"A Strikingly Rich Zone"—Nutrient Enrichment and Secondary Production in Coastal Marine Ecosystems

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ABSTRACT: Despite a recent review concluding that there is little or no reason to expect that the production of fish and other animals will increase with nutrient enrichment or eutrophication, there is a variety of evidence that anthropogenic nutrients can stimulate secondary production in marine ecosystems. Unique multiple-year fertilization experiments were carried out over fifty years ago in Scottish sea lochs that showed dramatic increases in the abundance of benthic infauna and greatly enhanced growth of fish as a result of inorganic nitrogen (N) and phosphorus (P) additions. These experiments appear to have provided a good qualitative model for the responses of the Baltic Sea to nutrient enrichment and resulting eutrophication. Historical comparisons by others have shown that the weight of benthic animals per unit area above the halocline in the Baltic is now up to 10 or 20 times greater than it was in the early 1920s and that the total fish biomass in the system may have increased 8 fold between the early part of the 1900s and the 1970s. While there are no similar data for the highly enriched central and southern North Sea, there is convincing evidence that the growth rates of plaice, sole, and other species have increased there since the 1960s or 1970s. Cross-system comparisons have also shown that there are strong correlations between primary production and the production and yield of fish and the standing crop and production of benthic macrofauna in phytoplankton-dominated marine ecosystems. Concerns over the growing nutrient (especially N) enrichment of coastal marine waters are clearly valid and deserve the attention of scientists and managers, but the recent demonizing of N ignores the fact that nutrients are a fundamental requirement for producing biomass. Decisions regarding the amount of N or P that will be allowed to enter marine ecosystems should be made with the full knowledge that there may be tradeoffs between increases in water clarity and dissolved oxygen and the abundance of oysters, clams, fish, and other animals we desire.

Introduction

It is possible that a meeting such as the one that stimulated this special issue of *Estuaries* could have been held a century ago, but the attendance would have been much smaller and the focus would have been quite different. Instead of hypoxia, toxic algal blooms, and fish kills, the emphasis would almost certainly have been on the positive impacts of nutrients on marine productivity. Our meeting at the turn of the last century would have been held in one of the Baltic or North Sea countries, rather than in Washington, D.C. A likely venue would have been Germany, where the Kiel Commission for the Scientific Study of the German Seas (a harbinger of ICES) was trying to apply newly developed quantitative sampling techniques to the problem of understanding variations in the yield of fish from different marine areas (Nixon et al. 1986; Mills 1989).

A critical step in developing such an understanding was the extrapolation to the sea of recently acquired knowledge about the importance of inorganic nutrients, especially nitrogen (N) and phosphorus (P), to agricultural production on land (Nixon et al. 1986). A keynote speaker might well have been Karl Brandt, who would have concluded as he did in a 1901 paper that,

> "The animals which inhabit the sea are developed in proportion to the quantity of their food. Now, since all this food comes directly or indirectly from plants, it follows that we can just as well estimate the real production of animal life in the water by means of the annual yield of vegetation as we can estimate the product of a farm by the quantity of grass and fodder that it affords. (Brandt 1901, p. 500)."

The early work by Brandt and others led to what the renowned marine fisheries biologist J. D. H. Cushing (1975) later called the agricultural model of production in the sea. The essence of this model is nowhere better captured than in one of the most influential marine science texts of its time, James Johnstone's (1908) Conditions of Life in the Sea, where food chains were simple, straight, and driven from the bottom up: diatoms-cockles-flounders-man, diatoms-oysters-man, peridinians-copepods-sprats-whiting-cod-man, and so on.

But agriculture is necessary precisely because nature is not so simple, and a hundred years of re-

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search has not surprisingly provided many other pictures of production in the sea, including food webs, cog and gear machines, system loop and flow diagrams of great complexity, and a diverse array of abstract theoretical equations borrowed largely from mathematics and physics (Nixon 1992; Raffaelli 2000). As a result, our views of nutrient enrichment in marine ecosystems have been changing (Cloern 2001; Elmgren 2001) and another dark side of marine eutrophication or increasing organic production has become increasingly apparent (Nixon 1995).

This is not to say that the agricultural model has been completely abandoned. Attempts to calculate the potential regional or global yield of fish often begin with primary production (e.g., Ryther 1969; Houde and Rutherford 1993; Pauly and Christensen 1995) and cross-system comparisons have provided evidence that there is a good correlation between ^{14}C uptake and fishery landings (Nixon 1982, 1988) as well as between estimated new production by phytoplankton and marine fish production (Iverson 1990). Similar cross-system comparisons have also shown a strong linear correlation between primary production and the average biomass of benthic macroinfauna in coastal marine systems (Herman et al. 1999). A more restricted comparison among 14 Danish estuaries found "A clear positive effect of nutrient load . . . on benthic biomass . . . The relationship was curvilinear with a leveling off or even depression of biomass at high total N load." (Josefson and Rasmussen 2000, p. 205). It should be noted that the two Danish systems showing declines were receiving well over 7 mol N m^{-2} yr^{-1}, a very high loading rate compared with a wide sample of other estuarine systems (Nixon and Pilson 1983; Nixon et al. 2001).

Caddy (1993, 2000, 2001) has also emphasized the positive impact of anthropogenic nutrient enrichment on fisheries yields from oligotrophic coastal areas, though his conceptual model suggests ". . . drastic and negative changes as nutrient input passes beyond a state that may be called mesotrophic" (1993, p. 57). Trophic states of the Caddy model remain undefined and it is not clear how they would align with the quantitative definitions proposed by Nixon (1995). The Caddy model is useful in emphasizing the probable importance of particular ecosystem features that may influence the response to nutrient enrichment (as does Cloern [2001] in his excellent review of the coastal eutrophication problem) and in noting that increasing the rate of primary production and increasing fishing pressure may have similar effects on the size and composition of fishery landings.

An unplanned test of Caddy's proposition that anthropogenic nutrient enrichment may start out

well but end badly may now be well underway off the coast of Egypt (Caddy 2000). Until the Aswan high dam was closed in 1965, the annual flood of the Nile discharged large amounts of inorganic nutrients onto the Egyptian shelf and stimulated a dramatic Nile bloom of diatoms (Halim 1960; Halim et al. 1967). With the loss of the flood, the bloom disappeared and the fishery collapsed (Dowidar 1984; Halim et al. 1995). The fishery remained unproductive for over 15 years, but began a dramatic recovery in the early-mid 1980s that has continued to the present. The recovery of the fishery has coincided with equally dramatic increases in the probable release of anthropogenic nutrients from Egyptian cities and agriculture that may have replaced the N and P (but not silica) once provided by the Nile flood (Nixon in press). Since the anthropogenic sources will almost certainly continue to increase, we may have the chance to follow an oligotrophic system and its fishery as they pass relatively quickly through the trophic gradient as discussed by Caddy (1993, 2000).

These exceptions aside, the agricultural model linking nutrient availability to increased primary production, phytoplankton blooms, and increased production of marine animals now seems out of favor among ecologists and environmentalists alike. There are at least four reasons. First, the last 100 years of marine research revealed a much richer and more complex marine environment than anyone working in 1900 could have imagined. Second, once it was shown that large-scale differences in fisheries yields were related to nutrient supply and primary production (i.e., open ocean gyres compared with Georges Bank or the Peru upwelling), the attention of fishery ecologists shifted to other problems. As Caddy (1993) pointed out, modern fisheries ecologists have tended to relate landings to recruitment as influenced by stock and climate or to fishing effort. Food supply may be studied at the finer scale of prey behavior, distribution, or nutritional quality, but seldom at the basic level of carbon fixation. Third, much of the excitement in biological oceanography during recent decades has involved a growing appreciation for the abundance of very small and very rapidly metabolizing plankton and for microbial loop processes and pathways. Both emphasize nutrient cycling rather than the traditional diatom-copepod-fish food chains described by Brandt, Johnstone, and others. Fourth, the amount of reactive N (and P) moving through the atmosphere and the landscape toward the coastal ocean has approximately doubled on a global basis since the turn of the last century (Smil 1990; Vitousek et al. 1997). The increase has been much greater in many bays and estuaries, as well as in such large systems as the

Black Sea, Baltic Sea, and North Sea (e.g., Nixon 1995; Rabalais et al. 1996; Caddy 2000; Elmgren and Larsson 2001). As a result, many coastal waters and enclosed seas have developed symptoms associated with over-enrichment by nutrients, including hypoxia, nuisance or toxic algal blooms, loss of seagrasses or corals, and fish kills. The title of this special issue of *Estuaries* and the symposium that gave rise to it reflects the level of concern in the scientific community with these issues, as does the recent publication of an increasing number of books and scientific symposia dedicated to problems associated with defining, diagnosing, describing, documenting, and controlling nutrient (especially N) over-enrichment (e.g., Vollenweider et al. 1992; McComb 1995; *Ophelia* 1995; Jørgensen and Richardson 1996; Vidal et al. 1999; National Research Council 2000; Committee on the Environment and Natural Resources 2000). The Ecological Society of America (2000) and the Hubbard Brook Research Foundation (2002), among others, have produced pamphlets to educate policy makers and the public about the dangers of nutrient enrichment and eutrophication.

Our concern is that all of these factors—the great taxonomic, spatial, and temporal complexity of marine ecosystems, the recent trends in plankton and fisheries research, and the various undesirable developments seen in many coastal areas (not all of which are necessarily linked to nutrient enrichment) have led to an emerging view that there is little or no truth to the basic tenet of the "agricultural model." So far have we come from the earlier view that a recent paper in the prestigious journal, *Science* (Micheli 1999, p. 1397), concluded that there was virtually no link between nutrient delivery or availability and secondary production in coastal marine waters:

> ". . . the generality of a weak coupling of N loading and phytoplankton productivity with higher trophic levels . . . implies that anthropogenic nutrient loading to coastal waters is unlikely to result in increased fish biomass, regardless of local physical and biological conditions and of the magnitude of nutrient enrichment."

Our purpose in this paper is to provide some historical balance to such conclusions about nutrient enrichment and its potential impact on secondary production of coastal marine ecosystems. As emphasized elsewhere (e.g., Nixon 1993) nutrients are not like many other pollutants. While estuaries would doubtless thrive with no inputs of anthropogenic metals or petroleum hydrocarbons, nutrient enrichment may well contribute in a positive way to the current levels of secondary production in many coastal systems. If so, then reduc-

tions in anthropogenic nutrient discharges to some systems may be accompanied by lower fish yields and reduced potential for aquaculture. To the extent that they occur, such tradeoffs need to be recognized and included in regulatory decision making.

An earlier review of nutrients and secondary production in marine systems (Nixon et al. 1986, p. 43) concluded that, "It is surprisingly difficult . . . to find quantitative evidence showing that estuaries, lagoons, or coastal waters respond to eutrophication by producing a larger biomass of animals." One reason it is so difficult to find such evidence is that marine ecologists have generally not been able to carry out the comparative or the long-term controlled nutrient enrichment experiments that proved so effective in the study of this question in lakes (e.g., Oglesby 1977; Hanson and Leggett 1982; Lee and Jones 1991). Marine ecologists have been forced to rely for the most part on time series monitoring from individual ecosystems, on relatively short-term and small-scale mesocosm experiments, or on numerical models of various types. All of these approaches can be instructive, but each also suffers from severe limitations. The monitoring of natural systems is usually confounded by large temporal and spatial variability, the lack of a reliable nutrient input history, changing methods of sampling and analyses, lack of replication, and the fact that nutrient inputs seldom, if ever, change in isolation. As nutrient inputs change, so do freshwater inputs, other pollutant inputs, and fishing pressure. Mesocosm experiments inevitably exclude larger and more mobile organisms, spatial heterogeneity, and larger-scale physical processes (Nixon 2001). Numerical models are forever hobbled by their inventor's knowledge, imagination, and assumptions.

Given this situation, it is surprising that the only two long-term controlled fertilization experiments yet carried out with natural, intact coastal marine systems have been largely ignored in the literature. Because of this neglect and because of their relevance to our present concerns, it seems useful to examine this work and the results in some detail.

The Scottish Sea Loch Experiments

While there were attempts as early as 1910 to increase the yields of shellfish from Norwegian oyster polls or ponds by adding fertilizer (reviewed by Orr 1947), the first (and perhaps only) extended experimental tests of the agricultural model in marine systems were carried out on the west coast of Scotland beginning in 1942. The work took place during the depths of the World War II and was motivated, at least in part, by a hope that the fertilization of coastal waters might increase the Brit-

TABLE 1. Comparison of the two Scottish sea lochs fertilized during 1942–1946 in hopes of increasing the production of fish. Data from Orr (1947) and Nutman (1950) for Loch Craiglin and Kyle Scotnish, respectively.

	Loch Craiglin	Kyle Scotnish
Area (ha)	7.3	61.4
Mean depth (m)	1.0	4.9
Max. depth (m)	6	21
Volume (10^3 m^3)	70	3,000
Temperature range (°C)	4–18	5–20
Salinity	20–30	28–33
Tide (m)	intermittent	~1–1.3
Macrophytes	*Zostera*	Traces
	Ruppia	
	Macroalgae	
Fertilizer Input	5 times (1942)	16 times (1944)
	6 times (1943)	14 times (1945)
		6 times (1946)
Fertilizer DIN/DIP	5.5 (1942)	16.9
	7.6 (1943)	
Mean Fertilizer Dose		
DIN (mmol m^{-2} yr^{-1})	38.7 (1942)	380 (1944)
	40.3 (1943)	263 (1945)
		390 (1946)
DIN (mmol m^{-3} yr^{-1})	38.7 (1942)	78 (1944)
	40.3 (1943)	54 (1945)
	79 (1946)	

ish food supply. The first effort was directed to Loch Craiglin, a very shallow (mean depth = 1 m) system with macroalgae and rooted macrophytes where inorganic fertilizer was added on 12 occasions between late 1942 and early 1944 (Table 1). In 1944, attention shifted to a nearby, but much larger and deeper (mean depth = 4.9 m) loch, Kyle Scotnish, which was fertilized at a higher rate during 1944–1946 (Table 1). The wartime conditions were obviously far from ideal for experimental ecology, and the measurements of system response suffered somewhat from undersampling. It must also be admitted that by present standards, there was a lack of statistical rigor in analyzing some of the data. In spite of these limitations extensive presentations of the results from both experiments in special issues of the *Proceedings of the Royal Society of Edinburgh* (1947, 1950) as well as in articles in *Nature* (Cooper and Steven 1948), the *Journal of Marine Research* (Raymont 1948), and the *Journal of the Marine Biological Association,* U.K. (Marshall and Orr 1948; Raymont 1949) seem compelling in their overall conclusion that the fertilized lochs became "a strikingly rich zone" (Raymont 1947, p. 54).

Loch Craiglin proved to be a problematic site for study in a number of respects. It had very little and only intermittent connection with the sea, so that there was essentially only wind mixing. Combined with high rainfall (~ 2 m yr^{-1}) and solar heating of the surface water during summer, the

lack of tidal mixing resulted in strong vertical density stratification and periods of anoxia in the deeper portions of the system (Orr 1947). The macroalgae, *Enteromorpha* and *Cladophora* became abundant during spring and apparently outcompeted the phytoplankton for fertilizer nutrients. The bloom of macroalgae was followed by luxurious growths of eelgrass, *Zostera,* and wigeon grass, *Ruppia* (Marshall 1947), which made sampling for benthic invertebrates and fish difficult. Lastly, the shallowness of the system made fish especially vulnerable to heavy predation by cormorants and herons (Gross 1947). In spite of these problems, Raymont (1947, p. 90, 92) reported an impressive enhancement of the benthos due to fertilization and Gross (1947) concluded that ". . . by the application of fertilizers the loch has been rapidly converted into a feeding ground for fish approaching—on a small scale—the richest feeding grounds known . . . the vast improvement in growth rate observed may be taken as an indication of a very rapid ultimate conversion of inorganic plant nutrients into fish flesh . . ."

Encouraged by such dramatic results even from a difficult site, the team switched their efforts to nearby Kyle Scotnish, a much larger and deeper phytoplankton-dominated loch. In this system, fertilization usually, but not always, ". . . produced an immediate but usually short-lived increase of the phytoplankton . . . and a very dense zooplankton population was maintained for two seasons . . . the productivity of Kyle Scotnish, in terms of plankton [was] doubled by the distribution of fertilizers" (Gaud 1950, p. 41, 51, 68). In this loch, there was also a dramatic increase in the numbers of benthic infauna (Fig. 1). This increase was in spite of grazing by large numbers of introduced fish, so that Raymont (1950, p. 105) concluded that, "The rises . . . are therefore all the more convincing proof of the efficacy of fertilization in stimulating the bottom fauna." The response of the fish was reported to be equally dramatic. According to Gross (1950a, p. 113), ". . . the addition of fertilizers . . . brought about an increase of almost four to five times the weight of Group 0 and about three times the weight of Group I plaice. The growth of flounders . . . also represents a remarkable acceleration . . . in weight three times faster than normal during the first year and between three and four times faster during the second year."

Despite these dramatic and important ecological results several circumstances converged to create an impression that the experiments were a failure. In the first experiment, anoxia and natural predation exerted a heavy mortality on introduced fish. In the second, large numbers of hatchery reared fry were introduced, but these also suffered
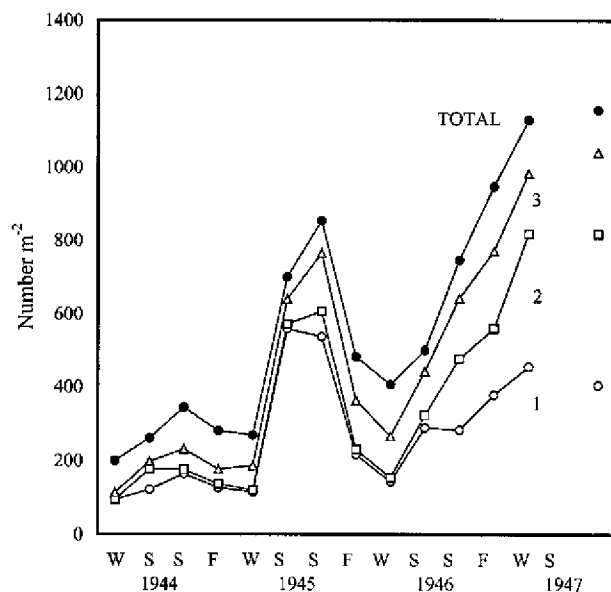
Fig. 1.   Mean abundance of benthic macroinfauna larger than 1 mm at eight regularly sampled stations in Kyle Scotnish, Loch Sween, Scotland. Measurements were made from winter 1944 (W 44) through summer 1947 (S 47) except for spring 1947. The loch was fertilized repeatedly in 1944, 1945, and 1946 (Table 1). Line 1 is for total polychaetes, line 2 is for amphipods, line 3 is for bivalves, and the top line is for the total of all groups (data from Raymont 1950).

a very high mortality. As the fish grew larger they also tended to migrate out of the open mouth of Kyle Scotnish. For these reasons, it was concluded that the economic return from enhanced fish yield would not justify the cost of fertilization. This practical failure seems to have over-shadowed the scientific value of the ecological results. This problem was noted early by Cooper and Steven (1948, p. 631), scientists not involved with the research, who wrote in strong appreciation of the Loch Craiglin work:

"The experiment suffered from many shortcomings which this group of able workers are the first to admit. The aim was set very high and the time that could be devoted to the project—mainly weekends—under the severe stress of war conditions was inadequate. The experiment failed in its primary objective of demonstrating that marine fish cultivation can be made to pay. In the series of papers embodying the results, one senses that this failure—a failure on the heroic scale—has infected the authors with so great a feeling of disappointment that in the end they have not dared to draw from their data even those conclusions that their results would seem to justify."

Cooper and Steven (1948, p. 633) concluded their

positive review in *Nature* magazine on an optimistic note, ". . . this unique experiment has provided such a mass of interesting and important facts as will stimulate academic research and practical endeavor in many parts of the world." But it was not to be so, even after the much more comprehensive and impressive results from Kyle Scotnish were published.

It is hard to know why this work, especially the Kyle Scotnish study, has had so little impact on current thinking in marine ecology. Cooper and Steven (1948) may have been correct that the failure of both experiments to demonstrate that fertilization could be an economic success distracted both the researchers and, by extension, the wider marine science community from the ecological value of the results. However, the quotations given here from some of the major papers do not suggest that the researchers were unimpressed with their findings. In his introduction to the special issue of the *Proceedings of the Royal Society of Edinburgh* devoted to the results of the Kyle Scotnish experiment, Fabius Gross (1950b, p. 3, 4) explicitly addressed the purpose of the experiments:

"When an experiment of this kind was first suggested . . . , it was hoped that a return of the money expended might be derived from the sale of the fish crop. However, by the time it was decided to undertake a small-scale experiment in Loch Craiglin it was clear that this would be of the nature of exploratory fundamental research, and neither our research team nor the representatives of Imperial Chemical Industries Ltd. [who provided the fertilizer and helped to finance the study] expected that it would pay its way. The objective of the experiment was "to test the possibility of increasing the fertility of a small sea-loch by the addition of nitrate and phosphate fertilizers, with the view of improving the growth rate and yield of fish."

In order to prevent any confusion with regard to our objectives, it should be pointed out that the second experiment, carried out at Kyle Scotnish, was also primarily concerned with scientific rather than economic problems of marine pisciculture, with the possibility of increasing production in an unenclosed area of the sea and of increasing the fish population of such as are with the aid of a hatchery. The paramount importance of the question whether marine cultivation can be made to pay was, of course, realized . . ."

Perhaps ecologists a half century ago were uncomfortable with the financial support provided for the work by the chemical industry. It seems more likely, however, that the dramatic shift in the center of marine research from Europe to North America

following the war made studies of Scottish sea lochs seem remote and of little interest. The issue of nutrients as a harmful pollutant in marine coastal waters would not emerge in a major way for another 25 years (Nixon 1995).

In our view, the two major limitations of the sea loch experiments were the lack of a longer time series of observations against which to compare the behavior of the systems being fertilized, and the lack of replicate lochs for control and manipulation. These same shortcomings have continued to confound our interpretation of virtually all planned and inadvertent manipulations of coastal marine ecosystems. There is no reason to exclude the results of the experiments from being an important part of our knowledge of how such systems respond to nutrient enrichment. The results clearly provide impressive evidence that both the standing crops and the growth rates of higher trophic levels (benthos and fish, respectively), can be markedly enhanced by anthropogenic nutrient inputs, at least under the circumstances of the experiments. Those circumstances had the singular advantage of including known amounts of nutrients added for multiple years to real, intact, and complete ecosystems containing natural plant and animal communities.

Comparisons with the Baltic Sea and the North Sea

It seems reasonable and useful to put the sea loch experiments in a larger context by comparing the fertilization used in the lochs and the biological responses observed with anthropogenic nutrient inputs and responses in larger systems. Two of the best known and intensively studied marine areas where nutrient enrichment has emerged as a serious concern are not far from the experimental area. Both the Baltic Sea and North Sea have been the subject of major international research and monitoring programs by leading universities and government laboratories for over 100 years. Both have also received increasing amounts of N and P from agricultural runoff, urban wastewater, and enriched atmospheric deposition for many decades (e.g., Postma 1978; Larsson et al. 1985; Boddeke and Hagel 1991; Wulff et al. 1994; Asman et al. 1995; Nixon 1995; Paerl 1995; Howarth et al. 1996; Elmgren 2001).

In spite of these increases, the average daily inputs of anthropogenic N and P per unit volume to the Baltic and to the most enriched central and southern portions of the North Sea remain far lower than the experimental additions to the sea lochs (Table 2). The comparison changes significantly if the nutrient inputs are expressed per unit area (Table 2). In the latter case, anthropogenic dis-

solved inorganic nitrogen (DIN) input to the North Sea exceeds that used in Loch Craiglin by about 7-fold and dissolved inorganic phosphorus (DIP) input is almost identical. Present anthropogenic DIN fluxes per unit area to the North Sea are approximately equal to those used in Kyle Scotnish in the less intensively fertilized period, while DIP inputs per unit area are about one-third those used in Kyle Scotnish. Total anthropogenic N and P inputs per unit area to the Baltic are roughly equal to the anthropogenic DIN and DIP fluxes to the southern and central North Sea, so that reactive N and P must be somewhat lower.

The Baltic Sea

When Nixon et al. (1986) reviewed the literature with regard to potential increases in animal populations in the Baltic in response to nutrient enrichment, they concluded that the most convincing indication was a comparison by Cederwall and Elmgren (1980) of benthic biomass data collected in the Baltic in 1920–1923 with similar data collected in 1976–1977 (Fig. 2). Their finding that benthic biomass above the halocline had increased by factors of 2–10, or even more, is dramatic and roughly consistent with Raymont's (1950) estimate of a 5–6 fold increase in the abundance of benthic infauna following fertilization of Kyle Scotnish (Fig. 1). Marked declines in biomass below the halocline were almost certainly due to declines in oxygen at depth in the Baltic that result from the long residence time of the bottom water and, quite likely, an increasing supply of organic matter from eutrophication (Elmgren and Larsson 2001).

A recent detailed examination of long-term fisheries data from the Baltic has now added another important piece of evidence that secondary production has increased. Based on his historical reconstruction, Thurow (1997) concluded that the biomass and yield of finfish in the system was relatively low during the first half of the 1900s, then increased sharply due to eutrophication after about 1950 (Fig. 3). Unfortunately, we can not directly compare the approximately 8-fold increase in fish biomass in the Baltic with the sea loch results because data on total fish weight were not obtained in the lochs. Thurow noted the negative impact of nutrient additions on bottom water oxygen concentrations and that this prompted some to argue for nutrient input reductions which ". . . would inevitably lead to a lower fish biomass (p. 460)". He also considered various other possibilities for the dramatic increase in fish biomass, including climate change and declining seal predation, but concluded that eutrophication has caused the increase in Baltic fish stocks since about 1950.

TABLE 2. Mean daily anthropogenic inputs of total nitrogen (TN), total phosphorus (TP), dissolved inorganic nitrogen (DIN), and dissolved inorganic phosphorus (DIP) in the Scottish sea loch experiments compared with recent anthropogenic inputs to the Baltic Sea and the central and southern portion of the North Sea. Inputs are expressed per unit area (mmol m^{-2} d^{-1}) and per unit volume (mmol m^{-3} d^{-1}). Mean depths are 55 m for the Baltic and 67 m for this region of the North Sea.

	Nitrogen		Phosphorus	
	Area	Volume	Area	Volume
Loch Craiglin (DIN, DIP)[a]	0.1	0.1	0.015	0.015
Kyle Scotnish (DIN, DIP)[b]				
Overall Average	0.7–1.1	0.14–0.22	0.041–0.065	0.008–0.013
North Basin	2.6–3.9	0.52–0.78	0.15–0.23	0.03–0.05
Central and Southern North Sea[c]				
DIN, DIP	0.73	0.01	0.013	0.0002
TN, TP	0.92	0.01	0.023	0.0003
Baltic Sea (TN, TP)[d]	0.52	0.01	0.01	0.0002

[a] Orr (1947).

[b] Nutman (1950).

[c] Nixon (2000) based largely on data from Turrell (2000) except that this estimate includes 0.19 mmol m^{-2} d^{-1} of direct atmospheric deposition (Paerl 1995; Asman et al. 1995). Includes 337 × 10^3 km^2 in subregions 3, 4, 5, and 7 or 62% of the total North Sea area. Discharges from Norway and Sweden not included.

[d] Based on data summarized by Nixon et al. (1996).

THE NORTH SEA

The impacts of increasing N input as well as recent declines in phosphate input to the central and southern North Sea appear less clear, in spite of at least two special International Council for the Exploration of the Sea symposia devoted to ecological change in the area (Hempel 1978; Daan and Richardson 1996). As noted by Daan et al. (1996, p. 879) in their introduction to the most recent proceedings, "The paradox is that the more data we

collect, the less we appear to know!", a situation for which any ecologist can find sympathy.

The North Sea has a longer record of zooplankton abundance than perhaps any other marine system, and one might look there first for signs of an impact of nutrient enrichment on animal biomass. The Continuous Plankton Recorder (CPR) Survey has sampled the open waters of the area on a reg-
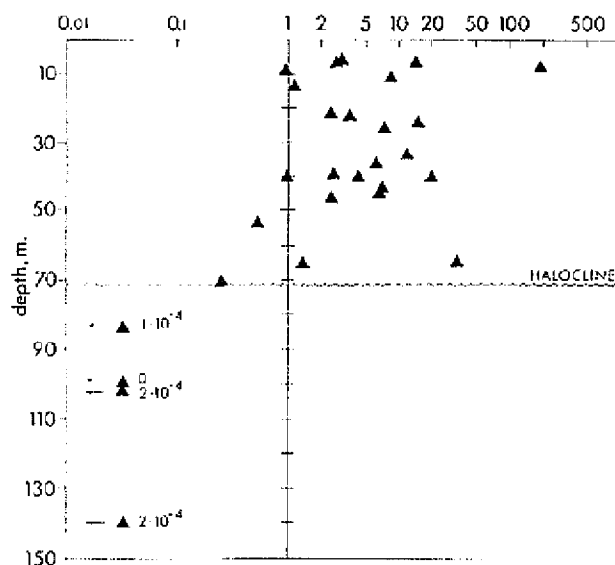

Fig. 2. Ratio of total wet weight biomass of benthic macroinfauna in the southern Baltic Sea in 1976–1977 to the biomass found in 1920–1923 as a function of depth. Note the marked increases above the halocline and decreases below (from Cederwall and Elmgren 1980).
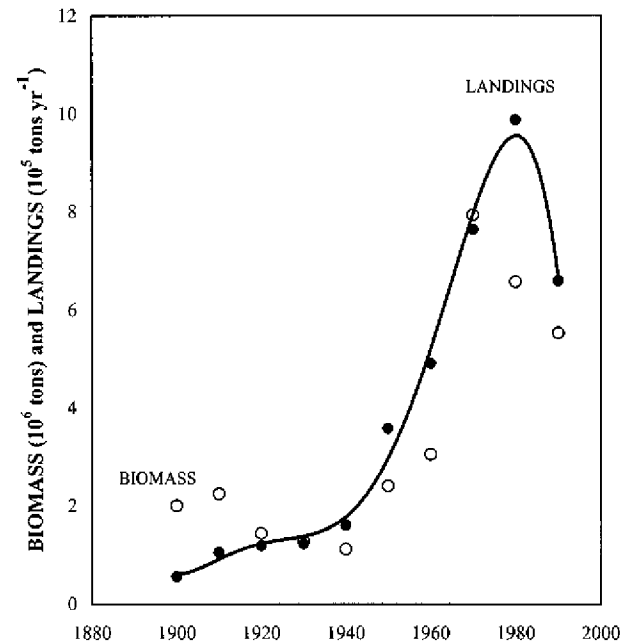

Fig. 3. Solid line is a polynomial fit through estimates of the total landings of fish over time from the Baltic. Open circles are estimates of total fish biomass in the Baltic over time (note different scales; from Thurow 1997).

ular basis since 1948, and the CPR Survey Team (1992) has shown long-term declines in the abundance of larger phytoplankton and zooplankton in the 1960s and 1970s that were followed by marked increases throughout the 1980s. There were also significant changes in the taxonomic composition of the zooplankton during the 1980s. It is unlikely that any of these major large-scale changes were related to anthropogenic nutrient inputs. At least two recent analyses have correlated year-to-year changes in the abundance of copepods in the North Sea CPR record with changes in the position of the north wall of the Gulf Stream (Frid and Huliselan 1996; Taylor 1996). It seems likely that the mechanism behind this relationship is that changes in the position of the Gulf Stream are associated with important weather shifts around the British Isles and North Sea area (Taylor 1996). Such large-scale climate-driven changes in the plankton must confound to some degree any potential impacts of anthropogenic nutrient enrichment on benthos or fish.

There appears to have been no study of central and southern North Sea benthos comparable to Cederwall and Elmgren's (1980) work in the Baltic. A 22-year record of benthic infauna at a station 55 m deep off the Northumberland coast of England shows that the abundance of animals > 0.5 mm was low and stable between 1969 and 1979, then increased in 1981 and 1982 to a less stable but approximately two-fold higher density that persisted through the rest of the record to 1994 (Frid and Huliselan 1996). It appears likely that this increase was a response to the large-scale plankton changes noted by the CPR record rather than a response to local eutrophication.

Because the North Sea seems much more subject to changes in climate and hydrography than the Baltic (e.g., Becker and Pauly 1996; Turrell et al. 1996), it is not surprising that the situation with regard to fish abundance is also more complicated than in the Baltic. Heessen (1996, p. 1079) analyzed data for 40 species sampled by the International Bottom Trawl Survey between 1970 and 1993 and concluded that "Among the 40 species, there are many more showing a positive trend during recent years than a negative one. However, the commercial species are all either declining or are stable." Over a longer time span Rijnsdorp et al. (1996, p. 1054) compared the results of trawl surveys in 1906–1909 with those in 1990–1995 and found a ". . . lower abundance in recent years for the total assemblage as well as for individual groups." They also reported that the fish community was less diverse and less even in its taxonomic composition. It seems likely that there has not been a marked increase in total fish biomass

TABLE 3. Increase in annual growth increment in female plaice in the North Sea during the period 1925–1949 compared with 1985–1994. Data were obtained by back calculation from otoliths by Rijnsdorp and van Leeuwen (1994) and reported by Rijnsdorp and Millner (1996). We combined the 1925–1934, 1935–1944, and 1945–1949 data reported by Rijnsdorp and Millner (1996) because of very small sample sizes in the earlier years.

Size Class (cm)	Increase in Growth Rate (%)
25–29	10
30–34	8
35–39	24
40–44	44
45–49	107
>50	115

in the North Sea comparable to that found in the Baltic, but the last effort to estimate the total fish biomass was focused on 1983–1985, and it did not include historical changes (Sparholt 1990).

There does appear to be ample evidence of increasing growth rates, at least for some of the major stocks that have been studied. In summarizing the conclusions of the 1975 ICES North Sea Symposium, Hempel (1978, p. 445) reported that "For both pelagic and demersal species, there is one phenomenon in common: an increase in growth rate, mainly observed in the first year's growth. Of the species considered in some detail, this holds true for herring, sprat, haddock, whiting, cod, sole, and plaice." He went on to note that the more rapid growth led to earlier maturation, higher fecundity, and possibly higher recruitment.

The more recent ICES special symposium reported detailed studies of the last two species Hempel noted, sole and plaice. Using age-at-length data reconstructed from otoliths, Millner and Whiting (1996) and Rijnsdorp and van Leeuwen (1996) analyzed growth rates for North Sea sole and plaice, respectively, back to pre 1945 and 1950, respectively. In contrast to Hempel's (1978) view that growth rate increases were largely confined to young of the year fish, both of these studies found increases in growth since the 1960s that were greater in larger fish (Table 3 and Fig. 4). In the case of sole, there was no increase in growth rate of fish during their first or second year, but for other size classes, at least up to age 6, larger sole showed increasing change, as did larger plaice. These growth rate increases were more modest than observed in the same species following fertilization of Kyle Scotnish (Gross 1950a), probably because the enhancement was generally confined to older, more slowly growing fish.

With this interesting acceleration of growth established, both studies attempted rather complex analyses in an effort to identify potential causes
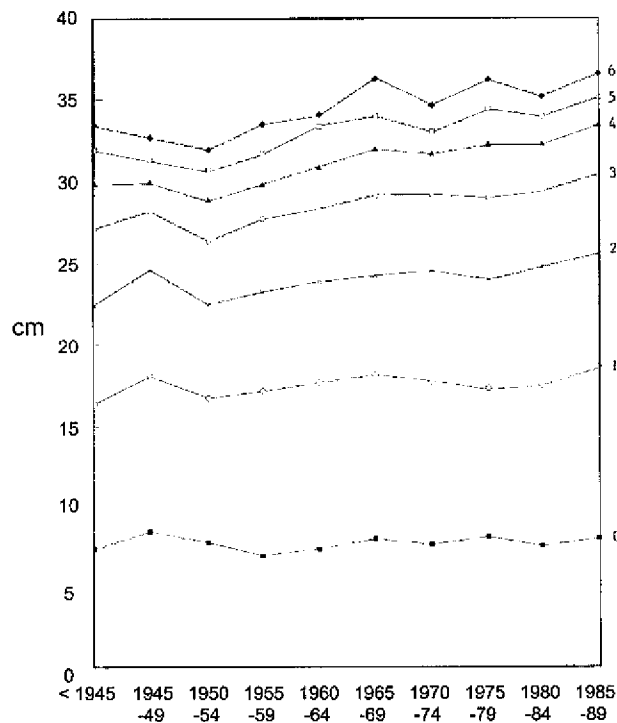
Fig. 4. Mean length at age by five-year periods (1945–1989) for sole in the North Sea. Age was measured at the end of each year's growth for ages 0–6 (from Millner and Whiting 1996).

through correlation. Both studies rejected temperature as being of importance, and both concluded that density-dependent crowding may have had some effect in reducing growth of some size classes during some periods. The most interesting conclusions for our purpose were those concerning the potential importance of eutrophication, defined here as an increase in the rate of supply of organic matter to the system (Nixon 1995).

Millner and Whiting (1996) concluded that eutrophication was not important for two reasons. First, the smaller sole that were found in shallow coastal areas showed no increase in growth rate. Yet such important nursery areas as the Wadden Sea had been shown to have greatly increased benthic infauna, presumably in response to increased nutrient input and primary production in the coastal areas (e.g., Beukema 1989, 1991; Beukema et al. in press). The younger fish were therefore not considered food-limited. They also dismissed nutrient enhanced primary production as being of importance for the observed growth increases of the larger sole because the growth increases did not correlate well with their index of eutrophication, which consisted only of the flux of DIP in the river Rhine at the German-Dutch border.

Rijnsdorp and van Leeuwen (1996) used a similar eutrophication index, although theirs consist-

ed of measured and estimated DIP concentrations off Helgoland in the German Bight. They concluded (p. 1207) that, for plaice, "The eutrophication index explained 6–10% [of the variance in growth rate] and was significant in size classes up to 30 cm with the exception of size class 15–19.9 cm, where [seabed disturbance] explained a significant part of the variance (9%)." They found no significant correlations with any factor they examined for plaice larger than 35 cm.

"Seabed disturbance" deserves some explanation because it figures prominently in both studies. The disturbance is due largely to tickler chains which run in front of the groundrope to activate flatfish so that they can be more effectively captured in trawls (Rijnsdorp and van Leeuwen 1996). A side effect is that the chains apparently dig out benthic infauna from softer mud and sand bottom areas and leave the dead or injured animals on the sediment surface where they can serve as easy food for fish, starfish, and crabs. While some tickler chains were used with otter trawls, many more could be used with beam trawls. Beam trawling for flatfish was introduced in the North Sea by the Netherlands and Belgium in the 1960s, then expanded to Germany and the United Kingdom in the 1980s (Rijnsdorp and van Leeuwen 1996). Since beam trawling is not practiced in shallow coastal areas, this factor may only be an important contribution to the enhanced growth of the larger sole and plaice. As noted by Rijnsdorp and van Leeuwen (1996, p. 1209), "The indices of both eutrophication and seabed disturbance explained a significant part of the variance [in growth of plaice], but the true effects of these two variables were less easy to determine, because they were mutually correlated . . . statistical analysis thus cannot be used in disentangling the possible causal factors further." Millner and Whiting (1996, p. 1193), however, concluded that, ". . . beam trawling was the only variable to be significantly correlated with length [in sole]," so we must assume that their slightly different eutrophication index did not covary as strongly with beam trawling effort.

An important point is that both the seabed disturbance hypothesis and the eutrophication hypothesis agree that the larger sole and plaice are food-limited, at least to some degree. One might also argue that if beam trawling kills increasing amounts of the benthic infauna over decades, then an increase in primary production and deposition of organic matter on the bottom may be required to support this additional anthropogenic predation. There are no adequate long-time series of primary production data from the open North Sea to evaluate this possibility (Joint and Pomroy 1993). While DIP fluxes in the Rhine appear to be well

correlated with DIP and chlorophyll concentrations along parts of the European coast (Laane et al. 1996), they seem a poor choice for a eutrophication index for the open waters of the central and southern North Sea, where Tett and Walne (1995, p. 376) report that "... nitrogen is the nutrient most likely to limit total phytoplankton production."

The prevalence of N limitation is important in considering the potential impact of eutrophication on the growth of larger sole and plaice for at least three reasons. First, the history of anthropogenic inputs of DIN and DIP to the North Sea must differ in some ways because fossil fuel combustion is a significant source for N but not for P. While N loading from sewage has continued, the use of detergents containing little or no P and advanced wastewater treatment have reduced the discharge of P from sewage treatment plants during recent decades. As a result, the addition of DIP to Dutch coastal waters peaked in 1981 (Boddeke 1996), and the flux of DIP in the Rhine declined by almost 90% between the early 1980s and the early 1990s (Rijnsdorp and van Leeuwen 1996). Eutrophication indices based on DIP discharge or concentrations will not correspond well with DIN loading and potential increases in primary production in the open North Sea, especially during the last 10–15 years of the record, when larger sole and plaice were increasing their growth rate.

Second, anthropogenic DIN inputs to the central and southern North Sea are currently about twice the background input of DIN through Dover Strait, while the anthropogenic DIP load is less than 75% of the background DIP input through the strait (Laane et al. 1993; Nixon 2000; Turrell 2000). The signal of anthropogenic N enrichment is much stronger than it is for P enrichment and should correlate more strongly with the observed increases in fish growth if eutrophication is an important causal factor. We have not found a well resolved historical reconstruction of the total N or DIN input from all sources to the North Sea.

Third, atmospheric deposition is an important pathway by which DIN reaches the North Sea, while it is only a very minor route for DIP transport. Since atmospheric deposition reaches the open North Sea directly, it provides an unambiguous N enrichment of the area where the larger sole and plaice grow. Measurements summarized by Paerl (1995) for various North Sea coastal areas during 1983–1985 and detailed model calculations for the Kattegat reported by Asman et al. (1995) suggest that direct atmospheric deposition of DIN may account for about 25% or more of the total anthropogenic DIN input to the central and southern North Sea. Atmospheric emissions of ammonia

and nitrogen oxides from Europe increased two and three fold, respectively, between 1950 and the mid 1980s (Asman et al. 1988), the time period covering the increase in growth of the larger sole and plaice.

For these three reasons, we believe that it is not correct to dismiss nutrient enhanced increases in primary production as being of importance in contributing directly and/or indirectly to the increasing growth rates of sole, plaice, and other North Sea fish. It is certainly premature without first repeating the correlation analyses using historical N input data.

While it appears that the sea loch fertilization experiments provided a useful qualitative model for at least some biological changes associated with nutrient enrichment in the Baltic and North Sea, it is clear that there are still major gaps in our understanding of the quantitative relationship between nutrient input and secondary production. Three examples from this very simplified summary illustrate some of the problems.

At the most basic level, it is remarkable that the Baltic Sea benthic and fish communities appear to have responded much more strongly than those of the central and southern North Sea, even though the nutrient enrichment rates of the two areas appear comparable on both an area and volume basis (Table 2). An obvious explanation might lie in water residence times, but while that of the Baltic Sea is longer, on the order of two decades or more (Larsson 1986), that of the southern and central North Sea is also long enough to capture more than a year of nutrient input, biological uptake, and regeneration (Laane et al. 1996; Nixon 2000). Does the greater exposure of the North Sea to cyclical climate change explain the lack of a more dramatic increase in benthos and fish biomass? Or do the much more energetic tidal currents of the North Sea suspend sufficient sediment that phytoplankton growth there is strongly limited by light and eutrophication of the system thus retarded by turbidity (Tett and Walne 1995; Cloern 1999)?

Second, the strong response of the Baltic Sea benthos and fish seems consistent with the responses of benthos and fish in Kyle Scotnish, but only if the nutrient inputs are compared on a unit area rather than a unit volume basis (Table 2). Yet, a long history of comparative nutrient loading and response in limnology has shown that mean depth is a critical scaling factor (e.g., Vollenweider 1968; Rigler and Peters 1995). How should we scale for depth in comparing the permanently stratified Baltic with the seasonally stratified or well-mixed North Sea?

Third, while the average daily inputs of nutrients are compared in Table 2, the experimental addi-

tions to the sea lochs took place only 5–16 times a year. The inputs to the Baltic Sea and North Sea are relatively constant (point sources) or varying by season (rivers, atmospheric deposition). How does secondary production respond to very large but less frequent pulses of nutrients compared with lower, but relatively steady loading?

Eutrophication and Secondary Production

The sea loch experiments, the historical changes in the Baltic, and, less convincingly at this point, the changes in growth rates of fish in the North Sea, all provide evidence that inorganic nutrient enrichment can have a positive effect on secondary production of particular coastal marine ecosystems. There are numerous other examples, ranging from dramatic declines in fish and sea bird abundances in the Peru upwelling ecosystem during El Niño years (Schaefer 1970) to positive correlations between coastal upwelling and the production of cultured mussels in Spanish rias (Blanton et al. 1987) to long-term changes in nutrient input, phytoplankton abundance, and benthic biomass in parts of the Wadden Sea and other coastal areas of the North Sea (Beukema et al. in press; Cadée and Hegeman in press; Colijn et al. in press). The developing story of the Egyptian shelf fishery may be another useful case study (Nixon in press).

The cross-system comparisons cited earlier provide compelling evidence for strong general links between primary production and secondary production of marine benthos (Herman et al. 1999) and fish (Nixon 1988; Iverson 1990). While it is important to recognize that such cross-system syntheses do not provide an unambiguous space-for-time substitution, it has been possible in at least one area, the Kattegat, to find evidence that changes in primary production and fishery landings over time are at least roughly consistent with the comparative system trend. The location of the Kattegat between the Baltic Sea and North Sea also makes it particularly appropriate for our discussion.

The first ^{14}C uptake measurements of primary production over an annual cycle by marine phytoplankton were made in the Kattegat during 1954–1960 (Steemann Nielsen 1964). More recent measurements for 1984–1993 were reported by Heilmann et al. (1994). In an interesting comparison, Richardson and Heilmann (1995) used Steemann Nielsen's original methods to adjust the Heilmann et al. (1994) data so that they could properly be compared with the earlier measurements. They concluded that primary production by the phytoplankton in the open waters of the Kattegat had increased over 3 fold, from a mean of about 65 g C m^{-2} yr^{-1} to a mean of about 230
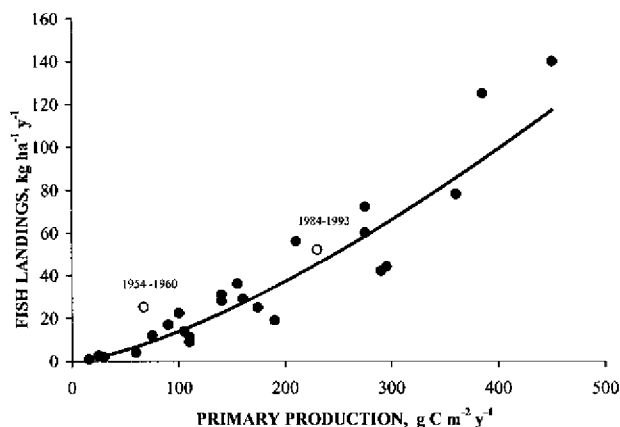

Fig. 5. Relationship between primary production (particulate ^{14}C uptake) and commercial fisheries landings in some phytoplankton-based marine ecosystems. The data are not necessarily contemporaneous (modified from Nixon and Thomas 2001). Open circles are data from the Kattegat during two different time periods. The increase in primary production is consistent with increases in nitrogen input (Richardson and Heilmann 1995). Landings per unit area are calculated from the Kattegat area of 22,177 km^2 given in Nielson and Richardson (1996).

g C m^{-2} yr^{-1}, during the 30-year period. In a subsequent paper, Nielsen and Richardson (1996) showed that total fisheries landings from the Kattegat also increased between these time periods to a level consistent with expectations from the cross-system comparison reported by Nixon (1992) (Fig. 5).

Demonizing Nitrogen

One of us recently published a paper in *Scientific American* with the too provocative title, "Fertilizing the Ocean to Death" (Nixon 1998). While the words were those of the magazine editors, the author of the piece let them stand and must accept his share of responsibility for contributing to the demonizing of N among marine ecologists and coastal managers. There are real reasons for concern about the dramatic increase in reactive N entering the coastal marine environment, and it has not been our purpose here to minimize these concerns or to argue that increasing inputs of N will necessarily lead to increasing secondary production in all coastal marine waters. We have not dealt with the very important issue of species changes in higher trophic levels that may be associated with increases in primary production, including the possibility that pelagic fish will replace bottom feeding fish as nutrient inputs increase (de Leiva Moreno et al. 2000). What we have tried to do is emphasize that nutrient supply is related in a fundamental way to the abundance and production of animals in marine ecosystems. There is a potential

positive dimension to nutrient supply that needs to be considered as part of the policy making process surrounding point and nonpoint nutrient reduction strategies. Nutrients are valuable resources with wide ranging potential impacts, some desirable, some not. Basic ecology and common sense dictate that we recognize this complexity.

ACKNOWLEDGMENTS

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