Physical energy inputs and the comparative ecology of lake and marine ecosystems

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Abstract

Although freshwater and marine systems both receive light and heat energy from the sun and are mixed by the wind, only marine systems receive additional mechanical energy from the tide. This input is very small relative to the flux of solar energy but may exceed that from wind. Some obvious physical consequences of this additional energy input include the development of intertidal habitats, the presence of stronger currents, and more vigorous vertical mixing. It is argued that these (and perhaps other) consequences lead to coastal marine ecosystems which differ in a number of important ways from temperate lakes.

There is some evidence that coastal marine systems generally maintain a larger standing crop of benthic animals and that these fauna are more effective in mixing the bottom sediments. As a result of better sediment mixing (and perhaps warmer and better oxygenated bottom water), organic matter deposited on the bottom of coastal marine areas may be more completely metabolized and less C, N, and P retained than in lake sediments. Materials that are more tightly bound to particles, like many metals, may behave similarly in lake and marine sediments. Although many lakes are strong sinks for nutrients and metals, marine bays and estuaries may be much less effective in retaining nutrients.

A major consequence of the input of tidal energy appears to be a more intensive yield of fish from marine systems compared with temperate lakes. The data suggest that this more intense yield is not due to the size or interconnection of marine areas or to higher primary production. Rather, the efficiency of transfer of primary production to fish appears to be greater. Tropical lakes appear more like marine systems in this regard, and this may be related to lower thermal stability and more efficient wind energy transfer because of a small Coriolis effect at low latitudes.

It is an editor's reward to have the chance to make some closing observations and speculations. I cannot claim that the following pages will synthesize or even summarize in any systematic and comprehensive manner all the papers that have come before. Certainly, my own thoughts have been helped greatly by reading all of the preceding reviews, but it would be unfair for me to put this chapter forward as anything more than my own contribution to the subject of this volume. Much of it is speculative, perhaps much of it will prove to be wrong. In any case, I am confident this last paper will not be the final word on the subject of the comparative ecology of freshwater and marine ecosystems.

This review carried me into waters both saltier and fresher than is my normal habitat and I was often over my head in both. In addition to those who prepared the reviews in this volume, many others tried to keep me afloat by providing insights, criticisms, data, and references. Among those I must thank are H. T. Odum, Michael Pilson, Virginia Lee, John King, Saran Twombly, Saul Saila, Jeff Frithsen, Jim McKenna, Candace Oviatt, Nelson Hairston, Rebecca Schneider, Ed Herdendorf, Anne Jones, Norb Jaworski, and Michael Prager.

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Comparative size and energy input

Surface area and depth—It seems useful to begin with some simple comments about the relative surface area and depth of freshwater, estuarine, and marine systems for two reasons. First, because many oceanographers—even those who work in coastal areas—seem to think of all lakes as small and shallow. Second, because the rest of this paper is devoted to the hypothesis that it is a difference in physical energy input that ultimately leads to some of the most profound, interesting, and important differ-

Table 1. Surface areas of the world's largest lakes compared with various estuaries, coastal and shelf systems, and major ocean regions.

Large lakes*		Bays and estuaries†		Coastal/shelf systems‡		Oceans§	
		(10³ km²)				(10⁶ km²)	
Caspian Sea	374	Casco Bay	0.42	Peru Current	1,000	North Pacific	11
Superior	82	Buzzard's Bay	0.59	Canary Current	690	Central Pacific	81
Victoria	68	Narragansett Bay	0.43	California Current	505	South Pacific	72
Aral	64	Long Island Sound	3.32	Benguela Current	630	Indian	75
Huron	59	Barnegat Bay	0.26	Benguela productive area	40	North Atlantic	11
Michigan	58	Delaware Bay	1.99	North Sea	570	Central Atlantic	22
Tanganyika	33	Chesapeake Bay	9.92	Gulf of St. Lawrence	226	South Atlantic	40
Baikal	32	Albemarle Sound	2.39	Mid-Atlantic Bight	97	Mediterranean	3
Great Bear	31	Pamlico Sound	5.25	English Channel	86		
Great Slave	29	Biscayne Bay	0.70	Scotian Shelf	62		
Erie	26	Mobile Bay	1.06	Georges Bank	53		
Winnipeg	24	Mississippi Sound	4.79	Irish Sea	48		
Nyasa (Malawi)	22	Galveston Bay	1.36	South Atlantic Bight	3		
Ontario	19	San Francisco Bay	1.17	Galapagos Islands wake	30–110		
Balkhash	18	Puget Sound	17.9				

* Herdendorf 1984a; 15 largest lakes in the world.
† Selected from NOAA 1985.
‡ Upwellings—Cushing 1971, Benguela productive area—Shannon and Field 1985, Galapagos wake—Feldman 1986, North Sea—Jones 1984, Gulf of St. Lawrence—Murty and El-Sabh 1985, English Channel and Irish Sea—Brander and Dickson 1984, Scotian Shelf—Mills and Fournier 1979, Georges Bank—Sissenwine et al. 1984, South Atlantic Bight—Atkinson and Yoder 1984.
§ Moiseev 1973.

ences between freshwater and marine eco-systems. And the input of physical or mechanical energy is linked to size and shape in a very fundamental sense.

In a recent inventory of the large lakes of the world, Herdendorf (1984a) identified 253 lakes with surface areas >500 km². Of these 75% contain freshwater and 48% lie in North America, mostly above 40°N. These northern lakes, like estuaries, are recent features existing only since the last glaciation (Schubel and Hirschberg 1978). Worldwide, over 80% of the large lakes are temperate systems found at latitudes >30°N or S.

Most of the larger lakes are similar to estuaries in terms of surface area. Over 90% fall in the range of 500–10,000 km², roughly the size range from Buzzard's Bay to Chesapeake Bay (Table 1), and 45% are between 500 and 1,000 km² in area (Herdendorf 1984a). The largest of the world's lakes, however, are comparable in size to some of the larger coastal shelf systems like Georges Bank or the most biologically active parts of some coastal upwellings (Table 1). There is no world inventory of estuaries comparable to Herdendorf's lake atlas, but on the basis of a recent review of U.S. systems

(NOAA 1985), it appears that large lakes are, on average, deeper (Fig. 1). Elsewhere in the world, however, there are estuaries and marine bays of much greater size and depth. For example, the Gulf of St. Lawrence covers about 226,000 km² and has a mean depth of 152 m (Murty and El-Sabh 1985).

Although large lakes are reported to contain almost 90% of all the world's liquid surface freshwater, there are also countless smaller, shallower lakes and ponds even as there are unnumbered smaller embayments, lagoons, and tidal creeks that are not included in any inventory. For our purposes, the important point may simply be that most of the world's surface liquid freshwater is captured in lakes that are of the same general size as many estuarine and coastal marine systems. In general, the larger lakes appear deeper than estuaries but shallower than many large bays or most of the coastal shelf (~100 m).

The great difference in scale between lakes and estuaries or bays of any size lies in the hydraulic link that all marine systems have with the oceans. Other papers in this volume have explored this link in terms of ecological diversity and evolution (e.g. Lehman
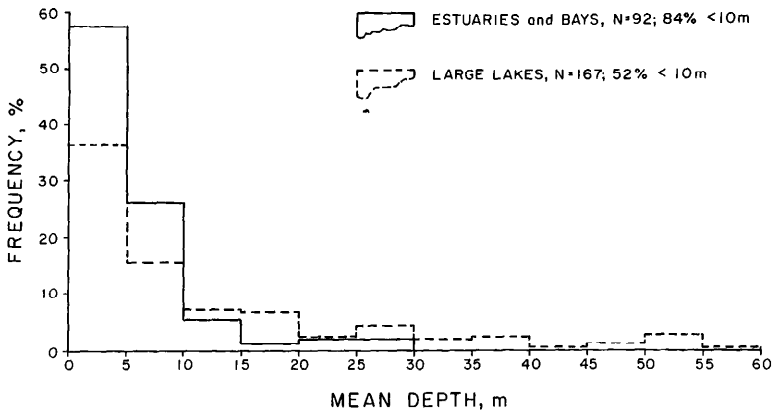
Fig. 1. Frequency distribution of mean depths reported for world lakes exceeding 500 km² in surface area (Herdendorf 1984a) and for estuaries and marine bays of the U.S. (NOAA 1985). Although the estuaries described in the NOAA atlas may not be a representative sample of world estuaries, there are certainly numerous embayments along the world coastline much deeper than those included in the NOAA atlas. On the other hand, Kjerfve (1986) and Deegan et al. (1986) have summarized the physical characteristics of many coastal lagoons with mean depths <5 or 6 m.

1988; Lopez 1988), but a central theme of my paper is that it is equally important in terms of physical energy.

Physical energy input — The gravitational force of the moon and the sun is dilute and cannot raise tides of more than a few millimeters within the confines of any lake (Hutchinson 1957). Even the Gulf of St. Lawrence is not large enough to develop an independent tide (Murty and El-Sabh 1985). Across the vast surface of the oceans (Table 1), however, the astronomical tide may reach an amplitude of centimeters to decimeters (Emery and Uchupi 1972; Murty and El-Sabh 1985). But because of the great depths of the oceans (84% of the world ocean is >2,000 m deep: Sverdrup et al. 1942), the resulting tidal currents are relatively slow and "the dissipation of tidal energy in the deep ocean is negligible" (Levine 1972, p.1). Most of the great store of tidal energy is left to be dissipated on the shallower shelf areas and in coastal bays and estuaries (Munk and MacDonald 1960; Miller 1966).

Most of the water motion in lakes is due to the wind (Csanady 1978) which is also, of course, a major force acting on coastal marine and oceanic systems. Although there has been a recent emphasis on the importance of wind for both local (Weisberg 1976; Weisberg and Sturges 1976; Gordon and Spaulding 1987) and for far-field (Kjerfve

et al. 1978) forcing of coastal circulation, the tidal energy input to marine bays and estuaries may be larger and is always in addition to the wind energy input (Table 2). For example, in their detailed analysis of Long Island Sound (LIS), Bokuniewicz and Gordon (1980a, p. 60) concluded that "the tide is the principal source of the power used in the estuarine processes of mixing and sediment transport in LIS."

The situation on much of the continental shelf may fall somewhere between that of large temperate lakes and that of most marine embayments or estuaries. As the progressive wave of the tide leaves the deep ocean and moves through the very much shallower water of the slope and shelf, its speed is reduced and its amplitude increased. As the tidal wave passes over the shelf toward land, its speed is reduced further by bottom friction and by reflection from the coast, with the result that its amplitude continues to increase, but the associated tidal current once again declines (Redfield 1955). As a result, the speed of the tidal currents is very low in the deep ocean, increases markedly along the outer shelf, declines across the inner shelf, and often increases sharply again in the shallow and constricted waters of bays and estuaries. The tidal currents generated in each bay or estuary will be determined by the

Table 2. Comparison of some energy sources for lakes, coastal marine areas, and the open ocean.

	ergs cm^{-2} s^{-1}
Lake Mendota—wind power above the water (Stauffer 1980)	
Winter–early spring	14–16
Summer	3–5
Narragansett Bay—mean tidal input from offshore (Levine 1972)	45
Long Island Sound (Bokuniewicz and Gordon 1980a,b)	
Mean tidal input	142
Wind, average winter month (dissipation below wave-affected zone)	87
Wind, "10-yr" storm (as above)	480
Irish Sea, south channel—tidal input (Taylor 1919)	1,640
Bay of Fundy—tidal input (McLellan 1958)	2,015
Georges Bank—crest-tidal current (Brown and Moody 1987)	2,000
Northeast Pacific—waves on exposed rocky coast (Leigh et al. 1987)	3×10^6
Open ocean (Faller summarized by Wright 1970)	
Rainfall	1
Wind stress (local = 24; large scale = 3)	27
Tidal (local near boundaries = 6)	7
Differential heating and cooling*	2.5
Pressure variations	"large"

* Wright 1970 concluded that for the North Atlantic this term was approximately equal to the wind stress.

depth, length, and general shape of the embayment as well as by the character of the tidal signal at the mouth. The latter may be strongly influenced by local geography and bathymetry as well as by the width of the offshore shelf (Redfield 1955).

There are also special areas of the continental shelf where deeper basins are found behind much shallower banks that are bisected by deep channels. Under such conditions, large volumes of water must be forced through a relatively constricted cross section and the tidal currents may be very strong over a large area (Emery and Uchupi 1972; Fig. 2). A well-known example is the Nantucket Shoals-Georges Bank-Browns Bank complex separating the Gulf of Maine and the Bay of Fundy from the North Atlantic.

The importance of physical energy

Intertidal habitats—An obvious consequence of the power of the tide is that many marine bays and estuaries contain large areas of intertidal mudflats, marshes, or mangrove swamps that develop where great volumes of water are moved. The importance of tidal inundation and flow (and/or river flow) for the productivity of these habitats is becoming clear (Steever et al. 1976; Odum 1980; Lugo et al. 1988), though in areas where the astronomical tide is small and topographic relief is slight, as along the U.S. Gulf Coast, water levels may still vary enough as a result of changes in mean sea level and wind set-up to create similar habitats (Madden et al. 1988).

Current speeds—The wind-generated currents of lakes are generally much weaker than those found in marine systems, especially those in estuaries, bays, or on shallow shelf banks. As Ruttner (1963, p. 49–50) put it, "when we now turn to . . . currents, we enter a field of science that has had a major development only in oceanography. In limnology, currents have been investigated only to a slight degree because the bodies of water usually studied are small with slow currents that are hard to measure." This is particularly true of near-bottom currents, which may be on the order of several centimeters per second or less in lakes (e.g. Lathbury et al. 1960; Sly et al. 1982) but reach several decimeters per second or more in bays and estuaries.

For example, near-bottom currents in the lower passages of Narragansett Bay commonly reach 30–60 cm s^{-1} (Levine 1972), and Schubel (1986) described tidal (surface?) currents up to 100 cm s^{-1} in Chesapeake Bay. Current speeds may be several meters per second in the Bay of Fundy (Daborn 1986). On the crest of Georges Bank, currents may exceed 75 cm s^{-1} (Butman 1982) while near-bottom flow is generally 10–20 cm s^{-1}, at least during calm weather, on the continental shelf off New Jersey (McClennan 1973; Fig. 2).

Among the consequences of the stronger currents in coastal marine systems is the presence of finer grained sediments in lakes than are found at an equivalent depth in marine environments (Sly 1978; Sly et al. 1982). Faster currents are also thought to thin the laminar layer against the leaves of seagrasses and the surfaces of macroalgae, thus enhancing the exchange of nutrients
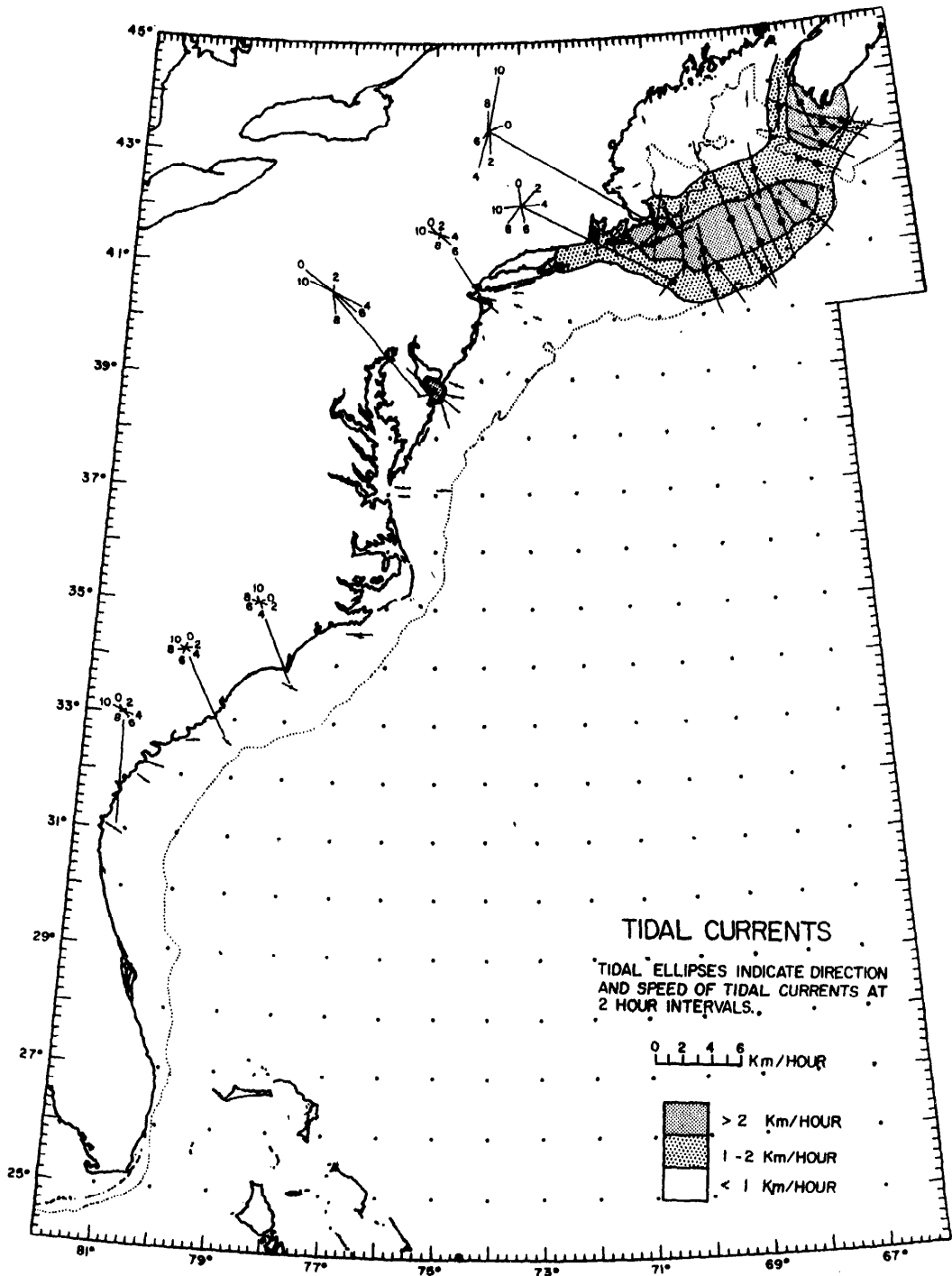
Fig. 2. Tidal currents over the continental shelf of the east coast of the U.S. and Canada showing the very high energy area associated with the most productive fishing grounds (from Emery and Uchupi 1972). Other coastal regions with especially high tidal energy dissipation are summarized by Murty and El-Sabh (1985) based on the age of the tide. Since records of water level are relatively common around the world compared to measurements of tidal currents, analyses of the age of the tide may provide a useful method for identifying areas of potentially high fisheries yield.

and metabolic gases and stimulating productivity (Conover 1968; Parker 1979; Wheeler 1980; Stevenson 1988).

Lopez (1988) has suggested that the lack of currents may be responsible for the virtual absence of tentaculate deposit-feeding bottom animals from lakes. It is also likely that the growth of suspension feeders and filter-feeding bivalves is enhanced in marine systems where they often constitute a major portion of the benthic biomass (Warwick 1980; Wildish and Peer 1983). Certainly there is nothing in lakes to compare with the great concentrations of animal biomass found in marine mussel beds, clam beds, and oyster reefs (Nixon et al. 1971; Dame 1976).

Vertical mixing—Schubel (1986, p. 18) described the tide in Chesapeake Bay as ". . . the egg beater that stirs up the water. . . ." And so it is. But only a small portion of the tidal energy may be needed for vertical mixing. In both Narragansett Bay (Levine 1972) and in Long Island Sound (Bokuniewicz and Gordon 1980a,b) only a small percentage of the tidal energy is needed to prevent density stratification. For wind, also, Kullenberg (1976, p. 159) found that "only a very small part of the energy is consumed by the local vertical mixing."

Vertical mixing results from several complex interactions, but it can be shown to be determined to a large degree by the simple relationship, U^3/Z, where U is the average speed of the tidal current and Z the depth of the water (Simpson and Pingree 1978; Riley 1982). I have inverted the usual presentation of the ratio to emphasize that an increase in current speed is particularly effective in promoting mixing. As a result, much of the preceding section on relative current speeds among open ocean, continental shelf, shelf bank, estuarine, and lake ecosystems translates rather directly into relative degrees of vertical mixing. For example, values of U^3/Z for some of the areas discussed earlier might be on the order of:

Lake Mendota—0.02
Inner continental shelf—0.02–0.40
Outer continental shelf—0.10–0.68
Narragansett Bay—10–30
Georges Bank crest—25–85

Even though vertical density gradients in the open ocean are usually small relative to those commonly found in coastal waters, the great depth and slow currents lead to little vertical mixing except under special circumstances. Some examples include upwelling, current interface shearing, and eddies and wakes behind islands (Sette 1955; Simpson and Tett 1986; Feldman 1986; Bowman 1986).

It is always difficult, frequently dangerous, and only occasionally rewarding to generalize, but my impression from much of the scientific literature is that most estuaries, coastal lagoons, and marine embayments are well mixed or only weakly stratified, at least during summer. The NOAA (1985) atlas describes 64% of the 92 sites inventoried as vertically homogeneous during the period of low freshwater inflow, and only 8.7% are classified as highly stratified. Some of the areas that do experience periodic stratification are microtidal systems like the Pamlico estuary that must rely on wind mixing (Copeland et al. 1984); others may have deep channels and very large inputs of freshwater like parts of the main stem of Chesapeake Bay (Officer et al. 1984a).

The situation in lakes is complicated by climate, altitude, area-to-depth ratio, wind, etc. According to Hutchinson (1957, p. 444), "most lakes in the eastern and central United States and Canada and in the interior of Europe exhibit the sharp continental type of stratification. . . ." As noted earlier, this includes a great many of the larger lakes in the world. It also includes a very large proportion of the lakes discussed in the scientific literature. In a recent review, Lewis (1987, p. 150) pointed out that "limnology has been predominately a science of high latitudes. . . ."

Tropical lakes—The situation in tropical lowland lakes is different and may provide additional evidence in an indirect way for the great importance of the enhanced physical energy input to coastal marine systems. Three factors come into play. First, although the temperature gradient between surface and bottom water in deep lakes is minimal near the equator and reaches a peak between 35°–50° lat, the rate of change in density of water increases substantially with

temperature. Lewis (1987) has calculated the stability that might be expected in an idealized lake at different latitudes as a result of the interaction of density change and temperature gradient, with the result that stability is lowest from 0° to 20° lat, then rises sharply to a broad maximum between about 25° and 40° lat. Empirical data from 52 African lakes analyzed by Kling (1988, p. 159) led him to conclude that "the differences in density gradients found in tropical and temperate lakes . . . are striking. For example, the mean of the maximum density differences within the water columns of the tropical lakes examined here was 0.00065 g cm^{-3} . . . whereas the density difference between 4° and 20°C in a temperate lake during summer stratification is about three times greater. . . ."

The second factor follows from the high temperatures of tropical lakes and the steep slope of the temperature–density curve. Since relatively small gains or losses of heat can produce a large change in stability, tropical lakes may commonly develop a regime of daytime stratification alternating with nighttime mixing or mixing resulting from a few days of cloudy weather (Lewis 1987; Kling 1988).

The third factor is that wind may be more efficient in generating currents and mixing in low latitude lakes. As explained by Lewis (1987, p. 163–164), "the Coriolis force deflects currents created by wind stress and thus reduces the current velocity that can be maintained by a given wind velocity. . . ." Since the Coriolis term falls rapidly to zero at the equator, Lewis (1987) calculated that a given wind speed will produce twice as fast a current between 0 and 10° lat as it would above 20°. In an idealized lake he suggested that this could translate into a mixed layer that is two to three times deeper at low latitudes.

All of these factors may come together to produce more frequent mixing in shallow tropical lakes and greater mixing depths in deeper tropical lakes than is found in comparable temperate waters (Kling 1988). If so, the greater thermal energy input and increased wind energy input to tropical lakes may produce some of the same conditions found in coastal marine systems.

Ecological consequences of vertical mix-ing—If there were a great dichotomous key to the aquatic ecosystems of the world, one of the earliest divisions would surely be on the basis of the extent and duration of vertical stratification. On one side would fall coastal upwellings and the shallow wind-mixed lakes of Africa, on the other, fjords and the Great Lakes of North America. It could be argued that the presence or absence of stratification may be every bit as important as the presence or absence of salt in determining the ecology of freshwater and marine ecosystems. And, of course, they are related.

As stratification is developed or destroyed in freshwater or marine systems, habitat will open or close, the kinds and abundances of organisms will change, and food webs will reform; rates of metabolism and nutrient cycling will change, a different stoichiometry may emerge, and substances will interact differently with particles.

Much of the impact of stratification, of course, follows from its effect on bottom water temperatures and dissolved oxygen concentrations. In stratified temperate lakes, the temperature of the bottom water during summer depends on several factors and may be quite variable from year to year. For example, at 24 m in Lake Mendota in mid-July, the temperature has varied from 7.6° to 14.5°C during a 28-yr record (Brock 1985). In general, however, hypolimnion temperatures commonly fall below 10°C. This contrasts with many temperate marine bays and estuaries where the water column may be virtually isothermal or the bottom waters and sediments are only a few degrees cooler than the surface. For example, in 20-m-deep water at the center of Long Island Sound, the surface is about 18.5°C in summer while the bottom water is 17.7°C (Gordon 1980). On high-energy shelf areas such as the crest of Georges Bank, the water column is isothermal to depths of 60 m during summer (Butman 1982).

The comparative reviews prepared for this volume do not suggest that there is any systematic difference between the potential rates of growth and metabolism of those organisms living in freshwater and those living in salt water or in the way these rates respond to temperature. It therefore seems reasonable to suppose that the realized rates

of feeding, respiration, excretion, and growth of organisms living below the thermocline of temperate lakes will generally be significantly slower than in the bottom waters and sediments of well-mixed marine systems. This may have a considerable impact on the ecology of a lake since a large area of sediment and volume of water may be involved. For example, about half the area of Lake Mendota lies below the summer thermocline (Brock 1985). Over half the total area of Lake Erie may fall below the thermocline in the Central Basin alone, along with almost 20% of the total volume (Herdendorf 1984b).

The capture of a significant area of sediment and volume of water below the thermocline may also expose the associated organisms and chemistry to hypoxic or anoxic conditions, especially in warmer and more productive lakes. During its worst year, some 45% of the bottom of Lake Erie was anoxic (Herdendorf 1984b). The lower oxygen concentrations can have profound effects on survival, growth, and reproduction of organisms as well as on biogeochemical cycles.

Hypoxia and anoxia are also found in some stratified coastal marine systems that experience large inputs of nutrients or organic matter. As noted earlier, such stratified areas are usually associated with weak tidal currents and/or large inputs of freshwater, deep channels, or obstructions to circulation such as dredge spoil banks, breakwaters, or sills. Several examples have been discussed in the recent "Nationwide review of oxygen depletion and eutrophication in estuarine and coastal waters" (e.g. Whitledge 1985; Rabalais et al. 1985). Large areas may be involved along the inner continental shelf south of Long Island and especially in the Gulf of Mexico from the mouth of the Mississippi River to Texas, where tidal currents are weak, considerable amounts of freshwater may accumulate in the surface layers, and mixing is largely dependent on the vagaries of the wind and the passage of storm fronts (Emery and Uchupi 1972).

In addition to its effects on temperature and dissolved oxygen, vertical mixing influences the exposure of phytoplankton to light and to the supply of nutrients from deeper water (e.g. Riley 1942; Demers et al. 1986),

couples heterotrophic bottom communities with the euphotic zone (e.g. Nixon 1981, 1986), and makes possible the conservative circulation pattern characteristic of many estuaries (Pritchard 1952; Schubel 1986). It is likely that the coupling of seaward-flowing surface water and landward-flowing bottom water contributes to the production of some commercially important species (Epifanio 1988).

Some ecological consequences of physical energy

Given the greater input of mechanical energy to marine ecosystems and the presumed importance of the intertidal habitats, strong currents, and vigorous vertical mixing that are associated with it, I was surprised not to see more dramatic contrasts with lakes emphasized in the preceding reviews. For example, Kilham and Hecky (1988) did not report a difference in primary production between well-mixed bays and estuaries and stratified temperate lakes.

It is very difficult to make such comparisons, of course, because the number of measured systems is small relative to the total, the range observed in freshwater (Wetzel 1983) and marine systems (Nixon et al. 1986a) overlaps, there is year-to-year variability in both environments, a variety of measurement techniques have been used, etc. Even within the marine environment, it has proven difficult to relate primary production to environmental factors (Boynton et al. 1982; Nixon 1983; Nixon et al. 1986b). In a study of 14 regions on the continental shelf from Cape Hatteras through the Gulf of Maine, O'Reilly and Busch (1984) reported a range of 260–470 g C m^{-2} yr^{-1}, or a difference factor of only 1.8 between the least productive inner shelf and Georges Bank. The same range includes almost all of the marine bays and estuaries as well as many of the coastal upwelling areas that have been described (Nixon et al. 1986b).

In his review of large lakes, Herdendorf (1984a) summarized primary production estimates for 25 lakes. Of these, 12 estimates were <200 g C m^{-2} yr^{-1}, three were between 200 and 300, and 10 were >300. Seven of the 10 most productive were tropical. Stratified temperate lakes can be as productive

as marine systems, however, just as the stratified inner shelf is similar in this regard to well-mixed bays (Table 3). More subtle, yet equally important differences may be found in the size distribution and species composition of plankton in stratified vs. well-mixed water and in the amount of production that is supported by "new" nutrients compared to the amount dependent on rapid pelagic and benthic recycling. Recent research on this topic in marine systems has been reviewed elsewhere (Demers et al. 1986; Peterson 1986).

I think there are, however, some major differences between freshwater and marine systems that may be related to a combination of the differences in habitat, currents, and mixing that follow from the focusing and concentration of tidal power in coastal areas.

Benthic biomass — In addition to the great concentrations of animals found in heterotrophic marine beds and reefs, it is likely that the average standing crop of benthic macroinfauna is generally greater in estuarine and coastal marine areas than in lakes. It is admittedly difficult to make such a claim with certainty for many of the same reasons discussed earlier with regard to primary production. For example, 500-μm mesh screens are commonly used to collect benthic animals, but mesh sizes from 100 to 1,000 μm have also been used; most benthic surveys measure abundance rather than weight; various conventions are used to report biomass values, including wet weight (shells?), preserved weight, dry weight, ash-free dry weight, etc.; most coring devices do not sample large animals adequately; benthic animals are notoriously patchy in distribution and vary with sediment type. In spite of these difficulties, I think there are enough reasonably comparable data available to show that there is generally a higher standing crop in marine areas. Since the abundance of benthic macrofauna declines with increasing depth (Lopez 1988), a greater frequency of higher biomass values might be expected from estuaries and marine embayments because they are frequently shallower than larger lakes (Fig. 1). Even when similar depths are compared, however, the benthic biomass of marine systems is com-

Table 3. Comparative rates of primary production (g C m^{-2} yr^{-1}) in some marine and freshwater ecosystems.

Temperate lakes*	
ELA (Experimental Lakes Area), Canada	6–170
Huron	100
Ontario	180
Michigan	130
Erie	500
Wingra	345
Mendota	295–390
Tropical lakes†	
Chad	620
Kivu	525
Rudolf	1,180
Tanganyika	640
Victoria	965
Lanao	620
Marine systems‡	
Bedford Basin, Nova Scotia	220
Narragansett Bay, Rhode Island	310
Peconic Bay, Long Island	190
Lower Hudson estuary, New York	690–925
New York Bight Apex	370
Mid-Chesapeake Bay	335–780
Pamlico River estuary, North Carolina	200–500
North Inlet, South Carolina	260
Inshore sounds, Georgia	300
Nearshore shelf, Georgia	285
Apalachicola Bay, Florida	360
Nearshore Louisiana	265
Burrad Inlet, British Columbia	350
Kaneohe Bay, Hawaii	165

* From summaries by Herdendorf 1984a and Brock 1985.
† African lakes from summary by Herdendorf 1984a. As discussed in text, production rates reported earlier for some of these and other African lakes are substantially lower (Melack 1976). Lake Lanao from Lewis 1974.
‡ From summaries by Nixon 1986 and Nixon et al. 1986b.

monly several times to many times greater (Fig. 3).

It would be desirable to compare the secondary production of freshwater and marine benthic communities, but there are probably too few direct studies to reach any meaningful conclusion. If Lopez (1988, p. 946) is correct that "there is no characteristic difference in $P:B$ ratios between marine and freshwater macrobenthos," then the production of marine areas may also be correspondingly greater. It would also be interesting to see if the higher benthic production of marine areas results in generally lower zooplankton production as suggested by Daborn (1986) and others.

It is worth noting that in addition to lower
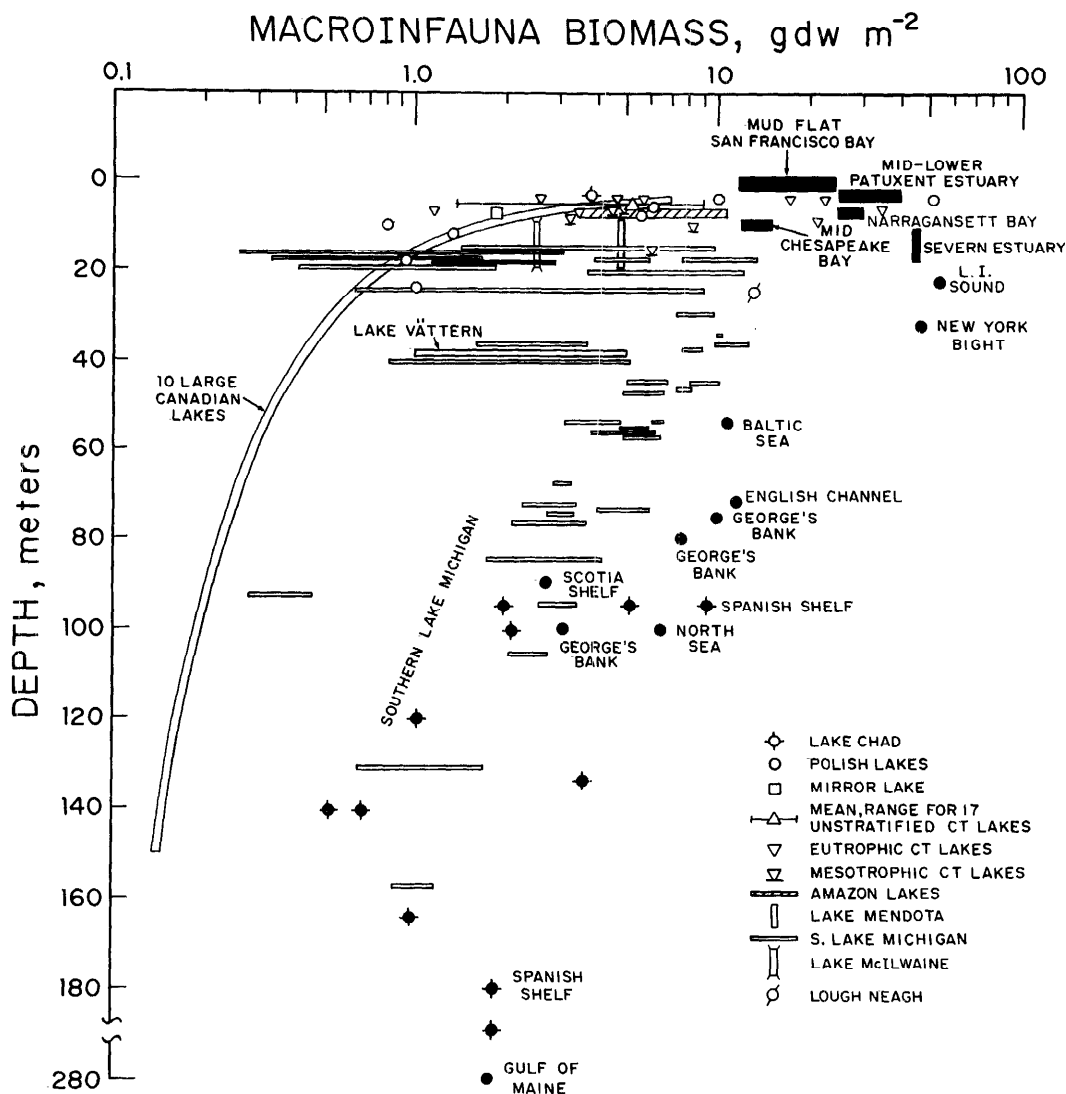
MACROINFAUNA BIOMASS, gdw m^{-2}

Fig. 3. Biomass of benthic macroinfauna as a function of overlying water depth in various lakes and coastal marine systems. Biomass data are shell-free or ash-free dry weight (dw). Screen sizes varied, but were <1 mm and usually close to 500 μm. Samples collected from sand areas have been excluded when possible. Bars indicate ranges or, in the case of Rawson's (1955) large Canadian lakes, a regression. Lake Michigan survey—Nalepa et al. 1985, Connecticut lakes—Deevey 1941, Polish lakes—Kajak and Dusoge 1975, Lake McIlwaine—Marshall 1978, Lake Vättern—Grimås et al. 1972, Lough Neagh—Carter 1978, Amazon lakes—Fittkau et al. 1975, Lake Chad—Davies and Hart 1981, Lake Mendota—Brock 1985, Mirror Lake—Strayer and Likens 1986. Marine data from Georges Bank—Maciolek-Blake et al. 1985, San Francisco Bay—Nichols 1977, Chesapeake Bay—Reinharz and O'Connell 1981, Patuxent estuary—Holland and Hiegel 1981, Severn estuary—Warwick et al. 1978, North Sea—McIntyre 1978, Long Island Sound—Sanders 1956, Baltic Sea—Elmgren 1984, Scotia Shelf—Mills 1980, northwest continental shelf off Spain—Tenore et al. 1984.

temperature, weaker currents, and hypoxia, the standing crop, production, and potential contribution of lake benthos to fish growth is often reduced further by insect emergence. For example, in Mirror Lake, New Hampshire, Strayer and Likens (1986) found that 25% of the zoobenthic production was accounted for by insect emergence, but only 15% was consumed directly by fish.

Sediment mixing and nutrient mass bal-

Table 4. Estimates of near surface mixing coefficients in some marine and freshwater sediments.

	D_m (cm^2 s^{-1} 10^{-6})
Marine systems*	
Narragansett Bay	
a. Santschi et al. 1979	0.01–0.1
b. Ludke and Bender 1979	0.2–0.4
c. Garber 1982	0.4–5.2
Long Island Sound	
d. Aller and Cochran 1976	1.2–2.5
e. Aller et al. 1980	0–1.5
Chesapeake Bay	
f. Officer et al. 1984*b*	0–3.2 (mean for 20 cores—0.3)
Freshwater systems†	
Lough Neagh	
g. Rippey and Jewson 1982	0.06
Lake Huron	
h. Robbins et al. 1977	−0.1 and 0.18
Susquehanna River mouth	
i. Officer et al. 1984*b*	0

* a. From tracer experiments with labeled microspheres. b. From tracer experiments with ^{141}Ce and ^{59}Fe. c. From ^{15}N-labeled organic matter added to cores. d. From in situ distribution of ^{234}Th. e. From the distribution of ^{234}Th and ^{238}U in 12 cores. f. From in situ distribution of ^{210}Pb, ^{137}Cs, and/or ^{239,240}Pu in 23 cores described by various workers. Mean is for all cores except three in which D_m was described as infinitely large.
† g. From in situ mixing of Chl *a*. h. From in situ distribution of ^{210}Pb. i. From in situ distribution of ^{210}Pb.

Table 5. Estimates of the thickness of well-mixed sediments in some marine and freshwater systems.

	Mixed depth (cm)
Marine systems*	
Narragansett Bay	
a. Nixon and Pilson 1984	5–10
b. Cochran 1984	25
Long Island Sound	
c. Aller and Cochran 1976	4
d. Cochran 1984	5–10
Chesapeake Bay	
e. Officer et al. 1984*b*	4–30
Freshwater systems†	
Lough Neagh	
f. Rippey and Jewson 1982	1–2
Lac Léman	
g. Krishnaswamy et al. 1971	0
Lake Pavin	
g. Krishnaswamy et al. 1971	4
Lake Lucerne	
h. Bloesch and Evans 1982	1–3
Lake Superior	
i. Bruland et al. 1975	2
Lake Huron	
j. Robbins 1982	1
Lake Michigan	
k. Robbins and Edginton 1975	0–4 (x = 0.83)
Susquehanna River mouth	0
l. Officer et al. 1984*b*	

* a. From distribution of C, N, and P in upper and lower bay cores. b. From ^{210}Pb. c. From ^{234}Th/^{238}U. d. From ^{210}Pb. e. From ^{210}Pb, ^{137}Cs, and/or $^{239/240}$Pu. Mean is for 14 cores showing clear evidence of mixing.
† f. From Chl *a*. g. From ^{210}Pb. h. From ^{210}Pb in six cores. i. From ^{210}Pb. j. From ^{137}Cs in 58 cores in southern portion of lake. Values were greater if porosity exceeded 0.9. k. Range and mean for seven cores analyzed for ^{137}Cs (lower value) and ^{210}Pb (upper). l. From ^{210}Pb.

ances—Given the extent of bioturbation or sediment reworking carried out by benthic macrofauna, it might be expected that a lower standing crop of animals would result in less mixing of the sediments of lakes. It is difficult to know if this is, in fact, the case because there appear to have been few measurements in either freshwater or salt-water sediments, and different taxonomic groups differ in the manner in which they carry out mixing. The few data I have found, however, are consistent with more rapid mixing and mixing to a greater depth in coastal marine sediments compared with lakes (Tables 4 and 5).

More vigorous mixing of the sediments by more abundant macrofauna and by faster currents may ensure more rapid and complete consumption of the organic matter deposited on the bottom in many marine bays and estuaries (Yingst and Rhoads 1980). Warmer temperatures and, in some cases, greater dissolved oxygen concentrations in bottom waters may contribute to the same

result. This could explain the relatively monotonous profiles of the concentrations of organic carbon, nitrogen, and phosphorus that have been found in the few estuaries where cores of sediment have been analyzed (Nixon and Pilson 1984; Boynton and Kemp 1985). In contrast to lake sediments, which often appear to preserve a historical record of increasing eutrophication and organic deposition from the overlying water (e.g. Kemp et al. 1972, 1976; Edmondson 1974), the coastal marine sediments of Narragansett Bay and Chesapeake Bay are enriched in C, N, and P only in the surface 5–10 cm, well within the zone of active mixing (Table 5). Below this zone, nutrient and carbon concentrations fall to background.

The behavior of these biologically active elements contrasts with that of less active

NARRAGANSETT BAY

ORGANIC C,   ORGANIC N,   ORGANIC P,   INORGANIC P,   Cu, μg g^{-1}

mg g^{-1} mg g^{-1} mg g^{-1} mg g^{-1}

LAC LÉMAN

ORGANIC C,   ORGANIC N,   ORGANIC P,   INORGANIC P,   Cu, μg g^{-1}

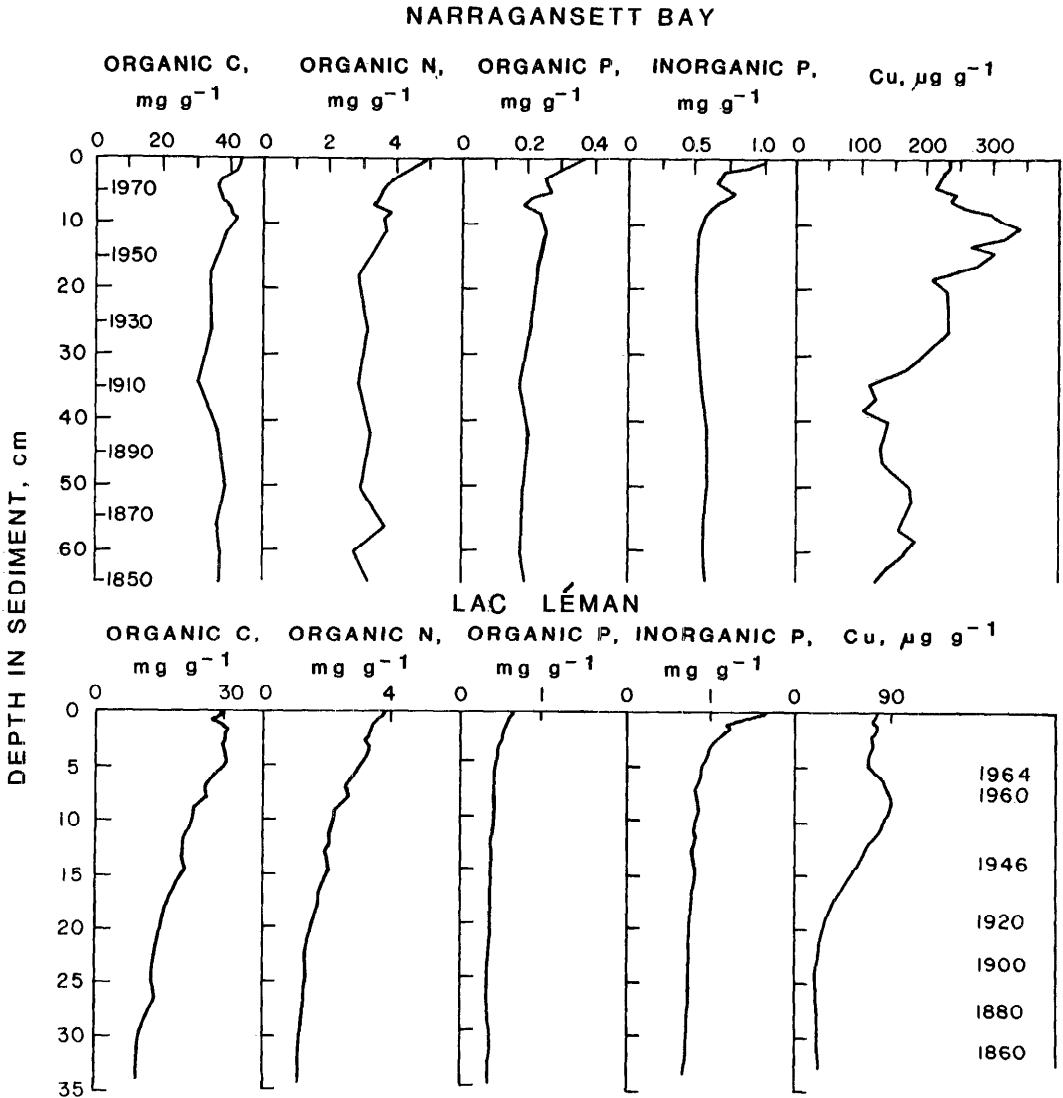mg g^{-1} mg g^{-1} mg g^{-1} mg g^{-1}

Fig. 4. Concentrations of organic carbon and nitrogen, organic and inorganic phosphorus, and copper at various depths in the sediments in dated cores from upper Narragansett Bay (Santschi et al. 1984; Nixon et al. 1986a) and Lac Léman (Vernet and Favarger 1982).

particle-bound materials like Cu and Pb. In Lac Léman (Lake Geneva), Switzerland, the sediments show increasing concentrations of organic carbon and nitrogen since the late 1800s that coincide with those of copper, which began to enter the lake in significant quantity around 1900 (Vernet and Favarger 1982; Fig. 4). In Narragansett Bay, Rhode Island, the sediments show increasing concentrations of Cu at a much greater depth

in the sediment than that at which C or N begin to increase (Fig. 4). Independent dating of the core using multiple isotopes (Santschi et al. 1984) showed that the Cu profile is a reasonable reflection of anthropogenic input. Since urban development preceded and increased with industrialization, and city water and sewer systems were under construction from about 1870–1880 on, the impact of C, N, and P enrichment

Table 6. Comparison of annual nutrient budgets for some lakes and estuaries.

	Lake Erie*	Lake Mendota†	Narragansett Bay‡	Chesapeake Bay§
Surface area, km²	25,212	39	255	11,500
Mean depth, m	18.6	12.4	8.4	6.5
Residence time, yr	2.4	6.2	0.07	0.5
Sediment deposition, g m⁻² yr⁻¹	1,190	715–1,100	250	260
P input, g m⁻² yr⁻¹	1.27	0.8	4.68	0.9
P retention, %	59–92	75	2.6	11–16
N input, g m⁻² yr⁻¹	5.1	12.7	27.6	10.7
N retention,‖ %	78	80	1.7	3–5

* Burns et al. 1976; Burns 1976; Kemp et al. 1976.
† Brock 1985.
‡ Chinman and Nixon 1985; Pilson 1985; Nixon et al. 1986a.
§ Schubel 1986; Nixon 1987.
‖ Lakes include sedimentation and denitrification.

is clearly not being recorded in this marine sediment (Nixon et al. 1986a). This is consistent with experimental studies showing that virtually all of the organic matter added to Narragansett Bay bottom communities is rapidly metabolized and the nutrients released to the overlying water (Garber 1982; Kelly and Nixon 1984).

An important consequence of this difference in the behavior of certain metals and nutrients in freshwater and marine sediments is that while lakes often act as strong sinks for both kinds of materials, estuaries and marine bays may retain and accumulate only a small portion of the nutrients that flow into them from rivers and anthropogenic discharges (Table 6). At the same time, a relatively large fraction of the metals that are not involved to a great extent in biological metabolism may be retained in coastal sediments (Santschi et al. 1984; Nixon et al. 1986a). For example, the retention of Cu (70–95%) and Pb (80–100%) in Narragansett Bay (Nixon et al. 1986a) is very similar to the 75 and 90%, respectively, retained in the Bodensee (Lake of Constance) (Sigg 1985).

Since the intensity of nutrient loading (mmol m⁻³ yr⁻¹) is generally much greater on estuaries than on even eutrophic lakes (Nixon et al. 1986a,b), it is a fortunate correspondence of nature that the same physical energy input that enhances the growth of heterotrophic bottom communities and promotes the efficient return of nutrients to the water column also provides a much more rapid exchange of that water (Table 6). If

lake benthos (including, of course, the microfauna) were as efficient in recycling nutrients, widely used empirical relationships linking nutrient loading and hydraulic residence time to lake water quality might be quite different (Vollenweider 1976). It may be necessary to make more than a simple stoichiometric conversion from P to N limitation and to include more elaborate descriptions of water residence time (see Lee and Jones 1981) when applying such lake models to higher energy estuarine and marine systems.

Fishery yields—It seems fitting to end this final paper with an observation that first stimulated my own interest in the comparative ecology of freshwater and marine ecosystems and helped to prompt the organization of the workshop that led to this volume. While preparing a review of coastal lagoons (Nixon 1982), it became evident that the fishery yields per unit area from estuarine and coastal marine systems were almost always much higher than those from well-developed lake fisheries. At first this may seem of only passing interest, since the catch of finfish, and perhaps shellfish, from any one marine area might represent the concentration of production from a much larger system. Fish harvested in a marine bay or estuary may have realized much of their growth offshore and the currents moving across an oyster bed can deliver phytoplankton produced over a wide area. Lake fisheries, on the other hand, must be largely self-supporting. This can be only part of the explanation, however, because the yield per
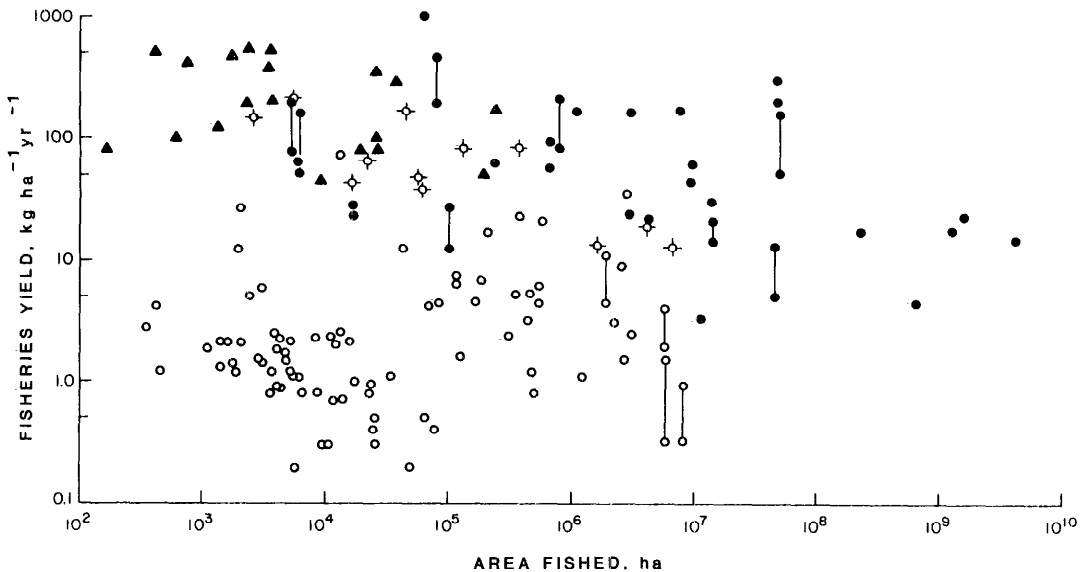
Fig. 5. Fisheries yield as a function of the surface area of the system from which the catch was taken. Since few small marine areas are fished intensively any longer, historical data from Goode (1887) were used (▲). More recent marine data (●) were taken from various sources, including many cited by Nixon (1982) and Nixon et al. (1986b). In some cases ranges are shown to indicate variability over a period of years. The four largest marine systems represent the total world ocean, the Pacific, the Atlantic, and the Indian Ocean total landings divided by the respective shelf and slope area of each (Moiseev 1973). The lowest marine point is the Gulf of Bothnia in the upper Baltic, an area that is almost fresh. Data for lakes (recent data—O; tropical lakes—◇) come from many sources: Rawson 1952; Melack 1976; Oglesby 1977; Schlesinger and Regier 1982; Youngs and Heimburgh 1982; Herdendorf 1984a. The yield from managed and/or enriched marine and freshwater fish culture areas may be much higher, and harvests from marine raft cultures, freshwater fishponds, etc. have not been included.

unit area from marine waters falls off very slowly as the area from which the landings data are collected increases over many orders of magnitude, and the intensity of yield from marine systems is greater than that from lakes at all scales (Fig. 5).

The greater intensity of harvest from marine fisheries also does not seem to reflect a general difference in primary production. Rather, the efficiency of conversion of photosynthetically fixed carbon to fish seems to be 5–10 times higher in marine waters and appears to increase with increasing primary production (Fig. 6). It is possible, however, that tropical lakes, especially those that are shallow, may fall within the trend for marine systems rather than within the trend for temperate lakes. Certainly, the yields from African lakes such as George (160 kg ha^{-1} yr^{-1}, 2.5-m mean depth), Kyoga (180 kg ha^{-1} yr^{-1}, 6 m), Malombe (130 kg ha^{-1} yr^{-1}, 4 m), and Upemba (225 kg ha^{-1} yr^{-1}, 0.3 m) exceed those from all but the most

productive marine areas (data of Henderson and Welcomme summarized by Schlesinger and Regier 1982; see Fig. 5).

Unfortunately, there seem to be no measurements of annual primary production available for the latter three lakes. Gross production data have been reported for Lake George (data of Ganf summarized by Melack 1976), but it is not clear how to convert the oxygen change measurements that have been used in almost all tropical lake studies (Melack 1976, 1979) into net carbon fixation to be consistent with virtually all the results from temperate lakes and marine ecosystems. The conversions used by Melack (1976) lead to estimates of 255–295 g C m^{-2} yr^{-1} for Lake George and place it on the upper slope of the fisheries yield–primary production trend for marine systems (Fig. 6). On the other hand, if one follows the $P_{net} = 0.75 P_{gross}$ conversion used by Lewis (1974) for oxygen data from Lake Victoria, the apparent production of Lake George is
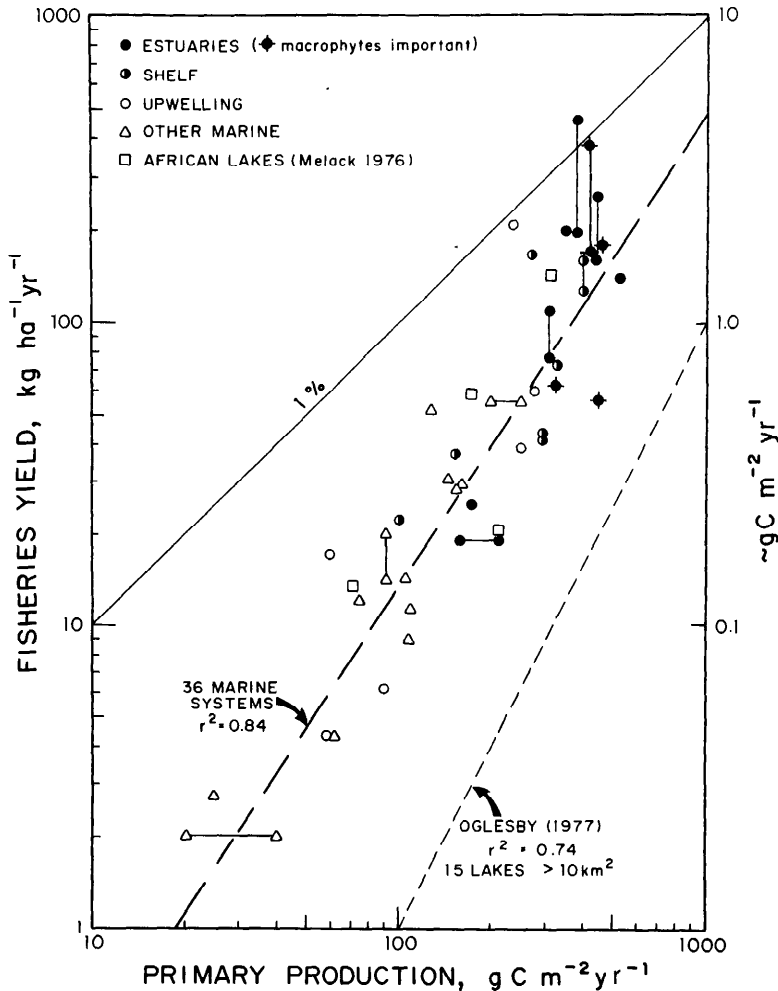
Fig. 6. Fisheries yield (FY) per unit area as a function of primary production (PP) per unit area in a variety of estuarine and marine systems compared with the regression obtained by Oglesby (1977) for large lakes. Regression line for the marine systems is ln FY = 1.55 ln PP − 4.49. A summary of regressions relating gross plankton production from O_2 changes to fish harvests from various intensively managed ponds is given by Liang et al. (1981). The fisheries landings have been converted to carbon assuming C is 10% of fresh weight (Gulland 1970). Data sources for marine systems given by Nixon (1982) and Nixon et al. (1986b).

increased to 940 g C m^{-2} yr^{-1} and the system falls between the marine and freshwater trends in Fig. 6. The more productive Winam Gulf area of Lake Victoria (mean depth, 6 m) also belongs with the marine group with primary production of 180 g C m^{-2} yr^{-1} and fisheries yield of 62 kg ha^{-1} yr^{-1} (Melack 1976).

Data summarized by Herdendorf (1984a) and by Melack (1976) place deep Lake Tanganyika with productive marine systems.

Lake Chad (mean depth, 4 m) has a relatively low fisheries yield of 14 kg ha^{-1} yr^{-1}, but extensive primary production measurements by Lemoalle (summarized by Melack 1976, 1979) also place it with the marine systems in Fig. 6. The greater energy input and more effective mixing of tropical lakes that was described earlier may account for the importance of latitude in numerous studies attempting to develop statistical relationships between fisheries yields and cli-

matic and morphoedaphic features of lakes (e.g. Brylinsky and Mann 1973; Ryder et al. 1974; Schlesinger and Regier 1982).

There are, of course, a number of problems with the use of fisheries statistics (e.g. underreporting, lack of data on recreational landings, accounting for effort, etc.; *see* Kerr and Ryder 1988; Bayley 1988), and the methods used to measure primary production also vary considerably. Moreover, in assembling the marine data used in Fig. 6 it was usually not possible to find contemporaneous measurements of primary production and fisheries landings. All of these factors, as well as annual variability, contribute to the "scatter" in the plot, but I think the great variety and number of systems considered as well as the size and consistency of the differences between marine areas and temperate lakes (Figs. 5 and 6) make a convincing argument that those differences are real.

Although it has long been assumed that there was a strong link between primary production and the yield of fish from the sea, Fig. 6 is the first empirical demonstration that such a link is strong enough to be seen (at least on a broad scale) against all the other variables that influence fish production (Nixon et al. 1986*b*). There has also been a long-standing appreciation among marine scientists for the importance of different vertical mixing processes as a mechanism for bringing inorganic nutrients to the surface and thereby increasing the fertility of certain parts of the ocean (Hutchinson 1950; Sette 1955; Cushing 1975; Bowman et al. 1986). What has not traditionally been recognized, however, is the important role that physical mixing and transport appear to play in creating an environment in which a larger fraction of primary production is channeled into harvestable fish production.

Coda—Limnologists and oceanographers . alike are comfortable thinking of copepods and clams and fish as highly transformed solar energy. And no one objects that the heat energy from the sun is important in regulating the speed of growth in plants and animals. It is more difficult, but no less real, to see the work of the wind in the rich catch of *Tilapia* from an African lake or the gentle pull of the moon made manifest in the great harvest from Georges Bank.

The energy input from the gravitational work of the moon is not easily measured, but from the slowing of the rotation of the earth and the acceleration of the moon's orbit due to tidal energy dissipation, Munk and MacDonald (1960) calculated a global value of 2.7×10^{19} ergs s^{-1}. If this is distributed over the world ocean of 361×10^6 km^2, it amounts to 7.5 ergs cm^{-2} s^{-1}. The gravitational work of the sun on the tide is much smaller, and the power in the wind is of the same order or within a factor of 10 greater (Table 2). Calculations by Miller (1966) suggest that the flux of lunar tidal energy out of the deep ocean is about 1.4–1.7×10^{19} ergs s^{-1}, though he cautioned that the potential error of this estimate may be equal to half its value.

The tidal energy flux is not uniform over the world shelf and varies from $\sim 25 \times 10^{17}$ ergs s^{-1} onto the Bering Sea shelf to $<1 \times 10^{16}$ ergs s^{-1} onto the shelf off the east coast of the U.S. between Cape Cod and Key West, Florida (Miller 1966). The area of the Mid- and South Atlantic Bight shelf is about 100×10^3 km^2 (Table 1), giving an average tidal energy input of <10 ergs cm^{-2} s^{-1}. The measured tidal energy flux into Narragansett Bay of 45 ergs cm^{-2} s^{-1} (Levine 1972) represents a focusing or concentration of over 4.5-fold compared to the general shelf average, but it is still a very small input compared with the flux of light and heat from the sun. The average total solar input to Narragansett Bay (approximately equally distributed between photosynthetically acting radiation and longer wavelengths) is about 1.7×10^5 ergs cm^{-2} s^{-1} or 3.8×10^3 times greater. This contrasts with the special situation on some rocky shores exposed to the open ocean where Leigh et al. (1987) suggest that the input of mechanical energy from waves may exceed the input of solar energy. For sites on Tatoosh Island, Washington, they calculated an average wave energy input of 3×10^6 ergs cm^{-2} s^{-1}, which contributed to a very great intensity of primary production by seaweeds.

Even relative to the much lower net primary production by phytoplankton in Narragansett Bay, the tide is a modest energy input. The reported primary production of 310 g C m^{-2} yr^{-1} (Furnas et al. 1976) converts to ~ 370 ergs cm^{-2} s^{-1}. This represents

a transfer efficiency of ~8.5% from total solar radiation and an input over seven times larger than that of the tide. But the tide is not amplifying the input of solar radiation and, perhaps, not even the photosynthetic fixation of carbon. Its great effect is seen at higher trophic levels. If Narragansett Bay were a lake with the same level of primary production, it might support a fishery yield of 10 kg ha^{-1} yr^{-1} rather than the 100 kg ha^{-1} yr^{-1} characteristic of a marine area (Fig. 6). The lower yield that could, presumably, be attained by solar and wind energy alone amounts to about 2 ergs cm^{-2} s^{-1} or only 4.5% of the tidal energy.

In retrospect, it does not seem so surprising that all of the energy entering an ecosystem plays some role in influencing the structure and functioning that we observe. Even the relatively small flows of physical energy from the wind and the tide set in motion a cascade of eddies and ecological effects that can alter dramatically the much larger flows of solar and chemical energy. The specific mechanisms by which these effects are realized may differ from place to place and there are doubtless many exceptions to the very general picture I have tried to develop in this review. I am sure the parallel between wind in the tropics and tide on the sea coast and their similar effects on currents and stratification and benthic animals and sediments and mass balances and fish is not a simple or perfect one. But I think there is enough that is correct in its fundamentals to put it forward for further consideration and research. If these links turn out to be real, they will serve as a fine illustration of the principle that large effects (especially those from weak forces) are difficult to see from within the system in which they operate. It is only from a new frame of reference that they become apparent. Certainly, this marine ecologist never appreciated the tides until he looked, at least a little, into lakes.

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