

Nutrient dynamics, primary production and fisheries yields of lagoons

Lagoon
Nutrients
Productivity
Fisheries
Coastal ecosystems

Lagune
Nutriments
Productivité
Pêches
Écosystèmes côtiers

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ABSTRACT

There is a great range in many of the characteristics of the lagoons which make up 13 % of the world coastline, including size (a few ha up to 800,000), shape, annual temperature range, fresh water input, exchange with the sea, anthropogenic inputs, and human uses. While these differences appear to have a marked influence on the species composition of lagoon ecosystems around the world, there are also some remarkable similarities in nutrient dynamics, the standing crop of phytoplankton, annual primary production, and fisheries yields of many lagoons. For example, in many of the systems reviewed, the annual phosphate cycle was similar in timing and magnitude, primary production amounted to some $200-400 \text{ g C m}^{-2} \text{ yr}^{-1}$, and fisheries landings were on the order of $50-100 \text{ Kg ha}^{-1} \text{ yr}^{-1}$. There appears to be an empirical correlation between primary production and fisheries yields in a great variety of marine systems which may be similar in slope to that found in large lakes. However, the yield of marine systems at any given level of primary production appears to be 10-20 times greater. The yield of lagoon fisheries per unit area is commonly as high or higher than that from the most productive coastal and offshore fisheries.

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RÉSUMÉ

Dynamique des nutriments, production primaire et rendements des pêches dans les lagunes.

Les lagunes, qui occupent jusqu'à 13 % du littoral mondial, présentent des caractéristiques très variées de taille (quelques ha à 800 000 ha), de forme, de régimes thermiques annuels, d'apports d'eau douce, d'échanges avec la mer, d'apports anthropiques et d'aménagements par l'homme. Bien que ces différences puissent avoir une influence marquée sur la composition spécifique des écosystèmes lagunaires, à l'échelle mondiale, il n'en demeure pas moins qu'on peut observer des similitudes remarquables pour beaucoup de lagunes dans la dynamique des nutriments, la production brute de phytoplancton, la production primaire annuelle et les rendements de la pêche. Par exemple, beaucoup de systèmes lagunaires présentent un cycle annuel de phosphate presque identique dans le temps et en amplitude ; la production primaire est comprise entre $200 \text{ et } 400 \text{ gC.m}^{-2}.\text{an}^{-1}$ et les rendements de la pêche sont de l'ordre de $50 \text{ à } 100 \text{ kg.ha}^{-1}.\text{an}^{-1}$. On peut constater empiriquement, pour un grand nombre de systèmes marins, une corrélation entre la production primaire et les rendements de la pêche qui rappelle celle observée dans les grands lacs. Cependant, le rendement général des systèmes marins apparaît 10 à 20 fois plus élevé que dans les lacs pour tous les niveaux de production primaire. Le rendement des pêches en lagune, calculé par unité de surface, est couramment aussi élevé, ou même plus élevé, que celui des pêcheries côtières ou hauturières les plus productives.

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INTRODUCTION

Many papers dealing with lagoons begin by trying to define them. The results are usually unsatisfying, but the continuing attempts reflect the fact that there are no generally accepted criteria which unambiguously separate lagoons from bays, estuaries, marshes and other parts of the coastal landscape (Mee, 1978). While most authors seem willing to exclude the wide mouths of major rivers and the large inland seas from their working concept of a lagoon, there is less agreement about the intertidal portions of the remaining shallow marine waters that are separated from the sea by some sort of barrier. In general, intertidal flats (where they are present) seem to be considered part of the lagoon (Cadée, Hegeman, 1974 *b*; Barsdate *et al.*, 1974 *a* and *b*) while emergent marshes and wetlands are thought of as coupled systems linked to the lagoon proper by tidal flows (Nixon, 1980). But even allowing for these exclusions, there is a great diversity of geomorphology, hydrology, chemistry, and biology that have gone into the development of lagoon ecosystems around the world. My hope in this paper is to emphasize some aspects of this underlying diversity with brief examples and then to examine some of the evidence which is available to tell us if these differences are reflected in various aspects of lagoon ecology. A comparative approach may be helpful in deciding which characteristics of any particular lagoon are unique and which more likely arise from features and processes common to coastal marine systems in general.

CHARACTERISTICS OF LAGOONS

Shape and size

Over 13 % of the world coastline consists of shallow marine waters lying behind barrier spits or islands (Cromwell, 1971). While these are the most common types of lagoons, there are also lagoons which lie between land and barrier reefs or mangrove islands, as well as some 400 open ocean atolls (Sournia, Ricard, 1975; Fig. 1). Even among the

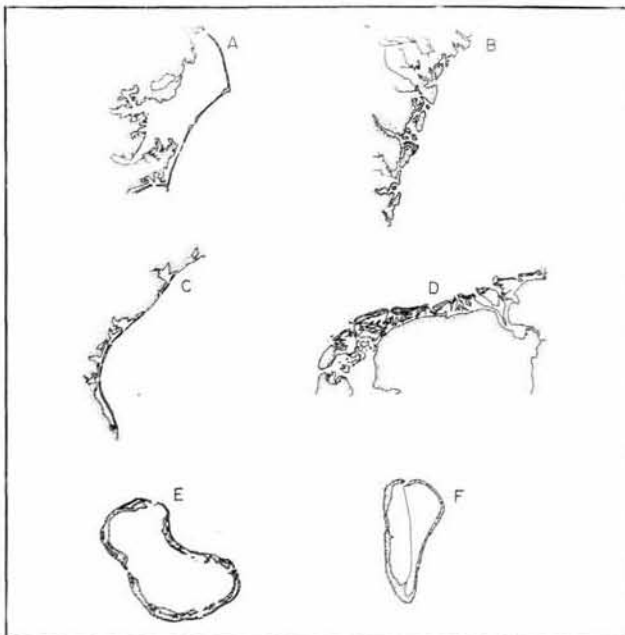


Figure 1

Various types of lagoons including (A) microtidal barrier spits of the Outer Banks of North Carolina (USA) with a very wide lagoon and large estuaries; (B) the mesotidal coast of Georgia (USA) with extensive salt marsh; (C) the microtidal coast of Texas (USA) with long narrow lagoons and limited fresh water input; (D) the mesotidal Dutch Wadden Sea with many inlets and extensive intertidal flats; (E) a « perfect » coral atoll at Fanning Island in mid Pacific; and (F) a lagoon set off by a fringing reef around one of the Laccadive Islands in the Indian Ocean.

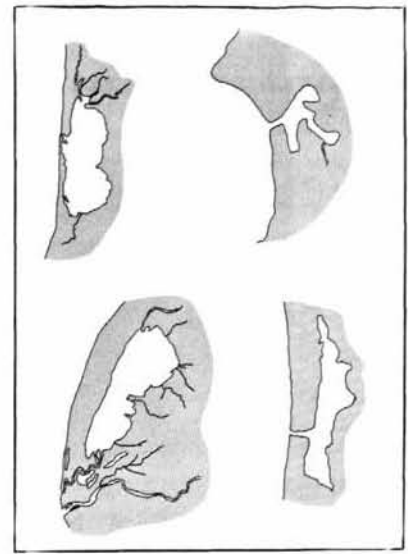


Figure 2

Different forms of lagoon along the Guerrero coast of Mexico (from Yáñez-Arancibia, 1978).

simplest of coastal lagoons there is much local diversity in size and shape, with additional complications caused by various patterns of association with streams and rivers (Yáñez-Arancibia, 1978; Fig. 2).

On a larger scale, it is possible to distinguish between at least two major forms of coastal lagoon (Hayes, 1979; Table 1). On microtidal coasts where the tide range is less than about 2 m, barrier spits tend to be long and narrow with few inlets. Sediment is carried into the lagoon and deposited on flood tide deltas as well as on washover fans inside the barrier during storms (Fig. 3). Well-known

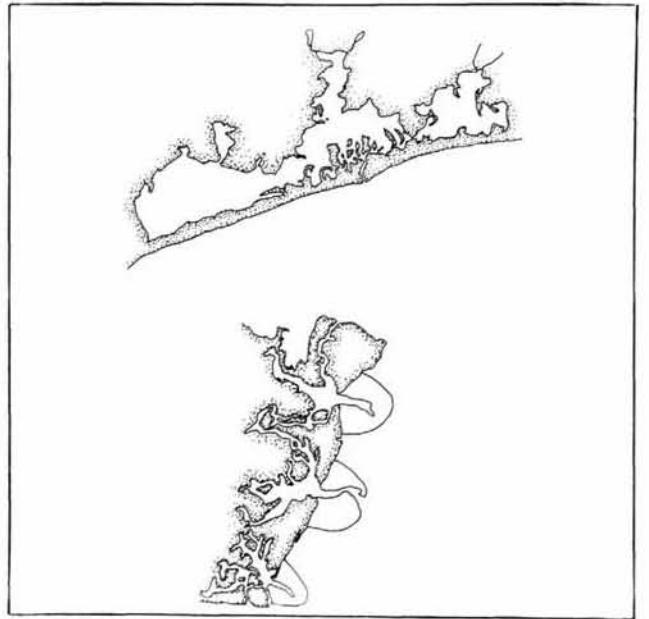


Figure 3

Top: Charlestown Pond, a microtidal lagoon on the ocean coast of Rhode Island (USA) with only one inlet, a well developed flood tide delta, and washover fans along the barrier spit. Bottom: the mesotidal coast of Georgia (USA) with frequent inlets, well developed marsh, and prominent ebb tide deltas.

examples are found along the coasts of New England, Texas and Mexico. Where the tide range is larger (2-4 m) but wave activity is not severe (Fig. 4), the barrier forms drumstick-shaped islands separated by frequent inlets with ebb tide deltas (Fig. 3). Such mesotidal coasts include well-studied areas like Izembek lagoon, Alaska, and the Wadden Sea in Europe (Fig. 1). The influence of tides and waves is reflected in lagoon flushing rates, salinity and temperature

Table 1

Some general geomorphologic differences between microtidal and mesotidal barrier islands on coasts of medium wave energy ($H = 60-150$ cm. From Hayes, 1979).

Barrier typer	Length	Shape	Washover features	Tidal inlets	Flood-tidal deltas	Ebb-tidal deltas
Microtidal	long (30-100 km)	elongated hot dog	abundant ; washover terraces & washover fans numerous	infrequent	large, commonly coupled with washovers	small to absent
Mesotidal	stunted (3-20 km)	drumstick	minor ; beach ridges or washover terraces ; washover fans rare	numerous	moderate size to absent	large with strong wave refraction effects

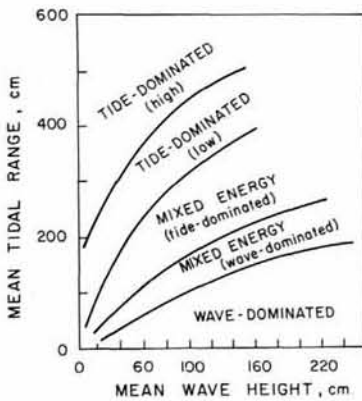


Figure 4

The interaction of waves and tides in determining the morphological classification of a shoreline. For the most part, coastal lagoons are found in areas of moderate to low wave energy and with tidal ranges less than 4 m. From Hayes (1979).

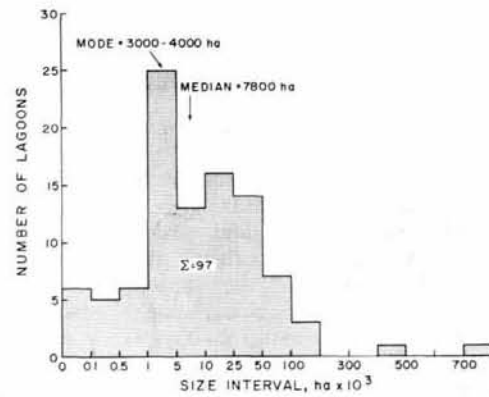


Figure 5

Size-frequency diagram for a number of lagoons described in the recent literature.

ranges, the amount of intertidal habitat, and a host of other characteristics.

Just as lagoons differ widely in form, they range in size over 5 orders of magnitude, from a few hectares up to the 800,000 ha Wadden Sea. For the most part, however, they are relatively small. The median size of almost 100 lagoons discussed in the recent literature is 7800 ha (Fig. 5). The only common physical characteristic of lagoons appears to be their shallow mean depth which, with few exceptions, ranges from about 1-10 m.

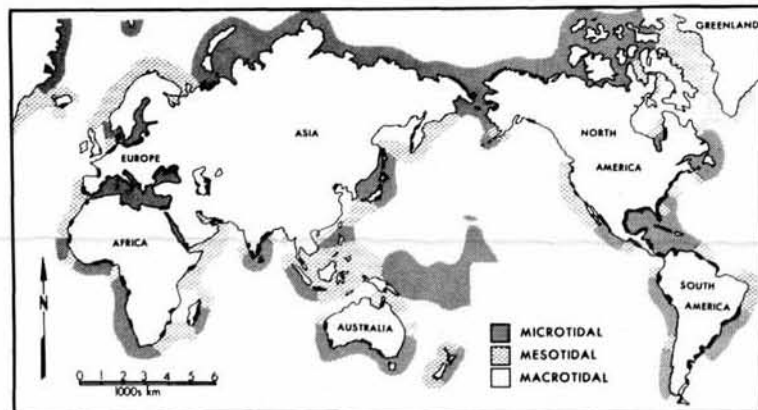
Temperature and salinity

Since lagoons are found at virtually all latitudes except those in extreme polar regions (Leont'yev, Nikiforov, 1965 ;

Hayes, 1979 ; Fig. 6), it follows that examples can be found of seasonal temperature patterns typical of tropical, temperate, and arctic environments. And in all of these cases, the generally shallow depth of lagoons makes them particularly susceptible to large diel changes in temperature (eg. Okuda *et al.*, ; 1965 a ; McRoy, 1970 ; Kwei, 1977). Similarly, the smaller volume of lagoons makes their salinity more responsive to changes in fresh water input and evaporative losses than most larger marine systems. The input of salt water to many lagoons is also highly variable as inlets through barrier spits open and close during the seasons in response to changes in long shore sediment transport, wave attack and water level inside the lagoon. As a result, it is possible to find lagoons with a great diversity of seasonal salinity and temperature patterns, including cases in which the waters become extremely hypersaline (Fig. 7).

Figure 6

Distribution of coastal lagoons around the world. From Hayes (1979).



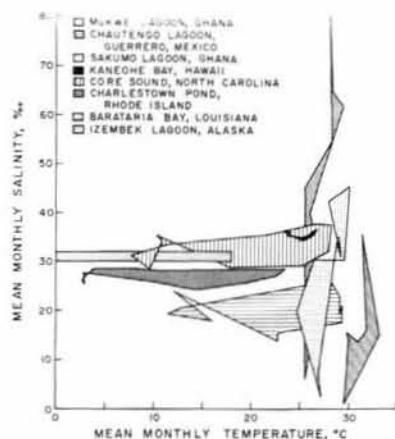


Figure 7

Annual temperature — salinity polygons for different types of lagoons. Data from Anonymous (1970) for Louisiana, Pauly (1975) and Kwei (1977) for Ghana, Smith (1981) for Hawaii, Nixon and Lee (1981) for Rhode Island, Yáñez-Arancibia (1978) for Mexico, Gamboa et al. (1971) for Venezuela, Thayer (1971) for North Carolina, and McRoy (1970) and Barsdate et al. (1974), Alaska.

Land use and human activities

The « land » surrounding lagoon systems varies from coral to mangrove swamp, from desert to lush salt marsh, and from glacial outwash to old fields and forests. In some cases intense agriculture reaches to the lagoon shore, in others the lagoon edge may be lawn and garden from high density suburban houses; in still others, marinas, shipping and industry many dominate the shoreline. Some lagoons receive sewage from major cities, some take part of the river discharge draining vast industrial complexes. A few lagoons are managed as salinas to produce solar salt while others are maintained at low or pulsing salinity to produce fish and shellfish.

Human activities have altered both fresh water and salt water inputs to many lagoons, as well as nutrient loading, sedimentation, and the input of a diverse assortment of toxic materials. Our concept of lagoons must include Fanning Island Atoll in the Pacific as well as Oyster Pond, Massachusetts; the Laguna Madre of Mexico as well as the Wadden Sea; Izembek Lagoon, Alaska, as well as the ancient city-lagoon of Venice.

COMPARATIVE ECOLOGY OF LAGOONS

Given the great diversity of lagoons in terms of size, shape, flushing rate, fresh water input, turbidity, sediment type, nutrient loading, seasonal patterns and values of temperature and salinity, human activities, and probably many other features, it would seem that few, if any, common ecological characteristics could emerge. Certainly the physical matrix must play a major role in determining the taxonomic structure of lagoon ecosystems, and it is obvious that species lists from a coral atoll, a hypersaline lagoon in Mexico, the Wadden Sea, and a lagoon in Alaska will not be very similar. But community structure is an elaborately detailed and responsive expression of the ecosystem (Slobodkin et al., 1980). If we look at the underlying rates and patterns of energy flow and nutrient cycling which come about from the combination of physical and biological processes, there may be more common ground.

In comparing the « total system metabolism » of the shallow bays and lagoons along the coast of Texas, Odum and b (1967) found that the overall flows of energy were remarkably similar among environments with different physical and biological characteristics. Sufficient data are now available to compare a greater number of lagoons from a much larger geographical range. It is also possible to take advantage of some of the more detailed data that are now available to

compare systems at a greater level of functional resolution than just total organic production and consumption.

Nutrients

Phosphorus

Like other estuarine and near-shore marine waters, and in contrast to the open sea, most lagoons are characterized by a summer phosphate maximum (Riley, 1941; Smayda, 1957; Taft, Taylor, 1976; Nixon, Lee, 1981; Postma, 1981; Fig. 8). This pattern has been attributed to the remineralization of organic matter carried into the lagoon from an earlier offshore phytoplankton bloom (Postma, 1981), and to the release of phosphate from the sediments where bottom waters become anoxic with summer stratification and high respiratory rates (Taft, Taylor, 1976). However, the summer phosphate maximum also develops in systems which do not import organic matter from offshore and in which bottom waters remain well-oxygenated throughout the summer (Nixon et al., 1980). It appears to be such a common feature of shallow marine systems that its occurrence may depend only on the storage of an appreciable amount of organic matter on the bottom which can be remineralized at warmer temperatures and the resulting phosphate mixed rapidly up into the water column.

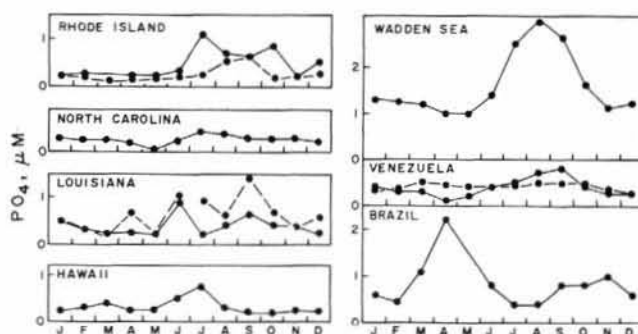


Figure 8

Annual cycle of phosphate in various lagoons. Data from Nixon and Lee (1981) and Nixon et al. (in prep.) for Rhode Island (— Pt. Judith Pond; — Charlestown Pond), Thayer (1971) for North Carolina, Anonymous (1970) for Louisiana (— Terrebonne Bay; — Barataria Bay), Okuda et al. (1965 a) and Gamboa et al. (1971) for Venezuela (— Tacarigua Lagoon; — Unare Lagoon), Tundisi et al. (1973) for Brazil, de Jonge and Postma (1974) for the Wadden Sea and Smith (1981) for Hawaii.

In addition to their common seasonal pattern of phosphate, there appears to be a great similarity in the range of phosphate concentrations found in lagoons around the world (Table 2). Of some 20 lagoons for which yearly nutrient cycles have been described, 85 % show an annual excursion of phosphate that remains within the concentration range of 1-5 μM . In order to capture 85 % of the lagoons in terms of their annual variation in inorganic nitrogen, the concentration range would have to be 1-100 μM for nitrate and about 1-15 μM for ammonia (Table 2). The fact that nitrogen is taken up and released in biological activities to a much greater extent than phosphorus contributes to the smaller amplitude of the seasonal phosphate cycle, but it does not necessarily account for the similarity in average concentrations among the different lagoons.

It is commonly assumed that sediments « buffer » the estuarine phosphate cycle (Pomeroy et al., 1965), but this concept has not been reconciled with the growing body of data showing that shallow water sediments virtually always release phosphate across a wide range of concentrations in the overlying water (Nixon et al., 1980). It is also unclear why differences in the loading rate for phosphorus among lagoons, which must be quite large, have not resulted in a larger range in the ambient concentrations. Since the

Table 2

Minimum and maximum inorganic nutrient concentrations (μM) observed during an annual cycle in various lagoons.

	PO_4	NO_3	NH_4
<i>North and South America</i>			
Pt. Judith Pond, RI (USA) ¹	0.22-1.11	0.13-4.95	0.10-2.04
Potter Pond, RI (USA) ¹	0.09-0.61	0.10-35.6	0.16-1.64
Charlestown Pond, RI (USA) ²	0.07-0.60	0.40-7.0	0-4.5
Great South Bay, LI (USA) ³	0.10-1.70	0.90-8.0	0.2-5.5
Hempstead Bay, LI (USA) ⁴	0.68-1.38	0.50-3.0	—
Peconic Bay, LI (USA) ⁵	0.25-3.80	0.10-3.5	0.9-2.0
Core Sound, NC (USA) ⁶	0.10-0.45	0.10-1.1	0.1-1.0
Apalachicola Bay, FL (USA) ⁷	—	3-175	6-33
Barataria Bay, LA (USA) ⁸	0.16-1.42	0-12.9	—
Unare Lagoon (Venezuela) ⁹	0.25-0.85	0.1-0.6	2-60
Laguna Grande (Venezuela) ¹⁰	0.09-0.78	0.6-4.2	0.8-6.0
Bahia de Mochima (Venezuela) ¹⁰	0.1-0.8	0.3-5.0	0.8-6.1
Tacarigua Lagoon (Venezuela) ¹¹	0.25-1.6	0.5-6.5	1.5-11.0
Canancia Lagoon (Brazil) ¹²	0.4-2.23	—	—
Izembek Lagoon, Alaska (USA) ¹⁸	—	0-10	0-9
<i>Europe</i>			
Wadden Sea (Netherlands, W. Germany) ¹³	0.9-3.1	0-22	0-12
Thau Lagoon (French Mediterranean) ¹⁴	1.52-4.58	1.03-4.8	—
Mauguio Lagoon (French Mediterranean) ¹⁵	0.45-2.29	7.1-37.8	0-10.3
Diana Lagoon (Corsica) ¹⁶	0-4.5	0-83	0-4.7
Urbino Lagoon (Corsica) ¹⁶	0-1.7	0-100	0-6.0
Biguglia Lagoon (Corsica) ¹⁶	0-12.7	0-1,100	0-3.5
Marsala Lagoon (Sicily) ¹⁷	0.06-0.25	0.08-0.25	0.53-3.41

¹ Nixon *et al.* (unpublished).² Nixon and Lee (1981).³ Buckner (1973).⁴ Mandelli *et al.* (1970).⁵ Bruno *et al.* (1980).⁶ Thayer (1971).⁷ Estabrook (1973).⁸ Anonymous (1970).⁹ Okuda *et al.* (1965 a).¹⁰ Okuda *et al.* (1968).¹¹ Gamboa *et al.* (1971).¹² Tundisi *et al.* (1973).¹³ de Jonge and Postma (1974); Helder (1974).¹⁴ Vaultot (pers. comm.); data from French National Sampling Survey « RNO, 1978-1979-1980, Recueil d'Observations, Ministry of Environment, CNEXO ».¹⁵ Vaultot (pers. comm.); data from Laporte (1978).¹⁶ Vaultot (pers. comm.); data from Frisoni (1981).¹⁷ Magazzu (1977).¹⁸ Short (1981).

seasonal cycle in the concentration of phosphate and other nutrients is largely the result of shifts in the rate of much faster short-term nutrient cycling processes, the relationship between these processes and nutrient loading must be worked out before we will have a very firm understanding of coastal marine nutrient dynamics.

Nitrogen

As with other coastal marine waters (Riley, 1941; Jeffries, 1962), the ratio of inorganic nitrogen to phosphorus in lagoons is usually much lower than the 16:1 found in the oceans (Redfield, 1934; Thayer, 1974; Buckner, 1973; Gilmartin, Revelante, 1978; Frisoni, Vaultot, 1981). This situation is particularly evident during summer when large amounts of organic matter are being remineralized on the bottom. Measurements of inorganic nutrient fluxes across the sediment-water interface in a variety of nearshore marine environments have shown that the N/P ratio of this flux is much lower than the 16:1 usually found during pelagic remineralization (Nixon *et al.*, 1976; 1980; Nixon, 1981 a). This effect is compounded by lower fresh water inputs (which are usually high in nitrogen relative to phosphorus) during summer and by the larger biological uptake of nitrogen relative to phosphorus.

One consequence of this low N/P ratio is the common observation that primary production in shallow marine systems is usually limited by the availability of nitrogen,

rather than phosphorus as in fresh water (c. g. Schindler, 1981). Direct measurements of denitrification in coastal marine sediments have shown that there can be a substantial loss of fixed nitrogen during remineralization on the bottom (Seitzinger *et al.*, 1980), but it is still not clear why nitrogen fixation is not a more active process in coastal marine waters where phosphorus is abundant.

There are exceptions to the generally low N/P ratio of lagoon waters, including some nitrogen-rich lagoons along

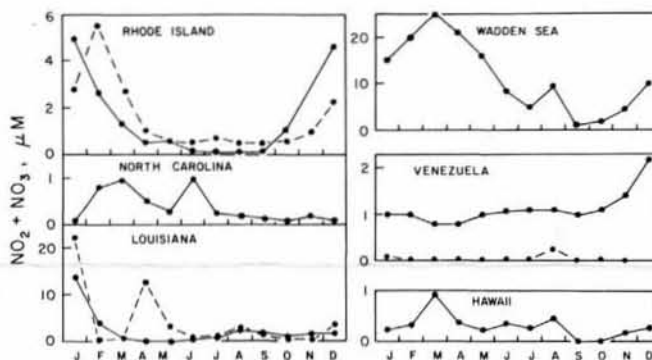


Figure 9

Annual cycle of nitrate in various lagoons. Data from the same sources as Figure 8 except: Wadden Sea from Helder (1974).

the coast of Venezuela (Okuda *et al.*, 1965 *a*; Gamboa *et al.*, 1971) and many temperate systems such as the Wadden Sea during periods when there is a large input of fresh water (Helder, 1974; deJonge, Postma, 1974). In coastal oligotrophic Mediterranean waters there is also evidence that phosphorus is the primary limiting nutrient (Berland *et al.*, 1977), though the N/P ratio of several lagoons in the area appear low (Frisoni, Vaultot, 1981).

As noted earlier (Table 2), there is a greater variability in the concentration of inorganic nitrogen among lagoons than there is for phosphorus. It is also more difficult to identify any common seasonal patterns in the abundance of inorganic nitrogen except that high nitrate levels are usually associated with fresh water input (Fig. 9 and 10). In contrast to phosphate, there may also be periods during which virtually all of the inorganic nitrogen is removed from the water column.

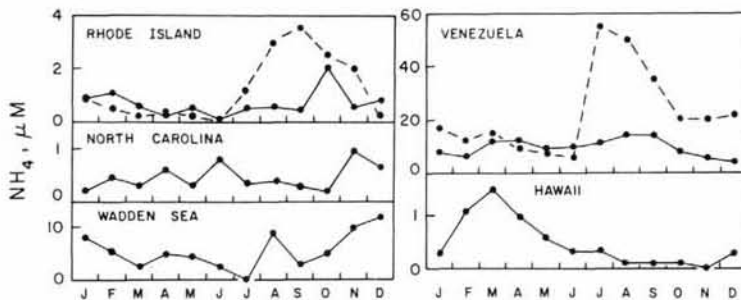


Figure 10
Annual cycle of ammonia in various lagoons. Data from the same sources as Figure 9.

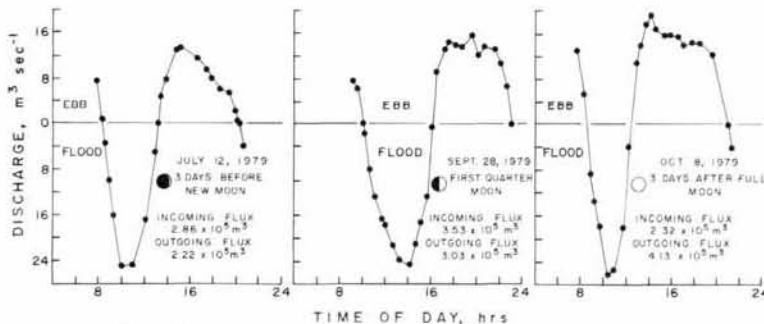


Figure 11
Flux of water through a narrow (mean cross section = 30 m^2) channel connecting Potter Pond lagoon on the Rhode Island (USA) coast with the sea. There is considerable day-to-day variation in the flood and ebb discharge and in the magnitude and direction of the net water flux. Measurements were made with a General Oceanics current meter at 3 depths at 4 stations.

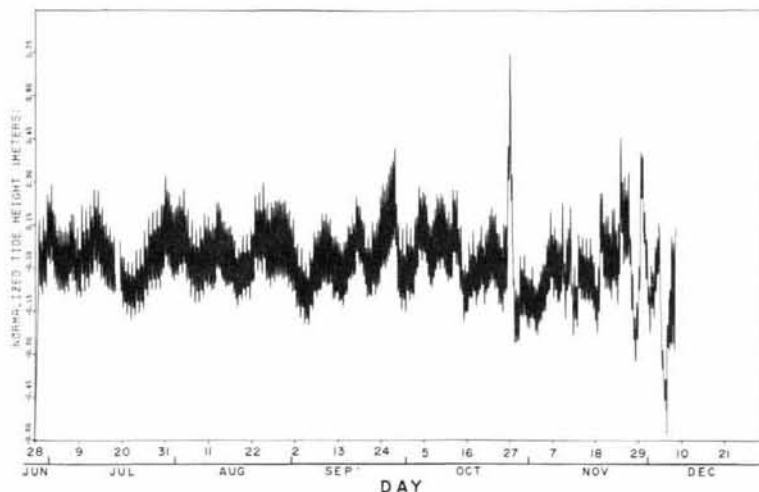


Figure 12
Water level in Potter Pond lagoon during summer and fall 1980 as measured by a Fisher-Porter recording tide gauge. All readings are given with respect to the mean for the period of record. Dramatic highs and lows are caused by wind and barometric pressure during fall storms.

Nutrient budgets

It would be extremely useful to compare the annual or even shorter-term nutrient budgets from various lagoons around the world, but there are few, if any, really well constrained budgets of any material yet available from a lagoon. In some areas, such as the Wadden Sea (van der Eijik 1979), impressive progress has been made in this direction, and in a number of other lagoons some preliminary analyses have also worked out (for example, Barsdate *et al.*, 1974 *a*; Nixon, Lee, 1981; Smith, 1981). But it is an extremely difficult problem requiring consideration of stream flow, surface run-off, ground water input, dry and wet atmospheric fallout, anthropogenic impacts, exchanges with the ocean through tidal inlets, biological exchanges with the atmosphere, and recycling within the lagoon itself. The direct atmospheric exchanges are usually (but not always) relatively unimportant, and inputs from land and fresh water are often discussed, but tidal exchanges and recycling have received less attention.

We have little knowledge about the relative importance of the open coastal waters as a source or sink for inorganic nutrients or organic matter in different lagoons. In a qualitative sense it may be possible to estimate the direction of net transport through an inlet by comparing the concentrations of material inside and outside of the barrier spit (e.g. Nixon, Lee, 1981), but the magnitude of flux is very difficult to determine (Boon, 1975; 1978; Kjerfve *et al.*, 1978; Nixon, 1980). The problem arises in large part because the concentration differences between flood and ebb tides are usually small relative to the imbalance in net water transport that is virtually always observed (Kjerfve, Proehl, 1979; Fig. 11). The net flux of water through an inlet on any given tidal cycle is a complex function of fresh water inflow, tide, wind and barometric pressure all acting over time. In order to get a meaningful direct estimate of the « average » transport of any material through an inlet, it seems necessary to measure the current field in detail over many tidal cycles (e.g. Lara-Lara *et al.*, 1980). The problem is further complicated by storms which may dramatically alter the exchange of lagoons with the offshore waters (Fig. 12).

Measurements of the nutrient cycling rates within lagoons are also difficult, and no thorough assessment of the remineralization of nitrogen or other material appears to have yet been reported for a lagoon system. It has, of course, been noted that in shallow water environments such as lagoons the decomposition of organic matter on the bottom may be particularly important (Mee, 1978). However, with the exception of a few measurements from Eel Pond, Massachusetts (USA) (Rowe *et al.*, 1975) there are no published data from lagoon sediments. Unpublished measurements from salt ponds on the ocean coast of Rhode Island (USA) suggest that shallow water sediments will

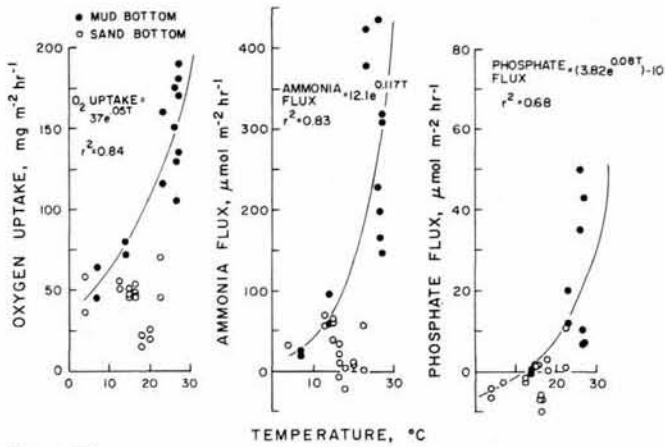


Figure 13
Net fluxes of oxygen, ammonia, and phosphate across the sediment water interface as a function of temperature in Potter Pond lagoon. Measurements were made in situ using dark chambers and 3-6 h incubations. Regression for mud bottom measurements only. Data from Nowicki and Nixon (in prep.).

behave in a manner similar to those of estuarine and near-shore environments which have been studied in much more detail (reviewed in Nixon, 1981 a). The rates of dark uptake of oxygen and the release of phosphate and ammonia from silt-clay sediments in Potter Pond, R.I. (mean depth 1m) were strongly influenced by temperature and indistinguishable from rates measured in nearby Narragansett Bay (mean depth 8.6 m; Fig. 13). In fact, after comparing the magnitude of benthic oxygen uptake and nutrient regeneration in a variety of near-shore marine environments, it appears that some 25-50 % of the organic matter fixed in or imported to the overlying water is decomposed on the bottom of these shallow systems regardless of the relatively small differences in their average depth (Fig. 14). The remaining, major portion of nutrient recycling must take place in the water column, though it is still unclear which group of organisms is most important in this regard (Nixon, 1981 a). Recent work in a North Carolina lagoon system (Smith, 1978) as well as elsewhere (e. g. Vargo, 1979) has shown that excretion by the larger zooplankton cannot support much of the primary production. And earlier views that microzooplankton were responsible for most pelagic nutrient regeneration (e. g. Johannes, 1964; 1969) have recently been challenged by studies showing the importance of bacteria (Barsdate *et al.*, 1974 b; Fenchel, Harrison, 1976; Wangerski, 1977; Harrison, 1978). A recent detailed analysis of marine plankton decomposition by Garber (1982) has emphasized the artificial nature of much of the past work in this field as well as the probable importance of autolysis in phosphorus cycling. His data

indicate that bacterial decomposition alone is probably not rapid enough to remineralize sufficient nitrogen to support the observed rates of primary production. The resolution may lie in the interaction of bacteria and microzooplankton as suggested by the experiments of Fenchel and Harrison (1976).

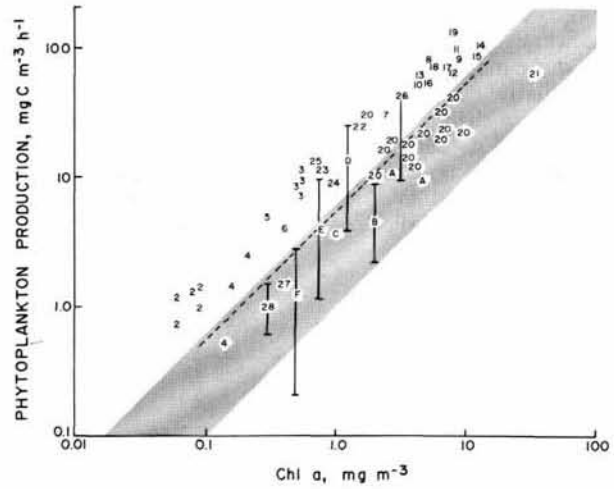
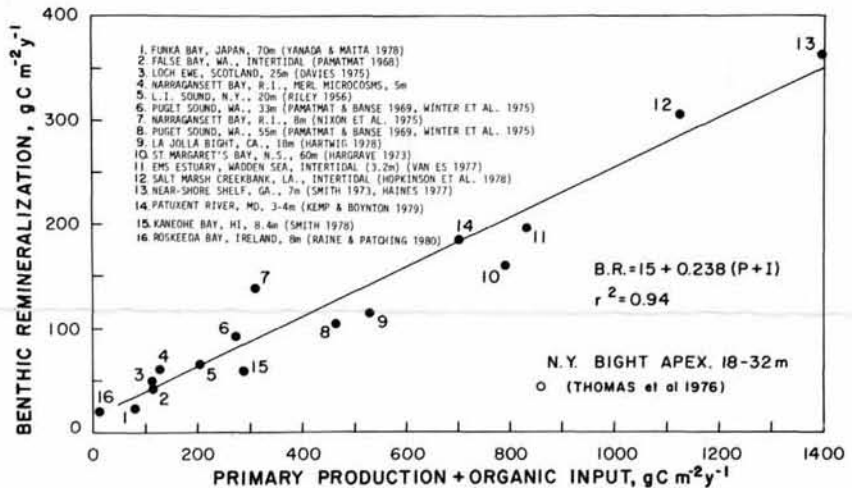


Figure 15
Assimilation efficiency of the phytoplankton in a variety of lagoons around the world (numbered points) compared with the annual range observed in other types of coastal waters (placed arbitrarily on abscissa), a regression developed from observations on 11 marine phytoplankton species during exponential growth in the laboratory (broken line; Glover, 1980), and a variety of offshore and open ocean measurements reviewed by Parsons and Takahashi (1973). Data from: 1 (Tiahura Lagoon, Moorea Island, French Polynesia, assuming 12 h light, Sournia and Ricard, 1976); 2 (Vairao Lagoon, Tahiti, same as 1); 3 (Fanning Island, Gilbert Islands, Gordon *et al.*, 1971); 4 (Kavaratti Lagoon, Laccadive Islands, Arabian Sea, Quasim *et al.*, 1972); 5-19 (Eastern Gulf of California Lagoons, Mexico, Gilmartin and Revelante, 1978); 20 (Inshore North Carolina Sounds, USA, monthly values over an annual cycle, Thayer, 1971); 21 (Manguio Lagoon, French Mediterranean, annual mean assuming 12 h day, 50 % active Chl a — Vaulot, pers. comm., Frisoni and Vaulot, 1981); 22 (Biguglia Lagoon, Corsica, same as 21); 23 (Thau Lagoon, French Mediterranean, same as 21); 24, 25 (Diana and Urbino Lagoons Corsica, same as 21); 26 (San Quentin Lagoon, Pacific Coast, Baja California, Mexico, June-July maximum, Lara-Lara *et al.*, 1980); 27, 28 (Western and Eastern Wadden Sea, annual range, Cadée and Hegeman 1974 a and b); A (San Francisco Bay, CA, USA, assuming 6 m depth, 9 and 14 h days, November and August data, Cloern, 1979); B (Port Valdeze, Alaska, USA, annual range, Goering *et al.*, 1973); C (Narragansett Bay, R.I., USA, annual range Durbin *et al.*, 1975); D (Surface water, nearshore, Louisiana, USA, annual range, Fucik 1974); E (Bedford Basin, N.S., Canada, annual range, Harrison and Platt, 1980); Saanich Inlet, B.C., Canada, annual range, Hobson, 1981).

Figure 14
Amount of organic matter decomposed on the bottom of a variety of coastal marine systems as a function of the organic matter fixed in and imported to the overlying water. Expanded from Nixon (1981a).



Primary production

There seems to be a general impression that lagoons are exceptionally productive systems (Vannucci, 1969). However, the data available suggest that this is only partially true. While the assimilation efficiency of lagoon phytoplankton may be somewhat higher than commonly reported for marine plankton (Fig. 15), the amount of carbon fixed in lagoons over an annual cycle does not appear to be significantly greater than found in estuaries or productive near-shore marine waters (Table 3; Nixon, 1980 and 1981 *a, b*). Similarly, the very impressive amounts of organic matter produced in shallow seagrass and seaweed beds are usually reduced considerably when apportioned over the entire area of a lagoon system. In fact, it is remarkable to see how similar the magnitude of annual primary production is in so many lagoons and other coastal marine systems that appear

very different in other respects. Even in very shallow lagoons, reduced phytoplankton production is supplemented by seagrasses, benthic algae and epibenthic microflora, so that the total production remains approximately the same (Table 3).

There are, of course, interesting extremes such as Izembek Lagoon in Alaska. Almost 80% of this system consists of intertidal flats with very productive eelgrass (*Zostera marina*) beds (McRoy, 1970; Barsdate *et al.*, 1974 *a*) which contribute some $800 \text{ g C m}^{-2} \text{ yr}^{-1}$ to the overall system. On the other hand, more than 50% of the Dutch Wadden Sea is covered by intertidal flats which have little or no seagrass, and the benthic microflora which do colonize the area contribute only some $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ to the lagoon as a whole (Cadée, Hegeman, 1974 *a* and *b*). The high eelgrass production of Izembek Lagoon places it among the most productive coastal marine ecosystems, along with St. Mar-

Table 3

Estimates of the annual aquatic primary production in various lagoons around the world. Data are for phytoplankton unless noted.

Lagoon	$\text{g C m}^{-2} \text{ yr}^{-1}$	Izembek Lagoon, Alaska (USA) ¹¹	
		Phytoplankton	20
		Macrophytes	810
			830
Charlestown Pond, Rhode Island (USA)		Kaneohe Bay, Hawaii (USA) ¹²	165
Seagrass ¹	235	Takapoto Atoll (French Polynesia) ¹³	~ 50-100
Macroalgae ¹	50	Vairoo Lagoon (Tahiti) ¹⁴	~ 1-10
Phytoplankton ²	30	Tiahura Lagoon (Moorea Island) ¹⁴	~ 35-150
	315	Fanning Island Lagoon ¹⁵	~ 245
Hempstead Bay, Long Island, New York (USA) ³		Pala Lagoon (American Samoa) ¹⁶	~ 300
Macrophytes	15	Kavaratti Atoll, Laccadives, Indian Ocean ¹⁷	
Phytoplankton	200	Phytoplankton	~ 10
	215	Macrophytes + corals	~ 1,220
Chincoteague Bay, Maryland-Virginia (USA) ⁴	180		~ 1,230
Core-Bogue Sounds, North Carolina (USA)		Cananúa Mangrove Lagoon (Brasil) ¹⁸	125
Phytoplankton ^{5, 6}	70	Cochin Backwater (India) ¹⁹	125
Macrophytes ⁶	255	Wadden Sea (Netherlands, W. Germany, Denmark)	
	325	Phytoplankton ^{20, 21}	65
North Inlet, South Carolina (USA) ⁷	260	Benthic Microflora ²¹	50
Inshore Sounds, Georgia (USA) ⁸	300		115
Apalachicola Bay, Florida (USA) ⁹	360	High Venice Lagoon (Italy) ²²	147
Barataria Bay, Louisiana (USA) ¹⁰		Mauguio Lagoon (France) ²³	225
Phytoplankton	165	Thau Lagoon (France) ²³	204
Macrophytes	195	Biguglia Lagoon (Corsica) ²³	289
	360	Diana Lagoon (Corsica) ²³	183
		Urbino Lagoon (Corsica) ²³	297

¹ Thorn-Miller *et al.* (in press).

² Nixon and Lee (1981).

³ Udell *et al.* (1969).

⁴ Boynton (1974).

⁵ Thayer (1971).

⁶ Dillon (1971).

⁷ Sellner *et al.* (1976).

⁸ Haines (1978).

⁹ Estabrook (1973).

¹⁰ Day *et al.* (1973).

¹¹ Barsdate *et al.* (1974 *a* and *b*).

¹² S.V. Smith (pers. comm.).

¹³ Sournia and Ricard (1975) extrapolated.

¹⁴ Sournia and Ricard (1976).

¹⁵ Gordon *et al.* (1971) extrapolated.

¹⁶ Krasnick and Caperon (1973) extrapolated.

¹⁷ Oasim *et al.* (1972) extrapolated.

¹⁸ Tundisi *et al.* (1973).

¹⁹ Qasim (1970).

²⁰ Cadée and Hegeman (1974 *a*; open water phytoplankton of $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ divided by 2 since 50% of Wadden Sea is intertidal flats over which phytoplankton contribute $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ or an additional $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ for whole system).

²¹ Cadée and Hegeman (1974 *b*; $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ on flats divided by 2 for whole system).

²² Vatova (1960).

²³ Frisoni and Vaulot (1981).

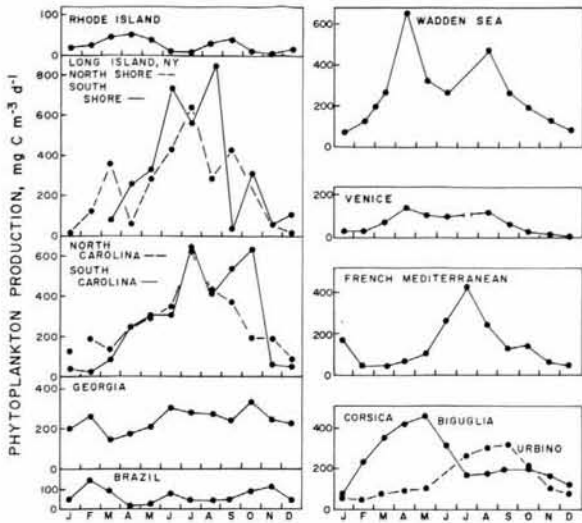


Figure 16 Annual cycles of phytoplankton production in various lagoons. Data from Nixon and Lee (1981) for Charlestown Pond, Rhode Island; Moll (1977) and Mandelli et al. (1970) for Long Island, Thayer (1971) and Sellner et al. (1976) for North and South Carolina; Turner et al. (1979) for Georgia, Cadée and Hegeman (1974 a and b) for the Wadden Sea, Vatova (1960) for Venice, and Frisoni and Vaulot (1981) for the French Mediterranean and Corsica.

garet's Bay, Nova Scotia, where phytoplankton and seaweed beds produce almost $800 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Platt, 1971; Mann, 1972 a, b), the mouth of the Hudson River estuary off New York City, where nutrient inputs from urban sewage support some $700\text{-}900 \text{ g C m}^{-2} \text{ yr}^{-1}$ of phytoplankton production (O'Reilly et al., 1976), and the Gulf of Cariaco, where intense upwelling along the Venezuela coast sustains a production of $800 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Margalef, 1971). For the most part, however, lagoons and other coastal waters appear to fix between $200\text{-}400 \text{ g C m}^{-2} \text{ yr}^{-1}$, despite great differences in all of the characteristics discussed earlier.

The distribution of primary production throughout an annual cycle varies somewhat according to latitude, and

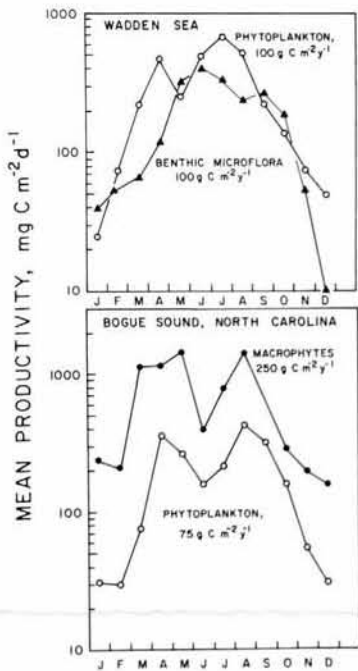


Figure 17 Comparison of the annual cycle of phytoplankton and benthic microflora production in the Wadden Sea (Cadée and Hegeman 1974a and b) and phytoplankton and macrophyte production in North Carolina, USA (Dillon, 1971).

there are clearly some interesting differences among lagoons (Fig. 16). For example, the mid-summer dip in phytoplankton production in the Wadden Sea during the year shown and the opposite pattern shown by the two lagoons on Corsica (Fig. 16). But overall, the daily phytoplankton production rates per unit volume are of the same scale in most of the lagoons where measurements have been made. In some cases, such as the north and south shores of Long Island, New York and the Carolinas on the southeast coast of the US, the seasonal patterns of production in different lagoons are virtually identical (Fig. 16). For the few areas where the seasonal pattern of production by other components of the system has also been measured, it seems that the growth of macrophytes and benthic microflora closely parallels that of the phytoplankton (Fig. 17; Dillon, 1971; Cadée, Hegeman 1974 b; Thorn-Miller et al., in press).

Primary production and nutrients

Since the concentration of nitrogen is generally considered a major factor limiting primary production in coastal marine waters (Ryther, Dunstan, 1971; Thayer, 1974), it is interesting to compare the seasonal distribution of nitrate and ammonia in lagoons (Fig. 9 and 10) with the seasonal pattern of primary production (Fig. 16 and 17). The fact that the rates of carbon fixation are usually highest during summer, when nitrogen is often least abundant in the water, suggests that any nitrogen entering the system is being rapidly removed and/or that most of the carbon fixation is being supported by nitrogen that has been somehow rapidly remineralized within the system. This point is made even more emphatically if primary production per unit volume is plotted as a function of inorganic nitrogen concentration using data from a number of different areas over an annual cycle (Fig. 18). While there are some periods, such as during a spring bloom, when primary production may draw on supplies of inorganic nitrogen (primarily nitrate) that have accumulated in the water, it is clear that there is little, if any, relationship between ambient nitrogen concentration and short-term carbon uptake during much of the year. This

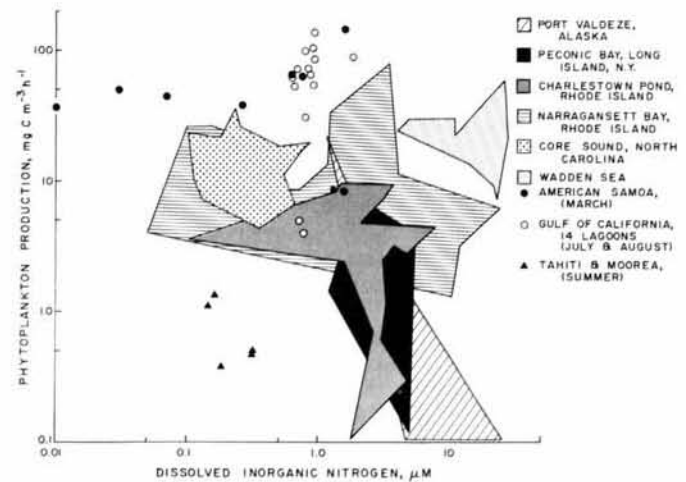
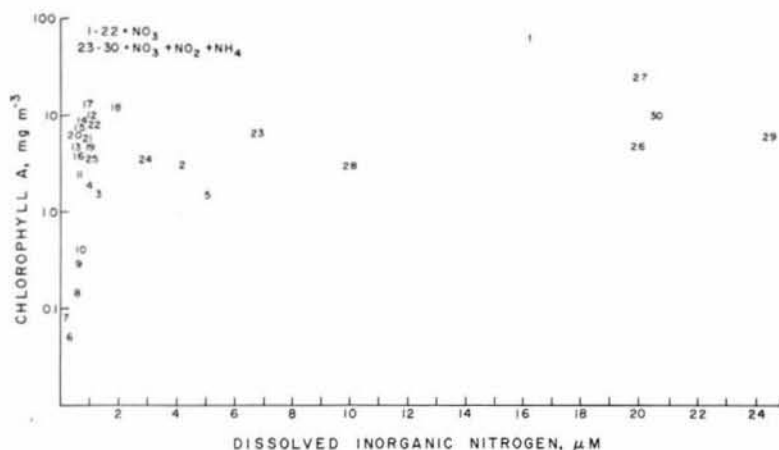


Figure 18 Phytoplankton production and dissolved inorganic nitrogen (NH_4 , NO_2 and NO_3 unless noted) concentrations at the time of measurement in a variety of lagoons and other coastal marine systems. Polygons describe an annual cycle of measurements. Data from Goering et al. (1973 a and b) for Port Valdez, Alaska; Bruno et al. (1980) for Peconic Bay, Long Island, N.Y. (assuming 8 m depth, 12 h days); Nixon and Lee (1981) for Charlestown Pond, R.I.; Durbin et al. (1975) and Nixon et al. (unpublished) for the mid-West Passage of Narragansett Bay; Thayer (1971) for the Core Sound area, N.C.; Cadée and Hegeman (1974 a and b) and Helder (1974) for the Wadden Sea; Krasnick and Caperon (1973) for Pala Lagoon, American Samoa; Gilmartin and Revelante (1978) for 14 Gulf of California lagoons in Mexico (NO_3 only); and Ricard (1976) for Vairao and Tiahura Lagoons on Tahiti and Moorea (NO_3 only).



conclusion is also supported by the relatively few nitrogen budgets that have been developed for various coastal marine environments over various time intervals (Haines, 1975; Furnas *et al.*, 1976; Mee, 1978; Harrison, 1980; Nixon, 1981 *a* and *b*).

There is a similar lack of correlation between average concentrations of inorganic nitrogen and the mean standing crop of chlorophyll in different lagoons, at least for systems in which nitrogen levels exceed $0.5 \mu\text{M}$ (Fig. 19). This behavior is in marked contrast to lakes, where Schindler (1978) found a highly significant correlation between mean annual phosphorus concentrations (the major « limiting nutrient » in fresh water) and average chlorophyll concentrations in some 80 different systems. While the data set available from lagoons and estuaries is much smaller than that from lakes, it does not seem likely that it will be possible to develop plots of primary production or algal standing crop as a simple function of nitrogen concentration (or perhaps even loading) in marine systems. It is a common observation that large nitrogen inputs can have a marked impact on local marine waters. But if nitrogen cycling and remineralization contribute much more to sustaining production in most marine systems than do inputs of « new » nitrogen, it follows that we may not be able to use nitrogen in the same way that the limnologists have so successfully used phosphorus (Dillon, Rigler, 1974; Vollenweider, 1976; Schindler, 1978 and many others). Again, it is evident that the remineralization of organic matter is very tightly coupled with the production of new organic matter in coastal waters (perhaps more so than in lakes), and that the relationship between nutrient loading, ambient concentrations, and recycling is not well understood. Most of our thoughts about eutrophication have been developed from studies of lakes, and at this point it is not at all clear how appropriate they may be for lagoons, estuaries, and other marine environments.

Fisheries yields

Limnologists have also been surprisingly successful in finding a relatively simple relationship between primary production and the fisheries yields of various lakes around the world (Oglesby, 1977). While there are certain difficulties with fisheries landings data (and with primary productivity data), they represent the only comparative information on secondary production available from many different systems. Moreover, after reviewing the data from a large number of lakes, Ryder (1965) concluded « that catch is a reliable estimate of fish production despite the variables affecting it ». While it is generally assumed that there is also a relationship between primary production and fishery

Figure 19

Mean concentrations of chlorophyll *a* and dissolved inorganic nitrogen (NH_4 , NO_2 and NO_3 except as noted) over various time periods in different lagoons. Data from Frisoni and Vault (1981) for NO_3 in Mediterranean lagoons, 1 (Mauguio, February-November), 2 (Biguglia, May-November), 3 (Thau, annual cycle), 4 (Diana, annual cycle), 5 (Urbino, May-November); Sournia and Ricard (1976) for NO_3 in Tiahura (6) and Vairao (7) lagoons during July and August; Qasim *et al.* (1972) for NO_3 in Kavaratti Atoll lagoon (8) during November; Gilmartin and Revelante (1978) for NO_3 in Gulf of California lagoons (9-22) during July and August; Buckner (1973) for Great South Bay and Moriches Bay (23) from June-December; Nixon and Lee (1981) for Charlestown-Green Hill Ponds (24) over an annual cycle; Thayer (1971) for the Core Sound area (25) over an annual cycle; Day and Seaton (1979) for brackish waters in the Barataria Basin (26-28) over an annual cycle; Cadée and Hegeman (1974) and Helder (1974) for the Western (29) and Eastern (30) Wadden Sea over an annual cycle.

yields in marine systems (e.g. Ryther, 1969; Hempel, 1973; Sheldon *et al.*, 1977), it has not been previously demonstrated.

Since the fisheries yields of lagoons are so often described as being « very » or even « extremely » productive, I thought it would be useful to see how they compared with other environments and to see if a relationship with primary production would be apparent once the necessary data were assembled. If there were such a relationship, the fisheries yield of lagoons might be expected to be very similar to other coastal marine systems, since there is such a relatively small range in their annual primary production (Table 3, Nixon, 1981 *b*).

There are obvious problems in trying to make such an analysis, and it has probably not been attempted because the outcome seemed so unpromising. But the result is at once reassuring and remarkable. There does appear to be a relationship between the catch of fish and the primary production of marine systems which is similar to that found in lakes — except that the fisheries yield of marine waters at a given level of primary production is some 10-20 times greater (Fig. 20). The reasons for this striking difference are not clear, but it persists through systems ranging in size from a few hectares up to the total shelf and slope areas of the world ocean (Nixon, in prep.).

Unfortunately, there are few lagoons for which both primary production and fisheries data are available. Those for which an assessment can be made seem to fall roughly within the range we might expect for productive marine systems (Fig. 20). Even without primary production, it is very difficult to find lagoons for which separate present-day fisheries statistics are obtained. Fortunately, a detailed collection of fisheries statistics was taken in the United States in 1879-1880 by G. Brown Goode and associates (1887) for the US Commission of Fish and Fisheries. At that time much of the activity was centered on coastal rather than offshore areas, and the census for Long Island, New York, where there are a number of lagoons and small estuaries was particularly thorough and specific (Mather, 1887). It could even be argued that the lack of income taxes made the statistics more reliable than they are today. In any case, the results of the Long Island survey give a dramatic picture of the productive potential and variability in terms of fisheries among a set of lagoons within a limited geographical area (Fig. 21). The data are not out of line with present day information on highly productive waters and show that the total yield per unit area of unpolluted, intensively fished lagoons can appreciably exceed that of such well-known fishing areas as the Peru upwelling, Georges Bank, and the North Sea (Fig. 20). If the landings of anadromous fish such as the alewife and migrating schools of menhaden which were also often taken in the

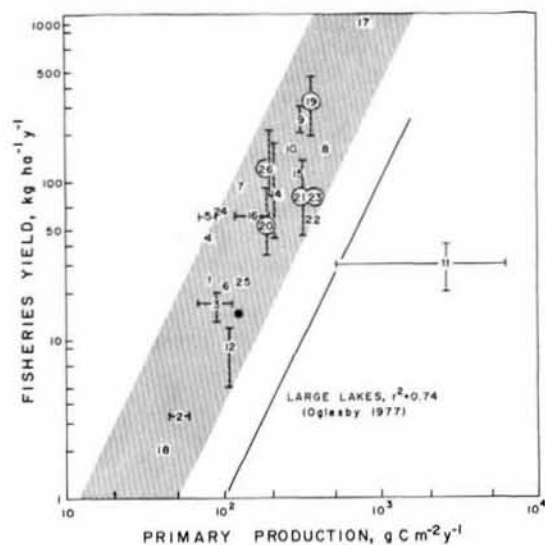


Figure 20
 The relationship between fisheries yield (first reference) and the primary production (second reference) of a variety of marine systems (points in shaded area) compared with the regression line developed by Oglesby (1977) for similar data from large fresh water systems. Range bars have been added to the marine data where practical and lagoon systems have been circled. Point 11 represents general ranges for coral reef systems reviewed by Marshall (1979) and DeVooys (1979). Other marine systems include: 1) Gulf of Finland (Thurow, 1980; Lassig et al., 1978), 2) Gulf of Bothnia (Thurow, 1980; Ackefors et al., 1978 and Lassig et al., 1978), 3) Adriatic Sea (General Fisheries Council for the Mediterranean, 1980; Kveder et al., 1971 and Pucher-Petkovic et al., 1971), 4) South Baltic Sea (Thurow, 1980; Lassig et al., 1978), 5) North Sea (Steele, 1974), 6) Scotian Shelf and 7) Scotian slope, NW Atlantic (Mills, 1980), 8) Georges Bank, NW Atlantic (Olsen and Sails, 1976 — ICNAF Zone 5 ZE, US and foreign fleet; Sherman et al., 1978, 9) Peru Upwelling (Paulik, 1971 - 1969-1970 catch), 10) Louisiana near-shore shelf, USA (Bahr et al., 1979; Sklar, 1976), 11) coral reefs (Marshall, 1979; DeVooys, 1979), 12) Black Sea, USSR (GFCM, 1980; Sorokin, 1964), 14) Long Island Sound, USA (upper bound = 1880 catch from Goode et al., 1887, lower 1975 catch from NMFS area 611; Riley, 1956), 15) Nearshore Rhode Island, USA (NMFS area 539 for 1975; Riley 1952 and Furnas et al., 1976), 16) Mid-Atlantic Bight (USA) — Cape Hatteras, NC to Nantucket Shoals, MA to 100 m isobath (McHugh, 1979-US catch only, data from early 1960's before foreign fleet was important; Emery and Uchupi, 1972), 17) Gulf of Cariaco, Venezuela (Margalef, 1971), 18) Caribbean and Gulf of Mexico (Margalef, 1971), 19) Barataria Bay, LA, USA (Day et al., 1973, production includes macrophytes), 20) Peconic Bay, LI, USA (upper bound = 1880 catch from Mather 1887, lower 1975 N.M.F.S. landings; Bruno et al., 1980), 21) Charlestown Pond, USA (upper bound when bay scallops abundant, lower without scallops from R. Crawford, pers. comm.; Nixon and Lee, in press and Thorne-Miller et al., 1981, production includes macrophytes), 22) North Carolina Sounds, USA (Taylor 1951; Thayer, 1971 and Dillon, 1971, production includes macrophytes), 23) Apalachicola Bay, FL, USA (National Estuary Study, 1970, Estabrook, 1973), 24) Sagami Bay, Japan (Hogetsu, 1979), 25) Seto Inland Sea, Japan (Hogetsu, 1979), 26) Wadden Sea, Netherlands, W. Germany (Postma and Rauck, 1979; cadée and Hegeman 1974 a and b). The heavy point represents the world ocean catch if it is assigned to the total world shelf and slope area (Moiseev, 1973; Platt and Subba Rao, 1976).

estuaries and lagoons are included, the yields frequently exceeded 1000 kg ha⁻¹. In the shallower lagoons the major portion of the catch came from shellfish which spend their entire life within the system, but it seems likely that much of their production is supported by an « auxiliary energy » subsidy from tidal and wind driven currents bringing in organic matter fixed over a larger area than the lagoon itself (Odum, 1967 b; Nixon et al., 1971). When the historical data are compared with recent information from New York and Rhode Island lagoons, it is evident that present day assessments may greatly underestimate the productive potential of lagoons in developed areas (Tables 4

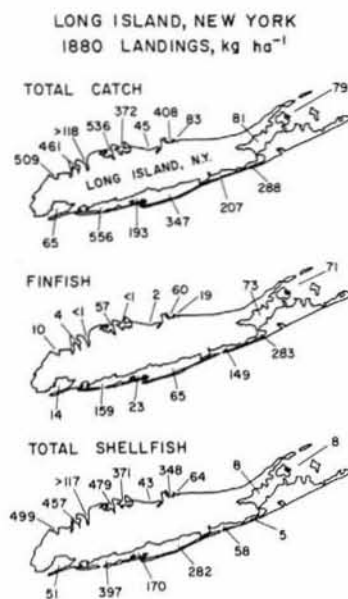


Figure 21
 Landings of finfish and shellfish from the coastal lagoons and embayments around Long Island, New York (USA) in 1880. Catch data from Mather (1887) divided by areas obtained by the author by planimetry of USGS charts.

Table 4
 Comparison of past and recent landings of finfish and shellfish from coastal lagoons on Long Island, New York (USA).

	Commercial and recreational landings, kg ha ⁻¹	
	1879	1960
Gardiners-Peconic bays		
Finfish	76.8	24.2 ^a
Shellfish	7.8	15.2
Total	84.6	39.4
Great South Bay		
Finfish	110 ^b	8.1 ^a
Shellfish	282	32.0 ^c
Total	392	40.1
Moriches-Shinnecock Bays		
Finfish	216	35.8 ^a
Shellfish	31	24.0
Total	247	59.8

^a Includes 2 kg ha⁻¹ of recreational catch for Gardiners-Peconic, 13.5 kg ha⁻¹ for Moriches-Shinnecock, and 6.8 kg ha⁻¹ for Great South Bay (Briggs, 1965).

^b Includes 45 kg ha⁻¹ of menhaden.

^c Recreational hard clam catch ~ 1% of commercial landings (Fox, 1981).

Table 5
 Changes in the landings of finfish and shellfish from a New England salt pond during the past 100 years. From Clark (1887) and Crawford (pers. comm.).

	Landings from Pt. Judith Pond, Rhode Island (USA), kg ha ⁻¹	
	1879	1979
Finfish		
Alewives	325	0
Smelt	48	0
White Perch	45	0
Bass	3	< 1
Flounder		6
Eels	many	18
Total finfish	> 430	~ 25
Shellfish		
Oysters	50	0
Clams	5	2
Scallops	0	0-155
Total shellfish	55	2-155
Total catch	> 490	25-180

and 5). Pollution, improper management, and the economics of large-scale offshore fishing often mask the potential of waters which were once prized and famous for their seafood. There is little, if any, evidence that the primary production of such lagoons has decreased during the past 100 years, and if they were more effectively managed they might yet find their place along the line of coastal marine systems shown in Figure 20.

Acknowledgements

One of the great pleasures and benefits that came with trying to prepare a general review of lagoon systems was the

opportunity to learn from the many people who have worked on various aspects of these systems around the world. Some of them are cited in this paper, but a number of others shared their experiences and information with me more informally, especially my fellow members of the University of Rhode Island Coastal Pond Research Team — Jon Boothroyd, Richard Chinman, Barbara Furnas, Stephen Granger, Marilyn Harlin, Virginia Lee, Stephen Olsen, Malcolm Spaulding and Boyce Thorn-Miller. I am also grateful to the Office of Sea Grant in the US Department of Commerce, NOAA, and to UNESCO — Division of Marine Sciences for the support which has made it possible for me to be a part of coastal lagoon research.

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