new food resources, estimates of their seasonal abundance can be used as an index of primary production in oceanic waters (*13*). We found that, like phytoplankton production, the densities of zooplankton, fish eggs, and fish larvae in the shallow and deeper waters are also closely coupled in time and space (Fig. 2, b and c). The population density of each component in both zones also reaches a peak in late summer.

All these parameters of the plankton community across the continental shelf thus have two features in common: (i) a seasonal synchronous increase and then decrease during the year, which peaks in late summer, and (ii) decreasing values as the water depth increases. Similar changes in salinity across the shelf result from the introduction of freshwater through coastal estuaries (Fig. 3) (*14*). The pattern that emerges exhibits an intense coupling between shallow and deeper portions of the shelf. Since the plankton community of the nearshore zone (*1*) is strongly influenced by what happens in the adjacent coastal estuaries, the coupling between estuary and continental shelf continues inshore. Irregular storms interrupt the predictable pattern of seasonal change. Because of their rapid turnover, phytoplankton and zooplankton tend to respond quickly to these storms. In contrast, the larger predators can adapt to the regular (seasonal) events but less readily to the irregular storm events. It is not surprising, therefore, that the abundance of fish larvae and eggs has a more sharply defined seasonal pattern than the rates of primary production or zooplankton density; perhaps fish eggs and larvae are actually being flushed out of the estuary along with the plankton, even stronger evidence of estuarine-shelf couplings.

Other couplings between estuaries and waters of the continental shelf include changes in sediment supply and circulation (*15*), transformations of riverborne nutrients (*16*), and the support of estuarine-dependent fisheries species which are harvested offshore (*17*). Many other areas along the world's coastlines are similar to this site, areas without either upwelling or major river plumes penetrating across the continental shelf to mask the subtle couplings of estuary,

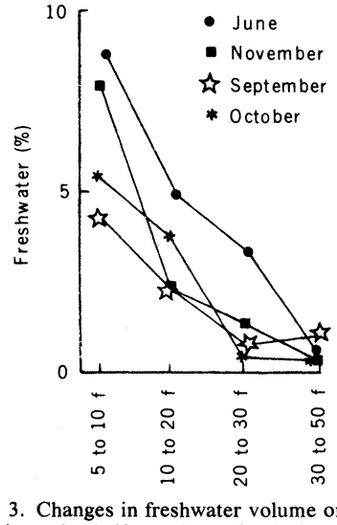

Fig. 3. Changes in freshwater volume on the continental shelf at four depth contours (*f*, fathom) (*14*).

nearshore, and offshore zones. Efforts to improve our knowledge of continental shelf ecosystems and of man's impact on them might well receive a boost if we do not underestimate these couplings and explore them in greater detail.

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5. On four cruises, the concentrations of particulate organic carbon on the shelf were 228 mg m^{-3}, and production was 480 mg of carbon per square meter per day (*4*). This is equal to an apparent doubling rate, averaged across the shelf and throughout the 20-m euphotic zone, of 1×10^{-2} doubling per day. This is a very low rate and reflects either high concentrations of detrital material or a low production per unit biomass.
6. The concentration of nitrates often found on the shelf (*3*), for example, are typical of oceanic oligotrophic plankton communities whose cellular physiology is undersaturated with respect to their ability to absorb nitrates [see T. Parsons and M. Takahasi, *Biological Oceanographic Processes* (Pergamon, New York, 1973), p. 90].
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8. Water samples were collected aboard the R.V. *Eastward* on 4 to 30 October 1972, 16 to 22 June 1972, 20 to 28 August 1971, and 9 to 16 November 1971. A submarine photometer was used to select the sampling depths. Productivity measurements were made at in situ temperatures, and two approaches were used. Simulated in situ conditions were created by the use of a gimbaled outdoor chamber fitted with neutral density filters. A fluorescent light bath was used to estimate the maximum rate of photosynthesis (P_{max}). Measurements of apparent net phytoplankton production (particulate only) were obtained by the ^{14}C isotopic dilution method. Inorganic carbon samples were collected for each sample. Duplicate light and dark bottles collected within 60 minutes of local apparent noon (LAN) were inoculated with 1 ml of stock ^{14}C solution at LAN. The incubation period was generally 2 to 3 hours and 0.5 day for fluorescent light and simulated in situ experiments, respectively. After the samples had been filtered through 0.45-μm membrane filters, they were exposed to fuming acid for 3 minutes and their radioactivity was measured with Geiger counters.
9. The linear regression of primary production determined by the simulated in situ method (y, in milligrams of carbon per square meter per 0.5 day) versus the P_{max} (x, in milligrams of carbon per cubic meter per hour) method is given by $y = 0.059 + 0.24\ x$; R^2 (coefficient of determination) = 0.74. The range of y is 0.016 to 0.41.
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18. The methods used by each research group varied somewhat. Haines and Dunstan (*4*) incubated their samples longer (24 versus 6 hours), used a rough approximation of light penetration (a secchi disk), and collected samples throughout the day. No single method of measuring primary production is acceptable to all researchers at the present time. These estimates are, at least, a good relative estimate of production across the shelf.
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20. We thank our colleagues at the Skidaway Institute of Oceanography, the Institute of Ecology of the University of Georgia, and the Coastal Ecology Laboratory, Center for Wetland Resources, Louisiana State University. J Gosselink, in particular, was a positive influence during the period of manuscript preparation. This work was supported by the Duke University Oceanographic Program, an Energy Research and Development Administration grant to L. R. Pomeroy, and the Louisiana Sea Grant Program maintained by the National Oceanic and Atmospheric Administrations. The U.S. government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon. Coastal Ecology Laboratory, Center for Wetland Resources, Publ. No. LSU-CEL-79-06.

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Expression of the *Escherichia coli* Cell Division Gene *sep* Cloned in a λCharon Phage

Abstract. *The* Escherichia coli *cell division gene* sep, *which probably codes for one of the penicillin-binding proteins, has been cloned into* λ*Charon 10 to form a viable* sep$^+$ *transducing phage. After infection with this hybrid phage, penicillin-binding protein 3 was overproduced and incorporated into the* E. coli *inner membrane.*

A 20.8-kilobase-pair (kbp) segment of *Escherichia coli* DNA around the minute 2 region of the standard map contains at least seven genes required for cell division, murein biosynthesis, or membrane permeability (*1, 2*). These genes include *sep* and *ftsA*, whose products function during septum formation; conditional mutants defective in these genes grow as long, nonseptate filaments at high temperature. The filaments retain some incomplete constrictions, which represent arrested septation (*2*). The *murE*, *murF*, *murC*, and *ddl* gene products function in murein biosynthesis; temperature-sensitive (ts) mutations in these genes cause lysis at high temperature (*1*). The *envA* mutants have increased permeability to a variety of agents and the cells grow in chains (*3*). All these genes are related in that they participate in cytoplasmic membrane–cell wall synthesis or function. Genetic and physical maps of this group of genes have been prepared by transduction and by heteroduplex analysis of DNA of defective λ transducing phages (Fig. 1A) (*2*).

The *sep* gene probably is identical to the *pbpB* and *ftsI* genes described independently by Spratt (*4*) and Suzuki *et al.* (*5*) and thought to code for penicillin-binding protein 3 (PBP-3), a component of inner membrane (*4*). This conclusion is based on the finding that a *sep* ts mutant lacks PBP-3 activity when assayed in vitro at 30° or 42°C and on a genetic analysis of independently isolated transducing phages (*6*). Therefore, the product of the *sep* (*pbpB*/*ftsI*) gene has two detectable properties—a function during septation and a function in penicillin binding.

As an approach to defining how septum formation (and consequently cell division) is regulated in *E. coli*, studies on the regulation of expression of *sep* might

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