FAO Fisheries Technical Paper No. 181 FIRM/T181

P. Gonzalez - Alberdi

SOME SCIENTIFIC PROBLEMS OF MULTISPECIES FISHERIES

Report of the Expert Consultation on
Management of Multispecies Fisheries
Rome, Italy, 20 - 23 September 1977

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1978

M-41
ISBN 92-5-100573-7

P. Gonzalez - Alberdi

PREPARATION OF THIS PAPER

This paper reports the discussions of an Expert Consultation on Multispecies Problems held in Rome in September 1977, which was organized by FAO in response to the recommendation of the Advisory Committee on Marine Resources Research (ACMRR) at its Eighth Session (Portugal, September 1975), that FAO should promote studies of these problems. The first draft of the report was prepared during the meeting, and the draft agreed by members of the Consultation by correspondence.

Distribution:

FAO Department of Fisheries
FAO Regional Fishery Officers
Selector SM
ACMRR

Bibliographic Entry:

Expert Consultation on Management of
Multispecies Fisheries, Rome, Italy,
20 - 23 September 1977 (1978)
FAO Fish.Tech.Pap., (181):42 p.
Some scientific problems of multispecies
fisheries. Report of the .....

Expert consultations - Rome (Italy).
Fishery management. Multispecies fisheries.
Mathematical models. Fishery surveys.
Yield. Population dynamics. Stock
assessment. ANW, Georges Bank. ISEW,
Thailand Gulf.

Abstract

Few fisheries exploit a single species in isolation although most studies of exploited fish stocks have been based on single-species models. Greater account needs to be paid to biological and technological interactions between fish stocks and fisheries on different species, as well as to the data requirements needed. This paper reviews the adequacy of single-species models in respect of the fisheries on Georges Bank and in the Gulf of Thailand. In some circumstances an extension of the simple Schaefer production model can be used. Where a large number of independent but similar bodies of water are concerned (e.g., African lakes), indices based on the size, morphology and simple biological characteristics of each body of water can provide a guide to its potential fish production. Proposals are made for work to improve these and other approaches, and for the types of data that need to be collected.

CONTENTS

1. INTRODUCTION

The first commercial fisheries to develop on a large enough scale to affect the stocks seriously enough to cause concern and raise questions of management were those in the waters around the industrialized countries in the late nineteenth and early twentieth century. The theory of fish population dynamics and stock assessment grew up in the following decades to provide advice on these fisheries, which were largely based on single species of particular value or abundance (plaice, cod, salmon, etc.). By 1950 there was a well-established body of theory on which scientific advice could be given to managers in respect of fisheries based on single species of fish.

Since then there has been a qualitative change in world fisheries, with a great expansion in the intensity of fishing and in the variety of species harvested. In virtually all parts of the world the local fisheries exploit several different species; in tropical areas the variety of species is particularly high. For example, fifty or more species can be caught in a single trawl haul in the Gulf of Thailand. The existing theory of single species, existing and exploited independently of any other species, is therefore no longer sufficient. It may be inadequate in at least three ways:-

(a) Technological interactions. This simply means that in fishing for one species (Species A) a second species (Species B) is also caught in appreciable amounts. Thus it is not proper to consider the problem of managing species A without considering the consequential effects such management may have on species B.

(b) Biological interactions. This simply means that the stock level of species A affects the stock level of species B. This might be caused by predation or by competition. Clearly this is a complicated subject since such interactions might take place at various points in the life history of the two species. For example, species A might eat the eggs of species B; alternatively, or at the same time, adults of species B might eat adults of species A. If such interactions took place they would clearly upset single species management.

(c) Data requirements. Most single species methods require extensive data. As more species become exploited it becomes increasingly impracticable to collect enough data to apply single species methods to each and every species of interest. In particular changes of emphasis of an existing fishery onto a new species means that advice may need to be given in respect of a heavily fished stock for which there is only a short time series of data.

Therefore there is a need for some new approaches to the problems of assessing and managing fisheries in which several species are caught. FAO convened a consultation to examine this question, which was held in FAO Headquarters, Rome, 20-23 September 1977.

The participants were:

H.A. Regier, Toronto (Chairman)
B.E. Brown, Woods Hole
Veravat Hongskul, Bangkok
J.G. Pope, Lowestoft

Members of the staff of the Fishery Resources and Environment Division, Department of Fisheries, FAO, also took part in the discussions.

During these discussions three distinct audiences were addressed - administrators, needing advice on how to manage multispecies fisheries, and especially advice on the reliance that can be placed on existing scientific assessments based on single-species models; their scientific advisers, needing guidance on the most suitable techniques and models to be used in studying multispecies fisheries; and the wider scientific community, who might find stimulating and useful ideas to pursue in relation to the development of improved techniques and more appropriate models. The multispecies problem has been noted (National Research Council, 1977) as being among those deserving special attention from the scientific community in relation to world food and nutrition. It is hoped that each of these groups will find all or part of this report of interest.

During the meeting particular emphasis was given to marine fisheries, partly deliberately because these account for the major share of the world's fish catch, and partly accidentally because the participants were, on the whole, more familiar with, and more interested in, marine fisheries. Nevertheless, it is felt that the report is also of interest to those concerned with inland fisheries. To provide equal coverage of case histories of inland fisheries and their particular problems would have greatly increased the volume of the report, and the time taken in issuing it. Readers with particular interest in inland fisheries are referred to the studies on inland fisheries in the bibliography, for example Henderson _et al._, 1973; Regier and Loftus, 1973; Regier and Hartman, 1973).

2. EXAMPLES OF MULTISPECIES FISHERIES

2.1 The southern part of the ICNAF area

The area from Georges Bank south to Cape Hatteras (subarea 5 and statistical area 6 of ICNAF - see Fig.1) has had a history of three centuries of fishing. Significant fishery research began in the 1930's, and has intensified steadily since, particularly since the establishment of the International Commission for the Northwest Atlantic Fisheries in 1949. The history of the fisheries since 1949 is described in detail in the various documents of ICNAF, particularly its Statistical Bulletin, its Redbook, containing _inter alia_ the reports of the Assessment Sub-Committee of its Standing Committee on Research and Statistics (STACRES), and working papers presented to STACRES.

As in other regions, early interest in ICNAF was in certain stocks of individual species - in the southern areas the main concern was with the haddock stock on Georges Bank - and particularly in mesh regulations to optimize the yield per recruit from these stocks. Events since 1961, however, completely destroyed the validity of single-species management.

Prior to 1960, almost all of the fishing in the southern area was carried out by U.S.A. vessels less than 300 GRT. After 1960 the distant water fleets of the U.S.S.R., Poland, Japan, the Federal Republic of Germany and other countries began fishing in the area. These fleets of large, highly mobile vessels steadily increased both in number and total tonnage (Table 1), and resulted in enlarging the scope of the total fishery with respect to species, area fished and intensity of fishing. While historically the U.S.A. fishery had concentrated on selected groundfish species (cod, haddock, redfish and flounders), greater catches of an increasing number of species (Table 2) have been reported since 1960 (ICNAF, 1962-1974).

Total catch increased approximately three times, while effort is estimated to have increased sixfold (Brown _et al._, 1976). Most of this fishery was conducted by relatively unselective otter trawl gear, with cod-end mesh sizes sometimes as small as 40 mm, though choices in the time and place of fishing enabled the fishery to be directed preferentially to particular species. Some species were taken as by-catch (i.e., catch other than the object of the fisheries) but many stocks such as Georges Bank herring and squid, which previously had been little exploited, became the focus of major directed fisheries. The entrance into specific fisheries often took place sequentially as intensive fishing reduced stocks which had temporarily increased in abundance due to a few strong year classes, classical examples being haddock and yellowtail flounder.

Studies of the individual species showed that, starting with haddock, each of them had become heavily exploited in succession, sometimes to the point at which productivity was seriously affected. As a result ICNAF has since given increasing attention to the need to

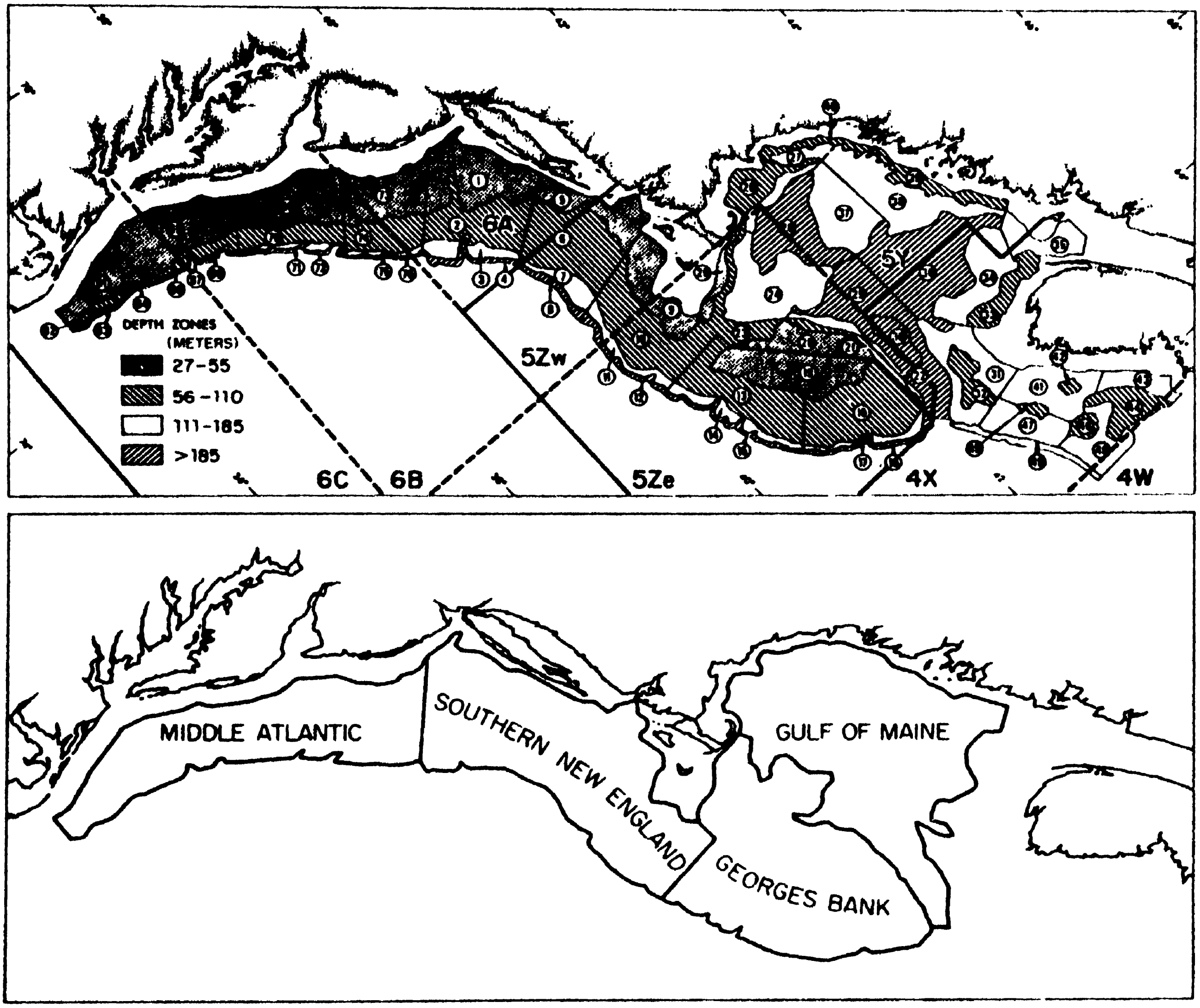

Fig. 1 Chart of the southern part of the ICNAF area

Table 1. Number of vessels (U.S.A., Others) fishing in SA 5 + 6 during 1959, 1965 and 1971 by tonnage class (A = less than 901 GRT[a] B = 901 GRT[a] and above)

		Number of vessels[b]						
		U.S.A.		Others		Total		
Year	Area	A	B	A	B	A	B	Total
1959	SA 5	301	-	26	-	327	-	327
1965	SA 5	323	-	244	110	567	110	677
1971	SA 5	299	-	447	213	746	213	959
		461		490	222	951	222	1173
1971[c]	SA 6	162	-	43	9	205	9	214

[a] GRT - Gross registered tons

[b] Data from ICNAF List of Fishing Vessels

[c] This includes only vessels which were listed for SA 5. SA 6 listings were not available for 1959 and 1965.

Table 2. Subarea 5 nominal catches as reported in ICNAF Statistical Bulletin Vol. 10 and 22 (ICNAF 1962 · Table 1; ICNAF 1974 Table 3)

Species	1960	1972
Cod	14,430	31,357
Haddock	45,801	6,669
Redfish	11,375	19,095
Yellowtail	13,581	29,620
Winter flounder	6,953	10,505
Summer flounder	1,255	5,454
Scup	3,779	1,229
Pollock	10,397	12,989
Silver hake	46,688	107,113
Red hake	3,410	60,062
White hake	2,483	3,084
Groundfish not stated	19,110	1,239
Herring	69,046	220,964
Mackerel	1,011	200,518
Alewife	8,669	8,656
Atlantic saury	-	3,429
Angler	8	4,332
Sculpins	-	4,862
Argentines	-	32,707
Sharks	801	13,154
Skates	128	8,735
Other fish not stated	-	21,661
Squid	741	26,111

control the total amount of fishing (Templeman and Gulland, 1965). Initially the method used was a limit on the Total Allowable Catch (TAC). The first TAC was set for haddock at the 1969 ICNAF meeting, and came into force for the 1970 fishing season; in 1972 at a Special Meeting in January ICNAF established a TAC for 1972 for herring which incorporated decisions not to lower spawning stock size below that to be at the beginning of 1973 (ICNAF 1972). At the 1972 Annual Meeting TAC's were established for cod, redfish, silver hake, red hake, pollock (ICNAF 1972) and at the 1973 January Special Meeting; mackerel and flounders other than yellowtail were added to the 1973 regulations (ICNAF 1973). TAC's for other finfish and squid were established in 1973 for the fishery in 1974 (ICNAF 1973)

Several of these TAC's were precautionary in that they were set above existing catch levels and were designed to prevent a too rapid development of a fishery prior to the establishment of an assessment data base. Species TAC's were based on several procedures depending on the data available for analysis. In some fisheries stock production models were used. Beverton and Holt yield per recruit models (using at first F_{max}, i.e., the fishing mortality giving the maximum yield per recruit, and later $F_{0.1}$, i.e., that fishing mortality for which the marginal increase in yield per recruit due to a small increase in fishing effort is 0.1 times the marginal increase in yield at very low levels of total effort) (Gulland and Boerema, 1973) applied to estimates of population size based on survey and cohort analysis data were used where sufficient data were available. In other cases historic catches were related to trends in the indices of biomass obtained from research survey cruises and judgements made of the magnitude of the sustainable yield.

Despite these measures, it soon became clear that they were insufficient to prevent a continuing general decline in the stocks, the clearest evidence coming from research surveys. These were initiated by the U.S.A. in the 1960's; the U.S.S.R. participated from 1967 onwards (Grosslein, 1968). The reasons for this were (i) the TAC's set for individual species did not, at least initially, take enough account of the by-catch of that species taken incidentally in fisheries directed at other species, (ii) it was difficult to set accurate TAC's for so many individual stocks (18, some including several species lumped together), especially when the time series of data for some stocks were very short, (iii) no account was taken of biological interactions between stocks.

Accordingly the Commission, following the October 1973 Special Meeting, established an additional overall control, setting a TAC on the total catch of all species. The overall second tier TAC for 1974 was 923 900 tons (942 000 tons were reported caught), 850 000 tons for 1975 (854 000 tons reported caught). These were designed to stabilise the total stocks. The lower TAC for 1976 - 650 000 tons (634 000 tons reported caught) and recommended for 1977 (520 000 tons) were designed to rebuild the total biomass.

Scientific procedures used to recommend overall TAC to ICNAF Commissioners

There were two approaches to recommending a second tier or overall TAC. The first was an examination of the expected fishery interactions, the underlying principles of which were discussed by Fukuda (1973). Utilising reported by-catch ratios in different fisheries in past years and the allocated TAC's in a linear programming procedure, a total catch was projected which would ensure that no individual species TAC would be exceeded (Brown *et al.*, 1973; Anthony and Brennan, 1974; Brown *et al.*, 1975 and Brown *et al.*, 1976). See Table 3 for example. Total TAC's estimated from a review of these simulations and from projections of possible declines in by-catch ratio under the imposition of the latest regulations were recommended. The reduction recommended by the overall TAC to serve as a forcing function for countries to reduce by-catch was usually in the neighbourhood of 20%.

The second procedure was to utilise a Schaefer yield curve applied to the total finfish catches and total standardised fishing days reported by all the fleets. In a first attempt Brown and Brennan (1972) indicated that the effort had reached a level above that giving MSY. This gave an estimate of the extent of reduction in effort and catch needed to achieve the given goals of first stabilisation and then recovery. Due to the difficulty

Sum of individual country's linear programming simulation of 1975 catches, maximising total catch ('000 tons), and using 1973 by-catch ratios

Species sought	Total allowable catch restraint	Directed catch	Total catch
Cod	45.00	16.39	31.48
Haddock	6.00	0.00	5.25
Redfish	25.00	18.24	22.25
Silver hake	175.00	74.69	85.72
Red hake	65.00	11.83	26.51
Pollock	21.30	9.57	20.28
American plaice	2.70	-	1.15
Witch	4.36	-	1.70
Yellowtail	16.00	11.02	15.06
Other flounder	18.00	-	6.54
Other groundfish	65.70	27.38	40.96
Herring	175.00	107.38	120.01
Mackerel	285.00	127.51	150.60
Other pelagic	26.90	16.97	26.45
Other fish	56.40	9.33	33.35
Squid	71.00	25.93	40.30
Total	1 058.30	456.24	626.75

Table 3B. Sum of individual country's linear programming simulation of 1975 catches, maximising total catch ('000 tons), and using 1971 by-catch ratios

Species sought	Total allowable catch restraint	Directed catch	Total catch
Cod	45.00	1.7	18.53
Haddock	6.00	0.0	5.23
Redfish	25.00	16.60	22.20
Silver hake	175.00	43.65	62.68
Flounders	41.00	1.32	36.25
Other groundfish	152.00	64.08	84.47
Herring	175.00	138.27	174.82
Other pelagic	311.90	189.07	210.48
Other fish	127.40	25.21	66.38
Total	1 058.30	479.90	681.05

in utilizing reported catch/effort data in fisheries that were developing rapidly, and switching from species to species the effort in many cases was adjusted by a "learning factor" derived from comparison with survey indices. This was intended to correct for the fact that fishermen moving into a new fishery need a little time to learn the best fishery grounds, and fishery tactics, and are usually more efficient in the second and later seasons. The procedures and results are described in Brown et al. (1976), although earlier ICNAF documents beginning in 1972 made attempts at using this approach. The yield curves in Brown et al. (1976) are given in Fig.2.

Initially the survey data could not be used alone because of differences in catchability between species which were particularly large between pelagic and demersal fish, but later further attempts were made to estimate total biomass from survey data by adjusting for differing catchabilities. Although attempts were made to estimate absolute biomass, for purposes of management using a Schaefer yield curve approach, a relative index is all that is necessary, provided the individual components are weighted correctly. The procedures used in these estimates are given by Clark and Brown (1977). Fig.3 gives these estimates of biomass decline.

At the ICNAF Mid-term Assessment Sub-Meeting in April 1975 the biomass at the MSY level was estimated to be 4 000 000 tons (Clark and Brown (1977) give 4 000 000 to 4 500 000). Judging the current stock to be depleted by 25% below this level by over-exploitation in 1970-1972 (Clark and Brown (1977) estimated 50%), and assuming a three-year biological lag time, the second tier TAC's - i.e., the Total Allowable Catch of all species combined, which was applied in addition to limits on each individual species - which were necessary to restore the biomass at different rates, were estimated as follows:

TAC	Years to Recovery
800 000 tons	13
750 000 tons	11
700 000 tons	9
650 000 tons	7

While steps were being made to introduce a second tier TAC, refinement of the assessments of individual stocks was continued. In addition, the Commission adopted more stringent objectives for managing certain stocks, e.g., fishing at $F_{0.1}$ rather than F_{max}, and acting to rebuild the stocks rather than simply to maintain the status quo. The net result of the combination of these factors resulted in significant reductions in the TAC's for many individual species. The most striking was for mackerel. The first TAC in 1973 (SA3-6 combined) of 450 000 tons was precautionary based on U.S.A. estimates from a Schaefer yield curve (300 000 tons) and U.S.S.R. estimates from hydroacoustic surveys. In 1973 the first analytical assessment was made. TAC's adopted were 1974: 359 000 tons; 1975: 355 000 tons; 1976: 310 000 tons and 1977: 105 000 tons. Cod in S.A.5 were first assessed using a Schaefer yield curve and a MSY value of 35 000 MT was established for the period 1973-76. An analytical assessment in 1975 resulted in a TAC of 20 000 tons for fishing at an F value between $F_{0.1}$ and F_{max}. For redfish in S.A. 5 the values from 1973 to 1977 were 30 000, 30, 000, 25 000, 17 000 and 9 000 tons. A comparison of the sum of individual TAC's and the second tier shows this convergence:

	Sum of TAC's ('000 tons)	Second Tier TAC's ('000 tons)
1974	1 056	924
1975	1 058	850
1976	826	650
1977	620	520

The result of applying this management procedure has resulted in a stabilisation of the total biomass as judged from the 1975 and 1976 surveys. With the extension of 200 miles

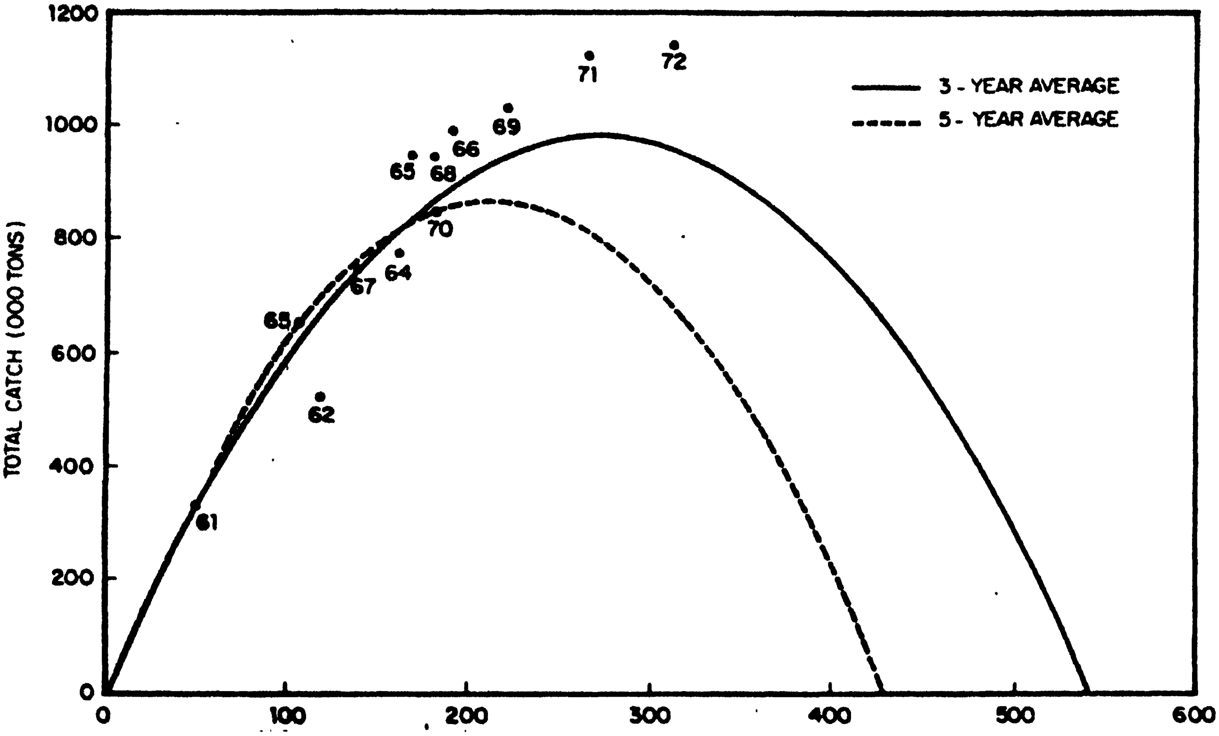

Fig.2 Yield-effort curves for ICNAF Southern Area based on the total biomass (from Brown *et al.*, 1976)

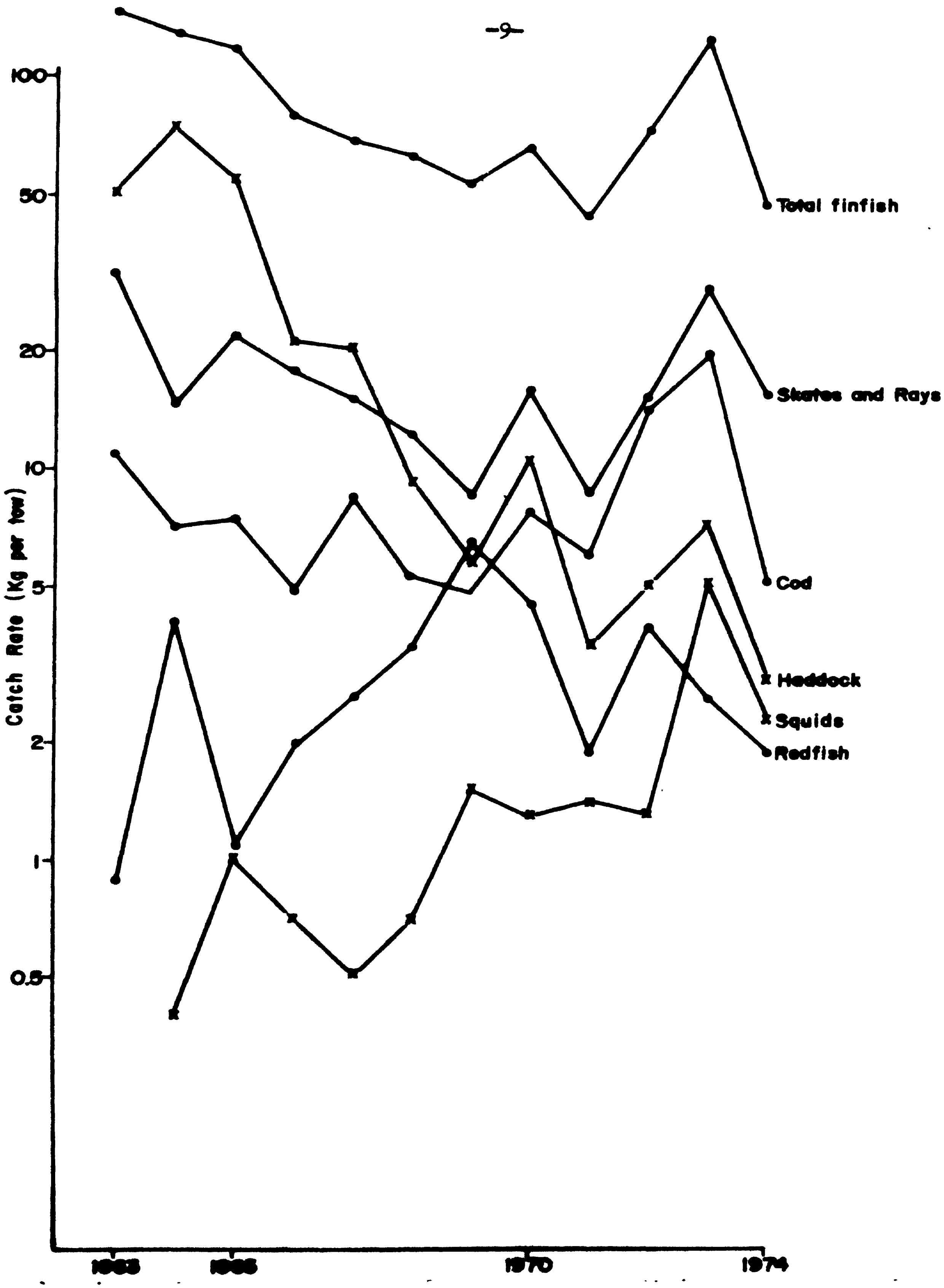

Fig. 3 Declines in the abundance of some major species on Georges Bank 1963–1974 (data from Clark and Brown, 1977, Table 4)

the basis for deciding on the objectives for fish stocks management have changed and thus a second tier TAC is not now being used in direct assessment and management procedure. However other restrictions even more stringent have been introduced which should result in a recovery of total biomass although certain components, e.g., yellowtail flounder, continue to be fished at levels not designed for individual stock recovery.

2.2 Gulf of Thailand Trawl Fishery

The development of the trawl fishery in the Gulf of Thailand started in the early sixties and the landing of demersal fish has expanded very rapidly in the last 15 years, from about 20 000 tons in 1956-1960 to over a million tons in 1972. However, since 1972 the catches have levelled off, despite the fact that the Thai fleet has been increasing in size, numbers and range of operations. In order to study the changes that occurred in the demersal fish populations, which are composed of more than 200 species, continuous trawl surveys have been conducted by the Department of Fisheries since 1963. These enormous amounts of data obtained from such surveys provided a strong data base for the study on this mixed-species fishery.

The average c.p.u.e. in this survey provided an index of abundance which, combined with the reported figures of total catch by Thai trawlers, enabled an index of effort to be calculated and the familiar techniques of relating between catch per unit of effort and total effort to be applied. This gave a good fit up till 1967 (see Fig.4) but later it was observed that there was an increasing deviation from the line of the points at higher effort, i.e., the c.p.u.e. and total catch were higher than expected from the level of effort. Though data on the location of fishing by Thai trawlers are poor, it seems reasonable to believe that, as the catch per unit of effort dropped and the fishermen became less successful in the traditional grounds, Thai trawlers have spread from the local grounds to other areas outside the Gulf of Thailand which were not covered by the surveys. Unfortunately, it has been difficult to obtain accurate information on where the boats have been fishing due to political and other reasons. Nevertheless, attempts have been made to estimate the sustainable yield of the demersal populations in the Gulf of Thailand by extrapolating the trend during 1961 to 1966. The resulting estimates of the MSY appears to be around 500 000 tons, which is close to that empirical estimate given by Gulland in 1972.

It is well acknowledged that the use of simple Schaefer's approach in estimating the total yield from this fishery has some limitations. Close examination of the changes in abundance of various species or group of species from the survey data reveals declining trends of most species, except for those of squid and crabs (see Fig.5). Such inverse relationship may indicate certain interspecific interactions between these species/groups although these interactive mechanisms are not well understood at present. As fishing has increased, it has become more desirable to determine the interactions between these species/groups and the effect of the fisheries on them, so as to manage the fishing of the different species and maximize the benefit to the major predator - the fisherman. Despite its simplicity together with questions of the validity of the assumptions, the surplus-yield model may be the only usable technique at present for the analysis of the complex fishery under study. It can establish the main dynamic properties of the fishery and can indicate the first steps required to regulate it for the management purposes which are urgently needed at present.

Certainly the present problems in the Gulf of Thailand are those of acting on the conclusions of the simple, overall biomass, analysis, and reducing the total amount of fishing. Once this is done and the fishery as a whole is in a more healthy state, further analysis may show that additional management action may be needed more specially directed towards one or other species group. However, until the first step, to reduce overall effort, is taken, detailed single species analysis is not needed for scientific advice to managers and the combined analysis is perfectly adequate.

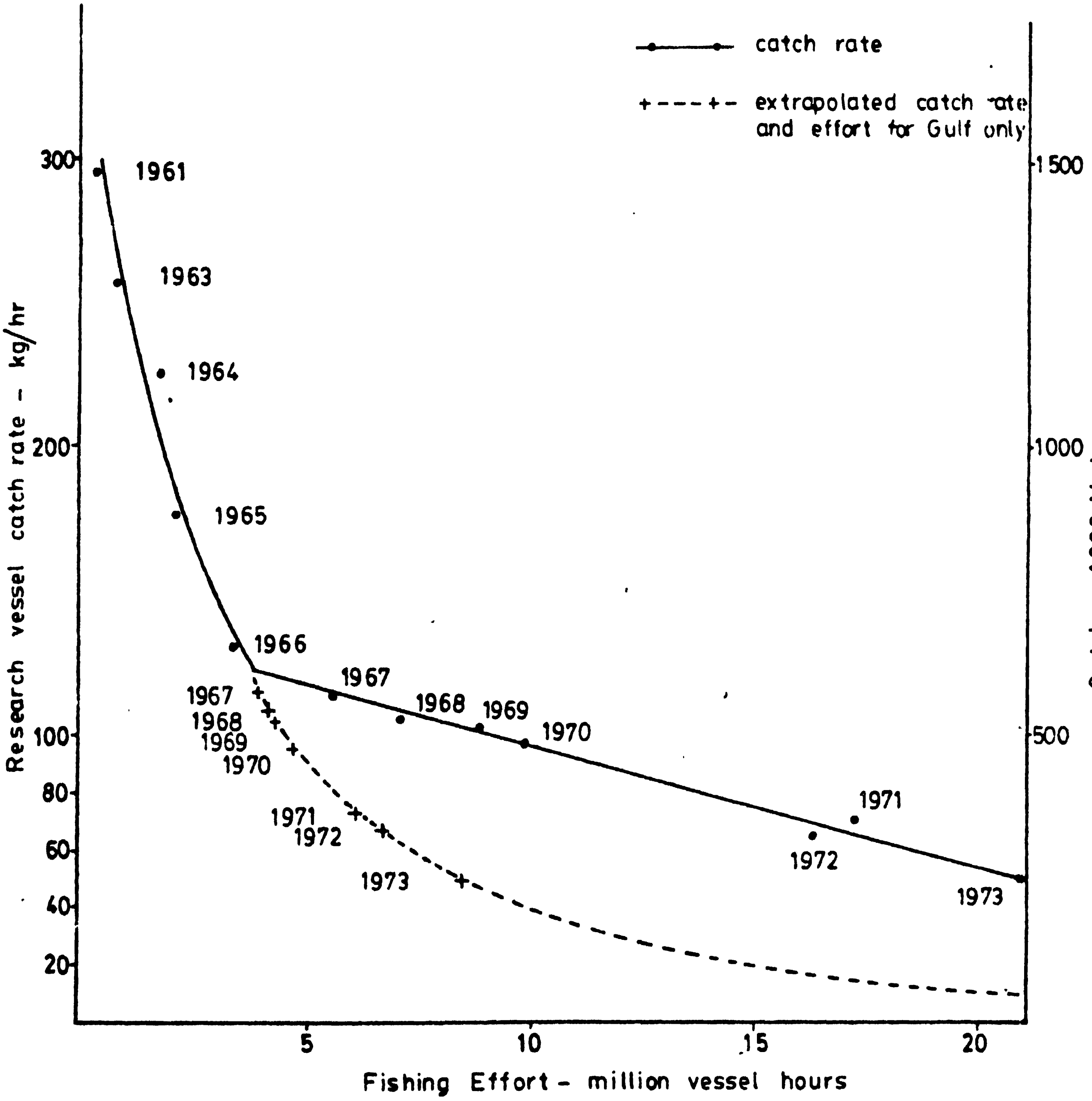

Fig.4(a) Relation of c.p.u.e. to total effort in the Gulf of Thailand, showing departures from the expected relation after 1966

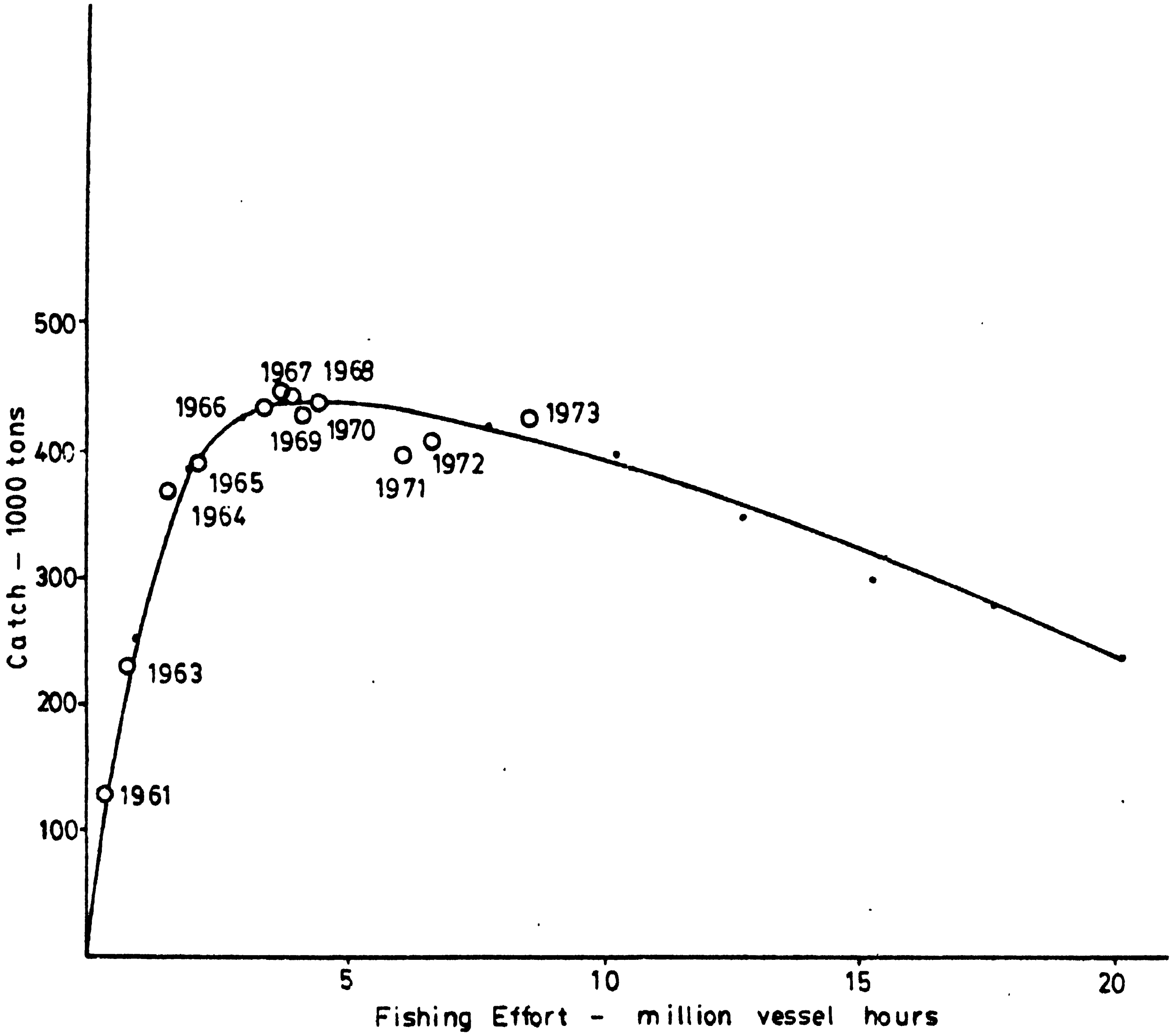

Fig.4(b) **Relation of total catch to total effort in the Gulf of Thailand, showing departures from the expected relation after 1966**

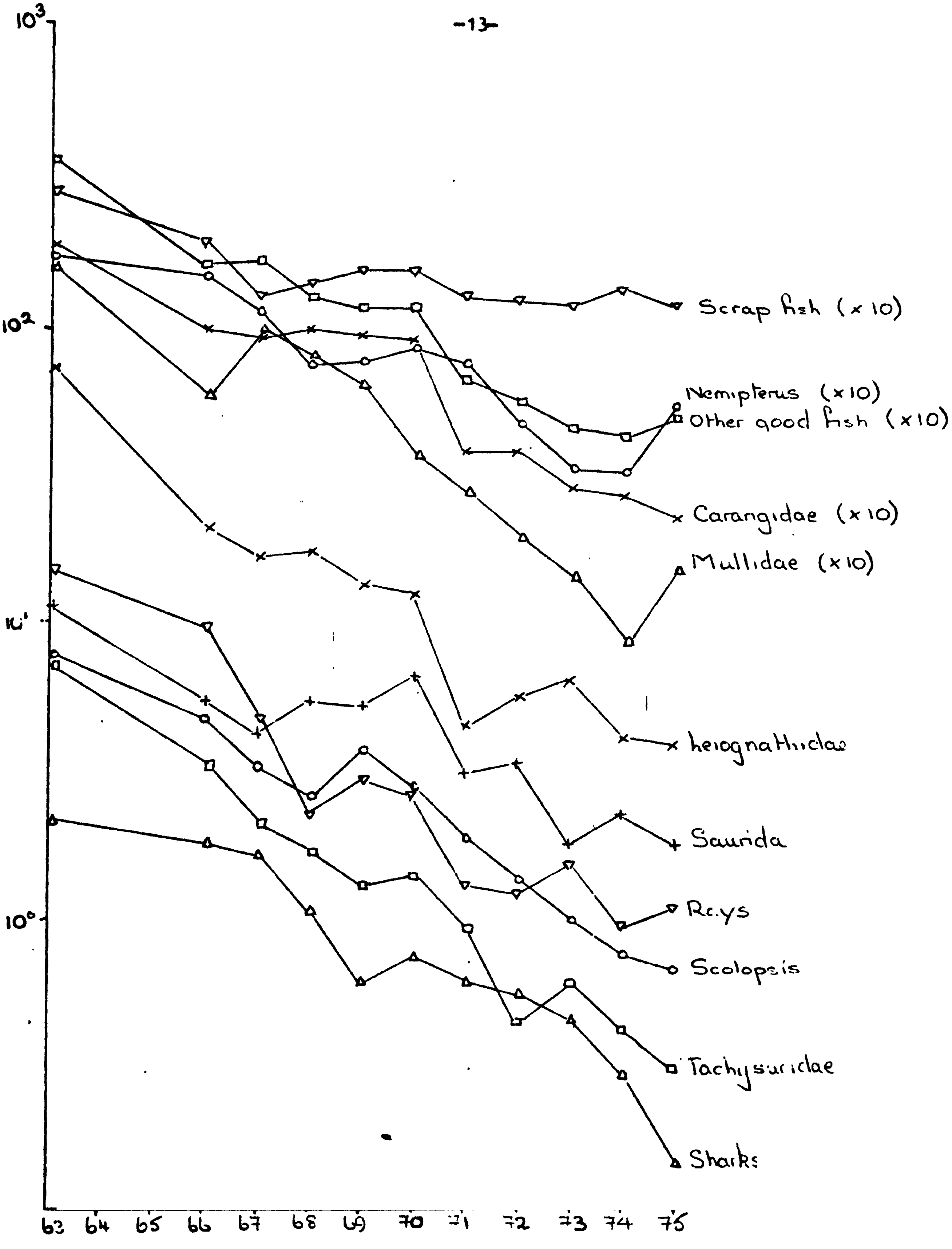

Fig.5 Declines in the abundance of major species or species groups in the Gulf of Thailand, 1963-1975

These two fisheries present both similarities and differences. Both were at first basically trawl fisheries for groundfish; pelagic stocks are now exploited in both areas, but whereas in the Gulf of Thailand the pelagic catches are mainly taken by purse-seine, and form to some extent a separate, and somewhat independent multispecies fishery on Decapterus spp., Rastrelliger, Caranx spp., etc. (though some pelagic fish are taken in bottom trawl), in the ICNAF area much of the pelagic fish were taken by trawlers, and the pelagic species contribute significantly to the multispecies problem. For both an approach considering only the total biomass provided sufficient guidance to determine effective management measures, whereas in ICNAF single species analysis alone was not sufficient. However, the ICNAF fisheries appear to be more complex (despite the smaller number of species). The relative simplicity in the Gulf of Thailand is indicated by the similarity of the change in abundance of different species in that area (mostly a steady decline, with some increases), compared with the greater variety of trends in the ICNAF area. A quantitative measure of this has been provided by principal component analysis. The first two principal components account for 80% of the variance in the Gulf of Thailand, considerably larger than in the ICNAF area.

2.3 Shoaling pelagic fish

Fisheries on small shoaling pelagic fish, especially clupeoids (sardines, herrings and anchovies) have exhibited some of the most dramatic collapses among world fisheries (see Murphy, 1977 for a compact review of the dynamics of these stocks). Fishery scientists have been singularly unsuccessful in providing advice (or at least advice that was acted on) in time to forestall these collapses, and the history of fisheries such as those on the Californian sardine, the Atlanto-Scandian and North Sea herring and the Peruvian anchoveta must be included among the worst failures associated with fishery science - though the failures have not infrequently been due to failure to act quickly enough on scientific advice, rather than on the advice itself. Analysis of the population dynamics of these stocks, using classical single-species methods has given little insight. The yield-per-recruit as a function of fishing mortality is a flat-topped curve with no dramatic features, and the collapses have been due to recruitment failures - which in itself is a description of the events rather than an explanation. Examinations of the relation of recruitment to parent stock for most individual stocks have been inconclusive, though Cushing (1971; 1977) by examining groups of species has suggested that clupeoids as a group has a stock/recruit curve in which the descending left-hand limb extends further to the right than in most groups, i.e., it is easier for these stocks to be reduced to a level at which recruitment becomes adversely affected. However, this analysis is still insufficient basis for the provision of quantitative advice in relation to an individual fishery.

In many cases of stock collapse there has been an increase in the abundance of some other pelagic species. For example, in the California Current system there has been a big increase in anchovy (Murphy, 1966). There is uncertainty whether this increase is purely coincidental, a result of the sardine decrease, or in part actually responsible for it, though there is some evidence (Gulland, 1971) that the survival of sardine larvae is related to the combined abundance of sardines plus anchovy. On the other hand, evidence from the occurrence of scales in anoxic bottom deposits (Soutar and Isaacs, 1969) shows that in the past couple of millenia both species have fluctuated, with the anchovy generally being the more abundant, but with no clear indication of any inverse relation. Despite this uncertainty there is a widely held view that the most positive step to encourage the recovery of the sardine stock would be the development of an intense fishery on anchovy.

Support for this view is greatest from the pelagic fisheries round Japan (Nagasaki, 1973). Several species (notably mackerel, horse-mackerel and sardine, and also squid) contribute to the landings. The catches of each of these have fluctuated widely. For example, sardines dominated the landings in the 1930's, with peak landings of 1.6 million tons (plus nearly another million tons in Korea), but collapsed to a very low level (less than ten thousand tons in 1965) only to recover to a remarkable extent in the last few years (60 000 tons in 1972, nearly 300 000 tons in 1973, and over 1 million tons in 1976). However, the total catch of all pelagic fish has remained remarkably constant; for example, apart from a low value of 1.9 million tons in 1964, it only varied between 2.3 and 2.8 million tons between 1958 and 1968 (Nagasaki loc.cit., Table 1). Further support for the idea of interaction is given by the fishery off south-western Africa. This had been based mainly on sardine, but when this showed signs of decline, fishing on anchovy was actively encouraged to the extent that by 1971 it made up more than half the total pelagic catch. This had seemed, at least until very recently, to have presented a collapse of the sardine stock, though concern about this stock was expressed at the 1977 session of the International Commission for the Southeast Atlantic Fisheries (ICSEAF).

In this way an empirical multispecies approach to management - encouraging fishing on species other than the traditional ones or those showing signs of stress - has at least been somewhat more successful than the single-species approach. At the same time the method lacks a sound theoretical background, and has not been matched by a similarly successful approach to the analysis of the situation. Certainly the method only seems applicable when there is a range of species present, and not when a single species dominates the system. For example, though sardines and mackerel seem to have increased since the decline of the Peruvian anchoveta, the magnitude of the increase in biomass of the former is far less than the decline of anchoveta biomass.

3. MODELS

3.1 General observations

A variety of descriptive and quantitative models are available to describe multispecies situations. They can roughly be classed as immediate extensions of single-species models - of either the surplus production/Schaefer or the analytic/Ricker-Beverton and Holt types - or more general models considering wider elements of the whole system.

It is unlikely that any one single model or method of analysis will be suitable in all situations or all stages of a fishery. In particular, considering the objectives rather than the techniques of the models, there is a range from the strategic considerations - the general state of the fishery and the direction in which changes should be made to improve the situation - to the tactical - what specific measures should be applied in the coming season. It is likely that the more general models, e.g., those based on the basic characteristics of the body of water in which the fish stocks exist, will be particularly valuable at the strategic level, while the more detailed analytic models, considering individual stocks, will be more useful at the tactical level, e.g., setting annual TAC's. If the ICNAF experience proves to be typical, then there is a tendency for the short term tactical models to lead to over-exploitation of a whole range of resources. It is important to use models with a longer-term view which give more robust and safer objectives for fish stock management. In practice it will probably be important for managers and their scientific advisers to apply as far as possible the full range of models to each situation, and not to rely on any one particular approach.

3.2 Analytic models

Analytic models, of the Ricker (1958b; 1975), Beverton and Holt (1957) type, which consider the effects of the individual parameters of growth, mortality and recruitment, have proved powerful tools in analysing the population dynamics of individual species. For single species they have been used in a number of ways:

(i) For well-behaved species (i.e., species without great natural fluctuations, easy to age, and with a convenient and reliable measure of fishing effort, e.g., North Sea plaice) they can provide a fairly complete and realistic description of the stock, including comprehensive advice for management.

(ii) They provide a better insight into how the stocks actually behave, and of the implications of different interpretations of production models, or catch/effort data. For example, for yellowfin tuna they show that different fits of the GENPROD model for different values of the parameter m imply different stock/recruit relations (ICCAT, 1975). This can help direct further research, as well as improving the fit of the production models.

(iii) They can be used for fine tuning of management based on other models, for example using year-class and growth data to calculate the TAC appropriate to maintaining some target population size based on Schaefer type models.

In principle, the same type of models can be applied to several species. Algebraically it is merely a matter of making the individual parameter for each species functions of the abundance of one or more other species. For example, mortality of prey species could include a term proportional to the abundance of predatory species; growth would increase with the increasing abundance of food species, but decrease with increasing abundance of competitors.

Practical application faces two major obstacles - of handling the mathematics, and of fitting parameters. Even with the simplest types of interactions, the algebra soon becomes much too complicated for explicit solution. This problem can be handled by computer models which can simulate the history of the fishery - usually over a long enough period at any given pattern of fishing to determine the equilibrium situation (if it exists) corresponding to that pattern, particularly as it regards the catch and biomass of each species. A number of such models have been constructed, notably in Canada and Denmark (Andersen and Ursin, 1977).

The choice of the nature of the interspecific relations and of the parameter values (e.g., the mortality caused in the prey stock by a predator stock of one thousand tons) presents difficulties that are less easily solved. The choice is extremely wide, especially - as is necessary if the potentially most significant interactions are to be dealt with - if the effects on recruitment are considered. If the only independent observations are the catches and biomass estimates for each species, the number of parameters to be estimated, i.e., the number of degrees of freedom, will considerably exceed the number of observations and the closeness of fit to past observations may measure little more than the skill of the model builder and his programmer. This situation is somewhat improved by taking account of other observations, e.g., of the actual numbers of herring, and their sizes, occurring in cod stomachs, or obtaining estimates of the growth pattern of cod in each year and correlating these with the abundance of herring. However, even at best there will remain considerable uncertainties about the values of the parameters. For example, one important interaction between herring and mackerel in the Gulf of St. Lawrence studied by Lett and Kohler (1976) was the reduction in herring growth with increasing abundance of 0-group mackerel. The corresponding parameter has an estimated value of 0.161 with a standard error of 0.056, i.e., taking limits of ± 2 x s.e., the confidence limits are 0.049 to 0.278, i.e., a five-fold range in the magnitude of this interaction.

At the present stage, therefore, it does not seem that this approach can provide quantitative predictions ("all prediction is difficult, especially about the future") of the effects of different patterns of fishing on the yields from interacting species. For example, they cannot be used to predict exactly how much less herring would be caught as a result of management action to increase the abundance of mackerel. However, these models, especially in their simpler forms, do seem to provide opportunities for insight into the nature of interactions, and the effects on different fisheries, and probably also into the possible range of magnitudes of these effects. This can give valuable results, e.g., in suggesting that the impact of mackerel on herring growth is most unlikely to be of practical significance, or that it might be so great as to question the wisdom of management action aimed at increasing mackerel abundance.

3.3 Production models

As applied to a given species, these models describe the growth of the biomass, i.e.,

$$\frac{dp}{dt} = f\ (p)$$

the simplest form for f (p) being given by the logistic (Schaefer, 1954; 1957), i.e.,

$$\frac{dp}{dt} = p\ (a - bp)$$

or

$$\frac{1}{p}\ \frac{dp}{dt} = a - bp \qquad \ldots\ldots\ldots\ldots\ldots(1)$$

The simplest way of extending this approach to the multispecies situation is to consider the equation as describing the changes in the total biomass of all species combined. This approach has been applied to various groups of stocks, e.g., Georges Bank (Brown *et al.*, 1976), Scotia Shelf (Halliday and Doubleday, 1976), Grand Banks (Pinhorn, 1976), Northeastern Pacific trawl fisheries (Hongskul, 1975), Irish Sea (Brander, 1977) and Gulf of Thailand (Marr *et al.*, 1976). These overall Schaefer models generally seem to fit the data rather better than the fits experienced with their various component stocks. This could occur for several reasons. Some of these are:

(a) Total biomass does react in a simpler way to overall fishing effort than does the biomass of individual stocks, i.e., the production model gives a more realistic description of total biomass than it does of the biomass of individual species.

(b) The better fit results simply from the averaging process.

(c) The overall biomass/overall effort fit is an artifact of the method of fitting in the time series of species exploitation. For example, exploitation starting on lower density high value species with low mortality, e.g., haddock, and then moving on to the high density low value high mortality species, e.g., silver hake.

(d) Because the shifts in the preference of the commercial fisheries between species are not taken account of in the statistics of nominal effort, the available effort data give a more accurate index of mortality exerted on the total biomass than they do of the mortality on any individual species.

Which of these is true only time will answer, but there is at least a possibility that (a) is the correct one and if it is, then total biomass models do provide reliable information on the behaviour of the fish stocks. Such a model suggests a simple biomass criteria for obtaining the overall yield from an entire system and while it does not explicitly refer to interactions between species, it must implicitly consider them.

The next most simple model to extend the Schaefer model is to include an explicit term in the equation of growth of each stock to account for the effects of other species. Various authors have contributed to this, notably Larkin (1963; 1966), Walters and Hogman (1971), Silliman (1975) and Pope (1976a). Pope (in press) gives a detailed development of the method. The state equations for stock p and stock q have extra terms (c, δ) introduced as follows in the steady state equations:

$$\frac{1}{p}\ \frac{dp}{dt} \qquad a - bp - cq - Kf_p \qquad \ldots\ldots\ldots\ldots\ldots(2)$$

$$\frac{1}{q} \qquad \hat{a} - \hat{b}q - \delta p - \hat{K}f_q \qquad \ldots\ldots\ldots\ldots\ldots(3)$$

where Kf_p denotes the effect of fishing on stock p.

Interactions are probably more complex than this but if we regard equations 2 and 3 as defining only the steady state (when $\frac{dp}{dt} = 0$) and not necessarily explaining transitional states, then equations 2 and 3 amount to a statement that when stock q is high the level of stock p will be reduced and when stock p is high stock q will be reduced.

If we altered the sign of $\hat{c}$ we would have a prey predator system with q as predator on p. Thus we might see equations 2 and 3 as being the simplest model containing interaction terms, and while we might not feel that it would necessarily hold in transitional states (where interactions might well be lagged) in a long term steady state situation this formulation has some of the simplicity and gives some of the insights we would expect from a strategic model.

Equations like 2 and 3 could be extended to contain interactions with any number of species but since the solution of the two stock model can be illustrated by diagrams and since the results obtained can be extended to the case of n stocks ($n > 2$) in a fairly obvious way, we will continue with a demonstration of the two stock interactive model. The right hand sides of equations 2 and 3 can be modified to give us the steady state yields Y_p, Y_q of the two stocks by multiplying by p and q, respectively. Thus since the yield Y_p is equal to pKf or pF_p, where F_p is the fishing mortality on stock p, we can write

$$Y_p = ap - bp^2 - cpq \qquad \text{..............}(4)$$

and

$$Y_q = \hat{a}q - \hat{b}q^2 - \hat{c}pq \qquad \text{..............}(5)$$

Thus total yield $Y = Y_p + Y_q$ is given by

$$Y = ap + \hat{a}q - bp^2 - \hat{b}q^2 - (c + \hat{c})\,pq \qquad \text{..............}(6)$$

If the yield is mapped as a function of the abundance of the two stocks, the contours of equal yield are concentric ellipses.

The yield can also be expressed as a function of the fishing mortalities on the two stocks as

$$Y = AF_p + \hat{A}F_q + BF_p^2 + \hat{B}F_q^2 + CF_pF_q \qquad \text{..............}(7)$$

This equation represents contours of equal yield that form concentric ellipses with their major and minor axis inclined to the axes of either F(p), F(q).

This situation is probably best explained using diagrams. Let us consider the case when the equations given below describe the yield of the two species:-

$$Y_p = .43p - 0.000143p^2 - 0.0000143pq \qquad \text{..............}(8)$$

$$Y_q = 1.10q - 0.001q^2 - 0.00005pq \qquad \text{..............}(9)$$

Then Fig.6 shows the form of the contours of equal yield when they are plotted against F_p, F_q. As it can be seen from the diagram the contours are concentric ellipses. Since the last terms in equations (8) and (9) which represent the interaction between species were smaller than the other terms, they do not have a great effect and the axes of the ellipses are nearly parallel to the F_p, F_q axes. The point of maximum yield is at the centre of the ellipses and is equal to 576 units. The lines p = 0, q = 0 are where one or other stock becomes zero. The elliptical contours break down beyond these lines.

Let us see what happens if we make the competition terms greater; for example, consider the equations:

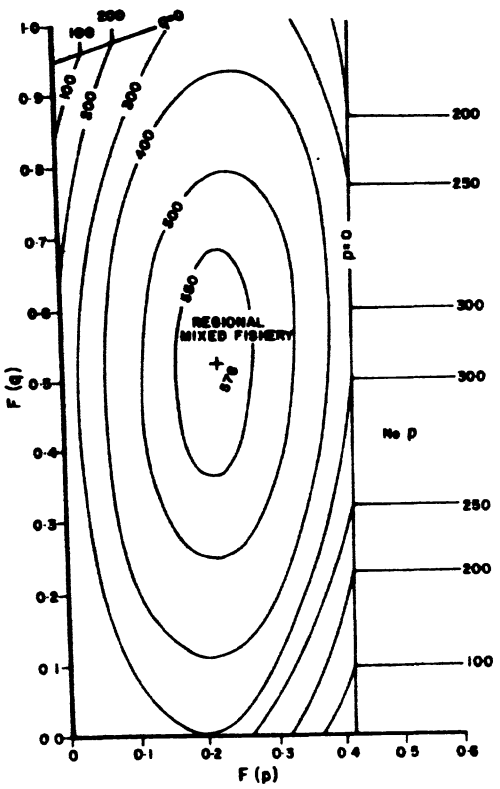

Fig.6 Yield-isopleth diagram for two species with weak composition

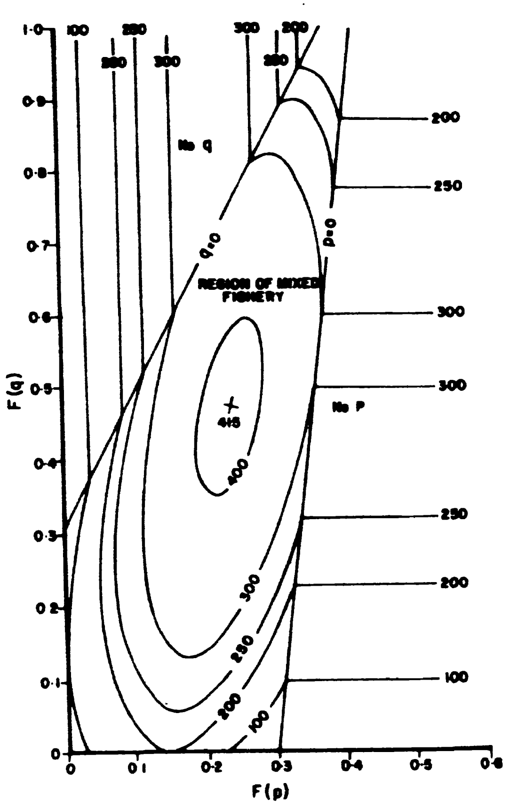

Fig.7 Yield-isopleth diagram for two species with strong competition

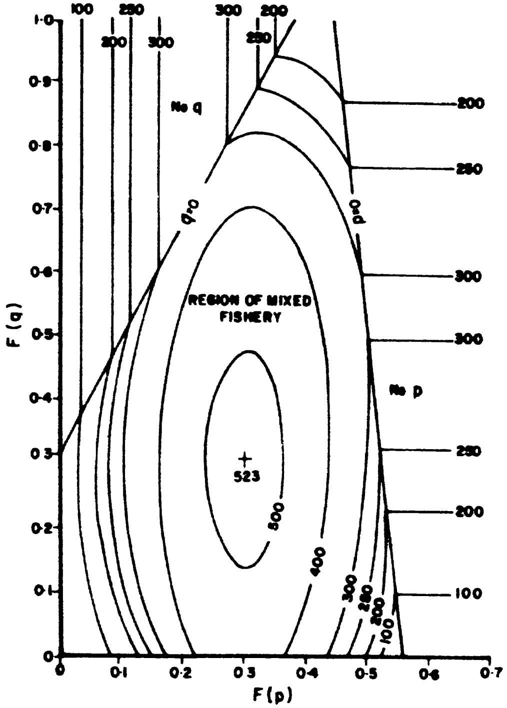

Fig.8 Yield-isopleth diagram for two species, one the prey of the other

$$Y_p = 0.43p - 0.000143p^2 - 0.000118pq \qquad \ldots\ldots\ldots\ldots\ldots(10)$$

$$Y_q = 1.10q - 0.001q^2 - 0.000266pq \qquad \ldots\ldots\ldots\ldots\ldots(11)$$

Clearly these equations only differ from (8) and (9) in the last term. Figure 7 shows the effect that this change has. The ellipses major and minor axis and the value of the maximum is lower at 415. The position of the maximum is also changed from about (0.24, 0.52) to (0.25, 0.48). The only obvious change is that the region in which the elliptical yield curves are valid is reduced. This means that the chance of one or other stock being eliminated is increased.

Another possible situation is where the interaction terms are of opposite sign. For example, modifying (10) to read:-

$$Y_p = 0.43p - 0.000143p^2 + 0.000118pq \qquad \ldots\ldots\ldots\ldots\ldots(12)$$

and with (11) remaining the same we would have a prey-predator system. Figure 8 shows what effect this change has on the contours of equal yield. It is obvious that the maximum yield is higher than in the previous case and is at a still lower value of F_q and still higher value of F_p. This is not surprising as we would expect to get more yield by fishing down the predator and leaving the prey less affected by fishing. It is also noticeable that the line $p = 0$ is altered and makes for a far larger area of elliptical yield contours.

It is worth bearing in mind that the equations developed here form the simplest hypothesis which describe interspecific interactions (it could be considered as a two order Taylor expansion of a more complicated system). It might thus be considered as a first approximation to what actually occurs in the sea. Consequently it should be useful in illuminating the effects of such interactions.

We may draw several conclusions from the general shape of the contours. Firstly it is clear that whether interactions are present or not the contours of equal yield form ellipses centred on the maximum yield of the system. From this it follows that as long as no stock becomes zero any fishery which develops with the fishing mortalities on its various component stocks in equal proportion, i.e., which progresses along a straight line in the F_p, F_q plane, will have a parabolic yield curve. This is true however many species are present as long as the multispecies Schaefer model is true. However, unless the various fishing mortalities are in the ratio which will take the line through the joint maximum sustainable yield, the yield curve observed will underestimate the maximum yield available. Furthermore the level of fishing effort required to achieve the maximum on a given line will not in general be the same as would be required to achieve the overall maximum yield. On the other hand, there is a considerable region in which a total yield near to the maximum is attained and these levels might well be shown by an overall Schaefer model provided that all species involved were being exploited to a reasonable extent. The overall Schaefer model would, however, give a poor result if some important stock were omitted. For example, Pinhorn's analysis of the northern Grand Bank and Labrador groundfish stocks obviously omits the capelin. Hence, his overall yield may well be a reasonable figure for the groundfish and of practical value when only groundfish were exploited, but it would not be satisfactory when capelin also became exploited on a large scale. Thus this more complicated model gives some support to the use of overall Schaefer models and also suggests where they might be less satisfactory.

Another conclusion that can be drawn is that if a fishery develops with mortalities in the various component stock in equal ratio through time, then the maximum yield will occur when the catch rate is half the virgin stock size. That is to say when $\sum Kp$ is $\frac{1}{2}\sum Kp_0$. Thus this more complicated model certainly provides insight into the use of overall Schaefer models. In practice its detailed use is limited since while it requires far less parameters than would a Beverton and Holt type multispecies model, it still requires a considerable number (equal to $(n + 1)^2 - 1$, where n is the number of stocks). Thus 10 stocks would have potentially 120 parameters although, of course, many of these would be zero or rather small. In some cases, however, it has been possible to fit such a model to a small number of stocks. This was done by Walters and Hogman (1971) to stocks of fish in Green Bay, Lake Michigan and by Pope and Harris (1975) for sardine and anchovy, Pope (1976b) for Newfoundland cod and redfish and by Silliman (1975) for artificial stocks of guppies and swordtails.

If we knew all the parameters of the models, then finding the maximum yield would simply be a question of solving the following equations for the populations of the various stocks (p_i).

$$\frac{\partial Y}{\partial p_1} = 0, \quad \frac{\partial Y}{\partial p_2} = 0, \quad \ldots\ldots \frac{\partial Y}{\partial p_r} = 0$$

These equations simply say that the rate of change of Y with respect to any population size is zero. For example, the two stock model gives:-

$$\frac{\partial Y}{\partial p} = a_1 - 2b_1 p - (c_1 + c_2)q = 0 \qquad \ldots\ldots\ldots\ldots\ldots(13)$$

$$\frac{\partial Y}{\partial q} = a_2 - 2b_2 q - (c_1 + c_2)\, p = 0 \qquad \ldots\ldots\ldots\ldots\ldots(14)$$

These two equations are solved for the value of p and q which will give the maximum.

This will be where:-

$$p = \frac{a_1 2b_2 - a_2(c_1 + c_2)}{4b_1b_2 - (c_1 + c_2)^2} \qquad \ldots\ldots\ldots\ldots\ldots(15)$$

$$q = \frac{a_2 2b_1 - a_1(c_1 + c_2)}{4b_1b_2 - (c_1 + c_2)^2} \qquad \ldots\ldots\ldots\ldots\ldots(16)$$

It is clear from this that the position of the maximum is determined by the parameters a, b, c. Consequently if we do not know these parameters we will be unable to say at what levels of the various populations the maximum occurs. This will certainly be the case if the only data available comes from groundfish surveys. What then should we do? If we assume that the fishing effort does not constrain us in the way described in the previous subsection, i.e., we can vary the ratios of the efforts applied to different species, then potentially we will be able to manage the fishery so as to achieve certain desired population biomasses. If this is the case, then it will be interesting to see the effect of reducing the biomass of each stock to half its virgin biomass. Obviously if there were no interactions this would achieve the overall maximum yield of the system. If there are interactions, however, how would this affect the result? Would the yield at the half virgin stock size level be a substantial proportion of the overall maximum yield, or would it be a small fraction? For the two stock model the ratio of the yield when p and q are half their unexploited levels to the maximum yield is

$$1 - \frac{(c_1 - c_2)^2}{4b_1b_1 - 4c_1c_1} \; : \; 1 \qquad \ldots\ldots\ldots\ldots\ldots(17)$$

Obviously if the interaction terms (c_1, c_2) are of the same size then the yield ratio will be 1 : 1. Equally obviously if the interaction terms c_1, c_2 are small with respect to b_1, b_2 then the ratio of the two yields will almost be 1 : 1.

The ratio will only be much smaller if c_1 and c_2 were of opposite sign. This can be seen from Fig.9. These show the same yield contours as were discussed earlier. The point half way along the line between $F_p = F_q = 0$ and $p = q = 0$ is the value of F_p, F_q which would give $p = \frac{1}{2}p_o q = \frac{1}{2}q_o$ where p_o, q_o are the population sizes when there is no fishing.

Figure 9a shows the case where interactions are small. The yield at $\frac{1}{2}p_o$, $\frac{1}{2}q_o$ is virtually the same as the overall yield. Figure 9b shows the interactions are larger but the yield at $\frac{1}{2}p_o$, $\frac{1}{2}q_o$ is still close to the maximum 400 : 415. Only in Figure 9c is there a substantial penalty for adopting the $\frac{1}{2}p_o$, $\frac{1}{2}q_o$ position. In this case the yield is 400/523 of the overall maximum. This case is where the interaction terms are of the same numerical size as for Figure 9b but of opposite sign. This is the case that equation (17) predicted would be worst. This case where the interaction signs are of opposite sign is similar to the classical Lotka-Volterra prey-predator model. Thus, if we reduce the predator stock we might expect to see an increase in the prey species assuming we are not reducing it heavily at the same time. If we see such an increase we may be wise to tend to reduce the predator rather beyond the half virgin stock size and the prey species rather less. This would only be done, however, on an experimental basis. In any case it would probably be better not to reduce the predator much beyond half of the virgin stock biomass.

Equation (17) gives the ratio for the two stock model. More generally if we have n stocks then we may imagine a (1 x n) matrix of the a's, A, a (n x n) matrix of b's, B, and a n x n matrix of the c's, C. This last matrix will have zero valued diagonal terms. The ratio of the yield, when each species is at half its virgin biomass, to yield at the overall maximum is given by the ratio of the two quadratic forms:-

$$1/4(a)^T(B + C)^{-1}(A) : \tfrac{1}{2}(A)^T(B + C\ (B + C)^T)^{-1}(A) \qquad \ldots\ldots\ldots\ldots\ldots(18)$$

As before, if the c's are small compared to the b's or if $C = C^T$ (equal interaction terms) then the half virgin biomass position will give practically the global maximum yield.

In conclusion therefore it would seem that to try to achieve biomasses for each species which are half the level of their unexploited biomass is a reasonable first approximation to the maximum yield. It therefore forms a very useful algorithm for managing multispecies fisheries where the parameter values are unknown. It is least satisfactory if there is a marked prey-predator type interaction. Such a relationship might be suspected either if a species has increased after another has been reduced or on general biological grounds (e.g., whales eat krill). If this were the case, then the rule might be modified to reduce the predator stock somewhat beyond the half virgin stock size level while reducing the prey stock by a lesser proportion. This rule of thumb supposes an ability to achieve the half virgin stock size level for each species separately. Clearly in a tropical multispecies fishery this may not be possible since the management strategy needed to achieve this might be hopelessly complex. It might be possible in the temperate and arctic fisheries where the commercial fleets can direct their attentions more selectively towards one species or another, and where it has been possible to introduce fairly complex management rules. In either case the rule of thumb would help in deciding which segments of the commercial fleet to encourage and which to discourage. For example, if the inshore fleet of subsistence fishermen catch proportionally more of lightly exploited species and proportionally less of heavily exploited species than an offshore trawl fleet, they should be encouraged to increase their share of the catch. In practice there may be other reasons for adopting this policy, while the biological characteristics of the various stocks and fishery may indicate that to achieve the objective of maximising physical yield, the reverse policy may be needed, i.e., the stocks exploited by the inshore fishermen are often the more heavily exploited.

A further good feature of this rule is that it makes biological sense since it imposes fishing mortalities on the stocks in the ratio of the stock specific a's. These terms in the equation could be regarded as the intrinsic rates of growth of each stock. Thus the

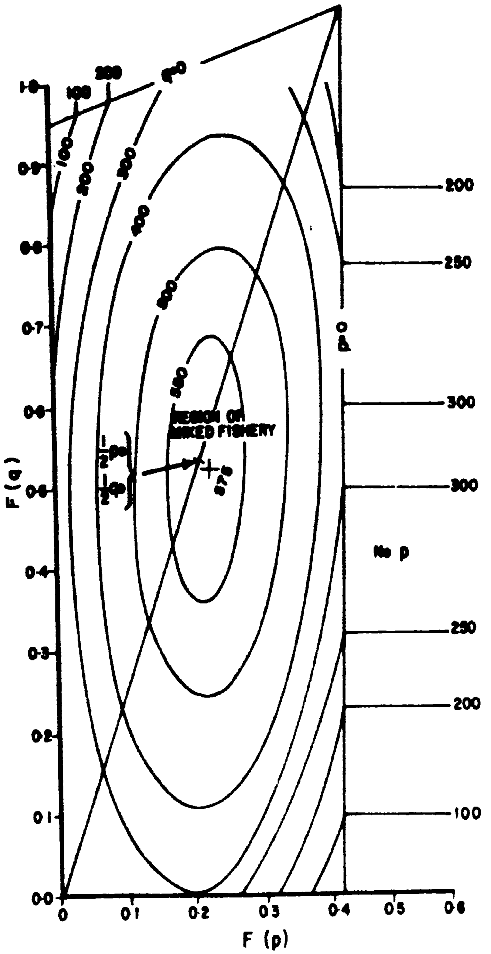

Fig.9a

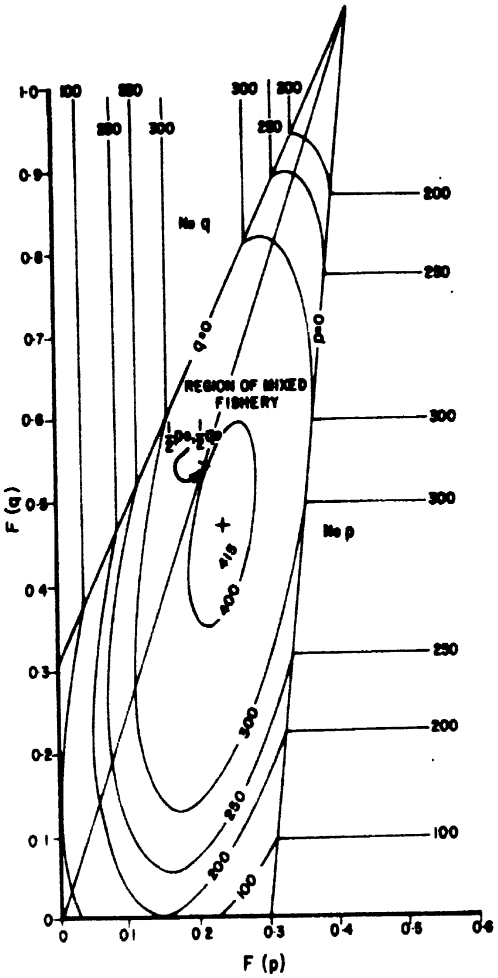

Fig.9b

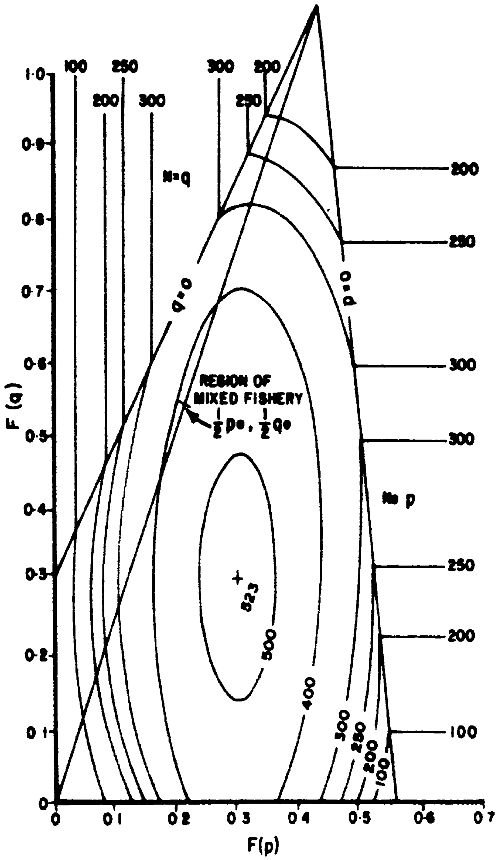

Fig.9c

Fig.9 Yield-isopleth diagrams showing the position corresponding to half the initial biomass for weak interactions (a), strong interactions (b) and predator/prey case (c) rule tends to exploit fast growing stocks at a high rate while exploiting slow growing stocks more gently.

Another interesting feature of this rule is that the yield at the half virgin stock size biomass ($\overset{0}{p}_i$) position is given by the formula:

$$\tfrac{1}{2}\overset{0}{p}_1\, a_1 + \tfrac{1}{2}\overset{0}{p}_2\, a_2 \ldots\ldots\ldots\ldots \tfrac{1}{2}\overset{0}{p}_r\, a_r \qquad \ldots\ldots\ldots\ldots(19)$$

If we know the p's (from a groundfish survey and a knowledge of the catchabilities) and if we know the a's then we can estimate the yield when all stocks are at half their virgin biomass. While the a's are not known as such their values might be guessed either from known examples of such species or on general biological grounds.

Conservative strategy might suggest a modification to their half virgin biomass rule. Both Doubleday (1976) and Sissenwine (1974) have simulated populations having an underlying Schaefer yield curve under conditions of environmental fluctuations and found that holding the biomass at 2/3 the initial stock, as opposed to one half, was an excellent compromise between goals of maximum yield, stability and conservation. Although this may not hold in multispecies fisheries since environmental fluctuations may have opposite and compensating effects on different species, for the present it might be a more prudent strategy. This would be particularly true where fisheries have developed very rapidly, and catches have been largely obtained by fishing up accumulated stocks and where the time series of survey data is short enough for the lack of precision in the estimates to cause serious difficulties in obtaining an accurate fit.

3.4 Whole system models

There are a number of approaches which use models, of greater or less complexity, that consider the system in which the fish stocks live as a whole. Of these the most productive, especially in fresh water, have been those that consider the catches in similar bodies of water, and relate them to simple observable characteristics of those water bodies.

Since the early years of this century limnologists have described and classified bodies of fresh water, and marine ecologists have done the same for marine and estuarial waters. Since about 1950 much attention has been directed to reservoirs. Bodies of water have been classified into sets according to numerous criteria. Various statistical relationships have been discovered between whole system variables within a set, particularly in fresh waters.

Some of the early motivation for limnology came from practical workers in freshwater fisheries and the latter have continued to work quite closely with the former - perhaps more so than was the case between marine fisheries and marine ecologists and oceanographers. This does not imply that marine fisheries scientists and ecologists did not collaborate effectively - only that it was apparently not as widespread as with fresh water situations. Even with fresh waters more collaboration would have helped both groups advance faster.

With fresh water lakes, reservoirs and rivers the fisheries workers have found that catches of fish per unit area (at constant effective effort) can be related to readily measured limnological variables. Some of the most significant variables have been found to be mean depth of water body, total dissolved solids or alkalinity, total phosphorus concentration at periods of complete mixture of the water body, amplitude of annual water fluctuations, some index of primary production such as mean summer concentration of chlorophyll a, and an index of annual temperature (Ryder, 1965; Jenkins, 1968; Henderson *et al.*, 1973; Ryder *et al.*, 1974; Welcomme and Hagberg, 1977; Oglesby, 1977; and Matuszek, 1977) (see Figs. 10 and 11).

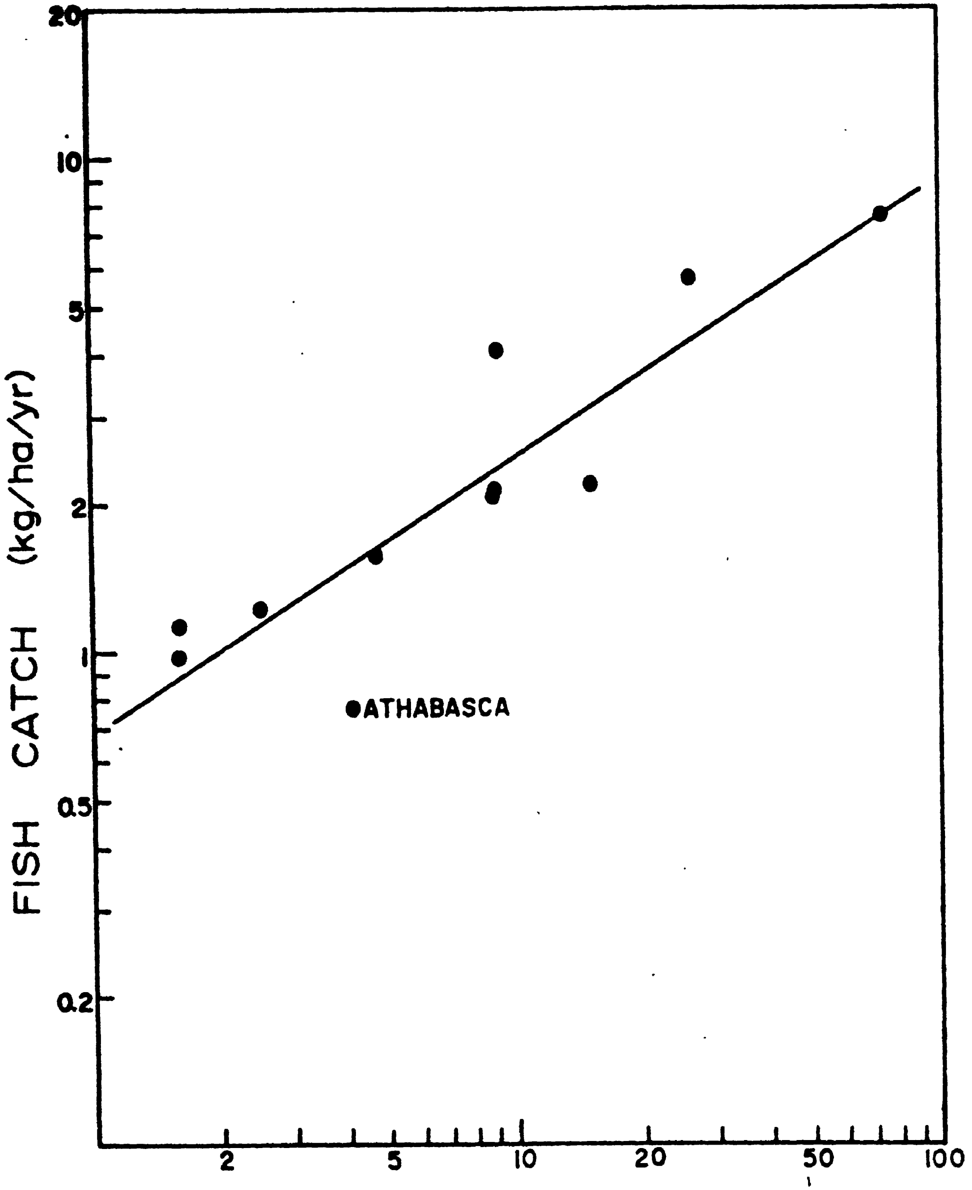

Fig.11 Fish yield in different lake basins as a function of bottom fauna standing crop (from Matuszek 1977)

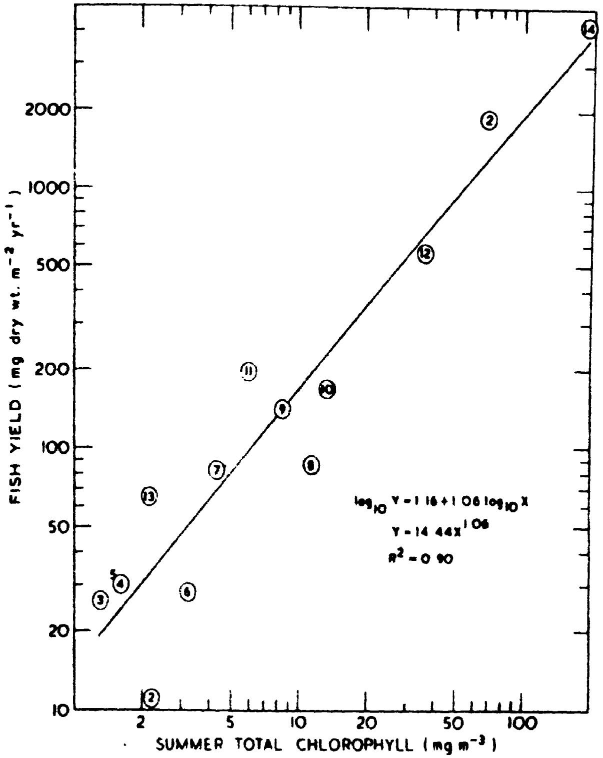

Fig.10 Fish yield in different bodies of water, as a function of summer chlorophyll (from Oglesby 1977)

Characteristically the statistical relationships between fish catch and various limnological variables have been developed using logarithmic transformations of all the data. This transformation is used for a number of reasons: the variables are usually distributed over two or more orders of magnitude even for water bodies within the same limnologically-defined class; also the variance of the scatter of points increases with the magnitude of the factors plotted, but is more nearly constant under a log transformation. The unexplained variance remains relatively large, so large that this approach in itself does not provide information of sufficient precision for tactical management of individual water bodies on a routine basis. At the strategical level, however, the data can be used to specify the approximate level of expectation which the prudent manager may entertain for his individual water bodies, and hence provide him with some broad general guidance on appropriate management action.

For example, where some statistical relationships of this type have been inferred for all waters of a given set from a study of some sub-set (which should be chosen according to some random sampling scheme, but which in practice may be chosen in some other way, e.g., accessibility, or attractiveness to fishermen, which could bias the conclusions), it is possible to specify the expected catch for any water body from a knowledge of the appropriate readily measured environmental covariates and also specify bounds on the estimate such that the probability is only 1 in 10, say, that the catch when fully realised will be greater than the upper bound or less than the lower bound. But such bounds as are obtainable by this approach may well extend from 0.5 E(C) to 2.0 E(C) where E(C) is the statistically derived expectation (mean) of the catch for that water body. An interval of this magnitude will likely be viewed as too wide except as a first approximation, and some additional scientific models and tools will be employed to fine tune the insights for purposes of achieving management goals. These supplementary and/or complementary techniques may be based on population dynamics concepts and/or on ecological concepts at the fish community level of organisation (see next section).

Whole-system variables as covariates of catch have been employed with: lakes of northern North America; reservoirs of the U.S.A.; lakes, reservoirs and rivers (separately) for Africa; some lakes of Scandinavia; and some lakes of Southeast Asia. The form of the relationships are generally similar within the various geographic-limnological classes and some attention has been directed toward explaining differences between sets (Henderson _et al._, 1973; Ryder _et al._, 1974). An international workshop has been planned for autumn 1978, under the aegis of the International Ecological Association, to bring together workers using this approach.

It seems likely that a similar approach could work with marine ecosystems. One problem relates to the fact that the marine fishery scientists have usually considered large units, with few, if any, replications - there is only one North Sea. Thus the direct statistical approach at this level of system is unlikely to be so immediately productive, though it was believed that posing questions such as "why is the Irish Sea considerably less productive per unit area?" could initiate some useful thought on the behaviour of these systems.

However, there are a number of marine situations, e.g., individual bays or estuaries, short lengths of coastline, especially when the shelf is narrow, which do offer the possibility of a number of replications. There are problems of interpretation due to the movements of fishing vessels, of fish and of the water itself that do not occur at least to the same extent in fresh water. For example, many fishing vessels operate over a wide area, without adequate reporting of where their catches were taken (see, for example, the problems in the Thailand trawl fishery). Also migration or currents may transfer fish or other organisms produced in one area to be caught or support fish catches in quite a different area. Nevertheless, the group felt that the comparative approach did have potential value in some marine situations, particularly in relation to inshore artisanal fisheries in which the fishermen do not move far, and from which the data are seldom adequate to make analysis by other methods.

Another basis for a comparative approach that has been found useful are various characteristics of the fish stocks themselves (ratio of the numbers or biomass of predatory to forage fishes, mean size of certain species, etc.).

Small ponds have long been managed intensively to produce fish for human consumption and/or recreational angling. Single-species aquaculture using domesticated species exists at one end of a spectrum, at the other are combinations of wild (genetically unselected) species. American experience with the latter is coming to be extended as a partial basis for managing American lakes and reservoirs (Swingle and Swingle, 1967; Jenkins, 1976b, personal communication) in the attempt to produce both "quality angling" and moderate crops of fish preferred as human food. Experience with sets of fish species selected ecologically for ponds in China (Tapiador et al., 1977), India and elsewhere in Asia might also provide useful bases for extrapolation to larger waters.

Recent work in the southeastern U.S.A. may serve as an instructive example. Beginning in the 1930's H.S. Swingle undertook a long series of experiments with various combinations of fish species using replicated ponds under experimental control as well as extensive field trials first in Alabama and eventually throughout much of North America. Subsequently other workers in Illinois, New York, Oregon, Missouri, Ontario and elsewhere conducted independent but related studies in part to test Swingle's experiences and in part to try out somewhat different ideas (Regier, 1962).

Swingle and his collaborators discovered a series of inexpensive, rapid diagnostic field tests to determine whether the fish community of a pond was "in balance" at the time. "Balance" was understood in his context as an ecological state in which satisfactorily large and sustained catches of large sport fish can be taken annually, about 100 kg/ha of bluegill and 20 kg/ha of largemouth bass in Alabama with Swingle's most favoured combination. Balance was defined operationally from the empirical studies and related to various biomass ratios such as predator to prey, adult to total, young of year to total, etc. Test seining (or cove poisoning in larger waters) provides samples of the total population from which the ratios can be calculated and state of balance diagnosed. For ponds of Alabama and nearby states it was possible to simplify the tests further: fine meshed seines were used to capture young of the year in summer, after annual reproduction had been completed, and state of balance could be inferred from the absolute or relative numbers of the young of various species captured. Swingle and his associates also discovered ways of correcting unbalanced communities using a variety of techniques including pond fertilization, destruction of spawning nests, seining out small bluegills, modification of pond morphometry, etc.

Jenkins (1976b,personal communication) has demonstrated that some of Swingle's diagnostic tests developed for small ponds also apply to reservoirs thousands of times as large and containing 10 to 20 times as many species as the ponds. It may now be possible, for example, to adjust commercial fisheries to harvest unnecessarily large masses of fish to bring an unbalanced association into balance or to help maintain an existing balance for the benefit of sport fishermen or other interests. It may not be an unsuperable step to extend this approach to larger, predominantly commercial fisheries in which various subsets of species are managed on a year to year basis by fishing them at different intensities. These intensities could be specified in relation to the simple types of ratio already mentioned, without involving complex assessments of individual species.

Another approach to modelling the whole system is to follow the flow of energy from primary production through to harvestable fish. There is a relatively robust ecological theorem that demands that transfer of energy from predator to prey cannot be complete or fully efficient. Data suggest that such transfer are rarely more than about 30 percent efficient. This concept has been conceptually treated as a pyramid of productivity in eco-systems in which the base is formed by primary producers elaborating food through photo-synthesis. Conventional theory also postulates a parallel pyramid of biomass (and of numbers). While this more or less holds for territorial systems, it is arguable in aquatic systems (Sheldon et al., 1972) and its relevance to aquatic systems has not been demonstrated. It is easy to show, however, that if the transfer of productivity is, say, 10 percent efficient, but the turnover rate of biomass of the prey is 10 times that of the predator, the biomass of the two should be about the same! This seems to be the case in Lake Tanganyika, where the predator species taken together and prey species taken together appear to fluctuate inversely from year to year (Henderson et al., 1973), and the changes in the biomass of the two groups as measured by the change in catch per boat, are about equal.

Gulland (1971) has noted that fishermen are more interested in high standing stocks than in high annual production, as the density or concentration of fish is what determines the cost of catching. Productivity seems to be higher in the tropics than in temperate seas, but it is the higher turnover rate in the tropics, accompanied by a moderate biomass, that is mostly responsible for the difference. For fishermen, therefore, there is no great advantage in this higher productivity.

Similarly, while fishes at the low end of the food chain may have a much higher productivity than the predators, there is little advantage to fishermen in utilizing the prey until harvesting has reduced the biomass of predators to low levels. It is for this reason in particular that the history of fishing in many regions of the world has been one of sequential shifts from long-lived predators toward shorter and shorter-lived plankton eaters or grazers. It is also one of the reasons why shifting harvests to lower levels of the food chain is not as effective in increasing yield to man as has often been assumed from simplified ecological theory.

This approach has been used to obtain quantitative estimates of the potential yield of fish from the whole ocean (Schaefer, 1965; Cushing, 1969; Ryther, 1969), and for major sea areas (e.g., off Peru, Ryther loc. cit., Cushing, loc. cit.). The difficulty with this is that small differences in the presumed trophic level, in transfer efficiency, or other factors (few of which have been measured with high precision) can make a big difference to the estimate of fish production. For example, interchanging Cushing's and Ryther's figures for overall transfer efficiency changes the estimate of fish production off Peru by a factor of 12 (Paulik, 1971). While calculations of this type can give some qualitative assurances that the limits of potential harvest obtained by other means are reasonable in trophodynamic terms, they are unlikely to be so useful for quantitative use. Indeed analysis of North Sea data (Steele, 1965; Gulland, 1976b), and the comparison of actual fish catches and primary production suggests that the transfer efficiencies are greater than generally supposed, and the trophodynamic approach would under-estimate the potential yield.

In the light of the various considerations it is clear that an examination of the structure of both the productivity (energy) and biomass pyramids can be useful in providing some insight into the system, but that it may be difficult from such an examination to obtain immediately applicable quantitative conclusions - not least because the fish being harvested may be playing a significant role in recycling nutrients and hence in determining the magnitude of primary production.

In the context of multispecies fisheries the main practical application of this approach may be in giving guidance on the likely effect of changes in species composition or species preference in the catches. Lateral shifts at the same trophic level (to the extent that any fish species can be considered as occupying a single well-defined level) should involve little change in total yield, whereas a shift to a higher (or lower) level is likely to involve a drop (increase) in catch. However, practical experience in fresh waters suggests that in the latter case the change is considerably less than the five or ten-fold change predicted by the accepted figures of ecological efficiency of 10-20%.

4. PROPOSALS FOR FUTURE ACTION

4.1 Improvements in models and methods of analysis

To improve current approaches the first need is for more data. This is taken up in section 4.2 following. In general, however, it should be accepted that fisheries theory has not yet reached its golden age but is very much in its infancy with very short time series and large area of complete ignorance. Consequently one of the most useful things we can do at present is to collect the right sort of data so that our successors will be in a better position to solve their problems than we are. At the same time the need to give advice now must not be ignored; we need a two-pronged approach, to ensure that we make good use of what data we have while ensuring that the scientists in future years will be in a position to give much clearer and accurate advice.

In terms of theory there is a need for models to be developed which bear a closer relationship with the real life fish stocks but which still retain features of mathematical tractability so that results from them may be generalised. Current approaches to fisheries problems have concentrated on studies at the population level, and they should be expanded as far as practicable. There are several possibilities here. One is multi-stock Schaefer models with time lags incorporated. Walter (1975) has made some progress in this direction. Another possibility is in cohort models based on a Leslie matrix approach. This gives steady states and also makes stability analysis possible. Pope (1976a) gives some details of such techniques, but obviously this will need considerable development if it is to become useful. Other possibilities are input/output models of the food web.

Population-level studies should be complemented by well-supported work at the fish community and aquatic ecosystems levels of organization. The approaches sketched in section 3 show promise that a well-balanced, broadly based set of approaches at higher levels can be developed to previde information useful for management with multi-species fisheries of the various types.

The development of ecological science at a particular level of organization, e.g., the ecosystem level, may be described as progressing through a series of stages:

(a) Description of systems and classification into sets using a variety of criteria, e.g., by use of statistical cluster analysis;

(b) Discovery of inter-relationships between descriptive variables within a set and between sets;

(c) Proposal and testing of explanations (or explications) of the relationships discovered, and of the lack of relationships between some variables;

(d) Development of testable theory to achieve generality, simplicity, richness of context, etc.

With freshwater lakes, reservoirs, rivers and floodplains the process sketched in rather stylised form above has proceeded into phase (b). Small groups of scientists are beginning to address phase (c) here and there. Scientists such as R. Margalef and M. Dunbar with major interests in the development of basic theory have proposed some ideas under phase (d). Progress should be stimulated at all levels.

In addition to these approaches others have been proposed from more theoretical viewpoints:

(a) Trophodynamic concepts developed within the International Biological Programme (Patten, 1975) are being applied on a trial basis within impact assessment activities in the U.S.A.;

(b) Regier and Henderson (1973) judge that concepts developed by R. Margalef, M. Dunbar, E.P. Odum and others could be used to manage fisheries to achieve desirable levels of production while safeguarding the ecological stability of the fish community;

(c) Kerr (1974) and his associates have brought together concepts of feeding size selectivity, physiological growth efficiency and organic particle size profiles as a possible framework for managing multispecies fisheries that harvest species in which the individual fish are of very different sizes.

The group felt that it is always desirable to develop at least two relatively independent scientific approaches to a problem or opportunity. These approaches may be at different levels of ecological organisation (such as population, fish community, ecosystem) or from different perspectives at the same level of organization (such as the analytical and surplus production approaches in population dynamics) or both.

The main approaches used in practice will vary with the particular situation faced by the scientists and the manager. Regier (1976; 1977; Regier and McCracken, 1975) has attempted to arrange situations into a logical pattern. Two main characteristics were used: the absolute magnitude of the object of study (the fish stock, the community, etc.) and its variability. Large stocks (cod, herring, tuna) can support the volume of research needed to provide accurate analysis using analytical single-species models; resources with low variability can be well described by Schaefer-type models, applied to single species, or total biomass. In general classical fishery techniques, especially in marine fisheries, have been addressed to this corner of the entire spectrum, whereas interest in high-variability-low magnitude situations has mainly been restricted to limnologists. Figure 12 (adapted from Regier and McCracken, 1975) illustrates this arrangement, with examples of significant publications (above), and types of resource (below) at different positions in the variability/magnitude matrix.

The position of a given resource in this matrix is not necessarily fixed. Man's activities can change their magnitude and their variability; in particular some forms of stress - heavy pollution, or intense exploitation - can increase their variability; clupeoids (anchovy, herring) being a noticeable example.

4.2 Data requirements

We recognize the need for data at a number of levels of specificity and of temporal and spatial scope. For strategic purposes it is sometimes useful to have very general and quite approximate measures of fish yield which may be obtained from data on conservative ecological properties that presumably already exist in the data files of oceanographers and limnologists. For year-to-year tactical purposes two other levels of advice are likely to be more useful: from production models of the Schaefer type, based either on total biomass or individual species in which the precision is moderately good; and from single species analytic models of the most important two or three species in which the precision is as good as it can be achieved practically.

Fishery managers as well as researchers would benefit from ready access to up-to-date information at all three levels. Each kind of information serves a somewhat different purpose, and thus the three kinds complement each other.

Ecosystem level data

Potential yield estimates, of sufficient precision to have strategic significance, have been obtained for freshwater lakes, reservoirs and rivers from inter-relationships between maximum sustainable yield for the combined fish community and several whole-system ecological variables.

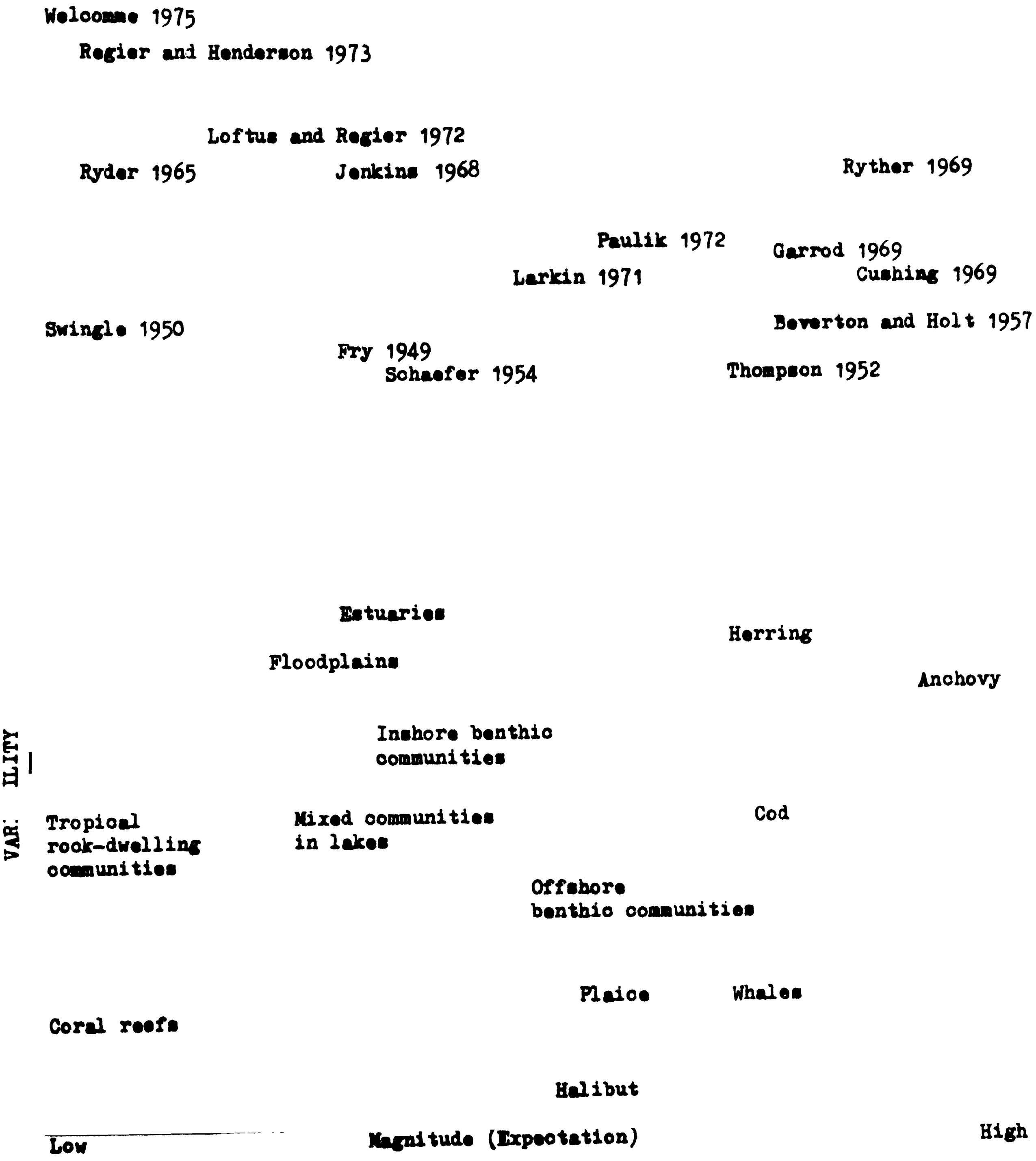

Fig. 12 Methods of approach, as indicated by significant papers (above), and typical species, groups of species, or communities (below) considered as functions of the magnitude (expectation) of the population, and its variability.

For freshwaters the most important variables may be classified as follows (not necessarily in order of world-wide significance):

Morphometric - mean depth;

Chemical fertility - total dissolved solids; alkalinity; annual phosphorus loading, or conductivity;

Ecological productivity - chlorophyll a concentration; primary production, or benthic biomass;

Climate - temperature, or degree days in growing season;

Current speeds or vertical mixing coefficients

Light - inorganic turbidity

All of the above tend to become interrelated in complex ways so that not more than three would be likely to enter significantly into a step-wise regression unless a very large number of ecosystems were included in the analysis (see e.g., analyses of more than 100 reservoirs by Jenkins, 1968).

It seems likely that similar variables could be identified that would also yield useful statistical interrelationships for marine ecosystems (smaller bays, estuaries or salt marshes might be good places to start). Some desk research using existing statistical and environmental data should be undertaken to explore such relationships. Presumably no new data would need to be collected by fisheries researchers to achieve an initial statistical characterisation. Since the variables to be entered are quite conservative, the relationship would likely not change rapidly through time. Periodic up-dates might be possible with relatively little data collection by fisheries agencies, on the assumption that most of the more useful variables will already be incorporated into the survey and monitoring programmes of oceanographers and marine ecologists, though this may well not be true in areas distant from the major centres of research, which are mostly in the larger developed countries.

Production models

The basic data necessary for the use of a Schaefer approach to assessing total mass are independent measures of two out of total catch, total effort, and an index of abundance. In single species fisheries it is normal to use the catch and effort statistics of the commercial fishery. When several species are concerned shifts in preference between species (which can be very difficult to measure, or even to detect with certainty) can invalidate commercial catches per unit effort (c.p.u.e.) as indices of abundance of any individual species. Total c.p.u.e. may be a somewhat more satisfactory index of total biomass (for example it has been used in some ICNAF areas), but an independent statistically sound resource monitoring survey will usually be needed.

Although surveys can reduce the need for effort statistics, it will always be essential to have reliable statistics of the total catch by the fishery, together with information on species composition at least to the detail of major species groups. In addition effort data can still be useful in interpreting the catch and survey information, in addition to its value in economic analyses and in the monitoring or enforcement of actual management measures.

The precision obtained from most individual surveys is low. The most valuable information for the present purposes comes from a series of observations over a period of years from which trends can be analysed. Therefore, when such surveys are set up there should be a commitment that resources will be made available to continue the surveys as a regularly scheduled time series.

Of the different types of survey available the most suitable for most multispecies situations is a bottom-trawl survey. The average catch per haul obtained will be some weighted index of the combined abundance of all species available to the gear. The weighting factor will be the catchability coefficients (q) of each species. For some situations, e.g., in the Gulf of Thailand where the commercial fishery has similar catchability coefficients, this index (unadjusted c.p.u.e. in the survey) may be satisfactory. In other cases, especially if the pattern of year-to-year changes in abundance is very different for different species, e.g., due to shifts in the target species in the fishery, adjustments need to be made to allow for differences in catchability between species or species groups. That is, an index of abundance of total biomass is obtained from a weighted sum of c.p.u.e. of individual species (or species groups), using weights equal to the reciprocal of the estimated catchability.

Although detailed analytical studies can be used to obtain refined estimates of these catchabilities, first approximations needed for immediate management can be made by knowledgeable scientists based on life history pattern knowledge of relative catchabilities for species with similar life histories reported in the literature, historic catch statistics, and experimental studies comparing commercial gear used for different species groups with the survey trawl.

The adjustments will be greatest for pelagic species, and clearly a bottom trawl is not suitable for a truly pelagic species that remains in mid-water the whole time. In practice this is rare; most pelagic species go near to the bottom at some time, e.g., at night, and can be sampled by a bottom trawl.

Pelagic species, and demersal species that are not too close to the bottom, can also be surveyed by acoustic methods. The doubts that still surround some approaches to estimation of absolute abundance by acoustic methods do not apply so strongly to indices of abundance, e.g., integrated signal strength received. However acoustic methods by themselves give little information about species. In the worst situation the index obtained may include signals not associated with the multispecies population of interest, e.g., from very small fish or other animals. In any case the index will be a weighted combination of different species, weighted according to their target strength. Fortunately the number of species involved is rarely large (much smaller than the variety of demersal species), and information on species composition can be obtained by fishing on samples of different types of echo while carrying out the survey. Adjustments can then be made, if desired, to allow for varying target strength.

Bottom trawl or acoustic equipment - or preferably the two used in combination - provide adequate survey instruments in most situations; exceptions include reefs, and some coastal and inland waters. Gill nets have been widely used in fresh water, and their use as a survey tool in shallow inshore areas is worth wider consideration. For reefs, traps are probably the most suitable.

Surveys will be of the greatest value when they are used by managers to control a fishery during its expansion phase, before over-expansion has incurred, and the biomass has been reduced below the level giving the maximum yield, or to the level where a reduction in fishing mortality (and hence for a period also in catch) is necessary in order to rebuild the stocks. This means that the surveys should be begun at latest as soon as there is a significant fishery. Failing that, it may be possible for knowledgeable fishery scientists to extrapolate the survey back to make an estimate of initial biomass accurate enough to be useful in making management decisions.

Biological data

Both for the application of analytic models, and for general insight into the behaviour of the fish community as a system, certain types of biological data are valuable.

Most obviously useful is the measurement of fish species on a routine basis, the collection of materials (scales, otoliths, etc.) by which the fish can be aged, where this is practical, and the collection of information on feeding habits.

The existence of a trawl survey often gives the opportunity for some biological sampling to be conducted for a fairly small extra cost in manpower and time. It is particularly desirable to use the survey to collect material for estimating total mortality so that it can be used later in estimating potential yield from the data on biomass (standing stock), using the relation $Y = 0.5\ MB_o$ or similar formula.

The priority given to these activities will, of course, be assigned by national resources and needs but the development of time series of such data will enable various types of mixed fishery models to be used. The existence of size/age distribution of fish apart from its obvious uses in the estimation of mortality will enable models based on broad classifications of fish size/cohort to be made. The combination of size and feeding data should assist in the development of cohort based models of interactions and lagged Schaefer models such as those suggested in section 3.3. Broad classifications of systems into competing systems and prey-predator systems and ideas of the degree of interaction should, at a conceptual level, assist in the interpretation of multispecies total yield contour models and suggest the likely levels of mortality or population levels for the MSY of the system. They might also make it possible to obtain indirect estimates of the 'a', 'b', 'c' parameters of such models (see equations 4 *et seq.*).

5. SUMMARY

The classical approaches to the dynamics of fish populations, and to the provision of advice to decision-makers on the utilization, management and conservation of fishery resources have been based on the analysis of populations of single species of fish. Intensification of exploitation onto a wider variety of fish species, interacting in various if undetermined ways, raises serious questions of the validity of such simple approaches.

Experience of fisheries in some areas (e.g., ICNAF) shows that management based on single-species analyses can fail to prevent serious declines in the stocks. On the other hand other experience (e.g., in the Gulf of Thailand, or in the ICNAF area) shows that fairly simple analyses, essentially ignoring species differences and considering only the total biomass, can provide useful advice on first-order management actions.

Some theoretical studies, expanding single-species production models to multispecies situations, show that such a simple approach should be valid for many situations involving interacting species, especially when the fisheries cannot alter the ratios of the effective fishing efforts on different species. Pending detailed analysis a cautious management strategy would be to maintain the biomass of each stock at not less than half its initial level.

Other approaches to multispecies fisheries that have been found useful, especially in fresh water, have included systematic comparisons between different water bodies in terms of environmental parameters (e.g., mean depth, conductivity, etc.) and characteristics of the fish stocks (e.g., ratios of predators to herbivores), as well as consideration of the trophodynamics of the systems.

None of these approaches are perfect, though all are useful in at least some situations. Efforts should therefore be made to refine them, as well as looking for alternatives; in practical applications it is important not to rely on any one method, but, especially when providing advice, to utilize as wide a variety of approaches as is practicable.

Any approach needs data and most need data over a series of years. It is important that action is taken now to ensure that systems of data are set up so that scientists in future years will have adequate material to work on. Types of data to be collected include statistics of total catch, and its species composition, and indices of stock abundance (particularly those obtained by surveys with bottom trawls and acoustic methods, possibly used in combination).

6. REFERENCES

Alverson, D.L. and W.T. Pereyra, Demersal fish exploitations in the northeastern Pacific
1969 Ocean - an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J.Fish.Res.Board Can., 26(8):1985-2001

Andersen, K.P. and E. Ursin, A multispecies extension to the Beverton and Holt theory of
1977 fishing, with accounts of phosphorus circulation and primary production. Meddr.Dan.Fisk.-Havunders.(Ny Ser.), 7:319-435

Anderson, L.G., Analysis of open-access commercial exploitation and maximum economic yield
1975 in biologically and technologically inter-dependent fisheries. J.Fish.Res. Board Can., 32(10):1825-42

Anthony, V.A. and J.A. Brennan, An example of the by-catch problem on directed fisheries
1974 for 1975. ICNAF Summ.Doc., (74/47) Serial No.3386 (mimeo)

Bell, F.H., The incidental capture of halibut by various types of fishing gears. Rep.Int.
1956 Pac.Halibut Comm., (23):48 p.

Beverton, R.J.H. and S.J. Holt, On the dynamics of exploited fish populations. Fish.Invest.
1957 Minist.Agric.Fish.Food G.B.(2 Sea Fish.), (19):533 p.

Brander, K.M., The management of Irish Sea fisheries - a review. Leafl.Dir.Fish.Food G.B.
1977 (New Ser.), (36)

Brown, B.E., A prospectus on the basis for fishery management on the northwest Atlantic
1976 continental shelf off the coast of the U.S.A. ICNAF Res.Doc., (76/102) Serial No.3925 (mimeo)

Brown, B.E. and J.A. Brennan, A preliminary evaluation of total fishing effort on the total
1972 fish biomass and first approximation of maximum sustainable yield for finfishes in ICNAF Division 5 and Subarea 6. Part 2. Estimates of total fishing effort and its relation to sustainable yield of finfish. ICNAF Res.Doc., (72/119) Serial No.2835 (mimeo)

Brown, B.E., J.A. Brennan and J.E. Palmer, Linear programming simulations of the effects
1975 of by-catch on national catches in ICNAF Subarea 5 and Statistical Area 6. ICNAF Res.Doc., (1975/68) Serial No.3552 (mimeo)

Brown, B.E., J.A. Brennan, E.G. Heyerdahl and R.C. Hennemuth, Effect of by-catch on the
1973 management of mixed species fisheries in Subarea 5 and Statistical Area 6. Redbook ICNAF, 1973(3):217-31

Brown, B.E., J.A. Brennan, M.D. Grosslein, E.G. Heyerdahl and R.C. Hennemuth, The effect
1976 of fishing on the marine finfish biomass in the Northwest Atlantic from the Gulf of Maine to Cape Hatteras. ICNAF Res.Bull., (12):49-68

Christie, W.J., Lake Ontario: effects of exploitation, introduction and eutrophication
1972 on the salmonid community. J.Fish.Res.Board Can., 29:913-29

Clark, S.H. and B.E. Brown, 1975 Changes in biomass of finfish and squid from the Gulf of Maine to Cape Hatteras 1963-74, as determined from research vessel survey data. ICNAF Res.Doc., (75/139) Serial No.3692 (mimeo)

__________, 1977 Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish.Bull. NOAA/NMFS, 75(1):1-21

Cushing, D.H., 1969 Upwelling and fish production. FAO Fish.Tech.Pap., (84):40 p.

________, 1971 The dependence of recruitment on parent stock in different groups of fishes. J.Cons.CIEM, 33:340-62

__________, 1976 Biology of fishes in the pelagic community. In The ecology of the seas, edited by D.H. Cushing and J.J. Walsh. London, Blackwell Scientific Publications, pp.317-40

Cushing, D.H., 1977 The problems of stock and recruitment. In Fish population dynamics, edited by J.A. Gulland. London, Wiley-Interscience Publication, pp.116-33

Doi, T., 1962 On the predatory and competitive relationships among fishes caught in the waters adjacent to Japan. Bull.Tokai Reg.Fish.Res.Lab., 32:49-121

Doubleday, W.G., 1976 Environmental fluctuations and fisheries management. Collect.Pap.Int. Comm.Northw.Atl.Fish., 1:141-50

Fry, F.E.J., 1949 Statistics of a lake trout fishery. Biometrics, 5:27-67

Fukuda, Y., 1973 A gap between theory and practice. J.Fish.Res.Board Can., 30(12):Pt.2:1986-91

__________, 1976 A note on yield allocation in multi-species fisheries. ICNAF Res.Bull., (12): 83-7

Garrod, D.J., 1969 Empirical assessments of catch/effort relationships in north Atlantic cod stocks. ICNAF Res.Bull., 6:26-34

__________, 1973 Management of multiple resources. J.Fish.Res.Board Can., 30(12):Pt.2: 1977-85

__________, 1973 Memorandum on the mixed fishery problem in Sub-Areas 5 and 6. ICNAF Res.Doc., (1973/6) Serial No.2908 (mimeo)

Grosslein, M.D., 1968 Results of the joint USA-USSR groundfish studies. Part 2. Groundfish survey from Cape Hatteras to Cape Cod. ICNAF Res.Doc., 68/67 Serial No.2075 (mimeo)

Grosslein, M.D. and E. Bowman, 1973 Mixture of species in Sub-Areas 5 and 6. Redbook ICNAF, 1973 (3):163-207

Gulland, J.A., 1971 Ecological aspects of fishery research. Adv.Ecol.Res., 7:115-76

________, 1972 Population dynamics of world fisheries, Chapter 13. Gulf of Thailand trawl. Mixed species-combined analysis. Wash.Sea Grant Publ., (WSG 72-1):268-90

________, 1976a The scientific basis for the management of fisheries. In Proceedings of the International Seminar on Fisheries Resources and their Management in Southeast Asia. Berlin, 19 November-6 December 1974. Organized by the German Foundation for International Development and FAO, edited by K. Tiews. Bonn, Druckerei Heinz Lammerich, pp.155-68

Gulland, J.A., Production and catches of fish in the sea. *In* The ecology of the seas,
1976b edited by D.H. Cushing and J.J. Walsh. London, Blackwell Scientific Publications, pp.283-316

Gulland, J.A., and L.K. Boerema, Scientific advice on catch levels. *ICNAF Res.Doc.*,
1972 (72/26) Serial No.2717 (mimeo)

Gundermann, J., H. Lassen and E. Nielsen, Splitting catch quotas of several species on a
1974 number of fisheries using linear programming. *ICES Doc.C.M.*, 1974/F:46 (mimeo)

Hackney, P.A. and C.K. Minns, A computer model of biomass dynamics and food competition
1974 with implications for its use in fishery management. *Trans.Am.Fish.Soc.*, 103 (2):215-25

Halliday, R.G. and W.G. Doubleday, Catch and effort trends for the finfish resources of
1976 the Scotian Shelf and an estimate of the maximum sustainable yield of groundfish. *Sel.Pap.ICNAF*, 1:117-28

Hartman, W.L., Lake Erie: effects of exploitation, environmental changes and new species
1972 on the fishery resources. *J.Fish.Res.Board Can.*, 29:899-912

Henderson, H.F., R.A. Ryder and A.W. Kudhongania, Assessing fishery potentials of lakes
1973 and reservoirs. *J.Fish.Res.Board Can.*, 30(12)Pt.2:2000-9

Hilborn, R., Optimal exploitation of multiple stocks by a common fishery: a new
1976 methodology. *J.Fish.Res.Board Can.*, 33(1):1-5

Hoag, S.H., Effects of domestic trawling on the halibut stocks of British Columbia.
1971 *Sci.Rep.Int.Pac.Halibut Comm.*, (53):18 p.

Hobson, E.S. and W.H. Lenarz, Report of a colloquium on the multispecies problem, June
1977 1976. *Mar.Fish.Rev.*, (9):8-13

Hongskul, V., Fishery dynamics of the northeastern Pacific groundfish resources. Ph.D.
1975 thesis. University of Washington, Seattle, U.S.A.

Hongskul, V., L.J. Bledsoe and J.E. Love, NORSIM I: A fishery simulation model for the
1972 study of multispecies exploitation. *Univ.Wash.NORFISH Tech.Pap.*, (19):72 p.

Horwood, J.W., Interactive fisheries: a two species Schaefer model. *Sel.Pap.ICNAF*,
1976 1:151-5

Huppert, D.D., D.J. Brown and V. Hongskul, NORSIM II: An expanded simulation model for the
1973 study of multispecies exploitation. *Univ.Wash.NORFISH Tech.Pap.*, (40):122 p.

ICCAT, Report of the Standing Committee on Research and Statistics. *In* Report for the
1975 biennial period 1974-1975. Part 1, 1974, pp.111-29. International Commission for the Conservation of Atlantic Tunas, Madrid

ICES, Report of the Working Group on the Assessment of Demersal Species in the North Sea.
1969 *Coop.Res.Rep.ICES*, (Ser.A.) (9):71 p.

ICNAF, Statistical bulletins for the years 1961-1973. Dartmouth, N.S., Canada, ICNAF
1962-1974

__________, Annual proceedings for the years 1971-1972. Dartmouth, N.S., Canada, ICNAF
1972

ICNAF, Annual proceedings for the year 1972-1973, Dartmouth, N.S., Canada, ICNAF
1973

Isarankura, A.P., Present status of trawl fisheries resources in the Gulf of Thailand and
1971 the management programme. *Proc.IPFC*, 14(2):105-14

———, Assessment of stocks of demersal fish off the west coasts of Thailand and
1971 Malaysia. Rome, FAO, IOFC/DEV/71/20, 20 p.

Jenkins, R.M., The influence of some environmental factors on standing crop and harvest
1968 of fishes in U.S. reservoirs. *In* Proceedings of the Reservoir Fishery Symposium
5-7 April 1967. Athens, Georgia, Southern Division, American Fisheries Society,
pp.298-321

———, Prediction of fish production in Oklahoma reservoirs on the basis of environ-
1976a mental variables. *Ann.Okla.Acad.Sci.*, (5):11-20

———, The influence of engineering design and other environmental factors on
1976b reservoir fishery resources. *J.Am.Water Res.Assoc.*, 16:110-6

Jenkins, R.M. and D.I. Morais, Prey-predator relations in the predator-stocking-evaluation
1976 reservoirs. Fayetteville, Arkansas, National Reservoir Research Programme,
U.S. Fisheries and Wildlife Service, 28 p. (mimeo)

Jones, R., Mesh regulation in the demersal fisheries of the South China Sea area. Manila,
1976 SCSDEVPRO, SCS/76/WP/34:75 p.

Keleher, J.J., Great Slave Lake: Effects of exploitation on the salmonid community.
1972 *J.Fish.Res.Board Can.*, 29:741-53

Kerr, S.R., Structural analysis of aquatic communities. *In* Proceedings of the First Inter-
1974 national Congress of Ecology. Wageningen, The Hague Centre for Agricultural
Publishing and Documentation, pp.69-74

Ketchen, K.S., Measures of abundance from fisheries for more than one species. *Rapp.P.-V.*
1964 *CIEM*, 155:113-6

Larkin, P.A., Interspecific competition and exploitation. *J.Fish.Res.Board Can.*, 20:
1963 647-78

———, Exploitation in a type of predator-prey relationship. *J.Fish.Res.Board Can.*,
1966 23:349-56

———, Simulation studies of Adams River sockeye salmon (*Oncorhynchus nerka*)
1971 *J.Fish.Res.Board Can.*, 28:1493-1502

———, An epitaph for the concept of maximum sustained yield. *Trans.Am.Fish.Soc.*,
1977 (106):1-11

Lett, P.F. and A.C. Kohler, Recruitment: a problem of multispecies interaction and
1976 environmental perturbations, with special reference to the Gulf of St. Lawrence
Atlantic herring (*Clupea harengus harengus*). *J.Fish.Res.Board Can.*, 33(6):
1353-71

Loftus, K.H. and H.A. Regier (eds), Proceedings of the Symposium on salmonid communities
1972 in oligotrophic lakes. *J.Fish.Res.Board Can.*, 29:613-986

Marr, J.C., G. Campleman and W.R. Murdoch, An analysis of the present, and recommendations
1976 for the future development and management policies programmes and institutional arrangements, Kingdom of Thailand. FAO/UNDP South China Sea Development and Coordinating Programme, Manila, Doc. SCS/76/WP/45

Matuszek, J.E., On empiric estimates of fish yields of large Canadian lakes. University
1977 of Toronto, M.Sc. thesis

Maurer, R., A preliminary analysis of interspecific trophic relationships between the sea
1976 herring *Clupea harengus* Linnaeus and the Atlantic mackerel *Scomber scombrus* Linnaeus. *ICNAF Res.Doc.*, (76/121) Serial No.3967 (mimeo)

Melack, J.M., Primary productivity and fish yields in tropical lakes. *Trans.Am.Fish.Soc.*,
1976 105(5):575-80

Murphy, G.I., Population biology of the Pacific sardine (*Sardinops caerulea*). *Proc.Cal.*
1966 *Acad.Sci.*, 34(1):1-84

__________, Clupeoids. *In* Fish population dynamics, edited by J.A. Gulland. London,
1977 Wiley Interscience Publications, pp.283-308

Nagasaki, F., Long-term and short-term fluctuations in the catches of coastal pelagic
1973 fisheries around Japan. *J.Fish.Res.Board Can.*, 30(12)Pt.2:2361-7

National Research Council, World fish and nutrition study. Supporting papers: Vol.1.,
1977 Washington, National Academy of Sciences

Oglesby, R.T., Fish yield as a monitoring parameter and its prediction for lakes. *In*
1977 Biological monitoring of inland fisheries, edited by J.S. Alabaster. London, Applied Science Publishers Ltd., pp.195-205

Parrish, J.D. and S.B. Saila, Interspecific competition, predation, and species diversity.
1970 *J.Theor.Biol.*, 27:207-220

Patten, B.C. (ed.), Systems analysis and simulation in ecology. New York, Academic Press
1975

Paulik, G.J., Anchovies, birds and fishermen in the Peru Current. *In* Environment: resources,
1971 pollution and society, edited by W.W. Murdoch. Stamford, Conn., Sinauer Associates

__________, Fisheries and the quantitative revolution. *In* World fishery policy: multi-
1972 disciplinary views, edited by B.J. Rothschild. University of Washington Press, Seattle, pp.219-28

Paulik, G.J., A.S. Hourston and P.A. Larkin, Exploitation of multiple stocks by a common
1967 fishery. *J.Fish.Res.Board Can.*, 24(12):2527-35

Pinhorn, A.T., Catch and effort relationships of the groundfish resource in Subareas 2 and
1976 3. *Sel.Pap.ICNAF*, 1:107-15

Pope, J.G., A note on the mixed species problem. *ICNAF Res.Doc.*, (119) Serial No.3620
1975 (mimeo)

__________, The effect of biological interaction on the theory of mixed fisheries.
1976a *Sel.Pap.ICNAF*, 1:157-62

__________, The application of mixed fisheries theory to the cod and redfish stocks of
1976b Subarea 2 and Division 3K. *Sel.Pap.ICNAF*, 1:163-9

__________, Problems of multispecies fisheries. FAO/UNDP South China Sea Programme,
Manila (in press)

Pope, J.G. and O.C. Harris, The South African pilchard and anchovy stock complex, an
1975 example of the effects of biological interactions between species on management strategy. *ICNAF Res.Doc.*, (133) Serial No.3685 (mimeo)

Rapport, D.J. and J.E. Turner, Economic models in ecology. *Science, Wash.*, 195:367-73
1977

Regier, H.A., On the evolution of bass-bluegill stocking policies and management recommenda-
1962 tions. *Progr.Fish.Cult.*, 24:99-111

——————, Science for the scattered fisheries of the Canadian interior. *J.Fish.Res.*
1976 *Board Can.*, 33(5):1213-32

——————, Fish communities and aquatic ecosystems. *In* Fish population dynamics
1977 edited by J.A. Gulland. London, Wiley Interscience Publications, pp.134-55

Regier, H.A. and W.L. Hartman, Lake Erie's fish community: 150 years of cultural stress.
1973 *Science, Wash.*, 188:1248-55

Regier, H.A. and H.F. Henderson, Towards a broad ecological model of fish communities
1973 and fisheries. *Trans.Am.Fish.Soc.*, 102(1):56-72

Regier, H.A. and K.H. Loftus, Effects of fisheries exploitation on salmonid communities
1972 in oligotrophic lakes. *J.Fish.Res.Board Can.*, 29:959-68

——————, Sequence of exploitation of stocks in multispecies fisheries in the
1973 Laurentian Great Lakes. *J.Fish.Res.Board Can.*, 30(12):1992-9

——————, Fish ecology and its application. *Mitt.Int.Ver.Theor.Angew.Limnol.*, 20:
1976 273-86

——————, Fish communities and aquatic ecosystems. *In* Fish population dynamics,
1977 edited by J.A. Gulland. London, Wiley Interscience Publications, pp.134-55

Regier, H.A. and F.D. McCracken, Science for Canada's shelf-seas fisheries. *J.Fish.Res.*
1975 *Board Can.*, 32(10):1887-932

Ricker, W.E., Maximum sustainable yields from fluctuating environments and mixed stocks.
1958a *J.Fish.Res.Board Can.*, 15(5):991-1006

——————, Handbook of computations for biological statistics of fish populations.
1958b *Bull.Fish.Res.Board Can.*, (119):300 p.

——————, Computation and interpretation of biological statistics of fish populations.
1975 *Bull.Fish.Res.Board Can.*, (191):382 p.

Riffenburgh, R.H., A stochastic model of interpopulation dynamics in marine ecology.
1969 *J.Fish.Res.Board Can.*, 26:2843-80

Ritragsa, S., Results of the studies on the status of demersal fish resources in the Gulf
1976 of Thailand from trawling surveys, 1963-72. Proceedings of the International Seminar on Fisheries Resources and their Management in Southeast Asia. Berlin, 19 November-6 December 1974, organised by the German Foundation for International Development and FAO, edited by K. Tiews. Bonn, Druckerei Heinz Lammerich, pp.198-223

Rosado, J.M. de Campos, Long-term changes in abundance of yellowfin and skipjack off the
1971 coast of Angola. J.Cons.CIEM, 34(1):65-75

Rothschild, B.J., Competition for gear in a multiple-species fishery. J.Cons.CIEM, 21
1967 (1):102-10

Ruamragsa, S. and A.P. Isarankura, An analysis of demersal catches taken from the experimental
1965 trawling operation in the Gulf of Thailand. Contrib.Dep.Fish.Bangkok,
(3):51 p.

Ryder, R.A., A method for estimating the potential fish production of north-temperate
1965 lakes. Trans.Am.Fish.Soc., 94(3):214-18

Ryder, R.A., S.R. Kerr, K.H. Loftus and H.A. Regier, The morphoedaphic index, a fish yield
1974 estimator-review and evaluation. J.Fish.Res.Board Can., 31:663-88

Ryther, J.H., Photosynthesis and fish production in the sea. The production of organic
1969 matter and its conversion to higher forms of life vary throughout the world
ocean. Science, Wash., 166:72-6

Schaefer, M.B., Some aspects of the dynamics of populations important to the management
1954 of the commercial marine fisheries. Bull.I-ATTC, 1(2):26-56

__________, The potential harvest of the sea. Trans.Am.Fish.Soc., 94(2):123-8
1965

Sheldon, R.W., A. Prakash and W.H. Sutcliffe, Jr., The size distribution of particles in
1972 the ocean. Limnol.Oceanogr., 17:327-40

Shiohama, T., Studies on measuring changes in the characters of the fishing effort of the
1971 tuna longline fishery. 1. Concentrations of the fishing effort to particular
areas and species in the Japanese Atlantic fishery. Bull.Far Seas Fish.Res.
Lab., (5):107-30

Silliman, R.P., Experimental exploitation of competing fish populations. Fish.Bull.NOAA/
1975 NMFS, 73:872-88

Sissenwine, M.P., Variability in recruitment and equilibrium catch of the southern New
1974 England yellowtail flounder fishery. J.Cons.CIEM, 36(1):15-26

Smith, S.H., Species succession and fishery exploitation in the Great Lakes. J.Fish.Res.
1968 Board Can., 25:667-693

__________, The future of salmonid communities in the Laurentian Great Lakes. J.Fish.
1972 Res.Board Can., 29:951-7

Soutar, A. and J.P. Isaacs, History of fish populations inferred from fish scales in
1969 anaerobic sediments off California. Rep.CCOFI, (13):63-70

Steele, J., Some problems in the study of marine resources. Spec.Publ.ICNAF, (6):463-76
1965

Svärdson, G., Interspecific population dominance in fish communities of Scandinavian
1976 Lakes. Rep.Inst.Freshwat.Res.Drottningholm, (55):144-71

Swingle, H.S., Relationships and dynamics of balanced and unbalanced fish populations.
1950 Ala.Polytech.Inst.Agr.Exp.Stn.Bull., (274):74 p.

Swingle, H.S. and W.E. Swingle, Problems in dynamics of fish populations in reservoirs.
1967 In Reservoir Fishery Resources Symposium. Athens, Georgia, American Fisheries Society Reservoir Committee, Southern Section, pp.229-243

Tapiador, D.D., H.F. Henderson, M.N. Delmendo and H. Tsutsui, Freshwater fisheries and
1977 aquaculture in China. FAO Fish.Rep., (168)

Templeman, W.E. and J.A. Gulland, Review of possible conservation actions for the ICNAF
1965 area. Ann.Proc.Int.Commn.N.W.Atlant.Fish, 15:47-56

Thompson, W.F., Condition of stocks of halibut in the Pacific. J.Cons.CIEM, 18:141-166
1952

Tiews, K., Fishery development and management in Thailand. Arch.Fischereiwiss., 24(1-3):
1973 271-300

Tiews, K., P. Sucondhamarn and A. Isarankura, On the change in the abundance of demersal
1967 fish stocks in the Gulf of Thailand from 1963/1964 to 1966 as a consequence of the trawl fishery development. Contrib.Dep.Fish.Bangkok, (8):39 p.

Turner, J.L., Changes in the size structure of cichlid populations of Lake Malawi result-
1977 ing from bottom trawling. J.Fish.Res.Board Can., 34:232-8

Walter, G.G., Graphical methods for estimating parameters in simple models of fisheries.
1975 ICNAF Res.Doc., (51) Serial No.3530 (mimeo)

Walters, C. and W. Hogman, Mathematical models for estimating changes in fish populations
1971 with application to Green Bay. Proc.Conf.Great Lakes Res., 14:170-84

Watt, K.E.F., The choice and solution of mathematical models for predicting and maximizing
1956 the yield of a fishery. J.Fish.Res.Board Can., 13(5):613-645

Welcomme, R.L., The fisheries ecology of African floodplains. CIFA Tech.Pap., (3):51 p.
1975

Welcomme, R.L. and D. Hagborg, Towards a model of a floodplain fish population and its
1977 fishery. Environ.Biol.Fish., 2(1):7-24

Wongratana, T., A check list of fishes caught during the trawl surveys in the Gulf of
1968 Thailand and off the east coast of the Malay peninsula. Contrib.Dep.Fish. Bangkok, (13):96 p.

Zuboy, J.R. and R.T. Lackey, A computer simulation model of a multispecies centrarchid
1975 population complex. Va.J.Sc., 26(1):13-9

NO; 11303