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Methods to analyse the dynamics of exploited marine populations: Use and development of models

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SUMMARY: The applicability of the current exploited fish populations dynamic models to the particular problems of Mediterranean fishing are studied. It is concluded that the age-structured models are more useful and appropriate to the Mediterranean than those based on catch-effort data analysis.

RESUMEN: Se estudia la aplicabilidad de los modelos que describen la dinámica de las poblaciones marinas explotadas, a la problemática particular de la pesca mediterránea. Se concluye que los modelos basados en el análisis de la estructura de las edades (o tallas) son más útiles para el Mediterráneo que los basados en el análisis de series captura-esfuerzo.

OBJECTIVES OF POPULATION DYNAMICS

The demography of living organisms constitutes the research object of population dynamics. Since changes in the number of individuals, and the age structure of a population, result from interactions between the biology of the species with the biotic and abiotic environment, population dynamics can be fully considered as a branch of ecology. As a quantitative discipline, population dynamics uses mathematical models as a main tool.

Some features of exploited marine populations have allowed the development of particular methodologies, yielding a set of concepts and models characteristic of this field. These features are:

a) Marine populations can not be observed directly. So, with some exceptions, a direct census is not possible.

b) Exploitation significantly affects the biomass and age structure of the population, so the catch data becomes the main source of information about the demography of the population.

There is some confusion about the objectives of this discipline. Population dynamics is used for assessment by fisheries managers, and because of the commercial importance of this activity, some people think that population dynamics is not a scientific field but a mere technique to evaluate stocks and calculate TACs. This is a misinterpretation of its actual research object: knowledge and comprehension of how populations work. The assessment of fisheries is a by-product of population dynamics.

THE MEDITERRANEAN PROBLEM

As in any other scientific discipline, the first questions solved were the simpler ones, that is, forming models of populations exploited by one gear in industrial fisheries (mainly North Atlantic fisheries, or fisheries in upwelling zones). The tropical and subtropical artisanal fisheries, characterized by a high diversity in species caught, number of competing kinds of gear, and difficulties in getting data, are complex exploitation systems and have more complicated approaches, and more hypotheses are required to substitute the data.

SOME REMARKS ABOUT MODELS

A model is composed by:

— A set of hypotheses expressed in mathematical form. This is the deterministic form of the model and can include submodels related to the parameters used.

— A set of data.

— A fitting procedure connecting data and equations. This is the stochastic form of the model and includes the error type (process or observation) and its distribution.

Data and hypotheses are partially complementary. For instance, the growth of individuals can be simulated by a model (i.e. von Bertalanffy) or can be entered as empirical data (i.e. lenght-age key). This means that the lack of information (as data) can be substituted by hypotheses, the model becoming more theoretical and less empirical, hence, a little bit far from reality. Nevertheless it can still be useful, and say something about the population studied.

CATCH-EFFORT DATA ANALYSIS (PRODUCTION —OR GLOBAL— MODELS)

This approach considers the fishery as a black box in which only the input (effort) and the output (catch) are observable, and was first developed by SCHAEFFER (1954).

Rationale

For any exploited population there is a stable equilibrium relationship between catch and effort (Fig. 1). It is described by a curve with a maximum called Maximum Sustainable Yield (MSY) representing an optimum from a management point of view.

Since the steady state is not the general case, in the plane catch-effort, the trajectory of an exploited population does not necessarily fall on the equilibrium curve and is rather described by short term particular predictive curves.

These short term predictive curves simulate the trajectories of a population from year to year. They

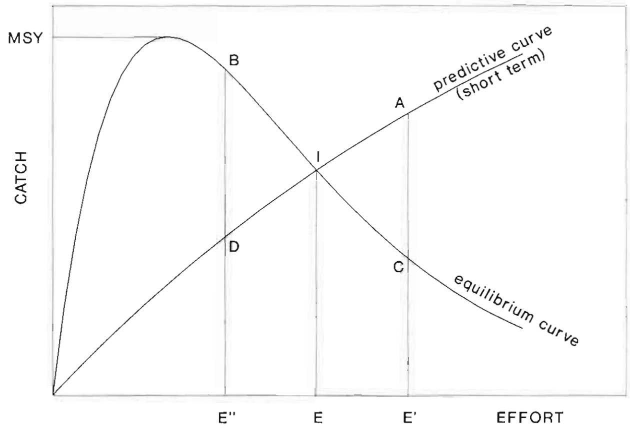

FIG. 1. — From a point I (in equilibrium in the example) corresponding to an effort *E*, the point A (or D) would be reached in the next year if the effort were changed to *E'* (or *E''*). Nevertheless, after some years mantaining the effort *E'* (or *E''*), the population would tend asymptotically to C (or B).

are monotonic from 0, when there is no effort, to an asymptotic catch value, corresponding to all the available biomass, as the effort increases. Around the actual values the predictive curve can be considered a straight line.

Every particular predictive curve is different from any other and depends on the situation of the actual catch effort point and of the actual biomass. The equilibrium curve is an attractor of the predictive curves.

Results

In almost all approaches the model has 3 parameters to be estimated: carrying capacity (or virgin biomass), rate of population growth (including mortalities, and individual growth), and catchability.

The trajectory of the population, and particularly those of the last points, relative to the equilibrium curve, allows one to know the exploitation level and the wealth of the population, its distance from the equilibrium and from the MSY considered as an optimum.

Forecasting

It can be done using the projection of the last point observed according to the particular (relative to actual biomass) short term prediction curve.

Data requirements

Data are easy to obtain from commercial statistics. No sampling is required.

Long series of data (the pairs catch-effort must be annual), are needed (30, or more, years are recommended).

As a regression model, a wide range of variation of the independent variable (effort), is strongly recommended.

Fitting

Non-linear regression is the most common estimation procedure.

Fitting the data series to the equilibrium curve is not correct. The data must be fitted to the corresponding short term prediction curves, and, hence obtain the parameters of the equilibrium curve. These fitting procedures are known as dynamic models (SCHNUTE, 1977).

Assumptions and warnings

A fundamental assumption of the method is that catch per unit effort (CPUE) is proportional to the biomass (that means constant catchability).

Recruitment, natural mortality are considered constant, and equilibrium is not needed. Catchability is also considered constant.

The time unit is the year, so nothing on a more detailed time scale can be asserted with this model.

Expansions

Sonn after SCHAEFER (1954), some alternative equations for population growth were developed (PELLA and TOMLINSON, 1969; FOX, 1970). DERISO (1980) and SCHNUTE (1985) connected production models with analytical ones, so recent approaches do not consider the fishery as a black box.

Gear competition for the same resource and multispecific production models are difficult to develop. The recent advances on catch-effort data analysis refer to fitting procedures, computational statistical problems, and distributional error problems. The main research in this field is done on the West coast of North America (Schnute, Hilborn, Walters, Ludwig, and others), and South Africa (Butterworth).

Application to exploited populations in the Mediterranean

The two main features of the data required by this model are: a long time series (more than 20 years), and a wide range of efforts to give contrast to the independent variable. Considering the exploitation patterns and the commercial structures, it can be asserted that Mediterranean fisheries data are not good enough to allow a reliable application of production models.

VIRTUAL POPULATION ANALYSIS (VPA)

The method is based on a formula describing the decrease in the number of individuals of a cohort. The method was formulated by GULLAND (1961).

Rationale

From the numbers of individuals caught at age of a cohort, the minimum number required at age, and the corresponding fishing mortalities, are obtained (Fig. 2).

Hence from a table of numbers caught at age and year, the corresponding tables of numbers of individuals at sea and the fishing mortalities are obtained.

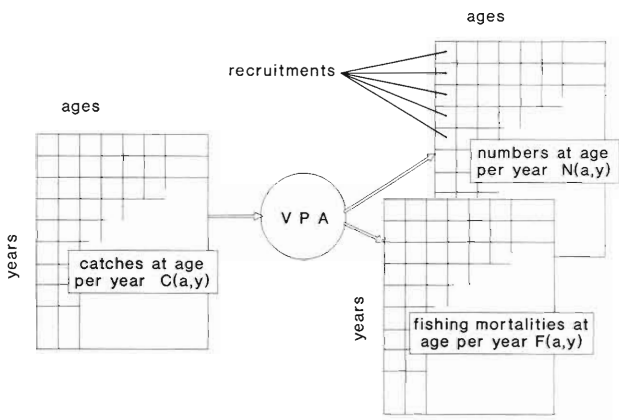

FIG. 2. — Scheme of the VPA process.

Results

VPA provides numbers of individuals at the beginning of each year and each age, and the mortalities. So, everything about the demography of the population becomes known.

In particular, series of recruitment values are obtained.

Forecasting

The projection of every age class to the next year can be done assuming a new vector of fishing mortality at age for the new year. Note that the forward projections diverge (as the backward ones converge).

Data requirements

Data series of number of individuals caught at age for several years (as many years as ages). This involves a long term sampling schedule, and a detailed knowledge of the biology of the species. In particular, mortality estimates, length-age relationships —or growth parameters— and length-weight relationships are strongly required).

In addition a lot of independent information would be very useful for tuning the analysis: total biomass and recruitment estimates, fishing efforts, gear selectivity, changes in exploitation pattern, etc.

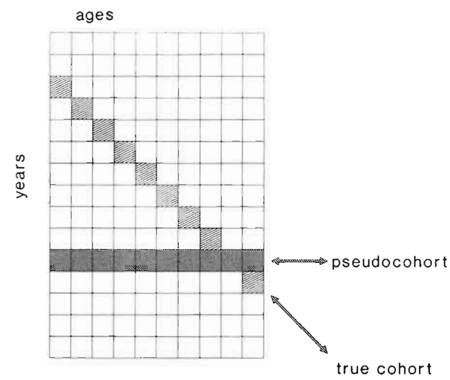

FIG. 3. — If the steady-state assumption were true, a pseudocohort is equivalent to a true cohort.

Assumptions

Recruitment. The recruitment series is estimated by the method.

Natural Mortality. Assumed (usually, but not necessarily, constant).

Equilibrium. Not needed.

Catchability. Since the effort is not directly involved in the analysis, q does not affect the analysis (there are some particular methods, such as the separable VPA or tunings, that need constant catchability).

Expansions and particular approaches

POPE (1972) developed an approach, called cohort analysis, to avoid the computing problem of solving the catch equation. Nowadays the availability of computing power makes this an obsolete method.

POPE and SHEPHERD (1982) assumed that fishing mortality by age and year could be separated into the product of a year effect and an age effect, and developed in such a manner the so called separable VPA.

The general VPA method avoids the equilibrium hypothesis, but requires many years of data. With the steady state assumption, a few years (or only one), are enough to carry out an analysis. The age structure of one year, actually constituted by as many cohorts as ages, represents the structure of the cohort in equilibrium (when every cohort is identical with any other). This false cohort is known as a pseudocohort (Fig. 3).

JONES (1982) developed the Length Cohort Analysis (LCA) allowing the analysis of length frequencies (all other methods require data arranged by ages). Two assumptions are required: a biunivocal relationship between age and length (usually, but not necessarily, the von Bertalanffy growth model), and the equilibrium hypothesis; this is because the unit of time used by all these methods is the year, and the relationship between age and length is usually non linear. Formerly this method employed "Pope's equation", but now the catch equation is (and must be) generally used.

Usually a length frequency has many more classes than the same data arranged by ages. This makes the LCA a method more precise than the methods by ages.

The age-structured models, their expansions and related topics (such as tuning, multispecific models, etc.) have been mainly developed in the ICES context.

Application to exploited populations in the Mediterranean

Complete catch-at-age matrices covering several years come from long term sampling programs that, for many reasons, are unusual in the Mediterranean area. Nevertheless this is, in my opinion, the right way to progress in Mediterranean population dynamics.

For the moment, equilibrium LCA is an acceptable method to do preliminary work, and to learn something about our exploited populations. It requires few years of length frequency samplings per gear and some estimates of biological parameters. Gear competition, a very important topic in the Mediterranean, can be easily studied using this method.

YIELD PER RECRUIT ANALYSIS (Y/R)

This method is based on the integration of biomass caught during the life of a cohort. It was first developed by BEVERTON and HOLT (1957).

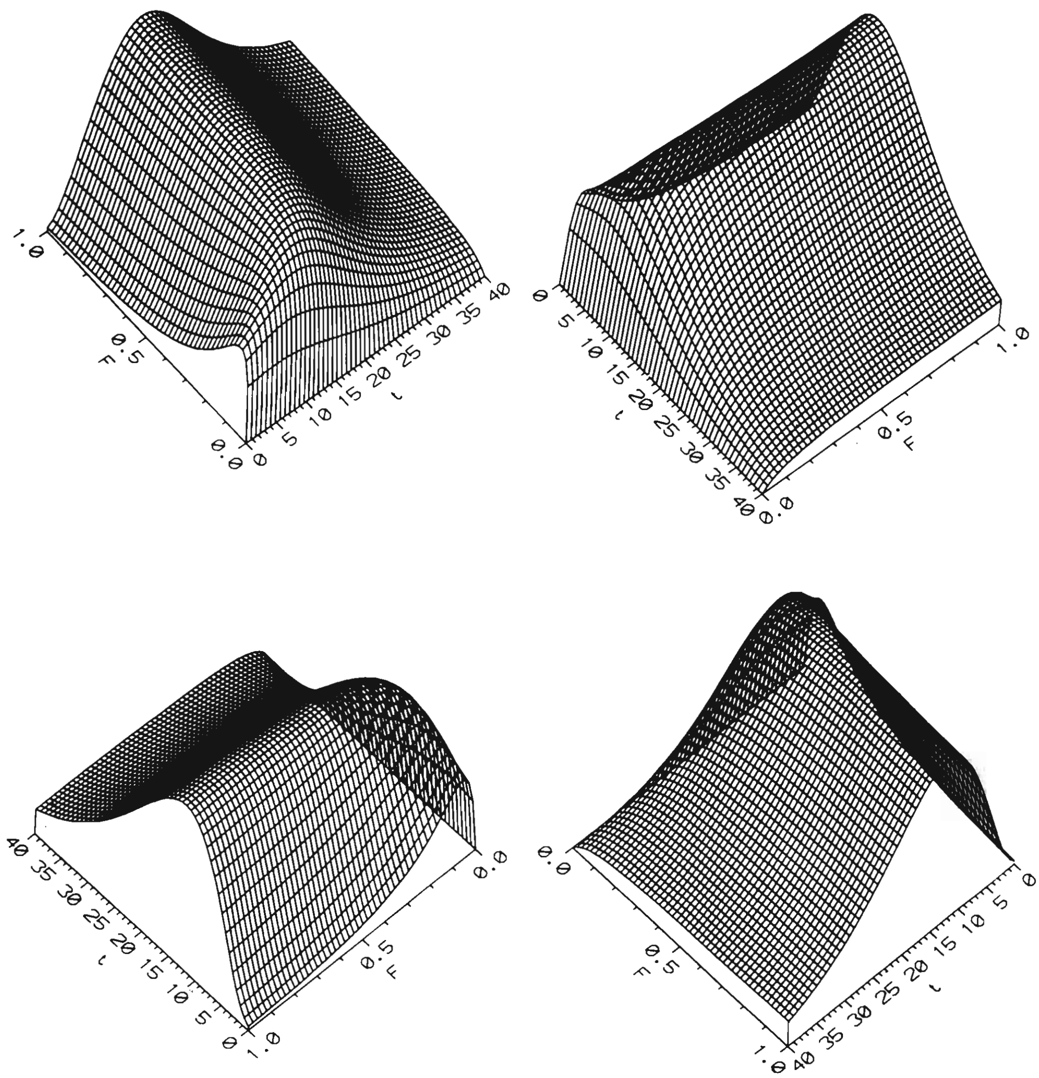

FIG. 5. — 4 views of the same Y/R equilibrium surface as a function of fishing mortality (*F*) and age at first capture (*t*). Conventional values.

Rationale

Knowing the natural and fishing mortalities at age, and the length-weight and length-age relationships, the yield (in biomass) of a recruit can be obtained.

The most interesting feature of this method is the computation of a set of Y/R values varying the fishing mortality vector. These variations can consist in multiplying every value of the vector by the same factor (simulating effort changes), or modifying some particular values to simulate selectivity changes.

Results

Y/R curves vs. effort (or fishing mortality), Y/R curves vs. mesh size, or Y/R surfaces vs. effort and mesh size, give us a very general idea of the status of the population.

The Y/R vs effort curve is equivalent to the production model curve and similar criteria can be applied in its interpretation. Nevertheless the methods are completely different and constitute independent approaches to the same system.

The use of Y/R analysis connected with VPA gives a very complete image of the population studied.

Forecasting

The curves (or surfaces) obtained are the equilibrium points of the exploited population and represent the stable situations of long term policies

(Fig. 4). Trajectories out of equilibrium would not be placed on these surfaces. Short term trajectories must be obtained by simulation procedures.

Data requirements

The fishing mortalities vector can arise from VPA or similar analyses. Length-weight and length-age relationships can be modelled (giving the classical Beverton and Holt model) or can be empirical.

Assumptions

Y/R refers to a cohort, but all Y/R studies are made on a pseudocohort, so, in fact the equilibrium hypothesis is assumed.

Since fishing mortalities are input variables, catchability considerations must be solved previously to the model. Natural mortality is assumed to be known (one value or a vector at age).

Since the results are expressed "per recruit", recruitment considerations are avoided.

Application to exploited populations in the Mediterranean

As a complementary method to the LCA, Y/R is very useful in Mediterranean studies, allowing one to analyze the effects of different exploitation strategies with several kinds of gear. Y/R adds to the detailed structure obtained by the VPA-type methods, and provides a general view of population demography.

IMPORTANCE OF BIOLOGICAL STUDIES

Most population dynamics models require previous work with biological models, or include them as submodels. In particular the following biological studies are of great importance:

Stock identification

Models in population dynamics refer to exploited demographic units, known as stocks. Genetic studies seem to be more appropriate than morphometric ones to characterize stocks.

Length-weight relationship

Data easy to obtain and to compute, allows one to convert numbers and lengths into weights.

Length-age relationship

This information can be merely empirical, in the format of length-age keys, or can be associated with a growth model.

The length-age keys allow conversion of length frequencies into age frequencies according to the probabilities observed. This is a very important step in preparing data for VPA.

The use of models requires a biunivocal relationship between age and length. The most common model is the von Bertalanffy one. In some cases it does not seem to be the most adequate.

Sex ratio

A number of species have sexual dimorphism which affect model parameters. Separate analyses by sex become necessary in this case, so reliable information about sex ratio per class (of length or age) is required.

Proportion of mature individuals

Knowledge of maturity ratios per age or length is necessary to compute spawning stock biomasses.

Trophic relationships

Studies, allowing one to know the rates of feeding of the species involved, are necessary to develop and apply multispecies models.

IMPORTANCE OF STATISTICAL STUDIES

The reliability of a result often has more significance than the value itself. So studies of the variance of model results become necessary to understand both the models and the actual system under study. The main problem in applying models does not depend on the deterministic form of the model chosen, but on the quality of parameters and data, and on the fitting method (the stochastic form of the model).

Most models use parameters estimated by other models, or simply assumed by the researcher according to previous studies, agreements, or common sense. Since several of these parameter values are doubtful, in order to obtain reliable results it is necessary to know how the errors pass from parameters to results. This kind of analysis is known as sensitivity analysis, risk analysis, etc. The most simplistic form consists in running the model with several parameter values and analyzing the results as a function of the parameters. Testing the effects on the Y/R results of inverse variation of natural mortality versus von Bertalanffy growth rate (*K*), is strongly recommended.

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