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WHY STUDY FISH POPULATION RECRUITMENT?¹

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ABSTRACT. Recent changes in world fisheries and in the Ocean Regime have substantially modified the scope of fishery science. Variability in fish stock abundance, a new concern for small-scale fisheries and conservation of littoral environments, and the weight of extensive mariculture have enhanced the priority of investigations on the ecology and dynamics of early stages of aquatic populations. Quantitative understanding of the regulatory mechanisms through which fish stocks regulate their numbers in response to environment fluctuations would contribute to the progress of marine ecosystems exploitation and coherent use.

1. INTRODUCTION

At the turn of this century, variability in fish stock abundance became a matter of concern for fishery science in the North Sea: Heincke (1898) demonstrated the existence of self-sustaining populations and Hjort (1914) hypothesized that fish population variability originates in processes taking place in the early, pelagic, phase of stock cohorts. Their work had a great influence on the development of fishery science, systematics and evolutionary biology (Sinclair and Solemdal, 1987).

However, attention to this topic dropped after World War I. Investigations on population recruitment variability were then restricted to assessing the effects of reduction in spawning biomass induced by fishing (Ricker, 1954; Beverton and Holt, 1957). Attention to fish population variability and its environmental causes has been recently revived at national and international levels (IOC, 1983; ICES, 1985), primarily among marine scientists and biological oceanographers. Such concern is justified by the role, played by

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the processes determining the recruitment success, in the regulation and evolution of aquatic population (Rothschild, 1986; Sinclair, in press).

This historical sequence raises the question of the timeliness and relevance of that topic for fishery science since academic interest is not in itself a sufficient motivation for targeted research: as potential contributions to the economic sector need to be taken into account when ranking research priorities .

The purpose of the present paper is to analyze to what extent a better understanding of the recruitment processes and sources of variability would improve fishery science potential contribution to the further development and better management of exploited fish populations--including the development of "fish ranching" opportunities and the need to conserve the carrying capacity of coastal environments. This assessment will be conducted by comparing developments in fishery science concerns to the specific issues associated with the successive steps observed in fishery development. This comparison is expected to indicate to what extent current scientific paradigms and research strategies are suited for investigating questions which have emerged with the full exploitation of world fishery resources and the adoption of a new Ocean Regime (see e.g. Rothschild 1972, 1983).

2. RESOURCE EVALUATION AND CONSERVATION

2.1 Historical Overview

Heincke's and Hjort's initial concern for fish population structure and fluctuations was clearly motivated by the intensive exploitation of North Sea stocks of major economic significance. The Western Norway herring fishery collapsed, for example, from 1870 to 1895; the Northern Norway segment did too in 1875; the Bohuslan stock was extremely low from 1810 to 1880 and, again, in 1980 (Devold, 1963). Herring population structure and interannual fluctuations in landings were directly connected issues and perceived as such, as shown by the two interpretations of divergent economic and political implications which were opposed one another at that time: that of a single stock migrating across the Northeast Atlantic against that of several discrete populations of fluctuating size spawning year after year in the same locations (Sinclair and Solemdal, op. cit.). There was also concern for the consequences of overfishing on demersal stocks subsequent to the introduction of steam propulsion and otter trawl (Went, 1972): as was later determined, signs of biological overfishing appeared first in 1890 on North Sea plaice and in 1905 on North Sea haddock.

A similar interest for the determinants of resource fluctuations was also noted in the French pilchard fishery which occurred as far back as the end of last century: "(il est) urgent de savior si l'irrégularité des rendements de la pêche est la résultat, comme certains l'affirment sans preuve, de l'action de l'homme ou échappe à

son influence" (Oudin, 1896, quoted by Durand, in press).

Investigations on recruitment variability stopped with World War I and were not resumed immediately afterwards for reasons that are not clear (Sinclair *et al.*, 1987). The likely explanation is that the rapid development of long-distance fisheries and the corresponding expansion through geographical expansion and stock diversification diverted attention away from the scientific issues associated with the politically less palatable task of resource conservation and fishery management. Confirmation of such hypothesis would require more detailed historical analysis for long-distance fishing started some centuries earlier and concerned small-scale as well as large-scale operations, in both developed and developing countries. Consequently, stagnant fisheries and expanding ones coexisted, e.g., in inshore and offshore segments or in different regions. However, it is during the inter-War period and, even more so, after World War II that long-range fishing expanded most rapidly, initially in the North Atlantic and Pacific and, then, throughout the World Ocean, as shown by the rise in world landings from about 7 million in 1920 to 72 million metric tons in 1972.

This expansion was paralleled by the development of the "theory of fishing" in three steps: (i) early observations and concepts relative to the effects of fishing upon stock abundance (e.g., Peterson, 1894; Garstant, 1900-3 and Heincke, 1913); (ii) formulation of a theory for rational exploitation of stock cohorts after recruitment (Russell, 1931 and Graham, 1935); and (iii) the development of computational models of operational applicability for stock assessment (Schafer, 1954 and 1957; Beverton and Holt, *op. cit.*; Ricker, 1958 and Gulland, 1965(2)).

These works provided the paradigm and the tools for assessing potential yields of stocks exploited by selective--in terms of target species landings, if not of catches--and capitalistic fisheries--inasmuch as the amount of fishing effort and balance between capital, manpower and resource were assumed to be easily modifiable. (It should be noted that the paradigm was oriented toward addressing only single species rather than the complex of species generally and taken any particular fishery).

Under the paradigm, opportunities for investments could be assessed and the conditions for coherent exploitation, in terms of fishing effort and size at first capture, determined. This phase of scientific development and application to fishery development planning culminated with the assessment of the world fishery potential yield (Gulland, ed., 1971).

The paradigm, however, disregarded the dynamics of cohorts during the early stages of their life history and the effects of environment upon their recruitment success. This exclusion was then considered as operationally appropriate for only spawning biomass can be

²Baranov's precursory contributions (1918) remained unknown and largely unused, even in his own country, before being unearthed in 1938 by the Western scientific community (Cushing, ed., 1983).

manipulated through the amount of fishing. Moreover, assuming only average environmental conditions and recruitment greatly facilitated the modeling of cohort yield as a function of fishing mortality and its distribution throughout the exploited phase. The recruitment/stock theory formulated by Ricker (*op. cit.*) and Beverton and Holt (*op. cit.*) can be interpreted as a straightforward extension of the dominant paradigm of the time as was, later, the distinction between two causes of biological overfishing, namely: (i) growth overfishing, *i.e.*, the decline in yield per recruit consecutive to the excessive fishing of recruited cohorts at young ages, and (ii) recruitment overfishing, *i.e.*, the fall in average recruitment and the increased risk of stock "collapse" as a result of excessive reduction by fishing of the parental biomass (Cushing, 1977; see however, Rothschild, 1986:244).

Variability in stock abundance did not initially raise excessive difficulties to long-distance fleets as fishing for accumulated biomass and the practice of pulse fishing provided alternatives for upsetting temporary and localized stock declines. Eastern European countries had a systematical recourse to that strategy by assessing cohort abundance before their entry into the exploited phase and optimizing year after year the geographical distribution of state-owned fleets over major world fish stocks.

As opportunities for expansion through geographical deployment faded away, long-distance fleets diversified the species basis of their harvests. Progressively, the single-species approach for stock assessment showed limitations. Already, analysts of limnetic, inshore and tropical fisheries were aware of the need for multispecies resource assessment, but no fully satisfactory methodology was available. The situation did not simply reflect the complexity of the ecological issue. It resulted also from the limited original research devoted to assessing small-scale fisheries at all latitudes. That this sector produced 27 million out of total 59 million metric tons used for human consumption and supports 10 million fishermen as compared to 0.5 million fishermen in the large scale sector (UNIDO, 1986) was largely overlooked. Eventually, the issue acquired recognition among fishery biologists (FAO, 1978), as did the trophic relationships among species components of exploited ecosystems (*e.g.*, Anderson and Ursin, 1977; Hempel, 1978a, 1978b; Laevatsu and Larkin, 1981).

In the early 1970's, the state and political context of world fisheries changed radically. From 1972--the very year the Peruvian anchovy fishery collapsed--until 1983, the annual increase rate of world landings dropped from an average of 6.5% which was maintained since World War II to a mere 1%. After 1983, this rate increased again, but in a chaotic fashion (FAO, 1987a): in addition to localized developments¹ in aquaculture, the recent improvement is due essentially to the episodic recovery of certain coastal pelagic stocks, such as the Japanese sardine, which yielded 5.9 millions tons in 1986 whereas its annual production remained below 10 thousands tons throughout the 1960's.

Despite this recent increase, the state of world fisheries has

not basically changed: most resources, notably the highly-valued ones, remain fully or excessively exploited; among those, some undergo fluctuations of large and unpredicted amplitude. Exhaustion of accumulated biomass and the restrictions now imposed by the New Ocean Regime against geographical deployments expose fishing fleets to the full amplitude of stock fluctuations, which tend to be magnified by the reduction in the number of year-classes in the catch. The adoption of annually-set catch quotas as the main measure for limiting the amount of fishing, *i.e.*, without the simultaneous adequate adjustment of the overall fishing capacity to medium-term productivity of accessible resources, does nothing to mitigate the detrimental effects of unexpected medium-term fluctuations.

Fishery collapses with catastrophic economic and social hardship were experienced apparently more frequently, notably in fisheries based upon coastal pelagic and bivalve molluscs. In some regions, fish stocks exploded, such as trigger fish or cephalopods off West Africa (Gulland and Garcia, 1984). The list and history of such dramatic events are now well documented (*i.e.*, Saville, ed., 1980; Sharp and Csirke, eds., 1984). What emerges from that history is the limited ability of fishery science to provide meaningful explanations of such phenomena, notably regarding the relative roles of natural and man-made causes of fluctuations and the implications on the relevance of scientific advice provided as a basis for designing fishing strategies likely to maximize the probability of stock recovery or to minimize future collapse risk.

For example, it was after the North Sea herring stocks had shrunk, and then recovered, and after a moratorium on their fishing had been adopted, and then relaxed, that the simultaneous occurrence of a hydrological anomaly was noted: the latter may have affected the drift and survival of herring larvae across the North Sea (Corten, 1984). Even if this explanation is not fully established as yet, natural factors seem to have played a critical role in the collapse of North Sea herring stocks. When the fishery was open again, deprived of supply, certain domestic markets had collapsed.

When in the mid 1970's, the Namibian pilchard stock began to collapse, the purse seine fleet was unable to harvest annual quotas (Troadec *et al.*, 1980): the stock declined faster than forecast by projections based on standard yield-per-recruit computations and prior recruitment trends.

As a consequence, for example, confronted by the simultaneous increase of the North-west African pilchard stock and its equatorwards extension, the Moroccan fishery administration could not be advised objectively on the respective merits of building new harbours and processing factories further south or seiners of longer operating range, for biologists were unable to assess the likely duration of the current stock high and southern extension.

Several stocks (*e.g.*, the Japanese sardine, the California sardine, the Peruvian anchoveta, the Greenland cod, the Bay of Brest (France) scallop, etc.) remained at extremely low levels for long and lasting periods after fishing has been banned or kept at minimum levels. Conversely stocks, such as the Japanese sardine, reached

abundances and yields never observed in the documented history of corresponding their fisheries.

As summarized by Hempel (*Op. cit.*): "The specific causes of fluctuations in fish population abundance are supported by a long list of speculations and a short list of facts."

2.2 State-of-the-art

From this brief historical overview, progress in the exploitation and conservation of fishery resources can be related to three basic sets of issues: (i) the yield of cohorts after recruitment and the condition for their rational exploitation; (ii) the variability in initial cohort number and partition of the cohort between natural and man-made causes of variability; and (iii) the trophic relationships within multispecies resources. This section reviews the present state-of-the-art respective to these issues and the suitability of available methods to investigating them.

2.2.1 Yield-per-recruit. Yield-per-recruit models are conceptually identical. They differ by the mathematical treatment, and its sophistication, of input data. Extensive routine applications shows that, provided adequate data are available, they give for many stocks operationally good answers to question (i) above.

Applications to short-term forecasts could be somewhat simplified, the more so that appreciable changes in the rate of fishing are not considered. Difficulty in accurately estimating natural mortality is, their major weakness, but its effects are less important for short term, *status quo* assessments (Shepherd, 1984).

In routine assessments, density-dependent and density-independent effects on growth and natural mortality of exploited cohorts are usually not taken in to account. The good fits generally observed between predicted and observed stock states confirm that, for a majority of finfish stocks, population regulatory processes are not concentrated on the adult phase. (This may not be the case for all taxonomic groups, notably bivalve molluscs). This does not exclude the possibility that appreciable changes cannot occur occasionally in the adult fish condition (fat content, mean weight at age, etc.) with parallel modifications in growth, fecundity and natural mortality rates. Such changes are usually observed in relation to sudden modifications in large marine ecosystems (e.g., El Nino; SELA-BID, 1984) or with changes in their boundaries (e.g., Icelandic summer spawning herring, Jakobsson and Halldorsson, 1984).

Thus Y/R models are efficient tools for short-term, operational forecasts but the undetermination of natural mortality and, more important of future recruitments limit their usefulness for medium-term, strategical projections as required for fishery policy making: assessments will be biased in case the error structure of future recruitments distribution does not replicate the one derived from past observations (Rothschild, *op. cit.*).

2.2.2 *Stock and recruitment.* As indicated earlier, S/R theory considers explicitly the effects of changes in parental stock size and disregards those in environmental conditions. Based on theoretical considerations, two mathematical functions have been proposed to represent the relation between recruitment and parent stock, namely:

- an asymptotic function (Beverton and Holt, *op. cit.*) and
- a dome-shaped function (Ricker, *op. cit.*).

A mathematical generalization of these two functions was later developed (Shepherd, 1982).

However, plots of annual recruitments versus parental spawning biomasses reveal for most stocks considerable dispersion (e.g., Garrod, 1982). Implications are twofold: (i) year-specific environment conditions, prevailing from spawning to recruitment, affect markedly the recruitment success, *i.e.*, the number of recruits per unit spawning biomass; and (ii) as such, the S/R plots have in most cases no operational utility.

Furthermore, recruitment strength distribution is not necessarily normal. Examination of time series of annual recruitments (e.g., Cushing, 1982; Rothschild, *op. cit.*) reveals the frequent superposition of:

- trends of varying durations and slopes,
- noise of moderate amplitude, and
- isolated explosions or drops of higher amplitude (Figure 1).

As for many climatological phenomena, the distribution of annual recruitment reflects the superposition of processes of different time and space scales: e.g., recruitment (Garcia and Le Reste, 1981); transoceanic events, such as ENSO or the North Atlantic low salinity anomaly (Corten, *op. cit.*); shelf and oceanic signals of smaller scale, such as storms affecting the stratification and density of plankton forage locally available for fish larvae (Lasker, 1975), etc.

Attempts have been made to relate recruitment success to certain environmental proxies (e.g., Bakun and Parrish, 1980). Occurrence of successive periods of relative environment stability enabled, for example, Watanabe (1977) to adjust three S/R curves of different heights to describe variations in Japanese mackerel recruitment as a function of parental biomass and environmental conditions.

Along with Kuhn's theory (1962), the introduction of environment indicators in S/R models can be interpreted as an attempt to internalize processes external to the dominant paradigm. As an investigation strategy, such an approach has little heuristic power. Aside from describing past states of fisheries, its efficiency is limited as it is not specifically tailored to the relevant processes, variables, and scales. Even for identifying environmental "signals", its discriminatory power is markedly reduced by the use of proxies measured on a time scale appreciably longer than that of the processes involved.

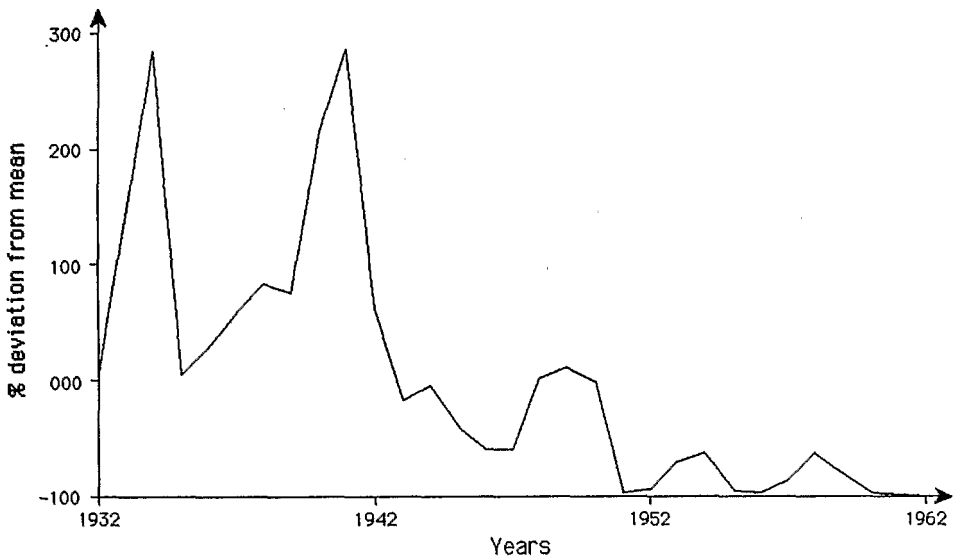


Figure 1. California sardine: fluctuations of annual recruitment. (after Garrod, 1982).

It is, therefore, no surprise if attempts at correlating recruitment and stock, annual estimates, derived as by-products of recruitment-stock assessments, have met little success. However sophisticated, subsequent mathematical processing cannot compensate for the lack of appropriate information in input data. Not backed by adequate field observations, mathematical functions proposed for representing certain past events (*e.g.*, compensatory mechanisms to explain stock collapses) appear largely speculative for explaining stock fluctuations of large amplitude. For example, to validate theory on "replacement" of one stock by another, processes involved between trophically related stocks as well as with environment signals need to be taken into account; similarly, recruitment overfishing cannot be ascertained as long as effects of medium-term environment fluctuations on recruitment are not accounted for.

These observations do not imply that investigating the S/R relationship is not important since even limited density-dependent effects would affect recruitment year after year in the same fashion. Knowing the shape of the S/R relationship will indicate whether it would be beneficial to maintain the biomass within certain limits to maximize average recruitment or above a minimum threshold to limit the risk of future declines in average recruitment.

2.2.3 *Surplus production and regenerative models.* Surplus production models (Schaefer, *op. cit.*) are an empirical procedure for representing the combined effects of fishing and past recruitments on stock size and yield. *De facto*, the model reflects past fluctuations in recruitment, incorporating density-dependent or density-independent factors. It may provide an operational tool for projecting the effects of changes in the amount of fishing upon multispecies communities whose components are trophically interrelated (May, *ed.*, 1984).

Regenerative models combine a Y/R function and a S/R relationship with annual recruitments randomly generated according to the statistical distribution adopted for representing the recruitment probability (Beverton and Holt, *op. cit.*; Walters, 1969; Laurec *et al.*, 1980).

Both approaches depend on annual estimates of exploited population parameters; consequently, they are ill-suited for investigating recruitment processes. Attempts have been made to incorporate climatic proxies into production models (e.g., Binet, 1982; Fréon, 1984, for West African *Sardinella*). Similar comments as those made in the previous section regarding Watanabe's treatment of Japanese sardine recruitment data also apply.

Although, in regenerative models, the analytical treatment of input data is precise, the choice of the mathematical function to represent the S/R relationship remains arbitrary as long as it has not been objectively determined through specifically designed investigations. On the other hand, regenerative models enable to incorporate selected recruitment distribution patterns for the years to come, which the production model does not.

As long as climate cannot be predicted with a sufficient lead time, the question of climatic effects on recruitment are difficult to deal with. Thus, Sissenwine (1974) and Doubleday (1976) stressed the risk of overoptimistic assessments of maximum potential yields for pulse fisheries, since those were generally initiated after a succession of above average recruitments.

Depending on whether future error structure replicates that which applies to past observed recruitments, requires consideration of two situations.

In the first, past recruitment frequency distribution could be used in regenerative models, with conventional Y/R and knowingly adjusted S/R models (which can be expected from investigations on recruitment). Historical information on past recruitment is therefore essential for determining the future recruitment probability distribution. Three sources of data, of varying accuracy and time coverage, can be used for that purpose: (i) scientific assessments of fish stocks provide yearly estimates of standing stock and recruitment; they are available for a growing number of fish stocks and a few cultivated ones; they seldom go more than a few decades backwards; (ii) historical fishery records give yearly landings; in a few cases, they extend backwards over a few centuries; they are limited to a small number of fisheries in Europe and Japan; and (iii) paleo-indices of stock abundance, such as those derived

from scale depositions in anoxic sediments in upwelling areas off California and Peru (Soutar and Isaacs, 1974; DeVries and Pearcy, 1982).

In the second case, applications of improved knowledge on processes linking environmental regime to recruitment success will depend on future developments in forecasting hydrodynamic events affecting recruitment at time scales matched to recruitment biology and major economic investments in the production sector, problems affecting the basic uncertainty affecting potential application of findings on recruitment.

2.2.4 *Multispecies resource assessment and ecosystem modelling.*

Appreciable research effort has been devoted to multispecies resource assessment (e.g., FAO, *op. cit.*; Anderson and Ursin, *op. cit.*; May, ed., *op. cit.*). Attempts at modelling whole marine ecosystems have also been made (e.g., Laevatsu and Larkin, *op. cit.*). However, developments of operational applicability remain so far limited. Reasons for slow progress are several: (i) trophic relationships vary markedly according to the successive life history stages of preys and predators making up ecosystems; (ii) strong divergences of opinions exist regarding the major processes determining recruitment success with strong supporters of effects of hydrodynamic processes on egg and larvae distribution and dispersion (e.g., Sinclair, *op. cit.*), predation (for a review, see Bailey and Houde, 1987), starvation, etc.; this may result from differences in the trophodynamics of particular ecosystems; in any case, it reflects a general lack of quantitative information, at the population level, needed for ecosystem modelling; and (iii) there are indications of various kinds suggesting that trophic relationships are less tight, at least for young and adults than for larvae and juveniles:

- as indicated earlier, estimates derived from Y/R projections, which do not take into account interspecies trophic relationships, fit usually well with observed stock states;
- this is supported by experiences from ranching (see next section);
- large-scale adult stock fluctuations are not accompanied by changes of comparable amplitude in their food abundance;
- according to Sinclair's "member/vagrant" theory, adult stock sizes would be determined predominantly by spatial processing taking place at early stages; in addition, adult populations are not necessarily food limited.

Such observations and considerations suggest that: (i) trophic relationships have probably not, for adult stocks, the importance it is frequently assumed; and (ii) progress in ecosystem modelling would depend on prior advance in the understanding and quantification of

regulatory mechanisms occurring during early stages at the population level.

3. RANCHING

Notwithstanding attempts towards intensification, the bulk of world aquaculture production still comes from extensive forms of cultivation in which depend primarily on the seeding of wild-caught or hatchery-raised juveniles (Table 1).

Table 1. World aquaculture production (in millions metric tons) in 1983 (FAO, 1987b).

<u>Finfish</u>	<u>Molluscs</u>	<u>Crustaceans</u>	<u>Seaweeds</u>	<u>Total</u>
4.45	3.25	0.12	2.39	10.21

Since the end of last century, various attempts have been made, mainly in the Northern hemisphere, to extend ranching to new species and areas. Efforts concentrated mostly on the production of young or juveniles called "seed." Comparatively less attention was devoted to the ecological and population aspects of such endeavours, i.e., to the survival of seed stocked in natural systems. In some cases, the strategy was directly inspired from the S/R paradigm: the objective was to artificially create a minimum spawning stock with the expectation that it will later further develop on its own. Most projects were approached in an empirical fashion; many failed. To quote Larkin (1977) in an assessment of the British Columbian salmon programmes: "Attempts to enhance salmon production by various "fish-cultural" activities were initiated almost a century ago in a wave of enthusiasm for hatcheries that was generated by the discovery that it was easy to collect salmon eggs, fertilize them and rear the progeny"... "However, it is almost impossible to document in detail the success with which... these efforts were attended, for most of them were on a small-scale and without a large research machinery for evaluation. Their effects were lost in the much larger-scale fluctuations of the natural system."

Considering the complexity of population regulatory mechanisms and their concentration on early stages on which we know the least, a better understanding of the population dynamics of recruitment appears the condition for apprising the ecological feasibility and determining the technical modalities for optimizing seed survival and return rates. In Japan, where such endeavours have been the most extensive in terms of areas and species (salmon, sea bream, scallop, abalone, penaeid shrimp, blue crab, etc.), remarkable success have been obtained for some species (salmon, scallop, abalone) while remaining to be demonstrated for others (Hénocque, 1984).

In this respect, the example of salmon ranching development in Hokkaido (Kobayashi, 1980) is interesting. Catches of chum salmon oscillated between 6 and 8 million fish, with an average of 7, between 1878 and 1892; then, they declined to an average of 3 million (ranging from 1 to 5) between 1905 and 1970; following an increase in the number of fry released and improvements in rearing techniques and releasing modalities, catches raised to an average of 9.6 millions (ranging from 7 to 16 millions) from 1971 to 1977. Simultaneously the S/R relationship changed radically with a threefold increase in return rate and, still, no apparition of saturation effects relative to the carrying capacity of the marine ecosystem for the adult stock (Figure 2). This corroborates experimentally an observation already made by Larkin (*op. cit.*) regarding Northern Pacific salmon stocks: "Apparently the various stocks and species collectively do not exploit the marine environment as to show striking relationships."

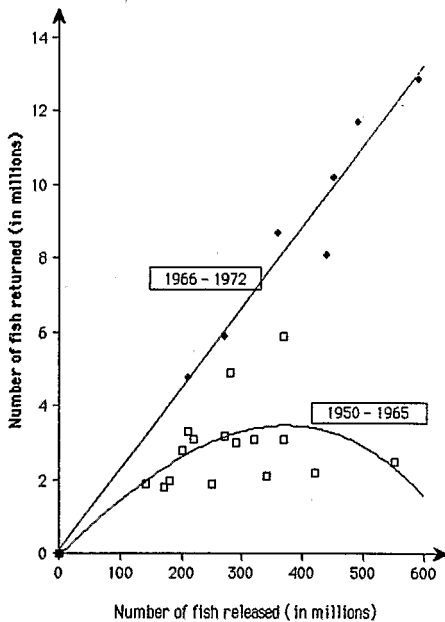


Figure 2. Development of salmon ranching in Hokkaido. (modified from Kobayashi, 1980).

In Mutsu Bay (Japan), the recruitment pattern of the scallop stock has been radically modified following the initiation, in the early 1970's, of systematic actions of various kinds: the setting of spat collectors of different types, the regular seeding on the bottom with spat harvested on collectors as well as artificially reared and the beginning of suspended culture. Simultaneously, the annual yield

which previously exceeded only occasionally 10 thousand tons, being very low the rest of the time, reached and remained between 20 and 40 thousand tons since (Figure 3). Unfortunately, as adequate observations were not carried out simultaneously, it is not possible to determine the respective roles of increased spawning stock, of the setting of collectors and of the regular addition of artificially-raised spat. Consequently, it cannot be established whether the enhanced stock can be self-sustainable only by the modification of its habitat (i.e., the setting of collectors), or whether regular additional stocking of artificially-produced seed is required. This understanding is critical both on scientific grounds as well as for further stock enhancement purposes.

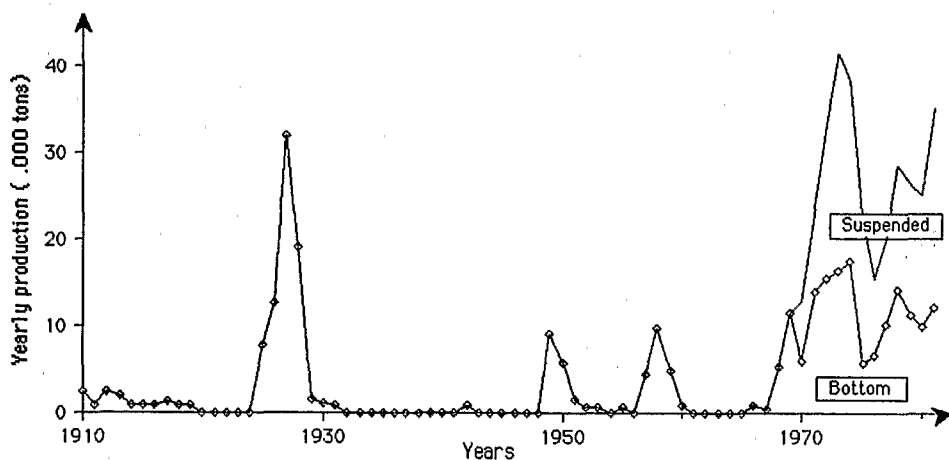


Figure 3. Scallop production from capture and culture in the Bay of Mutsu (Japan). (from data available at the Laboratory of Moura (Japan)).

The above example shows that, even in a semi-closed environment as a bay, natural ecosystems can sustain standing stocks of much higher biomass than usually observed under wild conditions.

In the Marennes-Oléron Bassin (France) where oyster production is ancient and intensive, the trophic saturation of a coastal marine ecosystem has been modeled (Figure 4). With Portuguese oyster (*Crassostrea angulata*), the standing stock regularly increased to reach almost 200,000 tons. The stock was close to that level when, from 1968 to 1971, it was decimated by a disease. Production resumed with Pacific oyster (*C. gigas*), following the same production/biomass relationship as observed for the development of Portuguese oyster. Biomass did exceed largely the level of about 80,000 tons corresponding to maximum annual yield (about 40,000 tons) and considerably more than existed under natural conditions (IFREMER, 1986).

These ranching examples are interesting because: (i) under natural conditions, natural mortality before recruitment can be so high that the recruited standing stock does not saturate the carrying capacity of natural systems; (ii) thus, high fluctuations of the recruited biomass do not depend on comparable fluctuations in

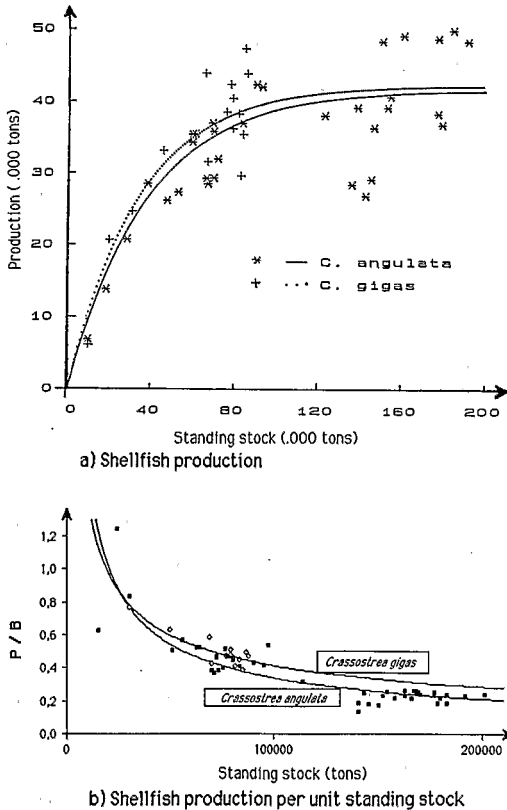


Figure 4. Yearly production and production per unit standing stock of oyster in the Marennes-Oléron Bassin (France). (after IFREMER, 1986).

plankton forage production; (iii) existence of different processes at the egg/larvae and juvenile/adult stages could explain why trophic relationships and energy transfer efficiency show little consistency at the upper trophic levels of the food web; if confirmed as a general principle, this would reduce the importance to be attached to trophic relationships within adult components of multispecies resources; and (iv) in the Marennes-Oléron oyster example, P/B

declines from 1.0 to 0.2 while standing stock (B) increased from 0 to 200,000 tons and yield (P) from 0 to 40,000 tons: the relationship between P/B and B changes markedly as B increases, P being more stable over a certain biomass threshold than P/B which declines monotonously; such ranges of variations are greater than those currently assumed in production analyses of ecosystem food webs.

Thus, investigations in ranching development offer facilities for experimental manipulation of natural ecosystems. Fishery science and oceanography are generally restricted to observing natural changes in systems or, in the former case, to observations on the effects of changes in the harvesting pattern but, with usually no possibility left to the scientist to direct changes. Well-selected experimental ranching projects would enable manipulation of habitat features, predator densities, etc. in addition to recruitment levels and, thus, help clarify the respective roles of spawning stock size, habitat modifications, predator removal, carrying capacities of the environment for particular stages in the life history, etc.

It is also worth noting that the "member/vagrant" theory on marine population structure and variability (Sinclair, *op. cit.*), makes homing a general feature in aquatic population behavior: otherwise, it is difficult to understand how those stocks can visit the same hatchery grounds year after year and succeed in maintaining their genetic pool within highly diffusive environments. If confirmed, this feature would widen perspectives regarding opportunities in ocean ranching.

Investigations on ranching offer the possibility of combining *in vitro* experiments with *in vivo* observations and experiments and of benefitting for that purpose from the sets of information, methods and expertise already accumulated in aquaculture research which will be long and costly to develop separately. Selecting coastal stocks of limited size can facilitate observations by making sampling efforts and experimental manipulations cheaper and easier. Also the existence of several discrete stocks of restricted geographical extension can provide replicates for comparative observations.

4. HABITAT MANAGEMENT AND ECOSYSTEM CONSERVATION³

Detection of anthropogenic impacts on marine populations are commonly attempted through observations and monitoring of environment changes supposedly induced by the development of certain human activities (e.g., nuclear plants). The implicit strategy is that impacts can be detected through correlations at the organism level (lethal effects, disease symptoms, contaminant contents, etc.).

Such an approach has a low discriminatory power for impacts on the abiotic environment usually generate weak signals as compared to the noise associated with the various time and space scales of natural ocean variability. In addition, such investigations do not say much about effects at fish population level, whereas it is those effects--through changes in growth, "natural" mortality and recruitment--which matter directly for fishing and culture

activities. Estimations of anthropogenic effects at fish stock level requires prior evaluations of population productivity under certain conditions of reference.

Quantitative measurements are few, except for impacts of large amplitude which can be estimated directly through simple correlations (e.g., the collapse of the Nile *Sardinella* stock in relation to the building of the Assouan dam and the subsequent reduction in freshwater outflow; Shaheen, 1975).

For similar reasons, positive effects of habitat modifications on fish stock productivity are hard to establish unless habitat management projects are "large-scale." With the methodology available, effects of artificial reefs on stock production and their differentiation from mere fish attraction are difficult to demonstrate unless they extend over large geographical areas. Owing to the current methodological shortcomings, this is seldom possible and biological effects and economic profitability cannot be assessed prior to implementations of costly projects.

Because aquatic populations concentrate their regulatory mechanisms on the early stages of their life history and it is at such stages that populations are most sensitive to environment modifications, improvement in the discriminatory power of analytical methods should result from progress in understanding and modelling of recruitment processes. Accurate determination of critical phases at which cohort survival is most sensitive to environment alterations would enable to refine standards for environment uses or for maximizing expected impacts of habitat management (e.g., localization of reefs).

The decline of oyster production in the Arcachon lagoon (France) was directly caused by a collapse in spat collection. This lasted for five years in succession (1977-1981) whereas, over almost a century, spat settlement never failed more than once every decade, on average. This was associated with mass mortalities of oyster larvae, directly and through a sharp reduction in their plankton forage, originally caused by organotin compounds in antifouling paints, (His and Robert, 1985 and 1986). There is, thus, a need to develop models interrelating recruitment success and environmental factors likely to be altered by human activities (e.g., temperature; Mclean *et al.*, 1981).

³Potential applications of early-stage dynamics of exploited populations to habitat management and ecosystem conservation would justify a development as extensive as the one devoted to ranching or fishery management. For keeping the present paper within an acceptable length, this section is restricted to an identification of major potential developments.

5. DISCUSSIONS

Interesting comparisons have been made between historical developments in fisheries and progress in fishery science.

Under the "theory of fishing", a powerful set of tools has been developed to assess the yield of cohorts after recruitment and the conditions for their exploitation. The theory provided answers to issues associated with the growth of world fisheries, notably the ocean wide spread of large-scale fishing operations. The underlying paradigm was based on the single-stock Y/R assessment approach, the hypothesis of average environment and recruitment conditions, the concept of stable maximum yield and the prevalence of fishing effort among the variables determining, recruitment, the state of fish stocks and their yields. This conceptual framework represented "a considerable advance that did much to organize and systematize thinking about mortality rates, growth, production, stock and recruitment, yield per recruit,..." (Rothschild, *op. cit.*).

However, since the 1960's, progress in fishery science has been "of computational rather than conceptual importance" (Rothschild, *op. cit.*). This situation reflects the very heavy involvement of fishery biology, initially in the assessment of world fishery resources, today in repetitive applications to fish stock monitoring and year-to-year yield projections for operational fishery regulation purposes. This workload is made heavier by current shortcomings in fishery management practices which do not tackle properly the economic and political causes of overfishing (Troade, in press).

This situation has impeded fishery biology to give adequate attention to the issues which have emerged in relation with the full exploitation of world fishery resources and the restrictions imposed to the geographical deployment of fishing operations, the recognition of the importance and specific features of small-scale fisheries, the development opportunities offered by extensive mariculture or the need to assess the effects, on fish stock productivity, of anthropogenic modifications of coastal environments.

Under the new Ocean Regime, the importance for fishery management of medium-term projections has increased: medium-term trends in fish stock abundance are needed for determining adequate balances between average fish stock productivity and fishing capacities operating in major fisheries. Simultaneously, a progressive reduction in the demand for short-term stock monitoring and support for operational fishery regulation can be expected from progress in fishery management, for resource conservation will be less demanding when excessive fishing capacities will be removed. On this aspect, the example of fishery management in Japan is relevant. Better performances are achieved on several aspects, notably the internalization of the management issue among fishermen, the reduction of conflicts, the limitation and distribution of fishing activities. These are not independent from the arrangements adopted in response to the political dimensions of the fishery management issue, *i.e.*, the regulation of access (Ruddle, 1987).

However, as compared to Western practices, less attention is given to short-term stock monitoring.

With more attention being given to recruitment variability, a change in the prevailing paradigm has already occurred. The importance of environment factors in stock variability, as opposed to spawning stock size, has acquired a more general recognition. Interpretations of certain collapses by recruitment overfishing have been reevaluated. Quantification of the respective roles of environment and spawning biomass, which can be expected from recruitment investigations, should improve long-term strategies for minimizing the risk of stock depletion as well as for stock rebuilding. For example, the principle of maintaining spawning stock size above a certain minimum level (which cannot be objectively determined with the methodology available) may appear unjustified for certain fish stocks. Such improvements can be achieved without the ability to forecast the hydroclimatic factors, influencing most the recruitment success.

The question of the prospects for forecasting climatic changes on a scale matched to the span of major investments in the fishing industry is a major one when assessing efforts to be devoted to recruitment investigations. Until such forecasts are feasible, trade-offs will have to be made between the amplitude and scales in stock variability, the forecasting capability, the time lags required by the industry to adjust its capacities and to open new markets, the costs involved for acquiring scientific information and optimizing the industry flexibility. These elements need to be assessed. Meanwhile, the means available to dampen the detrimental effects of stock variability have to be optimized: increasing the number of year-classes making up standing stocks; regulating the rate of fishing through the licensing of adequate fishing capacities; greater flexibility of fishing fleets to shift between stocks within fishing areas accessible to them, of the industry to process new species, to develop new products and markets; monetary compensation schemes, etc.

Ranching can be a major beneficiary from progress in recruitment studies. Challenging parallels have been made between certain theoretical developments concerning population structure and variability, and evidence drawn from ranching.

Performance of hatchery techniques are now such that the requirement of raising spat or fingerlings at an economically acceptable cost given the expected rates of return can be met for several species of molluscs, shrimp and finfish. Likely, more complex are the ecological aspects of stock enhancement and the institutional difficulties related to coastal ecosystem uses management.

In many instances, an empirical approach is likely to be insufficient: specifically tailored, innovative, scientific programs will be needed. Moreover, their size will have to be matched with that of the population or ecosystem to be manipulated. This is another argument for selecting, initially, stocks of limited geographical extension.

These considerations have a direct bearing on institutional and legal aspects. Effective development implies that action can also be taken on the modalities of exploitation at a scale corresponding to that of the resource. This may not be the least constraint. However, the issue is not specific to ranching. It is shared with fisheries, where some progress is currently observed. In a context of overall stagnation in production, advance towards production intensification (per unit sea area) could promote changes in legislation. Already, administrative and legal arrangements regarding, for example, site allocation and transfer are comparatively more advanced and making more progress in production systems, such as shellfish culture, which are well-developed and less complicated to administrate (sedentary organisms, self-contained eco- and socio-systems facilitating the internalization of the free competition).

Coherent use of exploited aquatic ecosystems depends also urgently on the ability to assess and allocate changes in fish stock recruitment among their respective potential causes: harvesting, fluctuations of climatic origin, restocking, pollution. So far, recruitment variability has received little direct attention except, at the turn of the century, in North Sea fisheries already confronted by overfishing. The methodology developed under the "theory of fishing" is not appropriate for investigating the ecology and dynamics of early stages. It is, therefore, no surprise if attempts made at approaching those issues within the traditional methodology have met little success. Probability of success will be substantially improved by adopting research strategies and protocols well-matched to the nature of the issue including: formulation of theories from which efficient research protocols can be designed; identification of appropriate time-and-space scales for observing processes; conduct of parallel field and laboratory activities; and modelling complex, multivariate phenomena.

Recruitment investigations fall predominantly in the field of ecology: the respective roles of spatial versus energetic processes in determining recruitment success, the coupling of hydrodynamic processes and larval behaviors, the role of discontinuities and heterogeneties in abiotic (fronts, upwellings, bottom, estuaries, etc.) and biotic (populations) structures of aquatic ecosystems, etc. are some of the topics to be investigated. This requires inputs from climatology, physical oceanography, planktology, population dynamics - including genetics, marine biology and aquaculture, in jointly designed multidisciplinary programs.

The historical review presented in the first part of this paper has shown that lags frequently appear between the emergence of fishery issues, the apparition of scientific concerns and the development of appropriate methods. One and a half decades ago, Kesteven (1972) noted already: "In its inability to predict, fisheries biology sits squarely and sadly beside ecology... In the terminology of Kuhn (*op. cit.*), fisheries biology is now operating with a paradigm whose potential of creativity is almost exhausted; employing its practices and models can serve only to confirm and

refine the results already established; its practitioners are mostly engaged on convergent research. And this is where I am finding justification in revolution: fisheries biology now needs divergent research."

Similar lags occur also between scientific understanding, the development of appropriate methodology and their application to fishery management. With respect to fishery management, the issue is not new: "During the first half on this century, a curious dichotomy existed between the emerging "theory of fishing" and the management measures then in vogue, which were mostly concerned with trying to ensure adequate reproduction and recruitment... For most species this preoccupation with recruitment seemed directly opposed to the accumulating scientific evidence of the time" (Ricker, 1977).

Qualitative progress in fishery science concepts and methods have been made generally when fishery biology addressed issues of strategic significance for fishery development and management and relied for their solution upon scientific findings in ecology and oceanography. Investigating the history of fisheries can help in comprehending long-term forces affecting the production sector and, thus, contribute to a better and more rapid adjustment of scientific concerns to emerging fishery issues. Now that physical growth is achieved in most capture fisheries, it is hard to see how fishery science will sustain further progress without specifically addressing the ecology and dynamics of early stages of populations in exploited ecosystems.

6. REFERENCES

- Anderson, K.P. and E. Ursin: 1977, 'A multispecies extension to the Beverton and Holt theory of fishing, with accounts on phosphorus circulation and primary production', *Meddr. Danm. Fish. -og Havunders. N.S.*, 7, 319-435.
- Bailey, K.M. and E.D. Houde: 1987, 'Predators and predation as a regulatory force during the early life of fishes', *Int. Cons. Explor. Sea. CM/mini*, Z:30.
- Bakun, A. and R. Parrish: 1980, 'Environmental inputs to fishery population models for Eastern Boundary Current', in G.D. Sharp (ed.), *Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes*, Intergovernmental Oceanographic Commission, UNESCO, pp. 67-104.
- Baranov, T.I.: 1918, 'On the question of the biological basis of fisheries', *N. -i Ikhtiologicheskii Int.*, I, 1, 81-128.
- Beverton, R.J.H. and S.J. Holt: 1957, *On the Dynamics of Exploited Fish Populations*, Fish. Invest. London, Ser. 2, 19, 533.
- Binet, D.: 1982, 'Influence des variations climatiques sur la pêche des *Sardinella aurita* ivoiro-ghanéennes: relations sécheresse-surpêche', *Oceanol. Acta* 5(4), 443-452.

- Corten, A.: 1984, 'The recruitment failure of herring in the Central and Northern North Sea in the years 1974/78 and the mid 1970's hydrography anomaly', *Int. Cons. Explor. Sea*, CM/GEN - 12:18 (mimeo).
- Cushing, D.H.: 1977, 'The problem of stock and recruitment', in J.A. Gulland (ed.), *Fish Population Dynamics*, New York, Wiley.
- Cushing, D.H.: 1982, *Climate and Fisheries*, London, Academic Press.
- Cushing, D.H. (ed.): 1983, *Key Papers on Fish Populations*, IRL Press, Oxford, Washington, D.C. 405.
- Devold, F.: 1963, 'The life history of the Atlanto-Scandian herring', *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 154, 98-108.
- DeVries, T.J. and W.G. Pearcy: 1982, 'Fish debris in sediments of the upwelling zone off central Peru: a late Quaternary record', *Deep-Sea Res.* 28, 87-109.
- Doubleday, W.C.: 1976, 'Environmental fluctuations and fishery management', *ICNAF Sel. Pap.* 1, 141-150.
- Durand, M.H.: La crise sardinière française: les premières recherches autour d'une crise économique et sociale, in press.
- FAO: 1978, 'Some scientific problems on multispecies fisheries', Report of the Expert Consultation of Multispecies Fisheries, *FAO Fish. Tech. Pap.* 181.
- FAO: 1987a, 'The state of world fishery resources', *FAO Fish. Circ.* 710, rev. 5.
- FAO: 1987b, 'Thematic evaluation of aquaculture', Joint study by UNDP, the Norwegian Ministry of Development Cooperation and FAO, 85 + ann.
- Fréon, P.: 1984, 'Des modèles de production appliqués à des fractions de stocks dépendants des vents d'upwelling: la pêche sardinière au Sénégal', *Océanogr. trop.* 19(1), 67-94.
- Garcia, S.: 1983, 'The stock-recruitment relationship in shrimps: reality or artefacts and misinterpretations?', *Océanogr. trop.* 18, 25-48.
- Garcia, S. and L. Le Reste: 1981, 'Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks', *FAO Fish. Tech. Rep.* 203.
- Garrod, D.J.: 1982, 'Stock and recruitment - again', *Fish Res. Tech. Rep.*, MAFF Direct. Fish. Res., Lowestoft 68.
- Garstang W.: 1900-03, 'The impoverishment of the sea', *J. Mar. Biol. Assoc. UK*, NS, 6, 1-70.
- Graham, M.: 1935, 'Modern theory of exploiting a fishery, and application of North Sea trawling', *J. Cons. int. Expl. Mer* 10, 263- 274.
- Gulland, J.A.: 1965, 'Estimation of mortality rates', Annex to Arctic Fisheries Working Group Report, *Int. Counc. Explor. Sea.*, Ann. Meeting (mimeo).
- Gulland, J.A. (ed.): 1971, *The Fish Resources of the Oceans*, Fishing News (Books), West Byfleet.
- Gulland, J.A. and S. Garcia: 1984, 'Observed patterns in multispecies fisheries', in R.M. May (ed.), *Exploitation of Marine Communities*, op. cit.

- Heincke, F.: 1898, 'Naturgeschichte des Herings. I. Die Lokalformen und die Wanderungen des Herings in den europäischen Meeren', *Abh. D; Seef. Ver.* 2 S CXXX VI u. 128 S
- Heincke, F.: 1913, 'Investigations on the plaice. General report. I. The plaice fishery and protective regulations', First part. *Rapp. Cons. Expl. Mer.* 17A, 1-153.
- His, E. et R. Robert: 1985, 'Développement des véligères de *Crassostrea gigas* dans le bassin d'Arcachon', *Rev. Inst. Pêches Marit.* 47(1 et 2), 63-88.
- His, E. et R. Robert: 1986, 'Observations complémentaires sur les causes possibles des anomalies de la reproduction de *Crassostrea gigas* (Thunberg) dans le bassin d'Arcachon', *Rev. Trav. Inst. Pêches Marit.* 48(1 et 2), 45-54.
- Hempel, G.: 1978 a, 'Symposium on North Sea fish stocks - recent changes and their causes', *Rapp. P.-v. Cons. int. Explor. Mer* 172, 5-9.
- Hempel, G.: 1978 b, 'North Sea fisheries and fish stocks - a review of recent changes', *Rapp. P.-v. Cons. int. Explor. Mer* 173, 145-167.
- Hénocque, Y.: 1984, 'Aménagement de la ressource côtière au Japon: effets des repeuplements marins', *Rapport technique ISTPM*, 11, 137 (mimeo).
- Hjort, J.: 1914, 'Fluctuations in the great fisheries of northern Europe viewed in the light of biological research', *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 20, 1-228.
- ICES: 1985, 'Report of the IREP Study Group', *Int. Cons. Explor. Sea CM/Gen* = 4, 43.
- IFREMER: 1986, 'Evolution et état du cheptel ostréicole dans le bassin de Marennes-Oléron, intérêt d'une régulation', *Document Technique IFREMER*. DRV. 86-6, AQ/TREM, 35 (mimeo).
- IOC: 1983, 'Workshop on the IREP component of the IOC Programme on Ocean Science in relation to Living Resources (OSLR), Halifax, N.S. (Canada), 26 Sept. 1983 *IOC Workshop Rep.*, 33, 17.
- Jakobsson, J. and O. Halldorsson: 'Changes in biological parameters in the Icelandic summer spawning herring', *Int. Cons. Explor. Mer CM/H*, 43.
- Kesteven, G.L.: 1972, 'Management of the exploitation of fishery resources', in B.J. Rothschild (ed.), *World Fisheries Policy. Multidisciplinary Views*, The University of Washington Press, Seattle.
- Kobayashi, T.: 1980, 'Salmon propagation in Japan', in J.E. Thorpe (ed.), *Salmon Ranching*, Academic Press, pp. 91-107.
- Kuhn, T.S.: 1962, *The Structure of Scientific Revolutions*, The University of Chicago Press, Chicago.
- Laevatsu, T. and H.A. Larkin: 1981, *Marine Fisheries Ecosystem: its Quantitative Evaluation and Management*, Fishing News (Books), Farnham, England, 162.
- Larkin, P.A.: 1977, 'Pacific Salmon', in J.A. Gulland (ed.), *Fish Population Dynamics*, A Wiley-Interscience Publication, pp. 156-186.

- Lasker, R.: 1975, 'Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding', *Fish. Bull.* 73, 453-462.
- Laurec, A., A. Fonteneau and C. Champagnat: 1980, 'A study of the stability of some stocks described by self-generating stochastic models', in A. Saville (ed.), *The Assessment and Management of Pelagic Fish Stocks*, *op. cit.*
- Maclean, J.A., B.J. Shuter, H.A. Regier, and J.G. MacLeod: 1981, 'Temperature and year-class strength of "Smallmouth Bass", *Rapp. P.-v. Cons. int. Explor. Mer* 178, 30-40.
- May, R.M. (ed.): 1984, *Exploitation of Marine Communities, Report of the Dalhem Workshop*, Berlin, 1984, April 1-6, Life Sciences Research Report, 32, Springer-Verlag, 366.
- Petersen, C.G.J.: 1894, 'On the biology of our flatfishes and the decrease of our flatfisheries', *Rep. Dansk. biol. Stat.* 4, 146.
- Ricker, W.E.: 1954, 'Stock and Recruitment', *J. Fish. Res. Board Can.* 11, 559-623.
- Ricker, W.E.: 1958, 'Handbook of computations for biological statistics of fish populations', *Bull. Fish. Res. Board Can.* 119, 300.
- Ricker, W.E.: 1977, 'The historical development', in J.A. Gulland (ed.), *Fish Population Dynamics*, A Wiley-Interscience Publication, 372.
- Rothschild, B.J., ed.: 1972, *World Fisheries Policy: A Multidisciplinary View*, Univ. Washington Press, Seattle and London, 272 pp.
- Rothschild, B.J., ed.: 1983, *Global Fisheries: Perspectives for the 1980's*, Springer-Verlag, New York.
- Rothschild, B.J.: 1986, *Dynamics of Marine Fish Populations*, Harvard University Press, 277.
- Ruddle, K.: 1987, 'Administration and conflict management in Japanese coastal fisheries', *FAO Fish. Tech. Pap.* 273, 93.
- Russell, E.S.: 1931, 'Some theoretical considerations on the "over-fishing" problem', *J. Cons. int. Explor. Mer* 6, 3-20.
- Saville, A. (ed.): 1980, 'The assessment and management of Pelagic fish stocks', *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 177.
- Schaefer, M.B.: 1954, 'Some aspects of the dynamics of populations important to the management of the commercial marine fisheries', *Bull. Inter-Am. Trop. Tuna Comm.* 1, 27-56.
- Schaefer, M.B.: 1957, 'A study of the dynamics of fishery for yellowfin tuna in the eastern tropical Pacific Ocean', *Bull. Inter-Am. Trop. Tuna Comm.* 2, 247-285.
- SELA-BID: 1984, 'Evaluacion de los recursos sardina, jurel y caballa en el Pacifico Suroriental', Informe Regional Final, 7a; *Reunion del Grupo Tecnico Cientifico*, Lima, Peru.
- Shaheen, A.H.: 1976, 'La pêche de sardinelles sur le littoral méditerranéen de l'Egypte', in Groupe de travail sur l'évaluation des ressources et les statistiques de pêche du Conseil Général des Pêches pour la Méditerranée (CGPM), Rome, 10-14 novembre 1975, *Rapp. FAO Pêches* 182, 35-36.

- Sharp, G.D. and J. Csirke (eds.): 1983, 'Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources', *FAO Fish. Rep.* 291, 1, 2, and 3.
- Shepherd, J.G.: 1982, 'A versatile new stock-recruitment relationship for fisheries and the construction of sustainable yield curves', *J. Cons. int. Explor. Mer* 40(1), 67-75.
- Shepherd, J.G.: 1984, 'The availability and information contents of fisheries data', in R.M. May (ed.), *Exploitation of Marine Communities*, *op. cit.*
- Sinclair, M.M. 'Marine Populations - An essay on population regulation and speciation in the ocean', in press.
- Sinclair, M.M. and P. Solemdal: 1987, 'The development of "population thinking" in fisheries biology between 1878 and 1930', *Int. Cons. Explor. Sea* CM/L = 11, 54.
- Sinclair, M.M., J.W. Loder, D. Gascon, E.P. Horne, I. Perry and E.J. Sandeman: 1987, 'Fisheries needs for physical oceanographic information within the Atlantic Zone', *Can. Tech. Rep. Fish. Aquat. Sci.* 1568: VIII + 166.
- Sissenwine, M.P.: 1974, 'Variability in recruitment and equilibrium catch of the Southern New Engl