A Comparative Study of Fish Yields from Various Tropical Ecosystems

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Abstract

There is an immense variation in actual and potential fish yields, both within and between different kinds of aquatic tropical ecosystems. The finfish catches from lakes, reservoirs, rivers, continental shelves and coral reefs all fall in approximately the same range of 0.1 to 30 tonnes/km^2/year, with most catches falling in the range of 1 to 10 tonnes/km^2/year and modal values falling in a range of 3 to 6 tonnes/km^2/year. The yields from estuaries and ponds can be considerably higher (up to 120 tonnes/km^2/year without supplementary feeding), and the yields from open ocean are considerably lower (.002 to .05 tonnes/km^2/year). Within the tropics, the best physical indicator of a fishery's potential yield is water depth, and the best biological indicator is primary productivity. Some ecosystems such as rivers, estuaries and ponds have relatively high fish yields for their primary productivity, presumably because of organic matter inputs. Other ecosystems such as coral reefs and open oceans have relatively low fish yields, presumably because of long food chains. However, no single indicator, including primary productivity, can predict fish yields very precisely. More refined yield assessments will have to be empirical in nature, recognizing the importance of fishing practices in assessing potential yields and giving particular attention to how the composition of fish communities in different habitats is altered by fishing and other human activities.

Introduction

There is an immense variation in fish yields in different parts of the tropics. The annual yield from a square kilometer of intensively managed fishponds can be as much as a million times the average annual fish catch from a square kilometer in the middle of the ocean. Even fisheries which are not intensely managed can vary by a factor of more than ten thousand in their yields, depending upon where they are located and the ecological conditions that prevail.

Sufficient information has accumulated on these fisheries to attempt an assessment of why they vary so much. This review examines the extent to which different fish yields are associated with different aquatic ecosystems such as lakes, reservoirs, rivers, estuaries, continental shelves, coral reefs and open ocean. Also, this review examines the extent to which fish yields can be explained by biological or physical characteristics of the different ecosystems and how these characteristics differ from one ecosystem to another.

One of the motivations for such an assessment is to assist inventories of the potential of tropical fisheries. Because it has not been feasible to conduct stock assessments and establish commercial catch record systems of the sort desired for management in all of the numerous lakes, rivers, estuaries, etc., that are situated in the tropics, there is a need for methods with limited data requirements to assess fishery potentials and the yield implications of present fisheries practices.

Methods

The basic information for this review comes from records of finfish yields (wet weight) in various ecosystems throughout the tropics. The analysis is not precise because the information is not precise. Large errors can be expected in fish yield statistics for a variety of reasons, many deriving from the artisanal character of multispecies tropical fisheries. One of the weakest points is the estimation of fishing effort, which is important to yield estimates because such estimates are customarily made by multiplying catch per unit effort (from a sampling of fish landings) by the total effort in the fishery. It can be extremely difficult, however, to know the effort of a fishery that consists of thousands of individual fishermen operating out of canoes along a complex shoreline where transportation and communications may be poor or non-existent. This may be further complicated if a fishery has restrictive regulations which encourage the fishermen to avoid reporting their catch faithfully.

It is important to appreciate the spatial scale of the yield estimates, which most often are highly aggregated. A single number may be used to represent the yield from a lake whose fishery production is ten times as great in its shallow inshore areas as its offshore areas. The estimate for a river may embrace both the highly productive flood plains and relatively sterile headwaters. The estimate for a coral reef fishery may cover an area that is a patchwork of highly productive coral and less productive sandy areas. Estimates from the open ocean come from areas that are thousands of square kilometers in extent and may be very heterogeneous.

The lower end of the scale of fish yields from each ecosystem is not well defined. The less productive fisheries, which by necessity have fewer fishermen, tend not to have catch records. In one sense the lower end of the scale is zero because there are places where each of the ecosystems is not fished at all. Even with regard to potential yield, the lower end of the scale is very low if the spatial scale is fine enough.

The upper end of the scale is reflected in maximum sustainable yields (MSYs). There are limitations in estimating the upper end of the scale because the MSY of a particular fishery can be inferred reliably only from actual yield experiences. However, in many instances none of the yields have been large enough to give suitable information concerning the maximum. This may be because the fishery has never been intensive enough to approach the maximum. The small-scale fisheries that are found on many tropical lakes and seashores are restricted to the inshore areas, so that offshore areas remain unexploited.

It may also be that the stocks have not been fished in the intricate fashion that would evoke the highest yield. This may involve the kinds of fishing gear that are used and the species of fish that are being harvested. Any history of yields, including the maximum from that history, is specific to a particular technology and may be considerably below the maximum possible yield.

Whenever possible, MSYs were estimated by tabulating the total annual finfish catches (summed over all species) for different years or different locations and plotting the catches against the fishing effort in those years or locations. In the absence of such information, the yields of fisheries with intensive fishing were considered to be representative of their MSY. It is possible that the yields of some of the intensely fished fisheries were depressed by overfishing, but we do not consider this to be a serious error because heavy fishing of a multispecies fishery does not usually result in significant reduction of the total catch, provided fishing activities do not lead to habitat destruction or other degradation of the resource base. Finally, in the absence of intensive fishing, MSY was estimated to be one-half the virgin biomass multiplied by natural mortality (when available).

Among indicators of potential yield, particular attention is given in this report to primary productivity because of its biological relationship to fish yield, and where possible we have tabulated fish yield and primary productivity figures from the same fisheries. The estimates are highly imprecise because of the spatial and seasonal variation in primary productivity, but the relationship seems to be strong enough to show through. For some ecosystems we did not find primary productivity and fish yield figures for the same fisheries. In those cases we assembled information on the range of primary productivities in the ecosystem in order to compare it with the range of fish yields.

Results

Lakes, Reservoirs and Ponds

Table 1 lists a number of tropical lakes (primarily African) in order of their catch per unit area. There is a range of 0.1 to 23 t/km^2/year.

Toews and Griffith (1979) reported a significant negative correlation between fish catch per unit area and the size of African lakes. This relation is probably due in part to the fact that smaller lakes tend to have a higher percentage of shallow water, and shallow water generally has higher fish production than deep water. This is reflected in the observations of Kud-

Table 1. Fish yields from tropical lakes.

Lake	Location	Area (km^2)	Catch (t/ km^2/yr)	Source
Upemba	Zaire	530	23	Henderson and Welcomme (1974)
Yercaud*	India	.08	22	Oglesby (1977)
Kyoga	Uganda	2,700	18	Henderson and Welcomme (1974)
George*	Uganda	250	15	Ganf (1975)
Mwadingusha	Zaire	393	13	Henderson and Welcomme (1974)
Malombe	Malawi	390	13	Henderson and Welcomme (1974)
Guiers	Benin	170	13	Henderson and Welcomme (1974)
Ooty*	India	0.34	10	Oglesby (1977)
Tanganyika* (north)	Tanzania	3,575	8.9	Mann and Ngomirakiza (1973)
Mweru	Zaire	4,580	6.8	Henderson and Welcomme (1974)
Edward	Uganda	2,300	6.8	Henderson and Welcomme (1974)
Victoria* (inshore)	Kenya	1,300	6.2	Melack (1976)
Chilwa	Mozambique	1,750	5.6	Henderson and Welcomme (1974)
Kodaikanal*	India	0.26	5.3	Oglesby (1977)
Rukwa	Tanzania	2,000	4.9	Henderson and Welcomme (1974)
Lanao*	Philippines	—	4.8	Frey (1969)
Chiuta	Mozambique	113	4.4	Henderson and Welcomme (1974)
Albert*	Uganda	5,600	4.2	Cadwalladr and Stoneman (1966)
Mweru-Wa-Ntipa	Zaire	1,520	3.8	Henderson and Welcomme (1974)
Kitangiri	Tanzania	1,200	3.4	Henderson and Welcomme (1974)
Baringo*	Kenya	160	3.3	Melack (1976)
Malawi (Southern portion)	Malawi	6,000	2.5	Turner (1977a, b)
Victoria* (offshore)	Kenya, Uganda, Tanzania	41,200	2.1	Kudhongania and Cordone (1974)
Chad*	Chad	16,000	1.4	Welcomme (1972a)
Bangweulu*	Zambia	2,733	1.3	Toews and Griffith (1979)
Tumba	Zaire	1,767	0.6	Henderson and Welcomme (1974)
Maji Ndombe	Kenya	1,300	0.5	Henderson and Welcomme (1974)
Rudolf	Kenya	7,200	0.3	Henderson and Welcomme (1974)
Kiru	Tanzania	2,699	0.1	Henderson and Welcomme (1974)

*Catch and primary productivity data also used in Fig. 3.

hongania and Cordone (1974) on Lake Victoria and Turner (1977a, b) on Lake Malawi that fish stocks are significantly larger in the shallow peripheral portions of the lake than they are in the deep, central area.

The main reason that shallow water has higher fish production is that primary productivity is higher in shallow water due to the availability and recycling of nutrients for photosynthesis. It is quite likely, however, that an even higher percentage of the primary production passes to fish in shallow water because of the more significant role of the benthic food chain. This is because plankton and detritus have a better chance of sinking to the bottom without being captured by the pelagic food chain if the water is shallow (see Jones, this vol.). Benthic food chains tend to be shorter than pelagic food chains because many benthic invertebrates which eat sediment are large enough to be fish food, whereas pelagic food chains start with microscopic organisms and pass through a series of progressively larger organisms before reaching a size sufficient for fish food. More of the primary production is translated to fish production when the food chain is short.

Small lakes also tend to be more productive because the nutrients and detritus which pass into them from outside can make a significant contribution to the lake's productive capacity in comparison with the biological production that originates in the lake itself. Finally, small lakes tend to be more intensively exploited, whereas the offshore areas of a large lake are not easily accessible to the small-scale fisheries which exploit them.

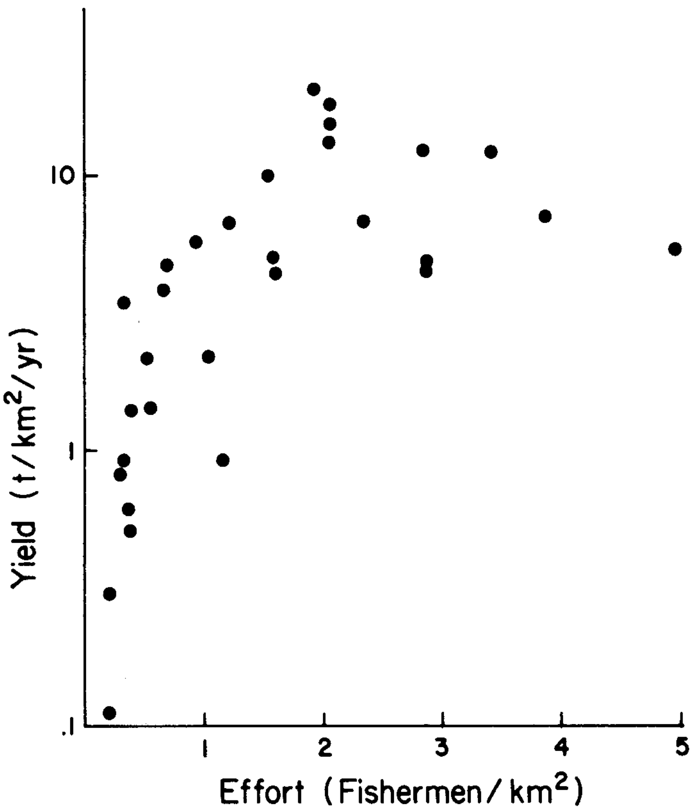

Fig. 1. Fish yields and fishing effort on African lakes (from Henderson and Welcomme 1974).

Although the yields in Table 1 vary by a factor of more than 100, the lower part of the range appears to correspond to lakes where the fishing intensity is not sufficient to yield a harvest near the maximum. Fig. 1 shows the relationship between fishing intensity (as measured by the number of fishermen per unit area) and catch per unit area for some African lakes. Since different lakes have different MSYs, it is not possible to infer the MSY simply as the maximum of the cluster of points in Fig. 1. However, Fig. 1 gives the impression that the range of MSYs may be approximately 1 to 23 $t/km^2/year$.

The main difference between reservoirs and lakes is that a reservoir was once a river or dry land before the river was dammed. As a consequence, a reservoir does not possess a full complement of lake fauna, even though the physical conditions of the reservoir are the same as those of a lake. This means that unless new fish are introduced, there may be parts of the reservoir that are virtually uninhabited by fish and their food, and the efficiency of translation of the reservoir's biological production to fish yields may be correspondingly reduced.

Fernando (1976) and Welcomme (1979) have reviewed the fish yields of reservoirs, and Table 2 lists the fish yields of some tropical reservoirs. The bottom end of the range is similar to that for lakes, but the upper end is 50% greater than for lakes. The upper end may be higher because many reservoirs can draw temporarily on the standing stock of trees and other plant materials which were inundated at the time the reservoir was formed. In addition, if the reservoir has an ecological vacuum, it is possible to introduce high-productivity fish such as the African cichlids and attain higher levels of production than would be possible with native fauna.

Henderson and Welcomme (1974) demonstrated a relationship between the morphoedaphic index (total dissolved solids/average depth) and fish yields in a series of African lakes. Although Fig. 2 shows a definite relationship between morphoedaphic index and yield, it is also apparent that most of the variation in yield is not explained by the morphoedaphic index.

Table 2. Fish yields from tropical reservoirs.

Reservoir	Country	Area km^2	Catch (t/ km^2/yr)	Source
Pacal	Indonesia	4	35	Sarnita (1976)
Pening	Indonesia	22	32	Sarnita (1976)
Dorma	Indonesia	4	28	Sarnita (1976)
Jombor	Indonesia	2	20	Sarnita (1976)
Lam praloung	Thailand	19	14	Chukajorn and Pawapootonan (1976)
Mwadingusha	Zaire	393	13	Henderson and Welcomme (1974)
Sirin thorn	Thailand	292	11	Chukajorn and Pawapootonan (1976)
Amaravathy*	India	9	11	Sreenivasan (1978)
Lam Poa	Thailand	230	11	Chukajorn and Pawapootonan (1976)
Sathanur*	India	13	10	Sreenivasan (1978)
Nzilo	Zaire	280	10	Henderson and Welcomme (1974)
Ayame	Ivory Coast	135	7.4	Henderson and Welcomme (1974)
Nam pung	Thailand	21	6.2	Chukajorn and Pawapootonan (1976)
Ubolratana	Thailand	410	6.0	Bhukuswan and Pholprasith (1976)
Prijetan	Indonesia	2	4.8	Sarnita (1976)
Volta*	Ghana	8,482	4.7	Henderson and Welcomme (1974)
Sentir	Indonesia	1	4.3	Sarnita (1976)
Kainji	Nigeria	1,270	4.2	Henderson and Welcomme (1974)
Kalen	Indonesia	1	4.0	Sarnita (1976)
Chulaporn	Thailand	12	3.3	Chukajorn and Pawapootonan (1976)
Tirumoorthy	India	5	2.8	Sreenivasan (1978)
Sandy Nulla	India	3	2.6	Sreenivasan (1978)
Stanley*	India	147	2.3	Sreenivasan (1978)
Lam takong	Thailand	44	2.2	Chukajorn and Pawapootonan (1976)
Jatiluhur	Indonesia	83	2.2	Sarnita (1976)
Nasser	Egypt	3,330	2.1	Henderson and Welcomme (1974)
Bhavanigasar*	India	79	2.0	Sreenivasan (1978)
Nam oon	Thailand	86	1.7	Chukajorn and Pawapootonan (1976)
Krishnagiri*	India	13	1.0	Sreenivasan (1978)
Kariba	Zambia	5,364	0.8	Henderson and Welcomme (1974)
Ghandi Sagar	India	660	0.7	Dubey and Chatterjee (1976)
Rihand	India	302	0.7	Natarajan (1976)
Nagaryanasagar	India	184	0.5	Natarajan (1976)
Konar	India	15	0.2	Natarajan (1976)
Tana	Kenya	3,500	0.1	Henderson and Welcomme (1974)

*Catch and primary productivity data also used in Fig. 3.

The morphoedaphic index has been reviewed by Ryder et al. (1974). The value of the morphoedaphic index for predicting fish yields presumably derives from its relationship with primary productivity. Total dissolved solids are related to the supply of nutrients required for primary production, and the depth of the water reflects the extent to which the nutrients are available at the lake surface where most of the primary production occurs. Of the two components of morphoedaphic index, depth is a better indicator of fish production than total dissolved solids (Matuszek 1978).

Melack (1976) and Oglesby (1977) have demonstrated a relationship between fish yields and primary productivity. We ran a multiple regression analysis of yield versus mean depth and primary productivity for the lakes and reservoirs in Table 3. The results indicated primary productivity to be a better predictor than depth. Comparing Fig. 3 with Fig. 2 suggests that primary productivity is also a better predictor of fish yields than the morphoedaphic index.

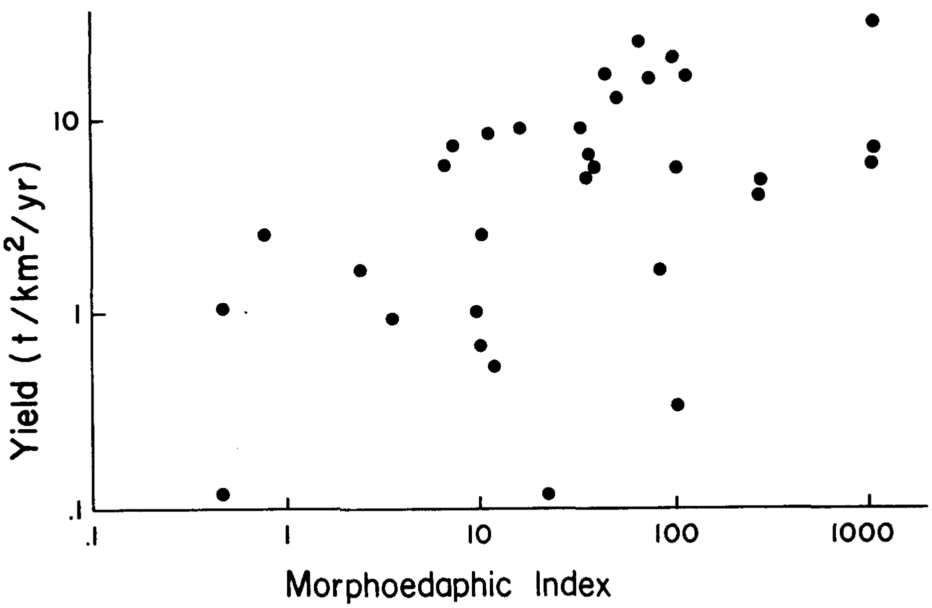

Fig. 2. Fish yields and morphoedaphic index (from Henderson and Welcomme 1974).

If a curve is put through the points in Fig. 3, it appears not to pass through the origin, suggesting that fish yields greater than zero are only possible once primary production exceeds a threshold. This would be expected from food-chain theory (Haussman 1971). There is also a suggestion of an upward curvature in Fig. 3, which implies that the efficiency of translation of primary production to fish production may be greater at higher levels of primary productivity. This may be because phytoplankton tend to be larger under highly productive conditions, requiring a shorter food chain (as particle size increases up the chain) in order to reach fish food size.

There is considerable variation in the fish yield (about fivefold) for any given level of primary productivity in Fig. 3. Part of the variation is undoubtedly due to errors in estimating yield and primary productivity, but it

Table 3. Physical and biological characteristics of some tropical lakes and reservoirs.

Lake	Primary productivity ($gC/m^2/yr$)	Depth (m)	Morphoedaphic index
George	1,500	2	83
Ooty	1,380	3	48-158
Amaravathy	1,175	12	4
Yercaud	1,060	2	55-100
Volta Res.	1,040	10	3
Tanganyika	1,040	330	2
Victoria (offshore)	1,000	63	2
Kainji	890	10	7
Albert	970	25	29
Volta	930	18	2
Victoria (inshore)	850	6	2
Bhavanigasar Res.	850	12	4-17
Stanley Res.	849	17	7-15
Sathanur	844	10	32-80
Krishnagiri Res.	565	5	47-108
Chad	370	4	103
Bangweulu	270	4	6
Baringo	200	7	83
Kodaikanal	160	2	14

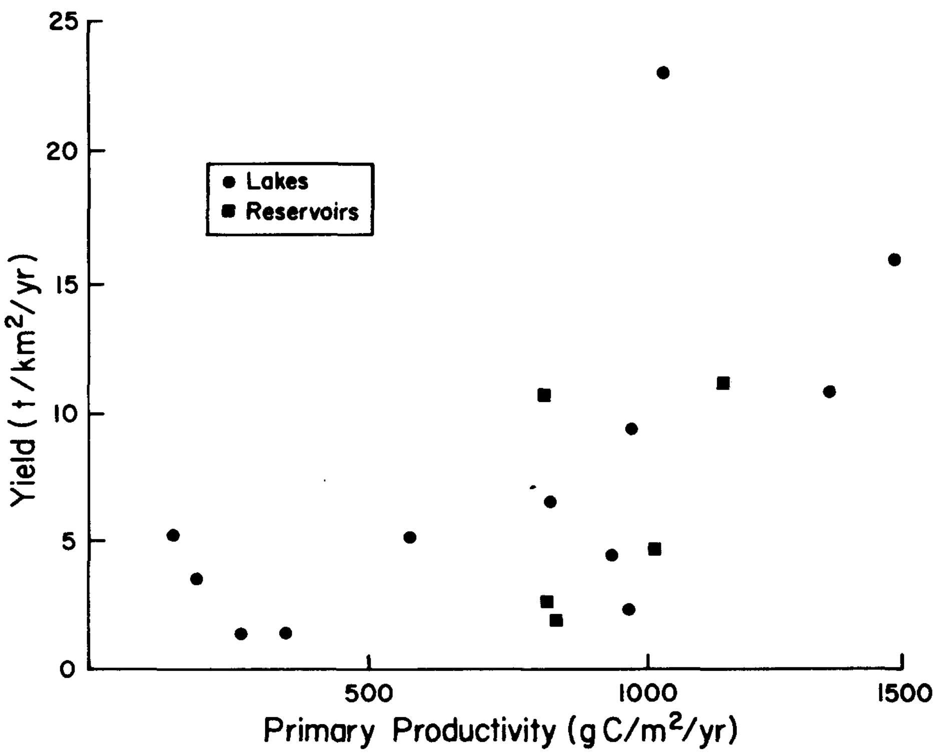

Fig. 3. Fish yields and primary productivity in tropical lakes and reservoirs, based upon lakes and reservoirs in Tables 1, 2 and 3 (r = .61).

appears the prediction would not be highly precise even in the absence of such errors. The loose relationship between primary productivity and fish yields is due in part to variation in the efficiency with which primary production is translated to fish yields. This may be due to the efficiency of the fishery (the fact that yield may be below MSY) or the efficiency with which primary production is converted to fish production through the food chain. Another limitation of primary productivity as a predictor is that the productivity of small lakes can derive in large measure from detritus and other organic materials that come from outside.

Oglesby (1977) explored other measures of the food available to fish as predictors of fish yield and found a closer correlation between yield and the standing crop of benthic fauna in temperate lakes. A similar relationship could have been sought for zooplankton and pelagic fish. The value of fish food abundance as a yield predictor may be limited, however, because the same standing stock of fish food could have a low or high production depending upon whether or not it is intensely harvested by the fish (Hayne and Ball 1956).

Fishponds, intensively managed with fertilization but without food supplementation, can show fish yields as high as 120 t/km^2/year (Bardach et al. 1972). This is partly due to the fact that the primary productivity of intensively managed ponds can be as much as three times the maximum primary productivity of lakes. It is also because fishponds can be stocked with fishes, such as carp and tilapias, which are highly efficient at translating primary production to yields. The yield from ponds can also be very high because they lack the predators which compete with fishermen for the fish harvest in natural water bodies such as lakes and rivers. The relationship between yield and primary productivity can be very close in fishponds (Fig. 4).

Rivers

Welcomme (1979) has reviewed the fisheries ecology of rivers. Table 4 lists the yields of some tropical rivers. Fig. 5 shows the relation between fish yields and the number of fishermen on some tropical rivers.

Rivers show a broader range of yields than lakes. The low end of the range in yields for rivers is lower than for lakes, and is associated with headwaters in areas of highly weathered soils which have a very low primary productivity and a correspondingly low fish production. The high end of the range for rivers is slightly higher than for lakes, even though the primary productivity of rivers is generally lower than that of lakes. The explanation may lie in the fact that rivers receive from the large watershed area that surrounds them a significant quantity of nutrients and organic material which contributes to the biological productivity of the fishery. Moreover, many of the rivers with high yields are flood-plain rivers that can draw upon the terrestrial productivity of the areas they flood, and the highest yields in Table 4 are probably due in large measure to the quantity of municipal sewage received by those rivers. Welcomme (1979) found the best predictor of fish yields from a river to be the total area of its drainage basin.

Rivers may also have relatively high yields because even large rivers are easier for fishermen to exploit fully than are large lakes. Furthermore, many of the fish that are caught in rivers have moved into them from lakes or the sea, so their growth has occurred primarily in ecosystems outside the river.

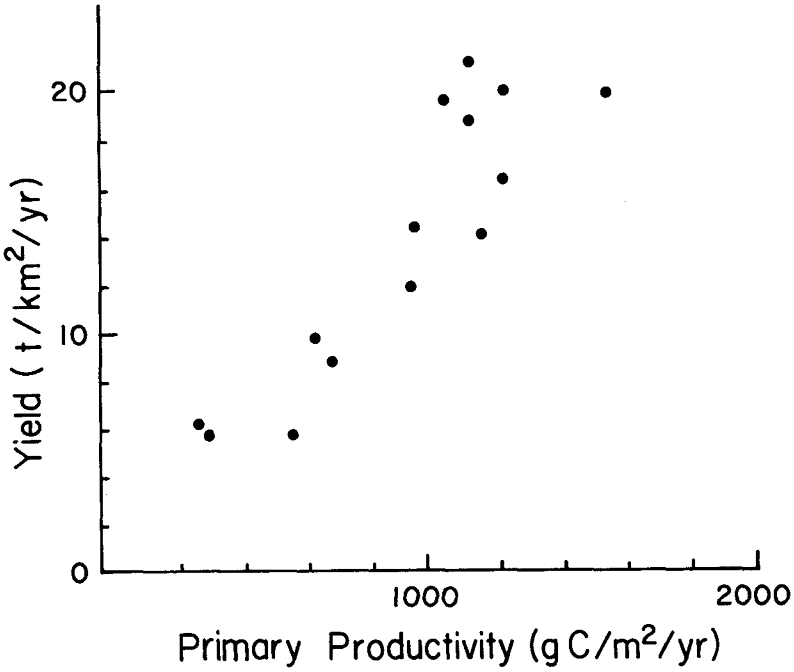

Fig. 4. Fish yields and primary productivity in tilapia ponds, based upon Almazan and Boyd (1978) (r = .89).

Table 4. Fish yields from tropical rivers.

River	Location	Catch[a]	Source
Ganges	Bangladesh	78	FAO (1976)
Niger	Benin[b]	44	Welcomme (1972b)
Lower Mekong	Viet Nam	41	R. Welcomme, pers. comm.
Mahaweli	Sri Lanka	34	Indrasena (1970)
Lubuk Lampan	Indonesia	24	Arfin and Arfin (1976)
Shire	Mozambique	13	R. Welcomme, pers. comm.
Kamulondo	Zaire	11	Poll and Renson (1948)
Oueme	Benin[b]	10	CTFT (1957)
Oueme	Benin[b]	6.5	Welcomme (1972b)
Niger	Niger	5.2	Dobrovici (1971)
Central Delta	Niger	4.5	Konare (1977)
Senegal	Senegal	4.3	Reizer (1974)
Pendjari	Benin[b]	3.5	Welcomme (1972b)
Magdalena	Colombia	3.3	Bazigos et al. (1977)
Benue	Nigeria	3.1	Mothwani (1970)
Niger	Nigeria	3.0	Mothwani (1970)
Kafue	Zambia	2.0	Zambia (1965)
Rufiji	Tanzania	1.9	R. Welcomme, pers. comm.
Kafue	Zambia	1.6	Zambia (1971)
Cross	Nigeria	1.0	R. Welcomme, pers. comm.
Barotse	Zambia	0.7	Zambia (1974)
Okawango	Namibia[c]	0.5	R. Welcomme, pers. comm.
Upper Amazon	Brazil	.02	FAO (1979)

[a] In t/km of river reach.
[b] Formerly Dahomey.
[c] Formerly S.W. Africa.

Estuaries and Lagoons

Estuaries and coastal lagoons have a mixture of freshwater and saltwater that may vary considerably in salinity at different times of the year. An estuary is subject to tidal mixing whereas a lagoon is not. Estuaries can have considerable impact on the adjacent marine fisheries because they serve as nursery areas for many fish that move out to sea at a later stage in life. Estuaries and lagoons are usually shallow, only a few meters in depth, and secondary production is often concentrated in the sediment (with its short benthic food chains) rather than in the water column. The sediment has an important role, even though it often does not itself contribute the major portion of the primary production (particularly when the water is turbid).

Saila (1975) has reviewed the ecology of estuarine fish production and Hickling (1970) has reviewed estuarine fish culture. Table 5 lists the fish yields of some tropical coastal lagoons and estuaries. The yields from both estuaries and lagoons are generally higher than the yields from lakes and rivers. This is due partly to the shallowness of estuaries and lagoons and partly to the nutrients they receive from rivers. It may also be due to the large quantity of plant materials they receive from their shoreline. This is particularly so for estuaries that are bordered by mangroves. The highest fish yields in estuaries and lagoons occur where intensive aquaculture is practiced.

Continental Shelf

Table 6 shows the demersal and pelagic MSYs of the fisheries of continental shelves on a broad geographic scale. In general, the pelagic and demersal components make similar contributions. The highest MSYs occur with anchovies and herring, which are species with short food chains, in upwelling areas which show the highest levels of primary production recorded in oceanic waters.

Table 7 shows the estimated MSYs of some demersal multispecies fisheries in tropical coastal areas, and Fig. 6 illustrates the information behind some of the catch-effort MSY estimates in Table 7. A regression analysis of MSY against primary productivity and depth showed a significant relation only with depth (Fig. 7), the higher MSYs appearing at depths less than 50 m. There was a weak positive correlation between primary productivity and fish yields ($r = 0.24$), but primary productivity explained none of the variation in yields beyond what was explained by depth. It is worth noting that Qasim (1979) found the average primary production of Indian coastal waters shallower than 50 m to be about six times that in waters deeper than 50 m. The MSYs above and below 50 m in Table 7 differ in about the same proportion.

Table 8 presents estimated MSYs for some tropical continental shelf pelagic fisheries. These MSYs have a significant relationship with primary productivity (Fig. 8), but not with mean depth. It is interesting to note that this is the opposite of demersal fisheries, where mean depth rather than primary production best predicted yields. An explanation for the stronger correlation between pelagic yields and primary productivity may be the direct connection of pelagic fish to the planktonic food chain (Petersen and Curtis 1980), whereas demersal fish may have much less direct connection to

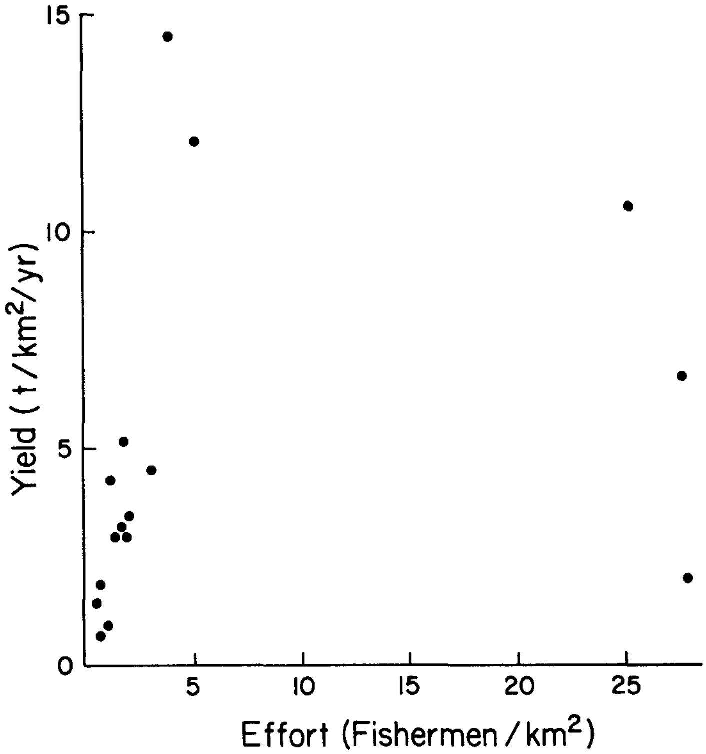

Fig. 5. Fish yields and fishing effort on tropical rivers (from Welcomme 1976).

Table 5. Fish yields from tropical estuaries and coastal lagoons.

Name of water body	Country	Area (km^2)	Catch (t/ km^2/yr)	Source
—	Taiwan (China)*		94-250	Lin (1968)
Aheme	Benin*, **	85	86	Welcomme (1972b)
—	India*		86-124	Pakrasi et al. (1964)
Nakove/Pio Novo	Benin*, **	157	56	CTFT (1969)
—	Philippines*		50-100	Frey (1947)
—	Philippines*		50	Tang (1967)
—	Philippines*		47	Rabanal (1961)
Ovidah, Grand Popo, Awo channel	Benin*, **	14	28	Welcomme (1972b)
—	Singapore*		25	Le Mare (1949)
—	Hawaii*		20	Cobb (1901)
Ebrié	Ivory Coast	556	16	Durand et al. (1978)
Sakumo	Ghana	1	15	Pauly (1976)
—	Java*		14-63	Schuster (1952)
Unare	Venezuela	54	14	Okuda (1965)
—	Morocco		13	Belloc (1938)
Cienaga Grande	Colombia	450	12	INDERENA (1974)
—	India		11-17	Pillay (1954)
Tacarigua	Venezuela	63	11	Gamboa et al. (1971)
Piritu	Venezuela	22	5.8	Carvajal (1972)
Mandapam	India	4	5.6	Tampi (1959)
Tamiahua	Mexico	659	4.7	Garcia (1975)
Chillca	India	1,036	3.7	Jhingran and Natarajan (1969)
Pangalanes	Madagascar	98	3.7	Lasserre (1979)
Anony	Madagascar	23	2.8	Moulherat and Vincke (1968)
Pulicat	India	392	2.6	Jhingran and Gopalakrishnan (1973)
Maracaibo	Venezuela	14,344	1.9	Nemoto (1971)
Jiquilisco	El Salvador	121	1.7	Hernandez and Calderon (1974)

*Includes aquaculture (without fertilization or feeding).
**Formerly Dahomey.

the primary production in the water column above. The lack of correlation between pelagic yields and depth may also be because coastal pelagic fishes probably range over a larger geographic area than demersal fish, so the depth in the area they are fished may not accurately represent the mean depth of their entire habitat.

Yesaki (unpub. data) observed a positive association between total multispecies fish yields and primary productivity when comparing a number of tropical and temperate continental shelf fisheries. He also observed a negative association between total yields and the number of species in the fishery.

Coral Reefs

The coral reef is an ecosystem in which the reef surface provides a substrate for growth of algae, both free-living and symbiotic with coral polyps. This fosters the maximum biological production possible within the limits of nutrients available in the surrounding water.

Table 6. Estimated maximum sustainable yields (t/km^2/year) for tropical continental shelf areas (from Gulland 1971 except where noted otherwise).

Region		Minimum			Maximum	
	Pelagic	Demersal	Total	Pelagic	Demersal	Total
NE Atlantic	0.8	0.6	1.4	7.3	8.0	15.3
NW Atlantic	1.8	1.8	3.6	7.0	7.0	14.0
NW Pacific	0.6	1.7	2.3	8.5	4.0	12.5
Indian Ocean[a]	0.7	1.4	2.1	4.3	5.5	9.8
E Central Atlantic	4.0	1.2	5.2	5.0	2.5	7.5
South China Sea[b]	0.2	0.8	1.0	2.4	4.3	6.7
W Central Atlantic	0.7	0.2	0.9	3.2	2.5	5.7
		Upwelling				
SW Atlantic	1.5	6.0	7.5	17.5	10.0	27.5
Peru[c]	—	—	—	1.0	21.9	22.9

[a]Yesaki (unpub. data).
[b]Menasveta et al. (1973).
[c]Murphy (1972).

Table 9 lists the fish yields of some coral reefs. The range is similar to that for other continental shelf fisheries, despite the higher primary productivity of coral reefs. Marshall (1980) reviewed potential fish yields from coral reefs and found a range of 0.8 to 5 t/km^2/year (see Fig. 9). He noted the observation of 14-20 t/km^2/year* for an intensively exploited reef in the Philippines (Alcala 1981) but questioned the generality of that observation. However, recent work by Wass (in press) on an intensively exploited reef in Samoa has estimated the finfish yield to be 18 t/km^2/year, suggesting that some of the lower estimates from previous studies may not reflect the yields of fully exploited reef systems. Fig. 10 shows the relation between the number of fishermen and the yield which has been realized on some coral reef fisheries.

*Editorial note: Marshall (1980) cites Alcala as having suggested a figure of 15 tonnes/km^2/year; it is the actual figures given by Alcala (1981) which are given here.

Table 7. Estimated maximum sustainable yield of tropical demersal marine fisheries.

Location	MSY ($t/km^2/yr$)	Depth (m)	Area (km^2)	Primary productivity ($gC/m^2/yr$)[a]	Estimation method	Source
North Coast Gulf of Mexico	6.7	0-110	111,210	135	Research Survey (0.5 B_o)	Klima (1977)
U.S. Atlantic Coast (N. Carolina—Florida)	5.5	0-110	125,000	135	Research Survey (0.5 B_o)	Klima (1977)
Gulf of Thailand	3.9	0-50	179,000	365	Catch vs. Effort (Fig. 6a)	SCS (1978)
Philippines	2.8	0-200	152,700	135	Research Survey (0.5 B_o)	Aoyama (1973)
North Coast of Java	2.6	0-50	26,160	180	Catch vs. Effort (Fig. 6b)	SCS (1979)
Sunda Shelf—South	2.3	0-50	267,900	75	Research Survey (0.482 B_o)	SCS (1978)
South China Sea	2.0	0-200	500,000	45	Research Survey (0.5 B_o)	Aoyama (1973)
West Coast of Florida	1.8	0-110	179,280	135	Research Survey (0.5 B_o)	Klima (1977)
Sunda Shelf—NW Borneo	1.7	0-50	62,900	75	Research Survey (0.482 B_o)	SCS (1978)
South Coast of Kalimantan (Borneo)	1.5	0-50	113,590	135	Research Survey (0.5 B_o)	SCS (1979)
Sunda Shelf—NW Borneo	1.1	50-200	69,700	75	Research Survey (0.482 B_o)	SCS (1978)
Gulf of Thailand	1.1	50-200	126,700	365	Research Survey (0.482 B_o)	SCS (1978)
Sunda Shelf	0.8	50-200	398,500	135	Research Survey (0.482 B_o)	SCS (1978)
U.S. Atlantic Coast (N. Carolina—Florida)	0.5	110-548	20,480	45	Research Survey (0.5 B_o)	Klima (1977)
North Gulf of Mexico	0.5	110-548	44,070	45	Research Survey (0.5 B_o)	Klima (1977)
West Coast of Florida	0.4	110-548	72,120	45	Research Survey (0.5 B_o)	Klima (1977)

[a]Primary productivity estimated from a world map in FAO (1972).

As a reef fishery is generally a patchwork of coral reef (which is highly productive) and sandy bottom (which is not so productive); the yield per unit area that is calculated for a reef can depend very much upon the size of the area and the percentage of that area which is actually covered by coral or other hard substrate. Some fisheries records cover a large area of many square kilometers, only part of which is actually covered by coral, whereas other records of fish yields apply to very small areas that are entirely coral reef. The productivity of a reef may also vary with the complexity of its vertical structure.

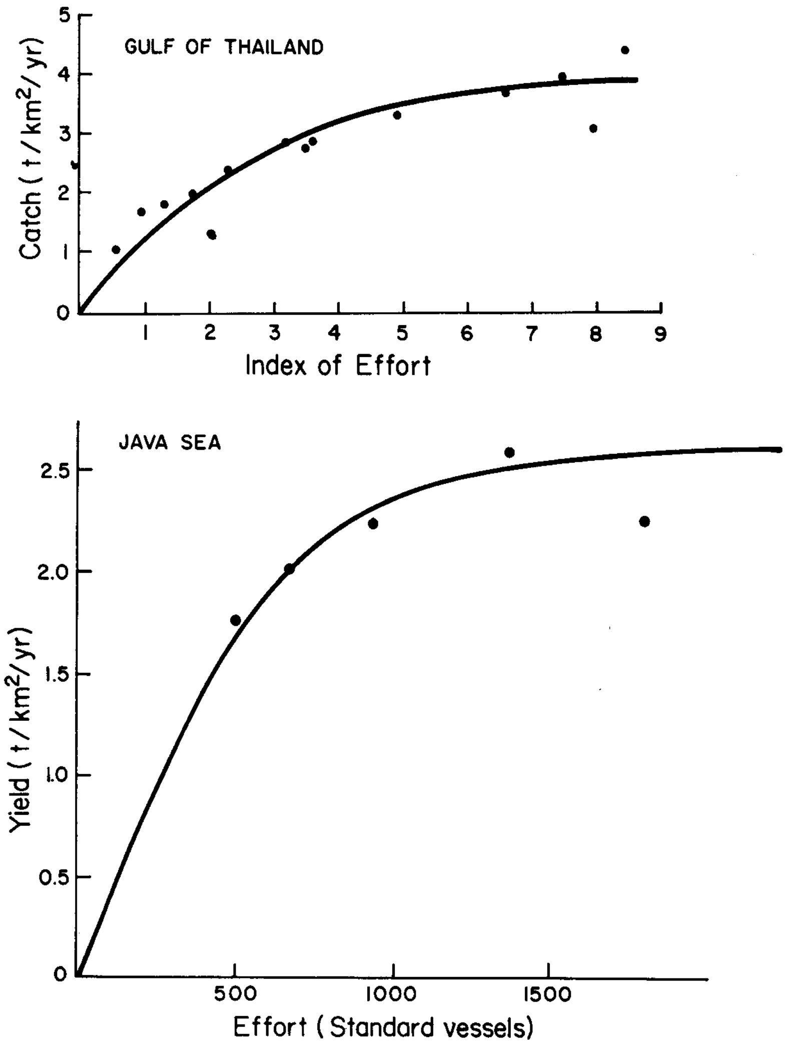

Fig. 6. Estimation of maximum sustainable yield for continental shelf demersal fisheries (from SCS 1978 and SCS 1979). The points in the graph represent different years in the history of the fishery.

Table 8. Estimated maximum sustainable yields of tropical pelagic fisheries.

Location	MSY ($mt/km^2/yr$)	Depth (m)	Primary productivity ($gC/m^2/yr$)	Estimation method	Source
Java Sea (N. Coast of Java)	6.02	0-50	180	0.5 B_o	SCS (1979)
South Atlantic	4.43	0-550	135	Research Survey (0.5 B_o) and Landings	Klima (1977)
Sumatra (West Coast)	4.28	0-40	130	Research Survey (0.5 B_o)	SCS (1979)
India (West Coast)	3.58	0-50	180	1978 Landing	Anon. (1979)
Malaysia (West Coast)	3.38	0-100	130	Landing 1973-1974	Yesaki (unpub. data)
Gulf of Mexico (coast)	3.20	0-550	90	Research Survey (0.5 B_o) and Landings	Klima (1977)
Atlantic (South America)	2.35	0-550	135	Research Survey (0.5 B_o) and Landings	Klima (1977)
India (East Coast)	1.98	0-50	180	1978 Landing	Anon. (1979)
India (West Coast)	1.03	0-200	135	1978 Landing	Anon. (1979)
Thailand (West Coast)	1.02	0-100	55	Research Survey (0.5 B_o)	SCS (1976b)
South China Sea	0.81	0-500	45	Research Survey (0.5 B_o) and Landings	SCS (1973)
India (East Coast)	0.70	0-200	90	1978 Landing	Anon. (1979)
Philippines (offshore)	0.55	200 and more	110	Research Survey (0.5 B_o) and Landings	Menasveta et al. (1973)

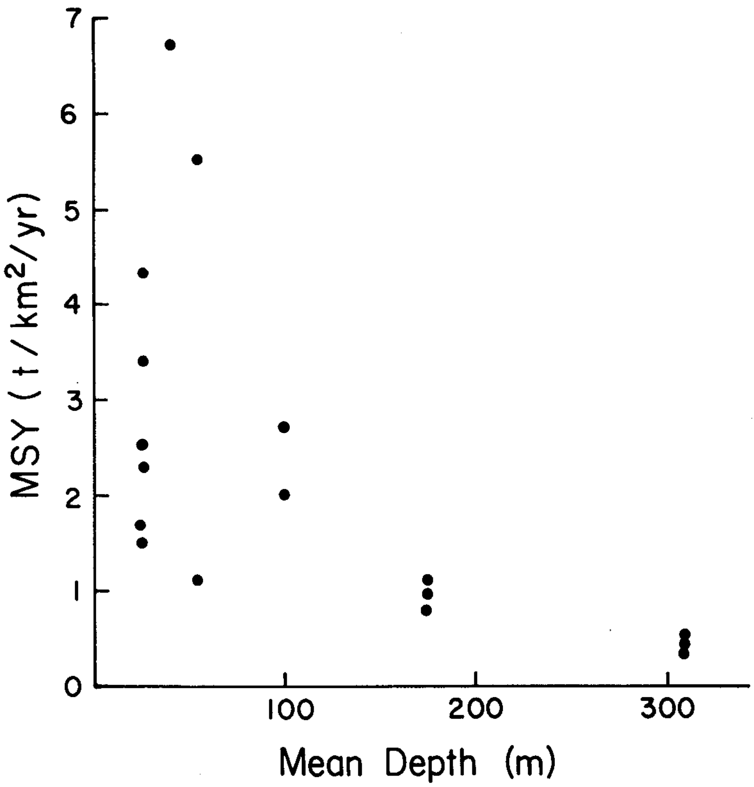

Fig. 7. Maximum sustainable yields and depth of continental shelf demersal fisheries, based on Table 7 (r = .86).

Open Ocean

Annual catches of tunas and billfishes by Japanese vessels in the western tropical Pacific, aggregated by 10-degree squares (data on file at the National Marine Fisheries Service, Southwest Center, Honolulu Laboratory) show a range of yields from 0.0025 to 0.04 $t/km^2/year$, with an average yield of 0.016 $t/km^2/year$. (This is an underestimate of the total catch because Korean vessels also fish this region but are not included in the statistics.) Catches of tunas and billfishes in the eastern tropical Pacific (Calkins 1975) suggest a range of yields from 0.002 to 0.04 $t/km^2/year$, with an average of 0.024 $t/km^2/year$. Finally, catches of tunas and billfishes in the 10-degree squares in the tropical Atlantic off the coast of Africa (ICCAT 1980) are as high as 0.05 $t/km^2/year$. The range of existing yields in the open ocean does not extend much below the range of MSYs for that ecosystem because much of the open ocean, like much of the continental shelves, is fished intensively by sophisticated fishing fleets.

Discussion

Relationship between Yields and Ecosystem Types

Fig. 11 summarizes the ranges of primary productivities and fish yields encountered in various tropical ecosystems. The range of fish yields is

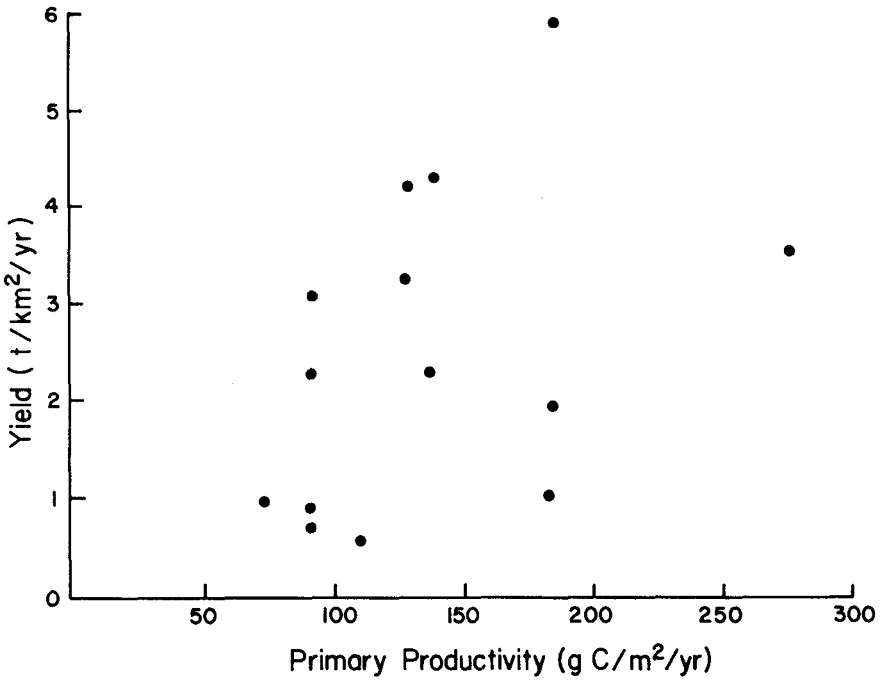

Fig. 8. Maximum sustainable yield and primary productivity of continental shelf pelagic fisheries, based on Table 8 (r = .61).

Table 9. Yields from coral reef fisheries.

Location	Area (km^2)	Catch (t/km^2)	Source
Samoa*	3	18[b]	Wass (in press)
Philippines	1	18[b]	Alcala (1981)
Samoa		8[b]	Hill (1978)
Ifaluk* (Pacific)	6	5.1	Stevenson and Marshall (1974)
East Africa		5[c]	Gulland (1979)
Mauritius*	350	4.7[a]	Wheeler and Ommanney (1953)
Fiji		4.4[a]	Bayliss-Smith (pers. comm.)
Jamaica*	2,860	4.1[c]	Munro (1978)
Bahamas		2.4[a]	Gulland (1971)
Puerto Rico*	2,300	0.8[b]	Juhl and Suarez-Caabro (1972)
Kapingamaringi* (Pacific)	400	0.7[b]	Stevenson and Marshall (1974)
Cuba*	55,000	0.5	Buesa Mas (1964)
Lamotrek* (Pacific)	44	0.45[b]	Stevenson and Marshall (1974)
Bermuda*	1,035	0.4	Bardach and Menzel (1957)
Raroia* (Pacific)	400	0.09	Stevenson and Marshall (1974)

*Catch and fishing effort appear in Fig. 10.
[a]MSY based on catch-effort relation over series of years.
[b]Probably near the MSY because of heavy fishing intensity.
[c]See Fig. 9.

different in each of the ecosystems, but the ranges are so broad that most of the ecosystems overlap considerably. As a consequence, ecosystem type alone is not a precise predictor of the potential yield of a particular fishery, at least at the coarse level of ecosystem classification employed here.

There is a positive association in Fig. 11 between the primary productivities of ecosystems and their fish yields, but the relation is not very tight. Some ecosystems with similar primary productivities have very different fish yields, and other ecosystems with similar fish yields have very different primary productivities. Furthermore, the overall range of fish yields through all ecosystems is much greater than the overall range of primary productivity, indicating that fish yield is not simply responding in proportion to primary productivity regardless of the ecosystem. Primary productivity is not useful to predict fish yields unless the ecosystem is specified.

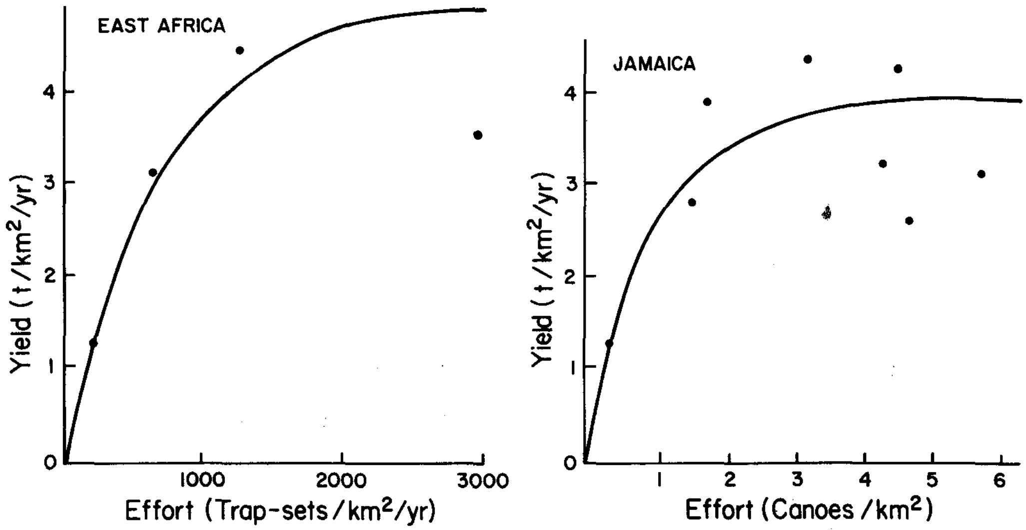

Fig. 9. Estimation of maximum sustainable yields for coral reefs [from Munro 1978 (Jamaica) and Gulland 1979 (East Africa)]. The points in the graphs represent different reef fishing locations in the same geographic area.

Table 10 shows the estimated range of efficiencies with which primary productivity is turned into fish yields in each of the ecosystems. (The real range in efficiencies for each ecosystem is probably more narrow because measurement errors would tend to broaden the range.) Lakes and reservoirs are quite similar. Rivers can have a higher efficiency, but it may be an artifact due to external inputs. The limited information on lagoons and estuaries indicates that the lower end of their range falls within the same range of efficiencies as lakes. The upper end is higher because of intensive aquaculture. Continental shelf fisheries appear to have a slightly higher efficiency than lakes, while upwelling areas have much higher efficiencies due to short food chains. The efficiency of coral reefs, which typically have a multitude of species, can be somewhat lower than the rest of the continental shelf. The efficiency of open oceans is less by an order of magnitude, presumably because of longer food chains.

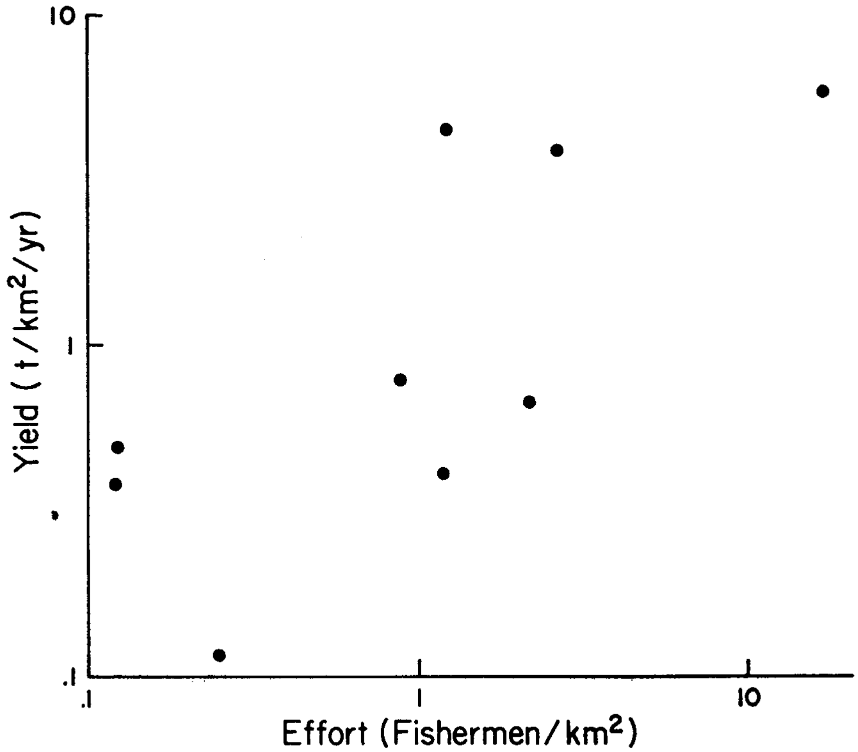

Fig. 10. Fish yields vs. fishing effort in coral reefs (based upon reef data in Table 9).

One reason the ecosystems appear to differ in their efficiencies is because some of them can exploit primary production that is elaborated outside the ecosystem, whereas others do not have an input of such materials. If the total productivity base of each ecosystem—including both primary production and organic matter from outside—were used in place of primary production alone, the relation between the productivity base and potential fish yield might be more universal regardless of the ecosystem. However, even with a better measure of the productivity base, different ecosystems could still differ in the food-chain structure which determines the efficiency of translating the resource base into fish yields.

Ecosystem and primary productivity can together predict potential fish yields better than either one alone. Nonetheless, there is considerable variation in yields that remains unexplained even when both are taken into account (Figs. 3 and 10), though it is possible the predictions could be more precise if the ecosystem classification were more refined. Even though such predictions can be helpful for rough inventories of potential fish yields, it is unlikely they will ever be precise enough for managing particular fisheries in the absence of other information about yields.

Yield Assessment and Management

The potential fish yield from an ecosystem cannot be inferred from catch records without reference to the fishing effort behind those records. The relationship between catch and effort is customarily displayed by means of graphs where different levels of effort are found at different locations within the same fishery (e.g., Fig. 9) or where different levels of effort have occurred at different times in the history of the fishery (e.g., Fig. 6). It is possible from catch-effort graphs to see if the fishing effort has been intense enough for the potential yield of the fishery to be expressed in actual yields. However, the yield from a multispecies fishery is not only a matter of how much fishing, but also what kind of fishing. Potential yields from different ecosystems can only be assessed in this context.

Table 10. Ratio of fish yields to primary productivity.[a]

Ecosystem	Range	Geometric mean
Coastal upwelling	.005 - .013	0.0081
Rivers	.005 - .01	0.0071
Ponds	.001 - .01	0.0032
Lagoons and estuaries	.0008 - .01	0.0028
Continental shelf	.0003 - .003	0.00095
Lakes	.0004 - .0016	0.00080
Reservoirs	.0002 - .002	0.00063
Coral reefs	.0002 - .0008	0.00040
Open ocean	.00001 - .0002	0.000045

[a]The ratios in this table are based on primary productivity estimates in Bunt (1975), Beadle (1974), Conner and Adey (1977), Cushing (1969), Edwards (1978), Gerlotto et al. (1976), Hempel (1973), Kaliyamurthy (1973), Kinsey (1979), Koblentz-Mishke et al. (1970), Likens (1975), Plante-Cuny (1977), and Rodriguez (1963). The ratios were calculated as the carbon yield of fish (assumed to be one-tenth of wet weight) divided by primary productivity (in carbon units).

There are two principal ways that the total harvest from a multispecies fishery can be increased by manipulating the kind of fishing:

— more intricate harvesting;
— restructuring the food web.

We have already observed that the highest yields from coral reefs occur where there is intense, intricate fishing. Higher yields can also be achieved by altering food web structure by:

— shortening the food chain between primary production and fish production;
— reducing fish consumption by predators which compete with fishermen.

Examples are the introduction of herbivorous or sediment-feeding fish to a fishery or the implementation of special measures to reduce predation (e.g., cage culture or intense fishing of predators).

The fishery of Lake Victoria (East Africa) illustrates these points. Lake Victoria has a multispecies fishery (12 commercial genera and more than a hundred species) which, like many other inland fisheries, shows signs of overfishing: declining fish sizes and disappearance of major commercial species. The diversity of fishing intensities and fishing gear around the shoreline of Lake Victoria has led to a similar diversity of yields and species composition in the catch. The result is a series of unplanned "experiments", which Marten (1979a, 1979b) has analyzed statistically to summarize the impact upon the stocks of the amount of fishing and the kind of fishing. The main interpretive tool was a curvilinear regression of catch versus effort,

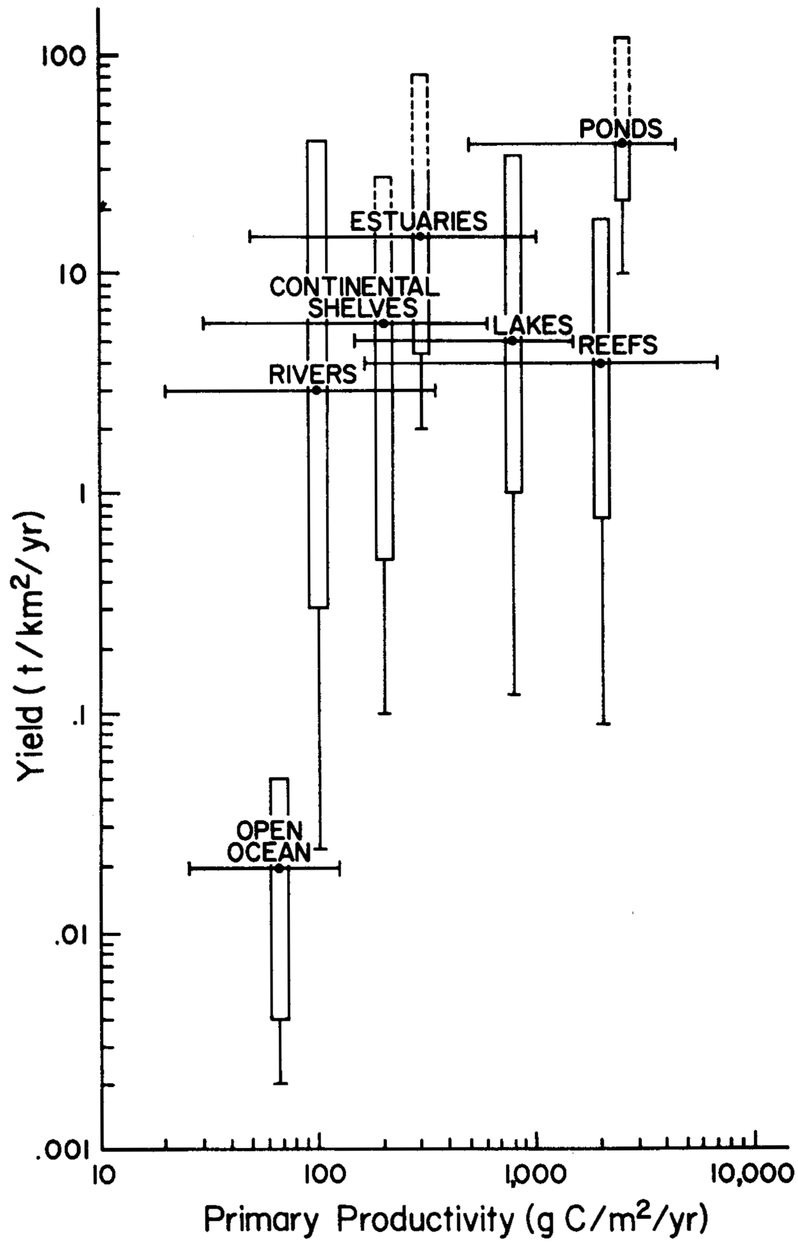

Fig. 11. Ranges of fish yields and primary productivities in various tropical ecosystems. Dots at the intersection of ranges represent modal values. Thickened portions of the bars represent the range of maximum sustainable yields. Dashed projections at the top of the ranges for estuaries and ponds represent elevated yields from aquaculture with fertilization (but not supplemental feeding). The dashed projection for continental shelves represents higher yields which occur in areas of upwelling. Primary productivity estimates are based on the references listed in Table 10.

in which the total catch (summed over all species) occupied one dimension and effort occupied six dimensions corresponding to six categories of fishing gear.

Above a certain fishing effort, the total multispecies catch in Lake Victoria is not affected much by fishing effort *per se*, but it is very much affected by the kind of fishing gear employed. There is no mix of gear which is optimal for all species in the fishery. What is optimal for one species may underexploit or destructively exploit another species. Fishing gear also has indirect ecological effects upon fish species that may not even be captured by that kind of gear, because of predation and competition, and these effects may lead to successional changes in the species composition of the fishery.

The optimal mix of gear for the fishery as a whole is a compromise. In the case of Lake Victoria, the optimal mix emphasizes intensively harvesting species at the end of short food chains (which are part of Lake Victoria's native fish fauna) and fishing down large fish that prey upon these species. There is no indication that even the heaviest fishing leads to lower yields if the optimal mix is employed. This suggests the practical conclusion that maximizing the yield from a multispecies fishery may be as much a matter of developing the infrastructure to encourage the right kind of intensive fishing as of restricting fishing practices which appear harmful.

Most of the management attention in fisheries to date has been devoted to yields, but the management of multispecies fisheries may be equally a matter of insuring a desirable species composition in the fishery. Although heavy fishing may not in itself significantly reduce the total yield from a multispecies fishery, it is quite common for heavy fishing (or the wrong kind of fishing) to change the composition, and therefore economic value, of the fishery. A change in species composition can also influence total yields to some extent because of food chain and predation effects.

A Habitat Perspective

A finer view of aquatic ecosystems than has been customary for fisheries purposes will be necessary for more effective management and yield assessment of multispecies fisheries. Substrate type is one way of distinguishing different habitats within the broader ecosystem, and Wanjala (1978) has shown that different sections of the Lake Victoria shoreline with different substrates (e.g., stony or muddy) are inhabited by different fish communities. The same is true in Hawaii, where different demersal fish communities are found at different depths offshore (Ralston and Polovina, in press); and different inshore substrates, such as lava and sand, each have their characteristic fish communities, potential yields and management needs, even though all are part of the broader shore ecosystem (Hawaii Coastal Zone Fisheries Management Program 1980). Each of these habitats has its own characteristic fisheries succession in response to fishing and each requires specific management decisions.

A habitat approach emphasizes attention to species composition (including a classification of fish communities), how different fish communities are associated with different habitats, and how community composition responds to human activities (including fishing practices) that impinge upon the fishery (Smith et al. 1973; Marten 1981). This perspective does not mean that massive amounts of quantitative data are required in much more detail than before. The data need only be roughly quantitative, but they must be sensitive to species composition. (This approach to species management is analogous in many respects to range management, where attention is given to forage species composition and how this changes under grazing pressure.) Habitats can be mapped (Aecos 1979), and because fishermen are generally precise about where they fish, it is possible at least in theory to maintain catch records on a habitat basis.

A habitat perspective in multispecies fisheries management and assessment may mean that the maintenance of habitat quality will be as important as the regulation of fishing effort. Although the production of a multispecies fishery can be manipulated to some extent by adjusting the harvesting regime, the yield from that fishery can be reduced immensely by habitat destruction. This includes destructive fishing practices such as the use of dynamite, poisons, and seines and trawls that scrape across the bottom and disrupt the production of fish food or spawning of fish. Equally important, however, are non-fishing activities that may cause even more serious destruction of fishery habitat, such as the siltation of coral reefs due to runoff from mining activities or pollution due to sewage, industrial effluents or oil spills. Pollution problems will increase as industrialization increases in the tropics, particularly under impetus from some countries to transfer their most polluting industries to developing countries.

This kind of fisheries management and assessment is complicated. It is not realistic to depend upon ecological theories to predict what will happen in every specific situation. Multispecies fisheries management and yield assessment will have to remain empirical, based on observations of how fish community composition and yields change under different circumstances, taking advantage of "experiments" provided by existing fishing activities in different places with different fishing conditions and different histories. It will have to be pragmatic and adaptive in the sense described by Holling (1978) for adaptive environmental management, relying upon monitoring to anticipate unwanted "surprises", and developing new approaches for keeping options open in dealing with such surprises.

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Discussion of the Paper by Drs. Marten and Polovina

Dr. Gulland suggested that a graph of total catch/km^2/year versus the number of fishermen/km^2, as in Fig. 1, may be of more use than the authors assumed. If a fishery approaches its maximum yield at the same density of fishermen, regardless of how large or small the MSY may be, then the cluster of level points in Fig. 1 would suggest that yields approximate the MSY whenever there are two or more fishermen/km^2. This question deserves further study. However, Dr. Marten was still of the opinion that lakes with a very low level of production could reach their maximum yield at a significantly lower number of fishermen.

Dr. Gulland asked what area was being used for river fisheries, and Dr. Marten replied that it was the area covered by the river at flood level. Dr. Gulland felt that it could make a big difference if the flood plain is included because it can add considerable production to the river.

Dr. Larkin commented that the level of exploitation of a lake depends very much on its location in relationship with the people who exploit it, citing the lakes in the north of Canada which are virtually unexploited because there are so few people around them. Dr. Sainsbury added that it is also a matter of what people are willing to do with the fishery. He wondered what yields would be like in the open ocean if people were prepared to eat myctophids or in coral reefs if they would eat pomacentrids. He has MSY estimates for the Australian northwest shelf that range from 4,000 t/year for an Australian-style fishery based on harvesting only large fish, to 30,000 t, if one is prepared to fish everything that is there.

Mr. Jones was impressed with the high productivity of shallow lakes and noted the importance of shallow, inshore areas as fish nursery areas. The total productivity of areas like the North Sea may be higher than is recognized because the higher inshore productivity is usually not taken into account. Dr. Murphy questioned the general importance of inshore areas as nurseries, citing the northwest shelf of Australia as an example where there is no evidence that inshore areas are nurseries. Dr. Marten commented that the inshore areas of Lake Victoria are nurseries for tilapia and that abuse of those inshore areas with seines appears to have contributed to the decline of tilapia. Dr. Pauly noted that graphs of fish size against depth invariably show the larger fish to be at greater depths. Dr. Gulland noted that it is difficult to know how much of the fish production has actually occurred inshore or offshore because many fish migrate from one area to the other.

Mr. Simpson pointed out that coral reefs that are directly offshore may have different yields from the barrier reef type. He also remarked that the high bird populations in many coastal lagoons may be taking a substantial portion of the fish production.

Dr. Sale suggested that, in addition to different food chains being responsible for the wide range of yields in the same ecosystem, different taxonomic groups and associated differences in the physiology of the fish may also be important. Some kinds of fish may be more efficient at converting their food to usable fish flesh than others. Mr. Jones cited the ability of *Sarotherodon niloticus* and one of the zooplankters in Lake George to digest the abundant blue-green algae that are indigestible for most animals. Dr. Marten speculated that the variation in digestibility of the organisms along the food chain could also influence the overall efficiency of transforming primary production to fish yields.

Following the observations on Lake Victoria that decline in total catch at high fishing efforts were a consequence of destructive fishing practices rather than an increase in fishing effort *per se*, there was a discussion of whether the total catch versus effort curve drops or remains high with increasing effort.

Dr. Pauly noted that the stocks of small fish species in the Gulf of Thailand have collapsed under fishing pressure, apparently due to the additional burden of heavy predation from larger fish, as has been the case with small fish like *Haplochromis* in Lake Victoria. However, Dr. Murphy felt that trawling the Gulf of Thailand should put as much fishing pressure on the small species as the large species and that a manipulation of gear-specific effort is only applicable to artisanal fisheries. Dr. Sainsbury expressed the need for better catch statistics because it is difficult to know with the present information just how hard the small species in the Gulf of Thailand have been fished.