I - EXECUTIVE SUMMARY

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1. INTRODUCTION

The workshop was held from 11 to 14 June 2003 at the Institute of Oceanography and Fisheries, located at the tip of the wooded Marjan Peninsula, now a protected natural area to the north-west of Split (Croatia). Seventeen scientists, originating from 11 different countries attended the meeting at the invitation of CIESM.

They were greeted by Ivona Marasovic, IOF Director, who recalled some major accomplishments of the Institute since its foundation in 1930, with current research ranging from plankton productivity, fishing and aquaculture resources, to ocean dynamics, sea water chemistry and anthropogenic impact.

In his opening remarks, Frédéric Briand, Director General of CIESM, expressed his warm appreciation on behalf of all participants to Professor Marasovic who had done her best to facilitate the preparation of the meeting. He recalled the long, close association of the Commission with the Dalmatian coast where marine research is particularly active, as *Acta Adriatica*, the well-known scientific Journal based at the Institute*, and CIESM Congresses regularly show. He remarked that the location of this seminar was no accident, but a tribute to the long-term vision of the Institute which still maintained a tradition of collecting monthly key oceanographic data at permanent stations in Kastela Bay and in open waters, yielding in the process the longest-running time series on plankton productivity in the Mediterranean.

He then turned to Kostas Stergiou, Head of CIESM sub-Committee on Living Resources, and thanked him for initially advocating the theme of the seminar and for agreeing to act as workshop coordinator. Together they presented the context, background and objectives of the event, which aimed to derive original perspectives on a subject largely neglected in the Mediterranean region, by drawing from the varied, combined experience of the participants.

1.1. Background and objectives

If humans have the perception of time and space, marine biologists will usually dispose of a narrow historical perspective bound by the limited time frame of their sampling programmes : rare are long-term environmental data sets initiated before the 1960s (see Duarte *et al.*, 1992).

Yet biological time series, used together with meteorological/oceanographic time series, are essential tools to track the long-term properties of marine systems, detect meaningful shifts and assess whether changes are attributable to human impact or other causes. This was well illustrated in recent studies (e.g. Jackson *et al.*, 2001; Christensen *et al.*, 2003; Myers and Worm, 2003; Baum *et al.*, 2003) where time series demonstrated beyond doubt the dramatic degradation of coastal and open sea ecosystems worldwide, following the rapid destruction of predatory fish stocks by industrial fishing. As remarked by Pauly and Watson (2003), "*should this continue we will be left with a diet of jellyfish and plankton stew*".

** The workshop participants had a chance to hear a brief, lively overview of the first 70 years of* Acta Adriatica *given by Anita Marusic, Technical Editor of the journal.*

Obtaining information on different marine food web components at regular time intervals is also critical for testing ecological theories on community dynamics, variability and resilience, enhancing our limited capacity for short- and medium-term forecasting, and for managing living resources.

In contrast with other areas of the world ocean (see Ultang and Blom, 2003), biological times series are quite rare in the Mediterranean Sea. At least this is the common perception. A preliminary aim of the workshop was to assess the reality of this assertion by identifying the availability, gaps, homogeneity and scales (up to the century level) of Mediterranean biological time series. Through presentations and in-depth discussions, the group was to further tackle additional challenges, each summarized in turn in the following pages:

- reviewing the many techniques, developed from diverse disciplines, that can be used to extract and identify trends and interrelationships from time series, as well as methods to deal with incomplete time series;
- identifying which higher-order questions can be uniquely answered by time series analysis;
- listing notable trends so far uncovered by the analysis of Mediterranean biological time series; and
- indicating priorities and recommendations for future research on Mediterranean biological time series.

2. DEFINITION : WHAT IS A TIME SERIES ?

A series of measurements of a variable at equal time intervals is known as a “time series” and the usual notation is Y_t, for t=1, 2, 3,…, K. Two of the most crucial characteristics of a time series are the *trend*, which can be either deterministic (i.e., long-term changes in mean with constant variance) or stochastic (the mean is constant and variance increases with time), and the *seasonality* (i.e., cycles of constant length occurring on regular basis). For a detailed account on trend and definitions of seasonality the reader will usefully consult Durand and Mendelssohn (1998).

3. METHODS FOR ANALYSING TIME SERIES

The group first examined the conceptual framework within which time series can be properly analysed, then reviewed the various families of techniques available for time series analysis, finally discussing the problem of how to deal with gaps or missing data.

3.1. The comparative approach

As marine populations and local climatic systems are hardly amenable to experimental controls, one must turn to the comparative method as a practical research tool. This method draws its multiple realizations from independent situations found in the natural world. The independence may come from wide geographic separation; alternatively the separation may be in time rather than in space. Thus, time series analysis can be seen simply as an application of the comparative method in the temporal, rather than in the spatial, domain.

A major problem in studying variations in hydro-climatic parameters, anthropogenic influences, or marine population numbers, is that they tend to occur over a rather long time period compared to the time frame of the time series. Accordingly, the available degrees of freedom are generally minimal or sub-minimal for addressing issues of significant complexity. This problem may in some cases be relieved by augmenting the scarce realizations in a local time series with similar time series obtained from somewhat analogous situations in other geographic locations. However, objective methods for dealing with this problem are not well worked out. Applications of interregional comparative time series analysis are currently a rather “creative” endeavour, involving a touch of “art” in addition to science. Nonetheless, these approaches offer a way to gain insight and understanding that would be otherwise unobtainable. The methodology is essentially “pattern recognition” (for examples of the application of the comparative approach to the marine realm, see Cury and Roy, 1989; Durand *et al.,* 1998).

A number of obvious opportunities for intraregional and interregional comparative studies present themselves in the Mediterranean. Certainly, the several separate basins offer opportunities of relative independent realizations. In terms of fish stocks, their degree of actual independence is indeed a scientific issue of great practical importance. To pursue with fish examples, other opportunities might exist in the fact that the very valuable but threatened North Atlantic bluefin tuna uses only two spawning sites located in extremely different environmental settings, one in the swift loop current of the Gulf of Mexico, the other in the Mediterranean Sea (see Ravier and Fromentin, 2001). A comparative study of the particular attributes of these two very different ecosystem settings might reveal much about the crucial factors controlling reproductive success in this species. The fact that anchovies and sardines not only appear to alternate in abundance within the Mediterranean Sea (e.g. Sinovcic, this volume), just as they do in very different environments elsewhere (Bakun, this volume), but that they do so synchronously with populations spread widely around the world, offers another possibility for comparative studies that could be extremely rewarding. Similar opportunities likely abound for other taxa.

3.2. Methods for time series analysis

The group reviewed various methods that can be used for modelling and/or forecasting time-series. Overall 35 different methods, varying in complexity, were discussed. They are categorised in Table 1 into four families: (a) regression methods, (b) time-series methods, (c) multivariate analysis methods, and (d) other models.

Fortunately the development of appropriate software for their application has rapidly expanded in recent years, including general statistical packages (e.g. S-Plus, SPSS, Statgraphics, Matlab) as well as specialised time series software such as Forecast Pro <www.forecastpro.com>, ForecastX <www.forecastx.com>, Econometric views <www.eviews.com>, Caterpilar SSA <www.gistatgroup.com/cat>, ForeTess (developed by the Polytechnic University of Catalonia: see Lloret, this volume).

Table I. List of methods available for time series analysis, accompanied by underlying assumptions, suitability, and usually two references (general: upper reference; application to a discipline: lower reference). **GAM** = Generalized additive models, **GLM** = Generalized linear models, **L**=linearity, **NL** = non linearity, **MF**=multivariate forecasting, **N**=normality, **P**=parametric, **NP**=non parametric, **TL**= time lags, **TS**=time series, **ST**=stationarity, **UF**=univariate forecasting,

METHOD	**ASSUMPTIONS**	**SUITABILITY**	**REFERENCES**
REGRESSION			
Time-varying[1]	N, L, P, no TL	For TS with gaps. UF	Makridakis *et al.*, 1983 Stergiou *et al.*, 1997
Linear regression[1]	N, L, P, no TL	For TS with gaps. MF	Makridakis *et al.*, 1983 Koslow *et al.*, 1987
GLM[2-4]	L, P, no TL	For TS with gaps. MF	McCullagh and Nelder, 1989 O'Brien, 1999
GAM[3-4]	P, NP, no TL	For TS with gaps. MF	Hasti and Tibshirani, 1990 Daskalov, 1999
Loess regression[4]	NP, no TL	For TS with gaps. MF	Cleveland *et al.*, 1992 Daskalov, 2003
Non-linear models[4-5]	NP, no TL	For TS with gaps. MF	Myers *et al.*, 1995
TIME SERIES[6]			
Smoothing methods	P, NP	For short TS, UF	Hastie and Tibshirani, 1990 Cury and Roy, 1989
ARIMA[7]	N, ST, TL	For long TS, UF	Box and Jenkins, 1976 Stergiou *et al.*, 1997
Decomposition methods[8]	N, STL-NP based on loess	For short TS, UF	Makridakis *et al.*, 1983 Daskalov, this volume
Intervention analysis[7, 9]	N, ST, TL	For long TS, MF	Box and Jenkins, 1976 Lloret *et al.*, 2000
Transfer function models[7,10]	N, ST, TL	For long TS, MF	Box and Jenkins, 1976 Lloret *et al.*, 2001
Dynamic regression[7]	N, TL,	For long TS, MF	Chatfield, 1984 Stergiou *et al.*, 1997

TIME SERIES[6] (continued)			
Vector autoregression[11]	N, TL	For long TS, MF	Chatfield, 1984 Stergiou *et al.*, 1997
Kalman-filters		Estimations of past, present, and future states	Kalman, 1960 Sibert *et al.*, 2003
Non-linear time series analysis	No N, No ST	MF	See section 3.2.1
Filters	P, NP		Cleveland, 1993 White *et al.*, 1997
MULTIVARIATE ANALYSIS[12]			
Ordination (i.e., PCA, MDS)[13]			Clarke and Warwick, 1994 Anneville *et al.*, this volume
Cluster[13]			Clarke and Warwick, 1994
MODELS[14]			
Age or size structured models (VPA, XSA, ADAPT, ICA, stock-synthesis, MULTIFAN[15]	Long TS, MF		Darby and Flatman, 1994 Hilborn and Walters, 1992
Spawning-stock recruitment[16]	L, NL, GLM, GAM	Long TS, MF	Ricker, 1975 Hilborn and Walters, 1992
Production models[17]	Generally based on regression	Long TS, MF	Shaefer, 1965 Abella *et al.*, 1999
Predator-prey models[18]			Berryman *et al.*, 1995
ECOPATH/ECOSIM[19]			Walters *et al.*, 1997 Pauly *et al.*, 2000 Christensen *et al.*, 2000
Neural networks[20]		MF	Bishop, 1995 Haralabous and Georgakarakos, 1996

1. Linear relationship between a continuous response variable and continuous predictor variable(s); normality of dependent and predictor variable(s).
2. The distribution of the dependent variable can be non-normal and does not have to be continuous; predict responses both for dependent variables with discrete distributions and for dependent variables which are nonlinearly related to predictors.
3. Allows various distributions of the response variable.
4. The shape of the function is not constrained by some *a priori* model but is flexible in relation to existing data; allows simultaneous smoothing of up to three independent variables.
5. Non-linear relationships between variables.
6. The participants also discussed the potential usefulness of others models which belong to this category: Mann-Kendall tests, spectral analysis, wavelength analysis, state-space- models and Bayesian analysis.
7. Take into account time lags (i.e. dynamic models). Handle all components of a time series (i.e., seasonality, trend, irregular component, cycles); strong verification of model adequacy; better forecasting power than other methods.
8. Handle seasonality and trend.
9. Detect and quantify non-random changes (anomalies).
10. Quantify the impact of external variables.
11. Very useful for modelling and forecasting two or more closely related variables as a system (e.g. predator-prey, competing species).
12. The participants also discussed the potential usefulness of multivariate regression and multivariate autoregressive models, which belong to this category.
13. Very useful for identifying changes in species composition of assemblages with time, regime shifts, or for identifying the best fitting/forecasting model in terms of accuracy measures.

14 The participants also discussed the potential usefulness of other methods belonging to this category: yield per recruit, Gadget/Fleksibest, other food web models and eigen-value frequency analysis.

15. Assumptions for natural mortality and terminal fishing mortality; requires a lot of data, reconstructs past history of stock numbers and mortalities; a standard stock assessment method.
16. A main assumption is that the number of recruits depends upon parental biomass; detects recruitment overfishing; inputs are difficult to be obtained.
17. Often assume equilibrium; easy and general indication of stock state; estimation of biomass from the relationship between effort and catch; data easy to be obtained.
18. Many assumptions depending on the model; complex; several models since Lotka-Voltera formulation.
19. Dynamic mass-balance models fitted to time series; global modelling with an ecosystem approach; modelling fish stocks in relation to habitat, fisheries and environment.
20. Many assumptions; analysis of unknown, complex systems; applicable when the relationship between the predictor variables and predicted variables is very complex and not easy to articulate in usual statistics.

A distinction must be made between modelling (i.e., fitting) and short-term forecasting (i.e., operational forecasting, 1-2 years in advance). First because methods that provide good fitting do not always perform well in terms of forecasting; and secondly, as many practicing forecasters might argue that forecasting models do not have to be “meaningful” in terms of the corresponding field (see Stergiou *et al.*, 1997). Fitting and forecasting performances must be evaluated using a variety of accuracy measures (i.e., standard, relative and other statistical measures), each suffering from certain limitations. For a detailed general introduction to accuracy measures the reader is referred to Makridakis *et al.*, (1983).

Many of the methods listed in Table I have been widely applied to marine time series (e.g. ARIMA, transfer function models, intervention analysis, decomposition and regression models) whereas others have not.

The group agreed that analyzing time series of population abundance data by non-linear time series models (also called non-linear stochastic process models) may reveal a complex and chaotic dynamics, which remains otherwise undetected when (linear) ARIMA models are used. In most stochastic population process models (in discrete time) the log reproductive rate, defined as the log ratio of succeeding population densities, is related to a set of previous population densities (hence, if more than one term is included, delayed density dependence is assumed) and, possibly, to a set of exogenous variables. Different non-linear functions, for example extensions of the Ricker model, have been applied. See Royama (1992) for an introduction to this kind of models, Van der Meer *et al.* (2000) for an application to the marine realm, and Perry *et al.* (2000) for a recent overview of applications to terrestrial ecology.

3.3. Dealing with gaps and missing values

In all scientific fields, time series are characterised by gaps (i.e., long periods without records) or missing values (i.e., few isolated time points without records). This is an important problem since both cases drastically restrict the application of many time series techniques. In fact, missing data imputation and handling is a rapidly evolving discipline by itself (see for example Little and Rubin, 1987; Allison, 2002; Howell, 2002), with appropriate software becoming widely available (e.g. MX, free download from <www.vcu.edu/mx>; NORM, free download from <www.stat.psu.edu/~jls>; AMELIA <gking.harvard.edu/amelia>).

Missing data and gaps can result from a variety of circumstances (e.g. logistics, equipment failure, sample loss, sample contamination, bad weather, sick observers, removal of outliers, corruption of databases, input errors, file/archive loss). In all such cases, the data are missing completely at random (MCAR), that is, the probability that an observation, Xt, is missing is unrelated to the value of Xt or to the value of any other variable (Howell, 2002). In many other cases, data are not MCAR but are simply missing at random (MAR), that is, data meet the requirement that missingness does not depend on the value of Xt after controlling for another variable. In both cases (MCAR or MAR), missingness is ignorable (i.e., there is no need to model the missingness property), as opposed to the case when data are not missing at random.

The simplest way for dealing with gaps and missing values is to completely ignore them, a fact resulting into two or more individual time series of shorter length and, obviously, in a loss of information. Whereas a few simple non-parametric tests (e.g. Mann-Kendall), regression models and many simulation models are not affected by the presence of gaps in the data, the application of time series methods, which involve lags of the dependent and/or the independent variables, does require completeness. As a result, one has to adopt some method for missing data imputation, e.g. mean substitution, regression method with or without adding uncertainty to the imputation of missing values, hot deck imputation, expectation maximization approach, raw maximum likelihood methods, wavelet analysis, chaos theory, neural networks (see Ahn, 1999; Khalil *et al.*, 2001; Hopke *et al.*, 2001; Elshorbagy *et al.*, 2002, for applications to specific disciplines).

Naturally, not all methods do perform equally and so the selection of a particular method will affect/restrict the subsequent analysis. Thus fish stock models often use temperature relationships to interpolate missing values, but then one cannot look for changes/cycles that might be caused by climate. The selection of a particular method must also not affect the statistical properties of the original series, a premise that is not met by all methods (e.g. mean substitution can result in distributions with truncated variance; Howell, 2002).

4. WHICH HIGH-ORDER QUESTIONS CAN BE ANSWERED BY TIME-SERIES ?

The participants first questioned to what extent time series analysis is simply “Exploratory Data Analysis” (EDA) or hypothesis testing. Judging significance in the case of EDA (which also generates hypotheses) might be a problem. If we assume $P < 0.05$, then there is a 1 in 20 chance of hitting a nonsense relationship. Thus if 100 species (of phytoplankton for instance) are considered, we will always obtain some significant results (as 1 in 20 will be spurious). However negative results are too rarely published in marine scientific journals (see Browman, 1999).

The group identified various tractable questions, grouped by level of biological organization which can be or have been uniquely addressed by time series analysis.

Population level:

- The relationship between recruitment variability and upwelling intensity (“optimal environmental window” at moderate levels of upwelling, Cury and Roy, 1989).
- The existence of regularities/periodicities in stock fluctuations (see section 4.1.1).
- How population and/or landing variability changes with time (see section 4.1.2) ?
- The relative importance of climate and internal stock dynamics/behaviour, including predator-prey cycles, for driving fluctuations in stocks (e.g. Ravier and Fromentin, 2001).
- The relative importance of climate and fisheries as drivers of fluctuations (Pauly *et al.*, 2002).
- The effects of fishing on demographic parameters of fishes (i.e., maximum length and age, weight-at-age, age and length structure, length and age at first maturity, reproductive potential).

Community level:

- The removal by fishing of large, long-lived predators from marine ecosystems (i.e., “fishing-down the marine food webs”, Pauly *et al.*, 1998a).
- The effects of fishing on species diversity (e.g. Greenstreet and Hall, 1996).
- The temporal variability of communities (Van der Meer, this volume)
- The fluctuations of anchovy and sardine in an opposite fashion-regime shifts (Bakun, this volume).
- Trophic cascades (see section 4.1.3).
- Phytoplankton assemblage succession (Anneville *et al.*, Zingone *et al.*, this volume) .
- Eutrophication and its effects (e.g. hypoxia).
- The effect of extreme events.

Ecosystem level:

- The effects of biology on the climate and composition of atmosphere (e.g. phytoplankton production influences “cloud condensation nuclei” and dimethyl sulphide, production).
- The impact of fisheries on ecosystems (the results of the “Sea Around Us” Project, see section 4.1.4).
- The paradigmatic study of the Peruvian upwelling ecosystem (Pauly and Tsukayama, 1987; Pauly *et al.*, 1989).

Among the above topics, some were the object of further discussion.

4.1. Climate change and regularities/periodicities

Many analyses of geophysical and biological time series have several signals with periods identical to those of astronomical cycles. It is natural to hypothesize that the latter are responsible for the former, and that the variables of the time series are being forced by the changing constellations of celestial bodies. The signal most commonly found in long time series, and often the strongest, has a period of 18.6 years, which points to the importance of the moon and the nodical cycle (see Wyatt, this volume).

Biomass fluctuations of many fish stocks seem to be synchronous on hemispheric or global scales (e.g. Bakun, this volume), either in phase for some species, such as *Sardinops*, or 180 degrees out of phase if we compare different species, such as sardines and anchovies or herrings. The little information available indicates that the Mediterranean Sea also conforms to this pattern.

The view that the nodal tide influences fish abundance has a very long history in the scientific literature, but has not attracted very much attention due to the problem of finding potential mechanisms through which the tide could force changes in population dynamics. This is probably due to the fact that in almost all routine tidal studies, only the vertical component of the tide is taken into account, and since the vertical amplitude of the nodal tide is extremely small compared with the better known tidal components, it intuitively appears to have little importance. But the picture changes if the horizontal component is considered, since it is unidirectional for nine years. For example the nodal tide contributes an impulse to the Atlantic inflow to the Mediterranean Sea, which runs in the same direction for nine years before reversing for a further nine years : it therefore introduces systematic changes into the Mediterranean environments in which fish populations live and reproduce.

A stationary nodal tide fluctuation in the Atlantic Ocean influences the atmospheric process. Atmospheric processes are reflected in the North Atlantic Oscillation (NAO) and NAO has an influence on weather and climate in Europe. A strong positive NAO winter index will lead to stronger winds and warmer air in the winter in Scandinavia and colder winter in the Mediterranean area. This climate oscillation between north and south is expecting to introduce a climate forced opposite fluctuation of biomasses in the North Sea and in the Mediterranean Sea.

In the meeting there were indications that some long-term time series in the Mediterranean Sea were related to this climate fluctuation. This suggests that the dominant biomass fluctuations in the Mediterranean Sea are controlled by climate change, an hypothesis which deserves to be tested by a wavelet analysis to identify cycle times and phase.

4.2. Variability of fisheries landings

Evidence that variability increases with the length of time over which it is estimated has been found for fisheries landings by Stergiou (1998), who analysed 103 time series of marine fish landings of Atlantic, Pacific and Mediterranean origin for the period 1970-1991. The more time – more variability pattern suggests that there is not any equilibrium yield (i.e., the basis of most conventional, steady-state models used for fisheries management). It also introduces uncertainty into various estimations from fisheries models, a fact affecting the effectiveness of traditional fisheries management schemes. An additional finding was that landing variability is significantly ($P<0.05$) higher in the four major upwelling areas of the world and lowest in the Mediterranean. This suggests that differences in variability with time are a function of the ecosystem characteristics of the given marine region (i.e., trophic potential, number of trophic levels, environmental dynamics).

4.3. Trophic cascades

Trophic relationships are important structural forces in marine ecosystems, as bottom-up (resource driven) and top-down (predation driven) controls may dominate the dynamics of the populations at different trophic levels and determine the trends in abundance. Historical time-series are obviously a useful tool for detecting bottom-up and top-down effects in predator and prey populations (see Cury *et al.*, 2000; Daskalov, 2002; Myers and Worm, 2003). Trophic cascades occur due to strong human driven (overfishing, alien invasion) or natural (climate shift) influences and may leave pronounced signatures in time series.

4.4. Impact of fisheries on marine ecosystems

Within the framework of the “Sea Around Us” project (SAUP), Pauly and his collaborators used a combination of fisheries landings, information from hydrographic databases, GIS modelling, statistical analysis and ECOPATH food-web models – representing both historic and recent periods –

to produce, among other things, fisheries maps, of half latitude-longitude degree resolution, showing declining patterns of (high trophic level) fish biomasses in the North Atlantic by two thirds during 1950-2000. The results for the North Atlantic have been recently summarised in Pauly and MacLean (2003). Analyses by Myers and Worm (2003) and Baum *et al.* (2003) of long time series of catch per unit of effort data provided strikingly convergent results. Time series are an essential component of such an imaginative approach, which did remarkably well in raising public and political awareness.

5. WHAT ARE AVAILABLE MEDITERRANEAN TIME SERIES ALREADY TELLING US ?

The participants summarized and discussed various trends revealed so far from analyses of existing Mediterranean time series. Some of the most interesting are noted below.

1. Many long time series in the Mediterranean Sea exhibit a strong signal with period of 18.6 years (see Wyatt, this volume).
2. Long time series of bacterioplankton from the Adriatic Sea show that abundance increased significantly in the 1980s (about 3-4 times the levels of the early 1960s, see Solic *et al.*, 1997), indicative of anthropogenic impact such as overfishing of suspension feeders (Jackson *et al.,* 2001).
3. The damming of the Nile River in 1965, resulting in a 90% decrease in the average annual discharge, led to a drastic decline in phytoplankton abundance and in the catches of sardine and shrimps (Wadie, 1984).
4. Available time series of FAO landings for the Mediterranean and Black Seas combined (FAO sub-area 37) during 1950-1994, of GFCM landings for the NW Mediterranean Sea during 1972-1998, of local landings from the southern Aegean Sea during 1964-1998, and of changes in the distribution of market fish prices (see Pinnegar *et al.,* this volume), all indicate that the mean trophic level of landings has declined.
5. Sardine and anchovy fluctuations in the Mediterranean Sea are out of phase (e.g. Spanish and Algerian waters, Larraneta, 1981; Mediterranean Moroccan waters, Turner and Bencherifi, 1983; Adriatic Sea, Alegria-Hernandez, 1983; Greek waters, Stergiou and Lascaratos, 1997) as they are elsewhere (see Bakun, this volume). Rainfall and wind activity are the main external factors driving sardine and anchovy fluctuations (Lloret, this volume).
6. The mean monthly total length of sardine in the north Aegean Sea declined significantly during 1996-2003, following a decrease in biomass due to overfishing (Voulgaridou and Stergiou, 2003).
7. Time series of stranded individuals of the Beaked Whale *Ziphius cavirostris* in the eastern Mediterranean revealed that stranding were related to NATO sonar tests during 1992-1997 (Frantzis, 1998).

6. MEDITERRANEAN TIME SERIES : AVAILABILITY / GAPS

6.1. Available time series (at the century level)

Apart from information spread in local government reports (e.g. French fisheries records for each port are available since 1885) or trade journals (e.g. Industrias Pesqueras, Spain: publishes fortnightly catches of anchovy and sardine), fisheries landings for the Mediterranean and the Black Seas are available from the FAO in two forms. First, landings referring to both areas combined (FAO sub-area 37) can be extracted from the global production FAO database for the years following 1950. Second, landings by different Mediterranean sub-areas and the Black Sea can be extracted from the GFCM capture database for the years following 1970. Both types of data series can be freely downloaded from the FAO website <www.fao.org>. Available time series can be manipulated, aggregated and filtered using FISHSTAT (downloadable from same site) (see Pinnegar, this volume). Finally, various time series on large pelagic species are available from ICCAT <www.iccat.org> (see Tserpes *et al.,* this volume).

Although FAO data suffer from many limitations (e.g. under- or over-reporting; Watson and Pauly, 2001), with the largest errors being introduced before data reach the national database, a number of factors (e.g. globalization of fisheries and fish markets, fisheries resources exploited almost everywhere) indicate that generally FAO data do reflect relative abundances. Therefore, to analyze global or regional trends there is little choice but taking the FAO or GFCM data at face value.

Fish price data are available from GLOBEFISH <www.globefish.org> since 1991 as well as locally from other sources (e.g. IREPA, Instituto di Ricerche Economiche per la Pesca e l'Acquacoltura, for individual Italian regions, available monthly since 1972; Hellenic Fishing News Magazine: monthly Greek wholesale values per main auction fishing port since at least the early 1980s; Industrias Pesqueras: Spanish fortnightly price data).

One of the most valuable time series of fishery independent data was initiated in 1994, within the framework of the EU-funded MEDITS (Mediterranean International Trawl Surveys) project, with the groundfish trawl surveys. It intends to produce basic information on benthic and demersal species (more than 50 species are monitored) in terms of population distribution as well as demographic structure, on the continental shelves and along the upper slopes at the global Mediterranean scale. MEDITS is realized through annual standardized experimental trawl surveys covering most trawlable areas of the northern Mediterranean basin at depths from 10 to 800 m. About 1000 stations are sampled each year. Details on sampling can be found in Abello *et al.* (2002). Access to the MEDITS data however is not easy and interested persons must contact the project steering committee.

Many European countries maintain National Marine Databases (or oceanographic data centres) where forms containing meta-data and detailed availability and contact persons are submitted regularly. The EU project MTP2/MATER Mediterranean Targeted Project II (MAss Transfer and Ecosystem Response <www.doga.ogs.trieste.it>) has assembled such meta-data for all northern Mediterranean countries and made them available on four CD-ROMs.

At the local scale, the longest biological time series are available for the Adriatic Sea, thanks to the unflinching efforts of the Institute of Oceanography and Fisheries, Split. Apart from a variety of abiotic parameters *, the Institute monitors coastal and open waters at monthly intervals for chlorophyll a since 1979, for primary production since 1962, and for bacterioplankton since 1968. Monthly phytoplankton composition is known through the period 1952-1985, and zooplankton time series since 1957 (e.g. Solic *et al.*, 1997).

With respect to fisheries data, long-term series exist for sardine (1875-2002; see Sinovcic, this volume; Wyatt, this volume), anchovy (1947-2002), sprat (1947-2002), Atlantic mackerel (1947-2002), chub mackerel (1947-2002), bluefin tuna (1947-2002) and Atlantic bonito (1947-2002). Biological data (i.e., migrations, distribution of eggs, larvae, juveniles and adults, population structure, sex ratio, feeding, reproduction, first sexual maturity, fecundity, growth) of sardine, anchovy, sprat, Atlantic mackerel, chub mackerel and bluefin tuna, are available since 1922, but with gaps. Finally, data for trawl fisheries are available since 1948, and for coastal fisheries since 1960 (see Jardas, this volume), but also with gaps.

In the NW Mediterranean several time series of oceanographic and biological data are available, such as the DYFAMED series on hydrography, nutrients and phytoplankton since 1991 (Marty *et al.*, 2002) plus various deep-sea ecosystem components since 1991 (Guidi-Guilvard, 2002); zooplankton abundance in Villefranche-sur-mer through 1974-1999 (with a gap in 1978-1983); and various time series of the biomass of small pelagics restricted mainly to the years following 1990 (Agostini and Oliver, 2002). Short time series (initiated between 1995 and 2000) of oceanographic and biological parameters exist at different locations along the Catalan coast. These time series include parameters such as water temperature and salinity, inorganic nutrients, bacteria, heterotrophic flagellates, microbial diversity, dissolved organic carbon, picoalgae, phytoplankton counts and phytoplankton pigments. Data belong to different research and

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** An automatic station operates in Kastela Bay since 1998, which measures twelve meteorological and oceanographic parameters at 10 min intervals with data presentation in real time through the Internet <www.izor.hr>.*

governmental institutions and are collected on a monthly, weekly, bi-weekly or daily basis. Long time series (>30 yr) of monthly landings and/or cpue, by species or groups of species, disaggregated or not by commercial size groups, are available from many Spanish ports (see Lloret, this volume). Total landings of the Catalan fisheries go back to 1910 (Lleonart, 1999).

Time series of Mediterranean seabird population densities mainly concern the years following the 1970s and are characterised by gaps. They can be found in Aguilar *et al.* (1993), Oro (2002) and Yesou and Sultana (2000). A recent study by Bosch *et al.* (2000) presents one of the longest seabird time series (i.e., population abundance of yellow-legged gull *Larus cachinnans*, Medes Islands, for 1960-1996) available for the Mediterranean Sea.

The SINAPSI project (Seasonal Interannual and decAdal variability of the atmosPhere oceanS and related marIne ecosystems) brings together time series on phytoplankton, zooplankton and zoobenthos from the Adriatic Sea. Most series are now fully computerized and available on the website <sinapsi.cineca.it>. Italian SINAPSI time series of phytoplankton are available from five Adriatic Sea sites and from three Tyrrhenian Sea sites, ranging from 12 to about 30 years in duration (e.g. Zingone *et al.*, this volume). Zooplankton time series are available for the Adriatic Sea from Trieste and for two sites of the Tyrrhenian Sea. They range from 17 to 32 years (frequency: weekly to yearly scale). Zoobenthos time series are available for 15 sites (frequency: fortnightly to yearly scale). The longest time series is from Clado (Tyrrhenian Sea) covering the period 1936-1996; the others range in duration from four to 15 years. With respect to fisheries data, long time series of sardine and anchovy landings and biomass are available since 1975, from IRPEM/CNR (Ancona): sardine and anchovy eggs/larval distribution and abundance from 1976, from LBMP University of Bologna in Fano (Agostini and Oliver, 2002). Finally, time series of trawl surveys (15 years) are available from the GRUND project (see Italian Ministry of Agriculture and Forestry <www.politicheagricole.it>) as well as from the Gulf of Castellamare (Sicily) before and after a trawl ban (see Badalamenti *et al.*, 2002). Time series of bottom fisheries in the central Mediterranean will also be found in Relini *et al.* (1999).

With respect to Greek waters, the only long time series on nutrients, chlorophyll a and abundance/biomass of all zooplankton taxa is derived from monitoring a coastal station in the Saronikos Gulf on a biweekly basis since 1989 (Christou, 1998). Fisheries landings statistics are collected by four independent organisations, each collecting and/or processing data for its own purposes. The time series recorded by the National Statistical Service of Greece (annual and monthly landings for 62 species, or groups of species, and fishing effort since 1964 for 16 statistical subareas) are the longest ones. Since the second half of 1995, a variety of fisheries data (i.e., engine horsepower, tonnage and days at sea; corresponding catch/day for a large number of species) are also collected by the Institute of Marine Biology of Crete on a monthly basis over 21 stations throughout the Greek Seas. Time series of biological parameters of sardine (e.g. mean length, length-weight relationship, condition factor) are available from the north Aegean Sea since July 1996 (e.g. Voulgaridou and Stergiou, 2003).

6.2. Mining historical data sources

Europe is probably richer in written “historic” resources than any other region of the world (see Hoffmann, 2001). There is a wealth of written “data”, often quantitative, going back many centuries, for example concerning levels of fishing or trade and movement of fish products. A huge variety of sources are available, including records kept by local authorities for tax collection purposes, shipping or railway inventories, tithe accounts, kitchen records, catch statistics and fish prices in trade magazines, newspapers, etc. These largely neglected records might allow biologists to extend their existing population estimates many centuries back in time. A successful example was provided by Ravier and Fromentin (2001) who managed to reconstruct a 300-year (1650-1950) time series of Mediterranean tuna catches based largely on the records of bankers and financiers. Wyatt (this volume) describes a similar attempt (by Zupanovic, 1968) to assemble a time series for sardine fisheries in the eastern Adriatic.

Anecdotal resources can also prove very useful. For example Francour *et al.* (1994) consulted long-serving marine scientists (with careers spanning the last 20-30 years) from around the western Mediterranean, whose records and memories suggested that many “thermophilic” fish species have become increasingly abundant, probably a reflection of a broad warming trend (Bethoux *et al.*, 1990). Benovic and Lucic (this volume) compared published species inventories for hydromedusae in the Adriatic Sea spanning 1912-2002, and suggested that the increased discharge of terrigenous material via rivers in the northern Adriatic may have caused changes in hydromedusan faunal assemblages and the depletion of many species. In the same region, written “historic” data sources might help scientists understand the occasional appearance of mucilaginous events (known as “mare sporco”), which have had a significant impact on the cultural and social life of communities in northeast Italy since times of antiquity.

Classical literature abounds with descriptions of fish and fisheries in the Mediterranean (see examples in Cushing, 1988; Radcliffe, 1921), and probably the best account is given by Opianos in his *Halieutika* (ca. AD 170). Homer (900-800 BC) described various fishing methods relying on hooks, nets and harpoon in both the *Iliad* and the *Odyssey*. The life and activities of fishermen were also described in the “Attic comedies” of Antiphanes (350 BC), and of Menander (about 300 BC). At about the same time, Aristotle referred to many fish species in his *Natural History*.

Stergiou (1999) has suggested that many Mediterranean top predators (e.g. *Coryphaena hippurus*) may have been all but “fished out” in antiquity, as even small amounts of fishing pressure can quickly deplete such species. Early fisheries, as depicted in Roman, Greek, Minoan or Egyptian frescoes, tended to involve highly selective gears, and it is therefore quite plausible that many fishing-induced changes occurred in Mediterranean fish assemblages long before scientific monitoring surveys were in place.

6.3. Socio-environmental proxies

Often, when no instrumental or scientific records are available, it is necessary to construct time-series using indirect methods and somewhat unconventional data. Entries in diaries or the recorded date of natural phenomena (the study of which is known as phenology) can often tell us something about the climatic conditions in a given year. One of the best examples (documented by Wyatt, this volume) is the date of the annual wine harvest in southern Europe, which is heavily dependent on summer temperatures. Leroy-Ladurie (1971) and Pfister *et al.* (1999) were able to construct time series spanning 1480-1880, since the warmer and sunnier the growth period, the swifter and earlier the grapes reached maturity and were harvested. Olive flowering dates also depend on temperature and it has been suggested that this may provide an early biological indicator of future climatic warming in the Mediterranean (Osborne *et al.*, 2000).

Other written sources might also yield useful (albeit indirect) information about the status of the marine environment in the Mediterranean, including records of employment in the fishing industry, the number of cans of tuna produced, the oil content of sardines (which reflects the availability of their preferred planktonic prey), records of fish consumption, etc. Pinnegar *et al.* (this volume) indicate how the prices of particular fish species on the markets might provide useful information about the availability of these species in the environment. Hence increased co-operation between economists, historians, sociologists and marine scientists is certain to yield a better understanding of the historic ecosystems.

6.4. Archaeological and sedimentary time series

Sometimes archaeological excavations or the extraction of sediment cores can allow very long-term time series to be constructed. One of the best-known examples involved counts of Pacific sardine *Sardinops sagax* and northern anchovy *Engraulis mordax* scales in cores taken from anaerobic sediments off California (Baumgartner *et al.*, 1992). These analyses showed that sardine and anchovy abundance had varied dramatically over the last 2000 years and that the collapse of the sardine stock in the latter half of the twentieth century would be only one of a series. Analyses of dinoflagellate cysts, foraminifera, pollen and coccolithophores in sediment cores can also provide useful information about past environments. Many of these techniques have been successfully applied in the Mediterranean (e.g. Sangiorgi *et al.*, 2002; Giunta *et al.*, 2003).

Archaeological excavation of fish middens (waste deposits) can yield important evidence regarding historical patterns of fish trade and consumption (see Barrett *et al.*, 1999). Desse and Desse-Berset (1993) demonstrated that inshore systems in Cyprus have been impacted by fisheries for millennia and that large specimens of certain species, notably sea breams (Sparidae) and groupers (Serranidae) are now much rarer than they were during the Neolithic (~6000 BC). The “Fish Working Group” of the International Council for Archaeozoology (ICAZ) contains several members from Mediterranean countries and holds regular workshops and symposia (see <www.nmnh.si.edu/icaz/workfish.htm>).

Museum specimens can also represent a valuable resource when attempting to construct historical time series. Several authors (Wainright *et al.*, 1993; Thompson *et al.*, 1995) have sampled archived materials (i.e., fish scales, feathers, bones, teeth, specimens in alcohol), assessing their carbon and nitrogen isotope composition. Changes in the isotope “signature” of animals collected at the same locality, but during different periods of time, can indicate changes in feeding preferences, and hence changes in the underlying ecosystem. For example Wainright *et al.* (1993) demonstrated a significant downward trend in the δ^{15}N of haddock on Georges Bank over the past 100 years, and the authors tentatively related this to changing patterns of fishery exploitation affecting the availability of prey resources.

6.5. Gaps in taxa, space and time coverage

In general, there are more non-biological than biological long time series, and the latter tend to be less frequent from higher to lower trophic levels (“researching down the food-web”). In other words, there are more time series for fish than for plankton and benthos, particularly long time series, and very few bacteria time series. Not surprisingly, the number of long time series decreases with distance from shore and with depth, with open- and deep-sea long time series almost missing (the DYFAMED-BENTHOS is among the longest ones, see section 6.1). Littoral benthos time series are also generally lacking (with the exception of a recruitment time series of sea urchins, Sala *et al.*, 1998).

Availability of biological time series, as opposed to meteorological/oceanographic ones, also generally declines from north to south Mediterranean either because very little actually exists or because whatever exists is not available to the scientific community (i.e., published in local reports, journals, magazines). This is not true of fisheries landings, in as much as all countries issue annual statistical bulletins of landings and effort. Despite the language barriers across the Mediterranean, which present a major problem for accessing existing scientific information, it was without saying that collaboration with the southern shore must be strongly encouraged.

With respect to time coverage, most time series originated only a few decades ago. Agostini and Oliver (2002) compiled a preliminary list of Mediterranean data sets on anchovy and sardine (i.e., biomass, eggs and larval surveys, acoustic surveys) and a few other biotic or abiotic parameters. With the exception of the Adriatic Sea time series, the vast majority started sometime in the 1990s. The limited longevity of time series is another concern: Duarte *et al.* (1992) showed that although the number of time series monitoring programs increased exponentially in European waters, few survived for periods longer than 10 years. Yet all participants agreed with the contention by Dickson (1995) that “*adding another year to a 60-year record may be inherently more valuable than starting a new* [series] *elsewhere*”.

The use of abiotic time series for the analysis and interpretation of biological time series is invaluable (e.g. Taupier-Letage and Millot, this volume). Many participants stressed that as the number and access of meteorological and oceanographic time series increase rapidly, the selection of what type of data (i.e., interpolated or actual data) and which time series to use may soon become a problem.

Finally, the participants expressed a concern regarding the time series of rare species as these are subject to sub-sampling problems (i.e., one never knows whether rare species do not show up because of inadequate sampling or whether they simply do not occur). Besides, certain species occur in certain areas only very occasionally because they are at the extreme edges of their distributions, whereas others are rare everywhere.

6.6. Evaluating the quality of time series

The participants agreed that it is generally unrealistic to assume that the methodologies used for collecting any data (e.g. sampling equipment, vessels, spatial coverage, sampling grid, taxonomic expertise) over long periods of time remain absolutely constant. In addition, both short and long time series can suffer from instrumental errors and malfunctions of various level of subtlety.

Examples abound in the marine realm. For instance, in plankton studies taxonomist expertise may change over time (e.g. as they become better trained or are particularly rushed in a particular year) and the misidentification of abundant phytoplankton species may occur for 20-30% (this percentage might be even higher for rare species). In addition, some taxonomists are "lumpers" and others "splitters", which renders recorded data inconsistent. For comparative purposes, for instance when combining plankton data sets from different institutions, it may be safer to carry out analyses at the lowest possible denominator (e.g. at the generic level).

In the case of fisheries surveys rarely has a long time series not been subjected to a change of research vessel. Even if the fishing methodologies and gears remain the same, the way the vessel "sails" can influence catches. In some cases standardisation studies have been carried out using parallel tows (pair trawlers). In fact, different survey gears can give a very different picture of fish populations, even though they are used in exactly the same areas. Finally, fisheries landings time series are highly heterogeneous because of changes in over- or under-reporting or in the ways that data are assembled over time (e.g. fishing ports deliberately miss-record landings as a different species, not covered by a TAC).

All these inconsistencies seriously affect the homogeneity of time series, making the separation of the "measurement" effect from the "real" changes in the underlying processes almost impossible. In addition, trends and imperfections in the quality of data can affect the probability of getting a statistical error. In fact only those involved in the data collection process will be aware of the inherent properties. Various mechanistic approaches for ensuring data quality (e.g. replicate measurements, reference to absolute standards, internal consistency between measurements, overlap of new sampling methods and people before changeover, inter-comparison and inter-calibration with other labs) will be found in Michaels (1995).

6.7. Parameters to be monitored

Time series should not be limited to species of importance for cultural, commercial, or public health reasons. Many other components of the marine ecosystem, which provide important ecosystem "goods and services", should also be monitored on a systematic basis.

The participants identified various easily measured parameters that would be valuable components of long-time series in order to monitor change:

(a) size spectra;

(b) ratios of different plankton taxa (e.g. *Calanus* species);

(c) community indices such as the Shannon diversity (however such indices might be less robust for phytoplankton data than for zooplankton, zoobenthos and fish data);

(d) species lists accompanied by information on their ranges and limit;

(e) ratios of various groups within the benthos (e.g. filter feeders *vs.* suspension feeders, r- *vs.* k-strategists, commercial *vs.* non-commercial species, pelagic *vs.* demersal species, warm- *vs.* cold-water species);

(f) number of eggs for seabirds and number of pups for seals;

(g) price and trophic level of fish and fisheries landings;

(h) maximum length and age, condition-factor, length at age, length and age at maturity of fishes, all of which are greatly impacted by fishing;

(i) fish egg/larval distribution; and

(j) primary production required to support fisheries.

6.8. Releasing time series on the Internet

The group stressed the usefulness of having access to reliable time series (or at least to some meta-data form) on the Internet. If time series of climatic/oceanographic data are already available in this way, as well as global fisheries landings data from FAO <www.fao.org>, biological data are only rarely available, and usually not on a free basis (in order to gain access it is necessary to work with the "owners" as full collaborators). Few notable exceptions exist (e.g. Myers' database of fish recruitment time-series, available at <www.fishbase.org>; the Sea Around Us project: <saup.fisheries.ubc.ca>).

There is a widespread tendency for scientists to hold on to their "own" data and not to respond to enquiries asking for access. As a result, important time series remain neglected in "desk drawers". Considerable efforts and period of time are required to create a time series either from field data (e.g. sitting over a microscope for 20 years) or from detailed information published in trade magazines. Hence it is understandable that people are "attached" to the data which they have themselves collected and are reticent to release these hard-earned data onto the internet.

The participants discussed how long personal data should remain in "drawers". The general sentiment was that scientists gathering data using public funds should be given five years to publish, and then that the data should be released. It was noted that in many European countries "freedom of information acts" exist, and that all data collected using EU funds are expected to be made freely available.

7. SPATIAL AND TEMPORAL SCALES

Ecological processes take place at different spatial and temporal scales. In this context, space-time scale diagrams are very useful tools for comparing physical and biological processes and to assess coupling between them. For instance Steele (1995) used space-time diagrams to compare the main atmospheric and marine physical processes with terrestrial and marine biological processes. This revealed that space-time scales for physical and biological processes largely coincide in the oceans, indicating a close physical-biological coupling.

The time and space scales of various events discussed by workshop participants are plotted in Figure 1 on a Stommel diagram. The increase in variance with wavelength (see Wyatt, this volume) is contoured with broken lines. The letters P, Z, and F show the characteristic scales of phytoplankton, zooplankton and fish population dynamics respectively from Steele (1977); more details for zooplankton are given in an elaborated version by Haury *et al.* (1977). The areas marked 1 to 4 show:

(1) "Lasker's world", where the day to day events which determine the success of larval fish feeding (and hence recruitment) are focused (Lasker, 1975; Cury and Roy, 1989);
(2) the scales of Mediterranean phytoplankton blooms (Zingone, this volume);
(3) mesoscale hydrodynamical features (Taupier-Letage and Millot, this volume);
(4) significant multiannual trends (Bakun, Daskalov, Sinovcic, and others, this volume).

The participants further discussed problems related with sampling frequency. They pointed out that according to Shannon sampling theory (i.e., signal theory) one should sample at least two times in each statistical sampling period (i.e., one should have at least two samples per cycle). The participants recognised that the collection of data at as smaller time scales as possible will be ideal because data at fine scales can then be aggregated to larger scales if required. Yet, this carries practical implications (e.g. keeping sufficient people employed over the whole time period to maintain and update the time series) such that at some point a compromise between availability of resources and effectively sampling in time and space is inevitable. Simple rules of thumb will prove useful. Thus, if a system is spatially homogeneous it is clearly better to put emphasis on increased sampling over time rather than space. The opposite will be true of a system not varying markedly over time.

It was also stressed that sampling frequency will determine the predictive power of the models build. In general, as sampling frequency increases the forecasting horizon is lowered, whereas forecasting accuracy increases: in other words high sampling frequency is useful for short-term detailed predictions.

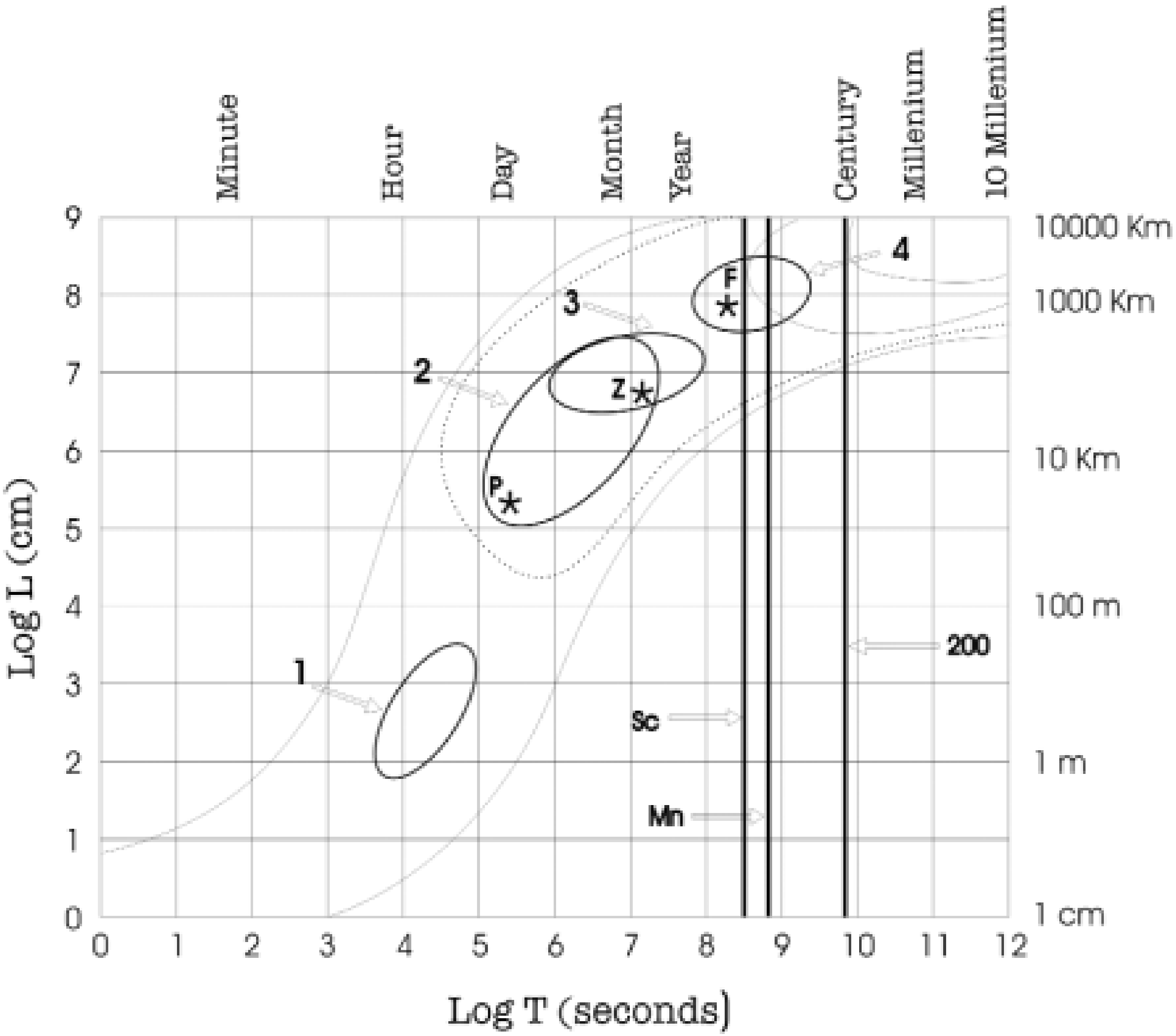

Fig. 1. Stommel diagram of the time and space scales of some of the topics discussed in this volume (modified from Wyatt 1995). The vertical bars show the sunspot cycle (Sc), the nodal cycle (Mn) and the Suess cycle, the first two of which (Sc, Mn) are plotted in the time domain Table 2 in Wyatt (this volume). For explanation of other symbols see text.

8. PRIORITIES FOR FUTURE ACTIONS – RECOMMENDATIONS

In conclusion the participants identified issues that call for further action. These were grouped along three main lines of actions.

8.1. Co-operation

The group noted that despite the accumulation of available biological data, hardly any cooperation and coordination are involved in the whole process. In addition the participants felt that much information is scattered in “grey” sources and could be advantageously assembled in the form of time series. Such information should be fully evaluated. Within this context the participants strongly recommended co-operation (in terms of planning, funding, maintaining, and inter-calibrating for quality control) between countries for assembling core time series and conducting comparative analyses of time series across European and Mediterranean waters. The group also stressed the importance of preserving existing datasets (avoiding losses due to staff retirement, computer format changes, …) and of sharing time series across the research community. The release of more meta-data on the Internet, and the organization of training courses or pilot projects on different time series issues, were highly recommended.

8.2. Interdisciplinarity

The participants recognised that the interaction and cooperation of biologists with scientists from other disciplines – who are rarely consulted by biologists – such as oceanographers, climatologists, economists, sociologists and zooarchaeologists, must be encouraged. The cooperation of scientists of different disciplines has much to offer in terms of methodology, for developing a "systems approach" and to better understand the relative importance of different mechanisms impacting ecosystems and embedded resources (e.g. climate-economy-resource interactions). This would certainly increase our medium- and long-term forecasting ability.

8.3. Building up new time series

The participants pointed out that the role of autonomous instruments is likely to greatly enhance our ability to gather and assemble new automated biological time series (e.g. chlorophyll, particle size, fish eggs and larvae). Finally, offshore autonomous monitoring stations will be useful for comparing and validating existing time series from inshore stations.

The participants also stressed that time series (or archives) of satellite images are increasing with time and such images, which provide relative values, offer potential time (and space) series that can be used to complement, or be compared with, existing biological time series. Already, as far as AVHRR images are concerned, daily, weekly and monthly SST composites can be found (free) on several Internet servers. Daily composites are usually posted within a few days. Several Institutions across the Mediterranean have receiving stations, and there should be a coordinated effort to cover the whole Mediterranean and ensure the availability of high resolution products to end-users.

With regard to the management of living resources, the participants noted that more effort should be directed towards the increase in the quality of fisheries time series and fishery-independent monitoring of stocks. They strongly recommended the build-up of long time series on cpue, recruitment, physiological indices, age and length structure, estimation of scales and cysts from cores taken from anoxic basins. Such data are at present lacking to a large extent for the Mediterranean Sea. Finally, the participants recommended using existing data (survey and commercial catches) as well as evaluating and using ECOPATH-ECOSIM models in the context of time series analysis and "back-to-the future" approach. For a more thorough discussion on these points the reader is addressed to a specific, recent CIESM workshop on the subject (CIESM 2000a).

CONCLUDING REMARK

In *The Art of Tracking*, the South African anthropologist Lieberberg describes the hunting skills of the Kalahari San as progression from the simple following of a prey animal's footprints, through a systematic hunt based on more varied data such as broken twigs or tufts of fur caught on bushes, to a speculative procedure in which hypotheses are based on data about the behavioural patterns of the prey, its habitual trails through the terrain and so on, "*a continuous process of conjecture and refutation to deal with complex, dynamic, ever-changing variables*". These stages are analogous to the ways in which we analyse biological time series, and, at the speculative level, attempt to relate the changes in the biological variable to external data such as climate or exploitation.

I - EXECUTIVE SUMMARY

This synthesis was drafted by Kostas Stergiou, and consolidated by significant inputs received from by John Pinnegar, Tim Wyatt, Josep Lloret, Georgi Daskalov, Harald Yndestad, Andrew Bakun and Jaap Van der Meer. Frédéric Briand took care of the final editing.

1. INTRODUCTION

The workshop was held from 11 to 14 June 2003 at the Institute of Oceanography and Fisheries, located at the tip of the wooded Marjan Peninsula, now a protected natural area to the north-west of Split (Croatia). Seventeen scientists, originating from 11 different countries attended the meeting at the invitation of CIESM.

They were greeted by Ivona Marasovic, IOF Director, who recalled some major accomplishments of the Institute since its foundation in 1930, with current research ranging from plankton productivity, fishing and aquaculture resources, to ocean dynamics, sea water chemistry and anthropogenic impact.

In his opening remarks, Frédéric Briand, Director General of CIESM, expressed his warm appreciation on behalf of all participants to Professor Marasovic who had done her best to facilitate the preparation of the meeting. He recalled the long, close association of the Commission with the Dalmatian coast where marine research is particularly active, as *Acta Adriatica*, the well-known scientific Journal based at the Institute*, and CIESM Congresses regularly show. He remarked that the location of this seminar was no accident, but a tribute to the long-term vision of the Institute which still maintained a tradition of collecting monthly key oceanographic data at permanent stations in Kastela Bay and in open waters, yielding in the process the longest-running time series on plankton productivity in the Mediterranean.

He then turned to Kostas Stergiou, Head of CIESM sub-Committee on Living Resources, and thanked him for initially advocating the theme of the seminar and for agreeing to act as workshop coordinator. Together they presented the context, background and objectives of the event, which aimed to derive original perspectives on a subject largely neglected in the Mediterranean region, by drawing from the varied, combined experience of the participants.

1.1. Background and objectives

If humans have the perception of time and space, marine biologists will usually dispose of a narrow historical perspective bound by the limited time frame of their sampling programmes : rare are long-term environmental data sets initiated before the 1960s (see Duarte *et al.*, 1992).

Yet biological time series, used together with meteorological/oceanographic time series, are essential tools to track the long-term properties of marine systems, detect meaningful shifts and assess whether changes are attributable to human impact or other causes. This was well illustrated in recent studies (e.g. Jackson *et al.*, 2001; Christensen *et al.*, 2003; Myers and Worm, 2003; Baum *et al.*, 2003) where time series demonstrated beyond doubt the dramatic degradation of coastal and open sea ecosystems worldwide, following the rapid destruction of predatory fish stocks by industrial fishing. As remarked by Pauly and Watson (2003), "*should this continue we will be left with a diet of jellyfish and plankton stew*".

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* *The workshop participants had a chance to hear a brief, lively overview of the first 70 years of* Acta Adriatica *given by Anita Marusic, Technical Editor of the journal.*

Obtaining information on different marine food web components at regular time intervals is also critical for testing ecological theories on community dynamics, variability and resilience, enhancing our limited capacity for short- and medium-term forecasting, and for managing living resources.

In contrast with other areas of the world ocean (see Ultang and Blom, 2003), biological times series are quite rare in the Mediterranean Sea. At least this is the common perception. A preliminary aim of the workshop was to assess the reality of this assertion by identifying the availability, gaps, homogeneity and scales (up to the century level) of Mediterranean biological time series. Through presentations and in-depth discussions, the group was to further tackle additional challenges, each summarized in turn in the following pages:

- reviewing the many techniques, developed from diverse disciplines, that can be used to extract and identify trends and interrelationships from time series, as well as methods to deal with incomplete time series;
- identifying which higher-order questions can be uniquely answered by time series analysis;
- listing notable trends so far uncovered by the analysis of Mediterranean biological time series; and
- indicating priorities and recommendations for future research on Mediterranean biological time series.

2. DEFINITION : WHAT IS A TIME SERIES ?

A series of measurements of a variable at equal time intervals is known as a “time series” and the usual notation is Y_t, for t=1, 2, 3,…, K. Two of the most crucial characteristics of a time series are the *trend*, which can be either deterministic (i.e., long-term changes in mean with constant variance) or stochastic (the mean is constant and variance increases with time), and the *seasonality* (i.e., cycles of constant length occurring on regular basis). For a detailed account on trend and definitions of seasonality the reader will usefully consult Durand and Mendelssohn (1998).

3. METHODS FOR ANALYSING TIME SERIES

The group first examined the conceptual framework within which time series can be properly analysed, then reviewed the various families of techniques available for time series analysis, finally discussing the problem of how to deal with gaps or missing data.

3.1. The comparative approach

As marine populations and local climatic systems are hardly amenable to experimental controls, one must turn to the comparative method as a practical research tool. This method draws its multiple realizations from independent situations found in the natural world. The independence may come from wide geographic separation; alternatively the separation may be in time rather than in space. Thus, time series analysis can be seen simply as an application of the comparative method in the temporal, rather than in the spatial, domain.

A major problem in studying variations in hydro-climatic parameters, anthropogenic influences, or marine population numbers, is that they tend to occur over a rather long time period compared to the time frame of the time series. Accordingly, the available degrees of freedom are generally minimal or sub-minimal for addressing issues of significant complexity. This problem may in some cases be relieved by augmenting the scarce realizations in a local time series with similar time series obtained from somewhat analogous situations in other geographic locations. However, objective methods for dealing with this problem are not well worked out. Applications of interregional comparative time series analysis are currently a rather “creative” endeavour, involving a touch of “art” in addition to science. Nonetheless, these approaches offer a way to gain insight and understanding that would be otherwise unobtainable. The methodology is essentially “pattern recognition” (for examples of the application of the comparative approach to the marine realm, see Cury and Roy, 1989; Durand *et al.,* 1998).

A number of obvious opportunities for intraregional and interregional comparative studies present themselves in the Mediterranean. Certainly, the several separate basins offer opportunities of relative independent realizations. In terms of fish stocks, their degree of actual independence is indeed a scientific issue of great practical importance. To pursue with fish examples, other opportunities might exist in the fact that the very valuable but threatened North Atlantic bluefin tuna uses only two spawning sites located in extremely different environmental settings, one in the swift loop current of the Gulf of Mexico, the other in the Mediterranean Sea (see Ravier and Fromentin, 2001). A comparative study of the particular attributes of these two very different ecosystem settings might reveal much about the crucial factors controlling reproductive success in this species. The fact that anchovies and sardines not only appear to alternate in abundance within the Mediterranean Sea (e.g. Sinovcic, this volume), just as they do in very different environments elsewhere (Bakun, this volume), but that they do so synchronously with populations spread widely around the world, offers another possibility for comparative studies that could be extremely rewarding. Similar opportunities likely abound for other taxa.

3.2. Methods for time series analysis

The group reviewed various methods that can be used for modelling and/or forecasting time-series. Overall 35 different methods, varying in complexity, were discussed. They are categorised in Table 1 into four families: (a) regression methods, (b) time-series methods, (c) multivariate analysis methods, and (d) other models.

Fortunately the development of appropriate software for their application has rapidly expanded in recent years, including general statistical packages (e.g. S-PLUS, SPSS, STATGRAPHICS, MATLAB) as well as specialised time series software such as FORECAST PRO <www.forecastpro.com>, FORECASTX <www.forecastx.com>, ECONOMETRIC VIEWS <www.eviews.com>, CATERPILAR SSA <www.gistatgroup.com/cat>, ForeTESS (developed by the Polytechnic University of Catalonia: see Lloret, this volume).

Table I. List of methods available for time series analysis, accompanied by underlying assumptions, suitability, and usually two references (general: upper reference; application to a discipline: lower reference). **GAM** = Generalized additive models, **GLM** = Generalized linear models, **L**=linearity, **NL** = non linearity, **MF**=multivariate forecasting, **N**=normality, **P**=parametric, **NP**=non parametric, **TL**= time lags, **TS**=time series, **ST**=stationarity, **UF**=univariate forecasting,

METHOD	ASSUMPTIONS	SUITABILITY	REFERENCES
REGRESSION			
Time-varying[1]	N, L, P, no TL	For TS with gaps. UF	Makridakis *et al.*, 1983 Stergiou *et al.*, 1997
Linear regression[1]	N, L, P, no TL	For TS with gaps. MF	Makridakis *et al.*, 1983 Koslow *et al.*, 1987
GLM[2-4]	L, P, no TL	For TS with gaps. MF	McCullagh and Nelder, 1989 O'Brien, 1999
GAM[3-4]	P, NP, no TL	For TS with gaps. MF	Hasti and Tibshirani, 1990 Daskalov, 1999
Loess regression[4]	NP, no TL	For TS with gaps. MF	Cleveland *et al.*, 1992 Daskalov, 2003
Non-linear models[4-5]	NP, no TL	For TS with gaps. MF	Myers *et al.*, 1995
TIME SERIES[6]			
Smoothing methods	P, NP	For short TS, UF	Hastie and Tibshirani, 1990 Cury and Roy, 1989
ARIMA[7]	N, ST, TL	For long TS, UF	Box and Jenkins, 1976 Stergiou *et al.*, 1997
Decomposition methods[8]	N, STL-NP based on loess	For short TS, UF	Makridakis *et al.*, 1983 Daskalov, this volume
Intervention analysis[7, 9]	N, ST, TL	For long TS, MF	Box and Jenkins, 1976 Lloret *et al.*, 2000
Transfer function models[7,10]	N, ST, TL	For long TS, MF	Box and Jenkins, 1976 Lloret *et al.*, 2001
Dynamic regression[7]	N, TL,	For long TS, MF	Chatfield, 1984 Stergiou *et al.*, 1997

TIME SERIES[6] (continued)			
Vector autoregression[11]	N, TL	For long TS, MF	Chatfield, 1984 Stergiou *et al.*, 1997
Kalman-filters		Estimations of past, present, and future states	Kalman, 1960 Sibert *et al.*, 2003
Non-linear time series analysis	No N, No ST	MF	See section 3.2.1
Filters	P, NP		Cleveland, 1993 White *et al.*, 1997
MULTIVARIATE ANALYSIS[12]			
Ordination (i.e., PCA, MDS)[13]			Clarke and Warwick, 1994 Anneville *et al.*, this volume
Cluster[13]			Clarke and Warwick, 1994
MODELS[14]			
Age or size structured models (VPA, XSA, ADAPT, ICA, stock-synthesis, MULTIFAN[15]	Long TS, MF		Darby and Flatman, 1994 Hilborn and Walters, 1992
Spawning-stock recruitment[16]	L, NL, GLM, GAM	Long TS, MF	Ricker, 1975 Hilborn and Walters, 1992
Production models[17]	Generally based on regression	Long TS, MF	Shaefer, 1965 Abella *et al.*, 1999
Predator-prey models[18]			Berryman *et al.*, 1995
ECOPATH/ECOSIM[19]			Walters *et al.*, 1997 Pauly *et al.*, 2000 Christensen *et al.*, 2000
Neural networks[20]		MF	Bishop, 1995 Haralabous and Georgakarakos, 1996

1. Linear relationship between a continuous response variable and continuous predictor variable(s); normality of dependent and predictor variable(s).
2. The distribution of the dependent variable can be non-normal and does not have to be continuous; predict responses both for dependent variables with discrete distributions and for dependent variables which are nonlinearly related to predictors.
3. Allows various distributions of the response variable.
4. The shape of the function is not constrained by some *a priori* model but is flexible in relation to existing data; allows simultaneous smoothing of up to three independent variables.
5. Non-linear relationships between variables.
6. The participants also discussed the potential usefulness of others models which belong to this category: Mann-Kendall tests, spectral analysis, wavelength analysis, state-space- models and Bayesian analysis.
7. Take into account time lags (i.e. dynamic models). Handle all components of a time series (i.e., seasonality, trend, irregular component, cycles); strong verification of model adequacy; better forecasting power than other methods.
8. Handle seasonality and trend.
9. Detect and quantify non-random changes (anomalies).
10. Quantify the impact of external variables.
11. Very useful for modelling and forecasting two or more closely related variables as a system (e.g. predator-prey, competing species).
12. The participants also discussed the potential usefulness of multivariate regression and multivariate autoregressive models, which belong to this category.
13. Very useful for identifying changes in species composition of assemblages with time, regime shifts, or for identifying the best fitting/forecasting model in terms of accuracy measures.

14 The participants also discussed the potential usefulness of other methods belonging to this category: yield per recruit, Gadget/Fleksibest, other food web models and eigen-value frequency analysis.

15. Assumptions for natural mortality and terminal fishing mortality; requires a lot of data, reconstructs past history of stock numbers and mortalities; a standard stock assessment method.
16. A main assumption is that the number of recruits depends upon parental biomass; detects recruitment overfishing; inputs are difficult to be obtained.
17. Often assume equilibrium; easy and general indication of stock state; estimation of biomass from the relationship between effort and catch; data easy to be obtained.
18. Many assumptions depending on the model; complex; several models since Lotka-Voltera formulation.
19. Dynamic mass-balance models fitted to time series; global modelling with an ecosystem approach; modelling fish stocks in relation to habitat, fisheries and environment.
20. Many assumptions; analysis of unknown, complex systems; applicable when the relationship between the predictor variables and predicted variables is very complex and not easy to articulate in usual statistics.

A distinction must be made between modelling (i.e., fitting) and short-term forecasting (i.e., operational forecasting, 1-2 years in advance). First because methods that provide good fitting do not always perform well in terms of forecasting; and secondly, as many practicing forecasters might argue that forecasting models do not have to be "meaningful" in terms of the corresponding field (see Stergiou *et al.*, 1997). Fitting and forecasting performances must be evaluated using a variety of accuracy measures (i.e., standard, relative and other statistical measures), each suffering from certain limitations. For a detailed general introduction to accuracy measures the reader is referred to Makridakis *et al.*, (1983).

Many of the methods listed in Table I have been widely applied to marine time series (e.g. ARIMA, transfer function models, intervention analysis, decomposition and regression models) whereas others have not.

The group agreed that analyzing time series of population abundance data by non-linear time series models (also called non-linear stochastic process models) may reveal a complex and chaotic dynamics, which remains otherwise undetected when (linear) ARIMA models are used. In most stochastic population process models (in discrete time) the log reproductive rate, defined as the log ratio of succeeding population densities, is related to a set of previous population densities (hence, if more than one term is included, delayed density dependence is assumed) and, possibly, to a set of exogenous variables. Different non-linear functions, for example extensions of the Ricker model, have been applied. See Royama (1992) for an introduction to this kind of models, Van der Meer *et al.* (2000) for an application to the marine realm, and Perry *et al.* (2000) for a recent overview of applications to terrestrial ecology.

3.3. Dealing with gaps and missing values

In all scientific fields, time series are characterised by gaps (i.e., long periods without records) or missing values (i.e., few isolated time points without records). This is an important problem since both cases drastically restrict the application of many time series techniques. In fact, missing data imputation and handling is a rapidly evolving discipline by itself (see for example Little and Rubin, 1987; Allison, 2002; Howell, 2002), with appropriate software becoming widely available (e.g. MX, free download from <www.vcu.edu/mx>; NORM, free download from <www.stat.psu.edu/~jls>; AMELIA <gking.harvard.edu/amelia>).

Missing data and gaps can result from a variety of circumstances (e.g. logistics, equipment failure, sample loss, sample contamination, bad weather, sick observers, removal of outliers, corruption of databases, input errors, file/archive loss). In all such cases, the data are missing completely at random (MCAR), that is, the probability that an observation, Xt, is missing is unrelated to the value of Xt or to the value of any other variable (Howell, 2002). In many other cases, data are not MCAR but are simply missing at random (MAR), that is, data meet the requirement that missingness does not depend on the value of Xt after controlling for another variable. In both cases (MCAR or MAR), missingness is ignorable (i.e., there is no need to model the missingness property), as opposed to the case when data are not missing at random.

The simplest way for dealing with gaps and missing values is to completely ignore them, a fact resulting into two or more individual time series of shorter length and, obviously, in a loss of information. Whereas a few simple non-parametric tests (e.g. Mann-Kendall), regression models and many simulation models are not affected by the presence of gaps in the data, the application of time series methods, which involve lags of the dependent and/or the independent variables, does require completeness. As a result, one has to adopt some method for missing data imputation, e.g. mean substitution, regression method with or without adding uncertainty to the imputation of missing values, hot deck imputation, expectation maximization approach, raw maximum likelihood methods, wavelet analysis, chaos theory, neural networks (see Ahn, 1999; Khalil *et al.*, 2001; Hopke *et al.*, 2001; Elshorbagy *et al.*, 2002, for applications to specific disciplines).

Naturally, not all methods do perform equally and so the selection of a particular method will affect/restrict the subsequent analysis. Thus fish stock models often use temperature relationships to interpolate missing values, but then one cannot look for changes/cycles that might be caused by climate. The selection of a particular method must also not affect the statistical properties of the original series, a premise that is not met by all methods (e.g. mean substitution can result in distributions with truncated variance; Howell, 2002).

4. WHICH HIGH-ORDER QUESTIONS CAN BE ANSWERED BY TIME-SERIES ?

The participants first questioned to what extent time series analysis is simply "Exploratory Data Analysis" (EDA) or hypothesis testing. Judging significance in the case of EDA (which also generates hypotheses) might be a problem. If we assume $P < 0.05$, then there is a 1 in 20 chance of hitting a nonsense relationship. Thus if 100 species (of phytoplankton for instance) are considered, we will always obtain some significant results (as 1 in 20 will be spurious). However negative results are too rarely published in marine scientific journals (see Browman, 1999).

The group identified various tractable questions, grouped by level of biological organization which can be or have been uniquely addressed by time series analysis.

Population level:

- The relationship between recruitment variability and upwelling intensity ("optimal environmental window" at moderate levels of upwelling, Cury and Roy, 1989).
- The existence of regularities/periodicities in stock fluctuations (see section 4.1.1).
- How population and/or landing variability changes with time (see section 4.1.2) ?
- The relative importance of climate and internal stock dynamics/behaviour, including predator-prey cycles, for driving fluctuations in stocks (e.g. Ravier and Fromentin, 2001).
- The relative importance of climate and fisheries as drivers of fluctuations (Pauly *et al.*, 2002).
- The effects of fishing on demographic parameters of fishes (i.e., maximum length and age, weight-at-age, age and length structure, length and age at first maturity, reproductive potential).

Community level:

- The removal by fishing of large, long-lived predators from marine ecosystems (i.e., "fishing-down the marine food webs", Pauly *et al.*, 1998a).
- The effects of fishing on species diversity (e.g. Greenstreet and Hall, 1996).
- The temporal variability of communities (Van der Meer, this volume)
- The fluctuations of anchovy and sardine in an opposite fashion-regime shifts (Bakun, this volume).
- Trophic cascades (see section 4.1.3).
- Phytoplankton assemblage succession (Anneville *et al.*, Zingone *et al.*, this volume) .
- Eutrophication and its effects (e.g. hypoxia).
- The effect of extreme events.

Ecosystem level:

- The effects of biology on the climate and composition of atmosphere (e.g. phytoplankton production influences "cloud condensation nuclei" and dimethyl sulphide, production).
- The impact of fisheries on ecosystems (the results of the "Sea Around Us" Project, see section 4.1.4).
- The paradigmatic study of the Peruvian upwelling ecosystem (Pauly and Tsukayama, 1987; Pauly *et al.*, 1989).

Among the above topics, some were the object of further discussion.

4.1. Climate change and regularities/periodicities

Many analyses of geophysical and biological time series have several signals with periods identical to those of astronomical cycles. It is natural to hypothesize that the latter are responsible for the former, and that the variables of the time series are being forced by the changing constellations of celestial bodies. The signal most commonly found in long time series, and often the strongest, has a period of 18.6 years, which points to the importance of the moon and the nodical cycle (see Wyatt, this volume).

Biomass fluctuations of many fish stocks seem to be synchronous on hemispheric or global scales (e.g. Bakun, this volume), either in phase for some species, such as *Sardinops*, or 180 degrees out of phase if we compare different species, such as sardines and anchovies or herrings. The little information available indicates that the Mediterranean Sea also conforms to this pattern.

The view that the nodal tide influences fish abundance has a very long history in the scientific literature, but has not attracted very much attention due to the problem of finding potential mechanisms through which the tide could force changes in population dynamics. This is probably due to the fact that in almost all routine tidal studies, only the vertical component of the tide is taken into account, and since the vertical amplitude of the nodal tide is extremely small compared with the better known tidal components, it intuitively appears to have little importance. But the picture changes if the horizontal component is considered, since it is unidirectional for nine years. For example the nodal tide contributes an impulse to the Atlantic inflow to the Mediterranean Sea, which runs in the same direction for nine years before reversing for a further nine years : it therefore introduces systematic changes into the Mediterranean environments in which fish populations live and reproduce.

A stationary nodal tide fluctuation in the Atlantic Ocean influences the atmospheric process. Atmospheric processes are reflected in the North Atlantic Oscillation (NAO) and NAO has an influence on weather and climate in Europe. A strong positive NAO winter index will lead to stronger winds and warmer air in the winter in Scandinavia and colder winter in the Mediterranean area. This climate oscillation between north and south is expecting to introduce a climate forced opposite fluctuation of biomasses in the North Sea and in the Mediterranean Sea.

In the meeting there were indications that some long-term time series in the Mediterranean Sea were related to this climate fluctuation. This suggests that the dominant biomass fluctuations in the Mediterranean Sea are controlled by climate change, an hypothesis which deserves to be tested by a wavelet analysis to identify cycle times and phase.

4.2. Variability of fisheries landings

Evidence that variability increases with the length of time over which it is estimated has been found for fisheries landings by Stergiou (1998), who analysed 103 time series of marine fish landings of Atlantic, Pacific and Mediterranean origin for the period 1970-1991. The more time – more variability pattern suggests that there is not any equilibrium yield (i.e., the basis of most conventional, steady-state models used for fisheries management). It also introduces uncertainty into various estimations from fisheries models, a fact affecting the effectiveness of traditional fisheries management schemes. An additional finding was that landing variability is significantly ($P<0.05$) higher in the four major upwelling areas of the world and lowest in the Mediterranean. This suggests that differences in variability with time are a function of the ecosystem characteristics of the given marine region (i.e., trophic potential, number of trophic levels, environmental dynamics).

4.3. Trophic cascades

Trophic relationships are important structural forces in marine ecosystems, as bottom-up (resource driven) and top-down (predation driven) controls may dominate the dynamics of the populations at different trophic levels and determine the trends in abundance. Historical time-series are obviously a useful tool for detecting bottom-up and top-down effects in predator and prey populations (see Cury *et al.*, 2000; Daskalov, 2002; Myers and Worm, 2003). Trophic cascades occur due to strong human driven (overfishing, alien invasion) or natural (climate shift) influences and may leave pronounced signatures in time series.

4.4. Impact of fisheries on marine ecosystems

Within the framework of the “Sea Around Us” project (SAUP), Pauly and his collaborators used a combination of fisheries landings, information from hydrographic databases, GIS modelling, statistical analysis and ECOPATH food-web models – representing both historic and recent periods –

to produce, among other things, fisheries maps, of half latitude-longitude degree resolution, showing declining patterns of (high trophic level) fish biomasses in the North Atlantic by two thirds during 1950-2000. The results for the North Atlantic have been recently summarised in Pauly and MacLean (2003). Analyses by Myers and Worm (2003) and Baum *et al.* (2003) of long time series of catch per unit of effort data provided strikingly convergent results. Time series are an essential component of such an imaginative approach, which did remarkably well in raising public and political awareness.

5. WHAT ARE AVAILABLE MEDITERRANEAN TIME SERIES ALREADY TELLING US ?

The participants summarized and discussed various trends revealed so far from analyses of existing Mediterranean time series. Some of the most interesting are noted below.

1. Many long time series in the Mediterranean Sea exhibit a strong signal with period of 18.6 years (see Wyatt, this volume).
2. Long time series of bacterioplankton from the Adriatic Sea show that abundance increased significantly in the 1980s (about 3-4 times the levels of the early 1960s, see Solic *et al.*, 1997), indicative of anthropogenic impact such as overfishing of suspension feeders (Jackson *et al.,* 2001).
3. The damming of the Nile River in 1965, resulting in a 90% decrease in the average annual discharge, led to a drastic decline in phytoplankton abundance and in the catches of sardine and shrimps (Wadie, 1984).
4. Available time series of FAO landings for the Mediterranean and Black Seas combined (FAO sub-area 37) during 1950-1994, of GFCM landings for the NW Mediterranean Sea during 1972-1998, of local landings from the southern Aegean Sea during 1964-1998, and of changes in the distribution of market fish prices (see Pinnegar *et al.,* this volume), all indicate that the mean trophic level of landings has declined.
5. Sardine and anchovy fluctuations in the Mediterranean Sea are out of phase (e.g. Spanish and Algerian waters, Larraneta, 1981; Mediterranean Moroccan waters, Turner and Bencherifi, 1983; Adriatic Sea, Alegria-Hernandez, 1983; Greek waters, Stergiou and Lascaratos, 1997) as they are elsewhere (see Bakun, this volume). Rainfall and wind activity are the main external factors driving sardine and anchovy fluctuations (Lloret, this volume).
6. The mean monthly total length of sardine in the north Aegean Sea declined significantly during 1996-2003, following a decrease in biomass due to overfishing (Voulgaridou and Stergiou, 2003).
7. Time series of stranded individuals of the Beaked Whale *Ziphius cavirostris* in the eastern Mediterranean revealed that stranding were related to NATO sonar tests during 1992-1997 (Frantzis, 1998).

6. MEDITERRANEAN TIME SERIES : AVAILABILITY / GAPS

6.1. Available time series (at the century level)

Apart from information spread in local government reports (e.g. French fisheries records for each port are available since 1885) or trade journals (e.g. Industrias Pesqueras, Spain: publishes fortnightly catches of anchovy and sardine), fisheries landings for the Mediterranean and the Black Seas are available from the FAO in two forms. First, landings referring to both areas combined (FAO sub-area 37) can be extracted from the global production FAO database for the years following 1950. Second, landings by different Mediterranean sub-areas and the Black Sea can be extracted from the GFCM capture database for the years following 1970. Both types of data series can be freely downloaded from the FAO website <www.fao.org>. Available time series can be manipulated, aggregated and filtered using FISHSTAT (downloadable from same site) (see Pinnegar, this volume). Finally, various time series on large pelagic species are available from ICCAT <www.iccat.org> (see Tserpes *et al.,* this volume).

Although FAO data suffer from many limitations (e.g. under- or over-reporting; Watson and Pauly, 2001), with the largest errors being introduced before data reach the national database, a number of factors (e.g. globalization of fisheries and fish markets, fisheries resources exploited almost everywhere) indicate that generally FAO data do reflect relative abundances. Therefore, to analyze global or regional trends there is little choice but taking the FAO or GFCM data at face value.

Fish price data are available from GLOBEFISH <www.globefish.org> since 1991 as well as locally from other sources (e.g. IREPA, Instituto di Ricerche Economiche per la Pesca e l'Acquacoltura, for individual Italian regions, available monthly since 1972; Hellenic Fishing News Magazine: monthly Greek wholesale values per main auction fishing port since at least the early 1980s; Industrias Pesqueras: Spanish fortnightly price data).

One of the most valuable time series of fishery independent data was initiated in 1994, within the framework of the EU-funded MEDITS (Mediterranean International Trawl Surveys) project, with the groundfish trawl surveys. It intends to produce basic information on benthic and demersal species (more than 50 species are monitored) in terms of population distribution as well as demographic structure, on the continental shelves and along the upper slopes at the global Mediterranean scale. MEDITS is realized through annual standardized experimental trawl surveys covering most trawlable areas of the northern Mediterranean basin at depths from 10 to 800 m. About 1000 stations are sampled each year. Details on sampling can be found in Abello *et al.* (2002). Access to the MEDITS data however is not easy and interested persons must contact the project steering committee.

Many European countries maintain National Marine Databases (or oceanographic data centres) where forms containing meta-data and detailed availability and contact persons are submitted regularly. The EU project MTP2/MATER Mediterranean Targeted Project II (MAss Transfer and Ecosystem Response <www.doga.ogs.trieste.it>) has assembled such meta-data for all northern Mediterranean countries and made them available on four CD-ROMs.

At the local scale, the longest biological time series are available for the Adriatic Sea, thanks to the unflinching efforts of the Institute of Oceanography and Fisheries, Split. Apart from a variety of abiotic parameters *, the Institute monitors coastal and open waters at monthly intervals for chlorophyll a since 1979, for primary production since 1962, and for bacterioplankton since 1968. Monthly phytoplankton composition is known through the period 1952-1985, and zooplankton time series since 1957 (e.g. Solic *et al.*, 1997).

With respect to fisheries data, long-term series exist for sardine (1875-2002; see Sinovcic, this volume; Wyatt, this volume), anchovy (1947-2002), sprat (1947-2002), Atlantic mackerel (1947-2002), chub mackerel (1947-2002), bluefin tuna (1947-2002) and Atlantic bonito (1947-2002). Biological data (i.e., migrations, distribution of eggs, larvae, juveniles and adults, population structure, sex ratio, feeding, reproduction, first sexual maturity, fecundity, growth) of sardine, anchovy, sprat, Atlantic mackerel, chub mackerel and bluefin tuna, are available since 1922, but with gaps. Finally, data for trawl fisheries are available since 1948, and for coastal fisheries since 1960 (see Jardas, this volume), but also with gaps.

In the NW Mediterranean several time series of oceanographic and biological data are available, such as the DYFAMED series on hydrography, nutrients and phytoplankton since 1991 (Marty *et al.*, 2002) plus various deep-sea ecosystem components since 1991 (Guidi-Guilvard, 2002); zooplankton abundance in Villefranche-sur-mer through 1974-1999 (with a gap in 1978-1983); and various time series of the biomass of small pelagics restricted mainly to the years following 1990 (Agostini and Oliver, 2002). Short time series (initiated between 1995 and 2000) of oceanographic and biological parameters exist at different locations along the Catalan coast. These time series include parameters such as water temperature and salinity, inorganic nutrients, bacteria, heterotrophic flagellates, microbial diversity, dissolved organic carbon, picoalgae, phytoplankton counts and phytoplankton pigments. Data belong to different research and

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** An automatic station operates in Kastela Bay since 1998, which measures twelve meteorological and oceanographic parameters at 10 min intervals with data presentation in real time through the Internet <www.izor.hr>.*

governmental institutions and are collected on a monthly, weekly, bi-weekly or daily basis. Long time series (>30 yr) of monthly landings and/or cpue, by species or groups of species, disaggregated or not by commercial size groups, are available from many Spanish ports (see Lloret, this volume). Total landings of the Catalan fisheries go back to 1910 (Lleonart, 1999).

Time series of Mediterranean seabird population densities mainly concern the years following the 1970s and are characterised by gaps. They can be found in Aguilar *et al.* (1993), Oro (2002) and Yesou and Sultana (2000). A recent study by Bosch *et al.* (2000) presents one of the longest seabird time series (i.e., population abundance of yellow-legged gull *Larus cachinnans*, Medes Islands, for 1960-1996) available for the Mediterranean Sea.

The SINAPSI project (Seasonal Interannual and decAdal variability of the atmosPhere oceanS and related marIne ecosystems) brings together time series on phytoplankton, zooplankton and zoobenthos from the Adriatic Sea. Most series are now fully computerized and available on the website <sinapsi.cineca.it>. Italian SINAPSI time series of phytoplankton are available from five Adriatic Sea sites and from three Tyrrhenian Sea sites, ranging from 12 to about 30 years in duration (e.g. Zingone *et al.*, this volume). Zooplankton time series are available for the Adriatic Sea from Trieste and for two sites of the Tyrrhenian Sea. They range from 17 to 32 years (frequency: weekly to yearly scale). Zoobenthos time series are available for 15 sites (frequency: fortnightly to yearly scale). The longest time series is from Clado (Tyrrhenian Sea) covering the period 1936-1996; the others range in duration from four to 15 years. With respect to fisheries data, long time series of sardine and anchovy landings and biomass are available since 1975, from IRPEM/CNR (Ancona): sardine and anchovy eggs/larval distribution and abundance from 1976, from LBMP University of Bologna in Fano (Agostini and Oliver, 2002). Finally, time series of trawl surveys (15 years) are available from the GRUND project (see Italian Ministry of Agriculture and Forestry <www.politicheagricole.it>) as well as from the Gulf of Castellamare (Sicily) before and after a trawl ban (see Badalamenti *et al.*, 2002). Time series of bottom fisheries in the central Mediterranean will also be found in Relini *et al.* (1999).

With respect to Greek waters, the only long time series on nutrients, chlorophyll a and abundance/biomass of all zooplankton taxa is derived from monitoring a coastal station in the Saronikos Gulf on a biweekly basis since 1989 (Christou, 1998). Fisheries landings statistics are collected by four independent organisations, each collecting and/or processing data for its own purposes. The time series recorded by the National Statistical Service of Greece (annual and monthly landings for 62 species, or groups of species, and fishing effort since 1964 for 16 statistical subareas) are the longest ones. Since the second half of 1995, a variety of fisheries data (i.e., engine horsepower, tonnage and days at sea; corresponding catch/day for a large number of species) are also collected by the Institute of Marine Biology of Crete on a monthly basis over 21 stations throughout the Greek Seas. Time series of biological parameters of sardine (e.g. mean length, length-weight relationship, condition factor) are available from the north Aegean Sea since July 1996 (e.g. Voulgaridou and Stergiou, 2003).

6.2. Mining historical data sources

Europe is probably richer in written “historic” resources than any other region of the world (see Hoffmann, 2001). There is a wealth of written “data”, often quantitative, going back many centuries, for example concerning levels of fishing or trade and movement of fish products. A huge variety of sources are available, including records kept by local authorities for tax collection purposes, shipping or railway inventories, tithe accounts, kitchen records, catch statistics and fish prices in trade magazines, newspapers, etc. These largely neglected records might allow biologists to extend their existing population estimates many centuries back in time. A successful example was provided by Ravier and Fromentin (2001) who managed to reconstruct a 300-year (1650-1950) time series of Mediterranean tuna catches based largely on the records of bankers and financiers. Wyatt (this volume) describes a similar attempt (by Zupanovic, 1968) to assemble a time series for sardine fisheries in the eastern Adriatic.

Anecdotal resources can also prove very useful. For example Francour *et al.* (1994) consulted long-serving marine scientists (with careers spanning the last 20-30 years) from around the western Mediterranean, whose records and memories suggested that many “thermophilic” fish species have become increasingly abundant, probably a reflection of a broad warming trend (Bethoux *et al.*, 1990). Benovic and Lucic (this volume) compared published species inventories for hydromedusae in the Adriatic Sea spanning 1912-2002, and suggested that the increased discharge of terrigenous material via rivers in the northern Adriatic may have caused changes in hydromedusan faunal assemblages and the depletion of many species. In the same region, written “historic” data sources might help scientists understand the occasional appearance of mucilaginous events (known as “mare sporco”), which have had a significant impact on the cultural and social life of communities in northeast Italy since times of antiquity.

Classical literature abounds with descriptions of fish and fisheries in the Mediterranean (see examples in Cushing, 1988; Radcliffe, 1921), and probably the best account is given by Opianos in his *Halieutika* (ca. AD 170). Homer (900-800 BC) described various fishing methods relying on hooks, nets and harpoon in both the *Iliad* and the *Odyssey*. The life and activities of fishermen were also described in the “Attic comedies” of Antiphanes (350 BC), and of Menander (about 300 BC). At about the same time, Aristotle referred to many fish species in his *Natural History*.

Stergiou (1999) has suggested that many Mediterranean top predators (e.g. *Coryphaena hippurus*) may have been all but “fished out” in antiquity, as even small amounts of fishing pressure can quickly deplete such species. Early fisheries, as depicted in Roman, Greek, Minoan or Egyptian frescoes, tended to involve highly selective gears, and it is therefore quite plausible that many fishing-induced changes occurred in Mediterranean fish assemblages long before scientific monitoring surveys were in place.

6.3. Socio-environmental proxies

Often, when no instrumental or scientific records are available, it is necessary to construct time-series using indirect methods and somewhat unconventional data. Entries in diaries or the recorded date of natural phenomena (the study of which is known as phenology) can often tell us something about the climatic conditions in a given year. One of the best examples (documented by Wyatt, this volume) is the date of the annual wine harvest in southern Europe, which is heavily dependent on summer temperatures. Leroy-Ladurie (1971) and Pfister *et al.* (1999) were able to construct time series spanning 1480-1880, since the warmer and sunnier the growth period, the swifter and earlier the grapes reached maturity and were harvested. Olive flowering dates also depend on temperature and it has been suggested that this may provide an early biological indicator of future climatic warming in the Mediterranean (Osborne *et al.*, 2000).

Other written sources might also yield useful (albeit indirect) information about the status of the marine environment in the Mediterranean, including records of employment in the fishing industry, the number of cans of tuna produced, the oil content of sardines (which reflects the availability of their preferred planktonic prey), records of fish consumption, etc. Pinnegar *et al.* (this volume) indicate how the prices of particular fish species on the markets might provide useful information about the availability of these species in the environment. Hence increased co-operation between economists, historians, sociologists and marine scientists is certain to yield a better understanding of the historic ecosystems.

6.4. Archaeological and sedimentary time series

Sometimes archaeological excavations or the extraction of sediment cores can allow very long-term time series to be constructed. One of the best-known examples involved counts of Pacific sardine *Sardinops sagax* and northern anchovy *Engraulis mordax* scales in cores taken from anaerobic sediments off California (Baumgartner *et al.*, 1992). These analyses showed that sardine and anchovy abundance had varied dramatically over the last 2000 years and that the collapse of the sardine stock in the latter half of the twentieth century would be only one of a series. Analyses of dinoflagellate cysts, foraminifera, pollen and coccolithophores in sediment cores can also provide useful information about past environments. Many of these techniques have been successfully applied in the Mediterranean (e.g. Sangiorgi *et al.*, 2002; Giunta *et al.*, 2003).

Archaeological excavation of fish middens (waste deposits) can yield important evidence regarding historical patterns of fish trade and consumption (see Barrett *et al.*, 1999). Desse and Desse-Berset (1993) demonstrated that inshore systems in Cyprus have been impacted by fisheries for millennia and that large specimens of certain species, notably sea breams (Sparidae) and groupers (Serranidae) are now much rarer than they were during the Neolithic (~6000 BC). The "Fish Working Group" of the International Council for Archaeozoology (ICAZ) contains several members from Mediterranean countries and holds regular workshops and symposia (see <www.nmnh.si.edu/icaz/workfish.htm>).

Museum specimens can also represent a valuable resource when attempting to construct historical time series. Several authors (Wainright *et al.*, 1993; Thompson *et al.*, 1995) have sampled archived materials (i.e., fish scales, feathers, bones, teeth, specimens in alcohol), assessing their carbon and nitrogen isotope composition. Changes in the isotope "signature" of animals collected at the same locality, but during different periods of time, can indicate changes in feeding preferences, and hence changes in the underlying ecosystem. For example Wainright *et al.* (1993) demonstrated a significant downward trend in the δ^{15}N of haddock on Georges Bank over the past 100 years, and the authors tentatively related this to changing patterns of fishery exploitation affecting the availability of prey resources.

6.5. Gaps in taxa, space and time coverage

In general, there are more non-biological than biological long time series, and the latter tend to be less frequent from higher to lower trophic levels ("researching down the food-web"). In other words, there are more time series for fish than for plankton and benthos, particularly long time series, and very few bacteria time series. Not surprisingly, the number of long time series decreases with distance from shore and with depth, with open- and deep-sea long time series almost missing (the DYFAMED-BENTHOS is among the longest ones, see section 6.1). Littoral benthos time series are also generally lacking (with the exception of a recruitment time series of sea urchins, Sala *et al.*, 1998).

Availability of biological time series, as opposed to meteorological/oceanographic ones, also generally declines from north to south Mediterranean either because very little actually exists or because whatever exists is not available to the scientific community (i.e., published in local reports, journals, magazines). This is not true of fisheries landings, in as much as all countries issue annual statistical bulletins of landings and effort. Despite the language barriers across the Mediterranean, which present a major problem for accessing existing scientific information, it was without saying that collaboration with the southern shore must be strongly encouraged.

With respect to time coverage, most time series originated only a few decades ago. Agostini and Oliver (2002) compiled a preliminary list of Mediterranean data sets on anchovy and sardine (i.e., biomass, eggs and larval surveys, acoustic surveys) and a few other biotic or abiotic parameters. With the exception of the Adriatic Sea time series, the vast majority started sometime in the 1990s. The limited longevity of time series is another concern: Duarte *et al.* (1992) showed that although the number of time series monitoring programs increased exponentially in European waters, few survived for periods longer than 10 years. Yet all participants agreed with the contention by Dickson (1995) that "*adding another year to a 60-year record may be inherently more valuable than starting a new* [series] *elsewhere*".

The use of abiotic time series for the analysis and interpretation of biological time series is invaluable (e.g. Taupier-Letage and Millot, this volume). Many participants stressed that as the number and access of meteorological and oceanographic time series increase rapidly, the selection of what type of data (i.e., interpolated or actual data) and which time series to use may soon become a problem.

Finally, the participants expressed a concern regarding the time series of rare species as these are subject to sub-sampling problems (i.e., one never knows whether rare species do not show up because of inadequate sampling or whether they simply do not occur). Besides, certain species occur in certain areas only very occasionally because they are at the extreme edges of their distributions, whereas others are rare everywhere.

6.6. Evaluating the quality of time series

The participants agreed that it is generally unrealistic to assume that the methodologies used for collecting any data (e.g. sampling equipment, vessels, spatial coverage, sampling grid, taxonomic expertise) over long periods of time remain absolutely constant. In addition, both short and long time series can suffer from instrumental errors and malfunctions of various level of subtlety.

Examples abound in the marine realm. For instance, in plankton studies taxonomist expertise may change over time (e.g. as they become better trained or are particularly rushed in a particular year) and the misidentification of abundant phytoplankton species may occur for 20-30% (this percentage might be even higher for rare species). In addition, some taxonomists are “lumpers” and others “splitters”, which renders recorded data inconsistent. For comparative purposes, for instance when combining plankton data sets from different institutions, it may be safer to carry out analyses at the lowest possible denominator (e.g. at the generic level).

In the case of fisheries surveys rarely has a long time series not been subjected to a change of research vessel. Even if the fishing methodologies and gears remain the same, the way the vessel “sails” can influence catches. In some cases standardisation studies have been carried out using parallel tows (pair trawlers). In fact, different survey gears can give a very different picture of fish populations, even though they are used in exactly the same areas. Finally, fisheries landings time series are highly heterogeneous because of changes in over- or under-reporting or in the ways that data are assembled over time (e.g. fishing ports deliberately miss-record landings as a different species, not covered by a TAC).

All these inconsistencies seriously affect the homogeneity of time series, making the separation of the “measurement” effect from the “real” changes in the underlying processes almost impossible. In addition, trends and imperfections in the quality of data can affect the probability of getting a statistical error. In fact only those involved in the data collection process will be aware of the inherent properties. Various mechanistic approaches for ensuring data quality (e.g. replicate measurements, reference to absolute standards, internal consistency between measurements, overlap of new sampling methods and people before changeover, inter-comparison and inter-calibration with other labs) will be found in Michaels (1995).

6.7. Parameters to be monitored

Time series should not be limited to species of importance for cultural, commercial, or public health reasons. Many other components of the marine ecosystem, which provide important ecosystem “goods and services”, should also be monitored on a systematic basis.

The participants identified various easily measured parameters that would be valuable components of long-time series in order to monitor change:

(a) size spectra;
(b) ratios of different plankton taxa (e.g. *Calanus* species);
(c) community indices such as the Shannon diversity (however such indices might be less robust for phytoplankton data than for zooplankton, zoobenthos and fish data);
(d) species lists accompanied by information on their ranges and limit;
(e) ratios of various groups within the benthos (e.g. filter feeders *vs.* suspension feeders, r- *vs.* k-strategists, commercial *vs.* non-commercial species, pelagic *vs.* demersal species, warm- *vs.* cold-water species);
(f) number of eggs for seabirds and number of pups for seals;
(g) price and trophic level of fish and fisheries landings;
(h) maximum length and age, condition-factor, length at age, length and age at maturity of fishes, all of which are greatly impacted by fishing;
(i) fish egg/larval distribution; and
(j) primary production required to support fisheries.

6.8. Releasing time series on the Internet

The group stressed the usefulness of having access to reliable time series (or at least to some meta-data form) on the Internet. If time series of climatic/oceanographic data are already available in this way, as well as global fisheries landings data from FAO <www.fao.org>, biological data are only rarely available, and usually not on a free basis (in order to gain access it is necessary to work with the "owners" as full collaborators). Few notable exceptions exist (e.g. Myers' database of fish recruitment time-series, available at <www.fishbase.org>; the Sea Around Us project: <saup.fisheries.ubc.ca>).

There is a widespread tendency for scientists to hold on to their "own" data and not to respond to enquiries asking for access. As a result, important time series remain neglected in "desk drawers". Considerable efforts and period of time are required to create a time series either from field data (e.g. sitting over a microscope for 20 years) or from detailed information published in trade magazines. Hence it is understandable that people are "attached" to the data which they have themselves collected and are reticent to release these hard-earned data onto the internet.

The participants discussed how long personal data should remain in "drawers". The general sentiment was that scientists gathering data using public funds should be given five years to publish, and then that the data should be released. It was noted that in many European countries "freedom of information acts" exist, and that all data collected using EU funds are expected to be made freely available.

7. SPATIAL AND TEMPORAL SCALES

Ecological processes take place at different spatial and temporal scales. In this context, space-time scale diagrams are very useful tools for comparing physical and biological processes and to assess coupling between them. For instance Steele (1995) used space-time diagrams to compare the main atmospheric and marine physical processes with terrestrial and marine biological processes. This revealed that space-time scales for physical and biological processes largely coincide in the oceans, indicating a close physical-biological coupling.

The time and space scales of various events discussed by workshop participants are plotted in Figure 1 on a Stommel diagram. The increase in variance with wavelength (see Wyatt, this volume) is contoured with broken lines. The letters P, Z, and F show the characteristic scales of phytoplankton, zooplankton and fish population dynamics respectively from Steele (1977); more details for zooplankton are given in an elaborated version by Haury *et al.* (1977). The areas marked 1 to 4 show:

(1) "Lasker's world", where the day to day events which determine the success of larval fish feeding (and hence recruitment) are focused (Lasker, 1975; Cury and Roy, 1989);
(2) the scales of Mediterranean phytoplankton blooms (Zingone, this volume);
(3) mesoscale hydrodynamical features (Taupier-Letage and Millot, this volume);
(4) significant multiannual trends (Bakun, Daskalov, Sinovcic, and others, this volume).

The participants further discussed problems related with sampling frequency. They pointed out that according to Shannon sampling theory (i.e., signal theory) one should sample at least two times in each statistical sampling period (i.e., one should have at least two samples per cycle). The participants recognised that the collection of data at as smaller time scales as possible will be ideal because data at fine scales can then be aggregated to larger scales if required. Yet, this carries practical implications (e.g. keeping sufficient people employed over the whole time period to maintain and update the time series) such that at some point a compromise between availability of resources and effectively sampling in time and space is inevitable. Simple rules of thumb will prove useful. Thus, if a system is spatially homogeneous it is clearly better to put emphasis on increased sampling over time rather than space. The opposite will be true of a system not varying markedly over time.

It was also stressed that sampling frequency will determine the predictive power of the models build. In general, as sampling frequency increases the forecasting horizon is lowered, whereas forecasting accuracy increases: in other words high sampling frequency is useful for short-term detailed predictions.

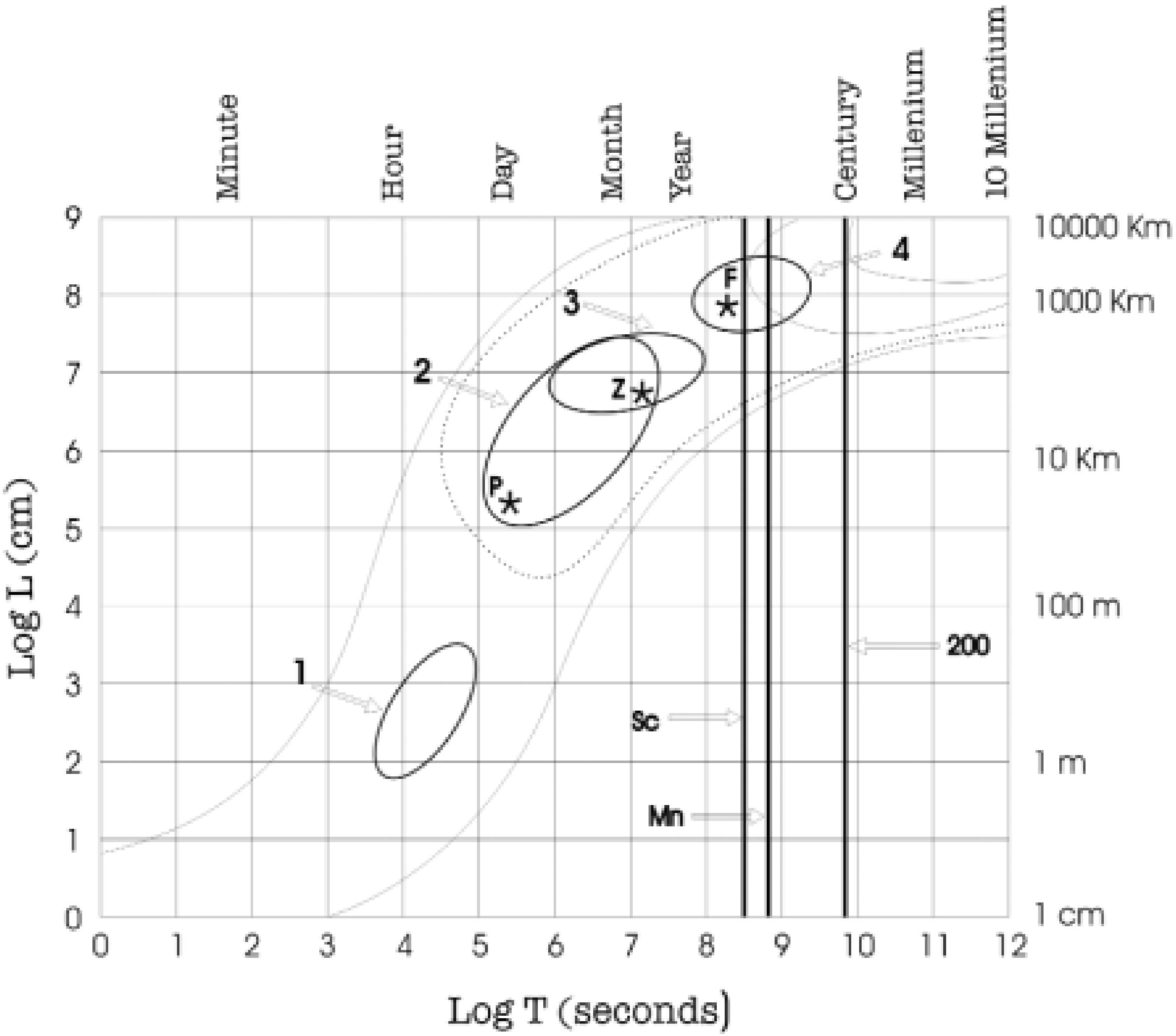

Fig. 1. Stommel diagram of the time and space scales of some of the topics discussed in this volume (modified from Wyatt 1995). The vertical bars show the sunspot cycle (Sc), the nodal cycle (Mn) and the Suess cycle, the first two of which (Sc, Mn) are plotted in the time domain Table 2 in Wyatt (this volume). For explanation of other symbols see text.

8. Priorities for future actions – Recommendations

In conclusion the participants identified issues that call for further action. These were grouped along three main lines of actions.

8.1. Co-operation

The group noted that despite the accumulation of available biological data, hardly any cooperation and coordination are involved in the whole process. In addition the participants felt that much information is scattered in “grey” sources and could be advantageously assembled in the form of time series. Such information should be fully evaluated. Within this context the participants strongly recommended co-operation (in terms of planning, funding, maintaining, and inter-calibrating for quality control) between countries for assembling core time series and conducting comparative analyses of time series across European and Mediterranean waters. The group also stressed the importance of preserving existing datasets (avoiding losses due to staff retirement, computer format changes, …) and of sharing time series across the research community. The release of more meta-data on the Internet, and the organization of training courses or pilot projects on different time series issues, were highly recommended.

8.2. Interdisciplinarity

The participants recognised that the interaction and cooperation of biologists with scientists from other disciplines – who are rarely consulted by biologists – such as oceanographers, climatologists, economists, sociologists and zooarchaeologists, must be encouraged. The cooperation of scientists of different disciplines has much to offer in terms of methodology, for developing a "systems approach" and to better understand the relative importance of different mechanisms impacting ecosystems and embedded resources (e.g. climate-economy-resource interactions). This would certainly increase our medium- and long-term forecasting ability.

8.3. Building up new time series

The participants pointed out that the role of autonomous instruments is likely to greatly enhance our ability to gather and assemble new automated biological time series (e.g. chlorophyll, particle size, fish eggs and larvae). Finally, offshore autonomous monitoring stations will be useful for comparing and validating existing time series from inshore stations.

The participants also stressed that time series (or archives) of satellite images are increasing with time and such images, which provide relative values, offer potential time (and space) series that can be used to complement, or be compared with, existing biological time series. Already, as far as AVHRR images are concerned, daily, weekly and monthly SST composites can be found (free) on several Internet servers. Daily composites are usually posted within a few days. Several Institutions across the Mediterranean have receiving stations, and there should be a coordinated effort to cover the whole Mediterranean and ensure the availability of high resolution products to end-users.

With regard to the management of living resources, the participants noted that more effort should be directed towards the increase in the quality of fisheries time series and fishery-independent monitoring of stocks. They strongly recommended the build-up of long time series on cpue, recruitment, physiological indices, age and length structure, estimation of scales and cysts from cores taken from anoxic basins. Such data are at present lacking to a large extent for the Mediterranean Sea. Finally, the participants recommended using existing data (survey and commercial catches) as well as evaluating and using ECOPATH-ECOSIM models in the context of time series analysis and "back-to-the future" approach. For a more thorough discussion on these points the reader is addressed to a specific, recent CIESM workshop on the subject (CIESM 2000a).

CONCLUDING REMARK

In *The Art of Tracking*, the South African anthropologist Lieberberg describes the hunting skills of the Kalahari San as progression from the simple following of a prey animal's footprints, through a systematic hunt based on more varied data such as broken twigs or tufts of fur caught on bushes, to a speculative procedure in which hypotheses are based on data about the behavioural patterns of the prey, its habitual trails through the terrain and so on, "*a continuous process of conjecture and refutation to deal with complex, dynamic, ever-changing variables*". These stages are analogous to the ways in which we analyse biological time series, and, at the speculative level, attempt to relate the changes in the biological variable to external data such as climate or exploitation.

Potential relevance of a “loopholes” conceptual framework to research studies of fish population dynamics in the Mediterranean Sea

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INTRODUCTION

The great evolutionary biologist, Ernst Mayr, has called the experimental method and the comparative method “*the two great methods of science*” (Mayr, 1982). The experimental method, where one assembles the set of multiple realizations of a process needed to draw scientific inference from a series of controlled experiments, is the one that most people think of first when considering the scientific method. However marine ecosystems, on the scales of large mobile fish populations and the coupled dynamic ocean-atmosphere systems in which they are imbedded, are hardly amenable to experimental controls. Fortunately, the comparative method, where one gathers the required set of realizations from naturally occurring spatial or temporal variability, offers an available alternative. Mayr (ibid.) in fact credits the power of the comparative method for “*nearly all of the revolutionary advances in evolutionary biology*” (another area where the enormity of scale, notably temporal in that case, tends to preclude application of experimental controls).

The following brief note is intended to (1) provide an example of the power of time series analysis, when employed in an interregional comparative framework to infer mechanisms, processes and relationships that would be difficult or impossible to address either experimentally or by analysis of time series data from a single area, (2) to suggest some fairly obvious potential applications, both intra-regionally within the separate basins of the Mediterranean Sea itself, and interregionally (e.g., addressing the two unique bluefin tuna spawning regions of the North Atlantic, one associated with the swift Loop Current of the Gulf of Mexico and the other within the Mediterranean Sea, etc.), and (3) to propose applicability of certain insights already gained from comparative studies of ecosystem situations – located mainly within the Pacific Basin – to ecological issues in the Mediterranean.

The Mediterranean Sea is known to be, on average, quite an oligotrophic sea. However, the fishery landings from the Mediterranean are remarkably high for an ocean area of its size (FAO, 1997). Moreover, the landings from most of the sub-basins are reported to have increased, or remained stable, over the past twenty years, despite the presumed increase in fishery mortality (Caddy and Griffiths, 1990a; Caddy, 1993; Estrada, 1996). The Mediterranean is reproductive habitat for the large tuna species, bluefin and albacore, which not only count among the most monetarily valuable fish in the world's oceans, but are among the most highly evolved of fish species groups. They have particularly voraciously-feeding early life stages (Hunter, 1981). These fish, as adults, are capable of, and do undergo, long migrations. They presumably would have been entirely capable of adaptive selection of spawning grounds in much more productive ocean areas. Nonetheless, their adaptive selection processes have evidently chosen the Mediterranean. The conclusion must be that somehow the relatively oligotrophic Mediterranean situation "works" for these fish.

Recently, a "loopholes" conceptual framework has met some success in rationalizing a number of paradoxes in the fisheries ecology of the Pacific Ocean (Bakun and Broad, in press). It is interesting therefore to ponder whether this concept could yield insight as to the paradox of remarkable fishery productivity, relative to primary productivity, that characterizes the Mediterranean.

RECAPITULATION OF THE "LOOPHOLES" RATIONALE APPLIED TO THE PACIFIC

The Pacific Ocean has a convenient attribute for analysis of ecosystem mechanisms, i.e., the El Niño perturbation which periodically, every few years, exerts a major stress on the evolved ecosystems. The main mechanisms of El Niño are relatively well understood (although forecasting abilities are not yet entirely reliable), and its characteristics are well described. During El Niño episodes the marine food webs in the ecosystems of the eastern Pacific tend to be decimated. Primary productivity declines drastically (Barber and Chavez, 1983). Zooplankton abundance declines accordingly, and large zooplankton species characteristic of productive coastal upwelling regimes are replaced by much smaller forms that typify much less productive oceanic conditions (Miller *et al.*, 1985). Most fish populations, notably the Peruvian anchoveta (Fig. 1), do extremely poorly. Salmon feeding in the California Current region return to the rivers in an emaciated condition (Pearcy, 1992). Seabirds and marine mammals experience reproductive failures that in strong El Niño episodes have led to serious population collapses (Wooster, 1960; Idyll, 1973). Local fishing industries are often devastated (Glantz and Thompson, 1981; Glantz, 1992). However, the sardine does relatively well (Arntz and Fahrbach, 1996).

Bakun and Broad (in press) applied the comparative method to try to deduce a common mechanistic "thread" which could explain the following puzzling issues:

A. the extreme fish productivity of the Peru-Humboldt Large Marine Ecosystem (LME);

B. the fact that sardines, which are species obviously adapted to highly productive ocean conditions (upwelling areas, etc.), often do better, at least in the eastern Pacific, during El Nino episodes – which are characterized by abruptly lowered primary productivity ?

C. a tendency for out-of-phase population oscillations of anchovy and sardines in any given regional ecosystem;

D. The apparent basin-scale (global?) synchronies in sardine population expansions and contractions during the 1970s and 1980s – even though the populations exist in very different types of ecosystems that would be expected to respond differently to the same large-scale forcing.

It was found that each of the items appears to become less enigmatic when the conceptual focus shifts from conventional trophodynamics to the idea that "loopholes" in the fields of biological controls (i.e., of predators of early life stages) produced by poor ocean productivity or by disruptive environmental perturbations, may in fact lead to remarkable reproductive success. For example, Sardines are a group of fishes that are clearly adapted to highly productive ocean situations. They occur in the richest subtropical ecosystems in the world: the various eastern ocean upwelling systems, the rich Kuroshio-Oyashio confluence region, etc. Even within these regions, sardines tend to concentrate in the richest parts of these systems, in many cases migrating as adults to feed directly on phytoplankton in the intense upwelling core regions of the regional upwelling systems (Bakun, 1996). It has been quite a puzzle, therefore, to understand the apparent paradox that in these eastern Pacific regions that are strongly impacted by El Niño episodes, rather than being devastated as one might expect *a priori*, sardines have on the contrary often experienced improved reproductive success during El Niño years (Arntz and Fahrbach, 1996), which are characterized by drastic decreases in ocean productivity.

Clearly, El Niño is not a good thing for a marine organism seeking to nourish itself in the eastern Pacific. But the point here is that it is bad for "everybody". For example, it should clearly be very bad for all the tiny organisms that prey upon sardine larvae. The numerous species of tiny short-lived medusas, ctenophores, predatory copepods, etc., that prey on sardine eggs and larvae may experience multiple successive reproductive failures during an El Niño episode. Adults of fish species that have voracious early life forms that may likewise predate on sardine early life stages may fail to amass the energy reserves needed for copious spawning. Predatory euphausids may be obliged to reduce or cease feeding activities in the ocean surface layers where sardine larvae occur, due to lack of sufficient prey concentrations (of all types, fish larvae ordinarily being only a very minor component of the plankton in this zone) to provide a positive energy return and consequently to spend more time in cooler deeper waters to conserve energy reserves.

Regime-scale variability in the 1970s

Sudden simultaneous expansions of the Japanese and South American sardine fisheries occurred in the early 1970s to mid-1980s from near total absence to unprecedented landed tonnages (Fig. 1), followed thereafter by simultaneous sudden declines. Many of the world's largest fish populations, particularly in the North Pacific (Hare and Mantua, 2000; Benson and Trites, 2002) but also in other regions around the world, experienced similar patterns of gyration at the same time (Bakun, 1996, 1998). In particular, the Peruvian anchoveta remained in extended decline throughout the period of the sardine increases (Fig. 1). The very large Japanese market squid fishery (*Todarodus pacificus*) also declined in opposite phase to the sardine rise (Hatanaka *et al.*, 1985). The very large salmon populations of the subarctic North Pacific all increased dramatically in this early 1970s to mid-1980s period (Fig. 2a). Likewise, many of the most massive demersal populations of the subarctic Pacific underwent sharp increases at the same time (Fig. 2b and 2c.). Pacific yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus palamis*) tuna populations also increased, while Pacific albacore tuna (*Thunnus alalunga*) appear to have declined. Marine mammal populations in the far north Pacific were doing well. This was a period

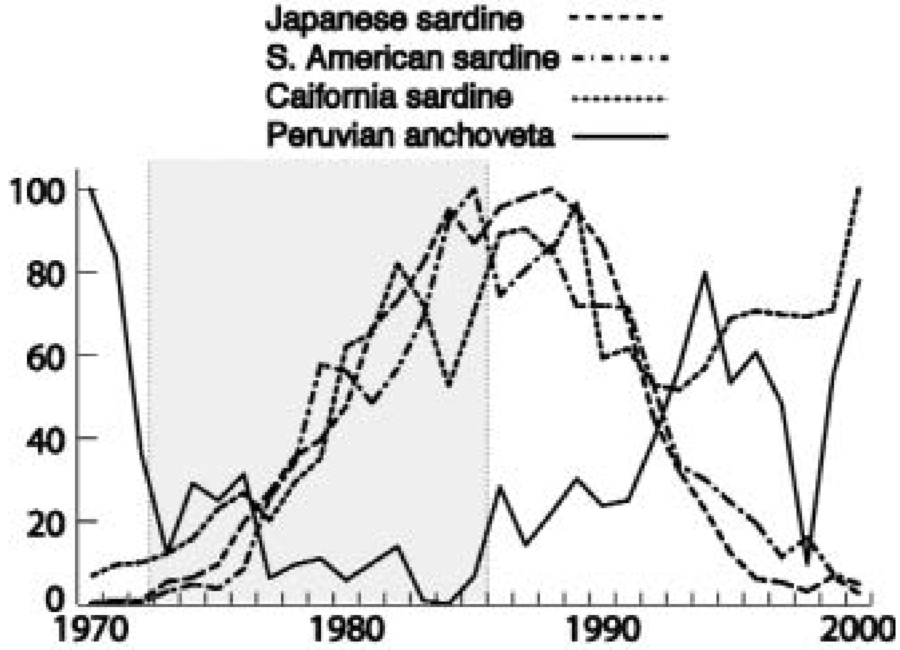

Fig. 1. Variations in abundance of the largest coastal pelagic fish stocks of the Pacific Ocean plotted as percentages of maximum annual values for the period 1970 to 2000, based on landings data taken from the FAO files. (Previous to the 1990s most California sardine landings were taken by the Mexican fishery inside the Gulf of California; Beginning in the mid-1990s increasing contributions came from U.S. and Canadian fisheries.) Shaded rectangle indicates the early 1970s to mid-1980s period of steep decadal trends in climatic indices (see Fig. 3 and discussion in text).

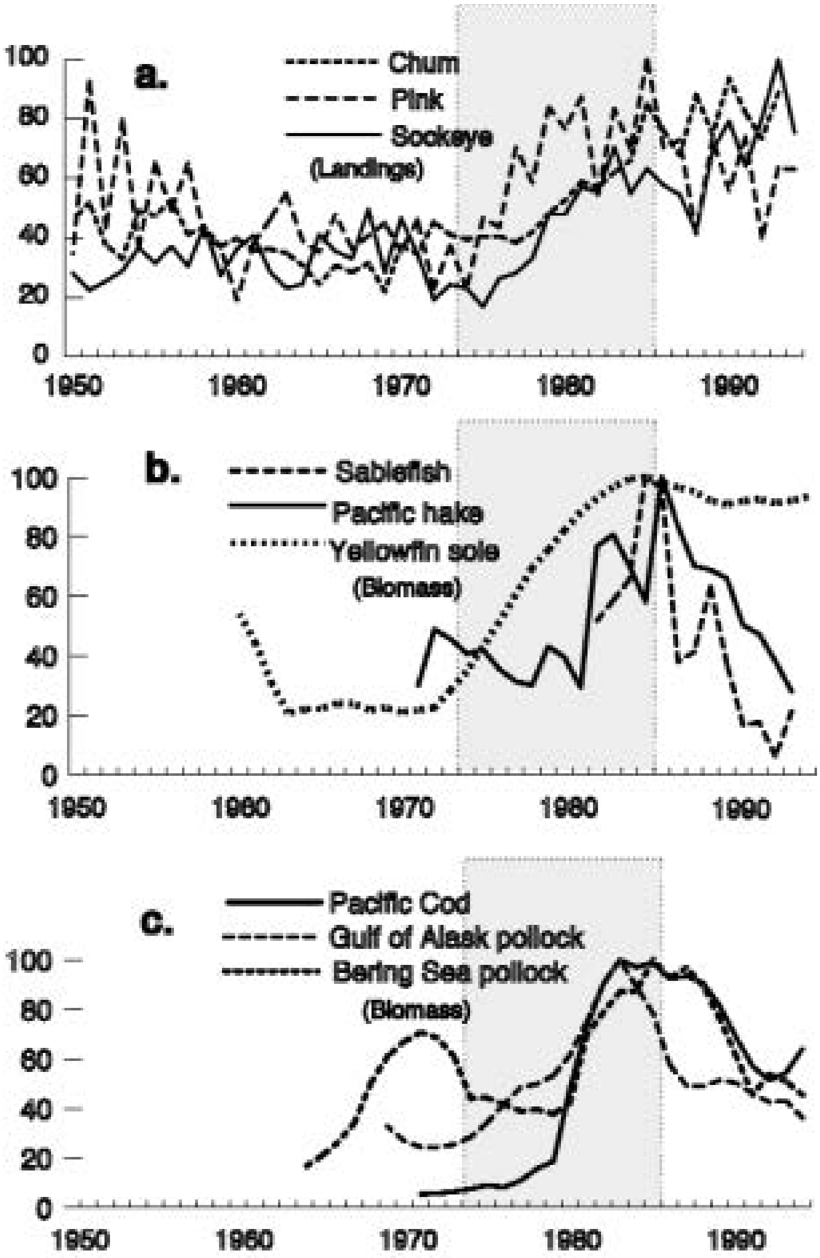

Fig. 2. Variations in abundance of some of the largest fish stocks of the subarctic North Pacific Ocean plotted as percentages of maximum historical annual values. Panel a is based on landings data taken from the FAO files). Panels b and c contain actual abundance estimates from Wespestad (1996) and from Anonymous (1996) (Figure modified from Bakun, 1998). Shaded rectangle indicates the early 1970s to mid-1980s period of steep decadal trends in climatic indices (see Fig. 3 and discussion in text).

when fishery resources managers were congratulating themselves on the efficacy of their methodologies.) However, after the mid-1980s the situation changed for most of these fisheries. The majority that had increased during the period tended to decline, the sardines off Japan and Peru collapsing particularly abruptly. The subarctic salmon (Fig. 3a) deviated somewhat from this pattern, merely pulling back briefly and then continuing on in a high abundance state for some years to follow. Many other important fish populations around the world reflected this pattern in one way or another (Bakun, 1996, 1998).

This was a period of particularly steep trends in many climatic index time series. The Southern Oscillation Index (SOI) went through a decadal-scale decline (Fig. 3) that was much deeper and more extended than had occurred in the previous several decades (the early 1970s to mid-1980s

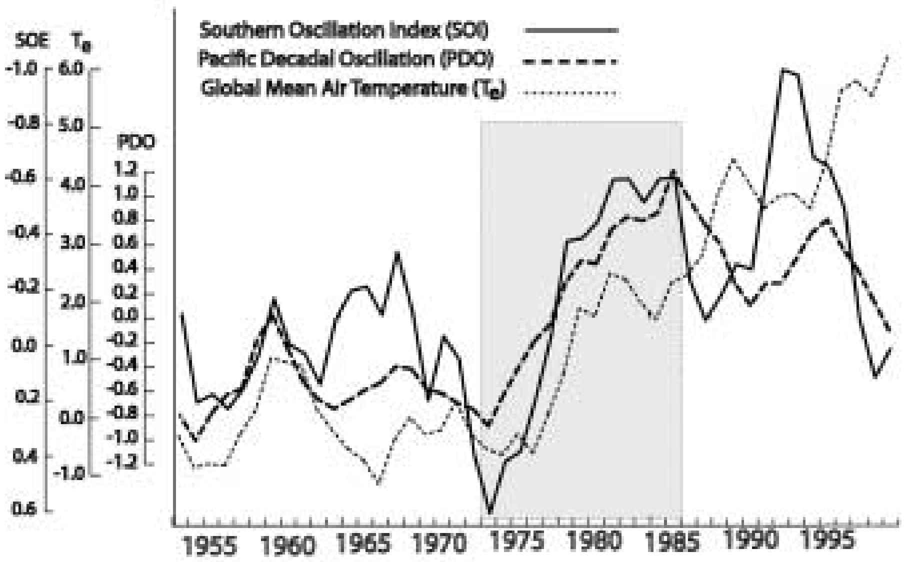

Fig. 3. "Low-passed" (via 5-pt running means of annual mean values) climatic index time series. The shaded rectangle indicates the early 1970s to mid-1980s period of steep decadal-scale trends discussed in the text. The Southern Oscillation Index (SOI) is tabulated as the difference between the standardized Tahiti Sea Level Pressure (SLP)and the standardized Darwin SLP measurements provided by the Climatic Prediction Center at <http://www.cpc.ncep.noaa.gov/data/indices>. (Note that the SOI is plotted in this figure with negative anomaly value increasing upwards.) The mean (i.e., global average) air temperature of the earth (Te) is as described in Hansen *et al.* (1999). The Pacific Decadal Oscillation (PDO) is as described in Mantua *et al.* (1997).

constituting a sort of decadal-scale analog to a standard annual-scale El Niño episode). The Pacific Decadal Oscillation (PDO) exhibited a corresponding decadal-scale increase (Fig. 3). The Aleutian low pressure cell, that dominates the seasonal behavior of the subarctic Pacific ocean-atmosphere system, intensified and expanded. Certain other index series exhibited similar features (Klyashtorin, 2001; Chavez *et al.*, 2003). Even global-scale indices such as the mean air temperature of the earth (Fig. 3) (Kawasaki and Omori, 1988) and the rate of the earth's "solid body" rotation (Beamish *et al.*, 1999; Beamish *et al.*, 2000) also showed particularly steep sustained trends during this period. Indications of substantial effects also in the Atlantic have been noted (Bakun, 1995; Roy and Reason, 2001).

"LOOPHOLE" PATTERNS IN LARGE TUNA SPECIES OF THE PACIFIC

The North Pacific albacore tuna (*Thunnus alalunga*) are caught as juveniles in surface fisheries in the richly productive temperate-zone ecosystems both of the Kuroshio-Oyashi confluence of the western North Pacific and the California Current upwelling system of the eastern North Pacific. Adults are caught in longline fisheries over very large areas of the tropical and temperate North Pacific. However, rather than spawning in food-rich regions, the albacore travel to the many thousands of kilometers to tropical zone of the west-central North Pacific to spawn, which is a region of quite low average primary productivity (FAO, 1972).

Large tunas are oceanic "top predators". But they are top predators only as adults. Earlier in life, they are definitely prey. And the fishes that prey upon these early tuna life stages are generally much smaller as adults than are the adult tunas, and so tend to have significantly shorter life cycles. Thus the tunas have no possibility of using such potential life-cycle length dependent mechanisms as "school-mix feedback" (Bakun, 2001) to evade devastating effects of predation at the stages of their lives at which their population dynamics is largely determined. From this frame of reference, rather than the lordly top predators that they otherwise appear to be, large tuna species are seen as the "fugitives" of the ocean system, being forced to migrate widely to find spawning grounds where conditions are so poor that even the predictable appearance of tuna early stages may not be sufficient to make it worthwhile for potential predators to concentrate their feeding within those areas at those times. The situation thus may be rather similar to that for the sardine where particularly poor conditions may impact predators on larval or juvenile stages to the degree where it constitutes a "loophole" within which the benefit of decreased predation may outweigh detrimental effects of poor feeding conditions.

Recall the long-term decline in the Southern Oscillation Index (Fig. 3) during the mid-1970s to mid-1980s period, which signals a decadal-scale relaxation of the trade wind circulation in the near-equatorial zone of the Pacific. Correspondingly, one expects that the equatorial upwelling that is a major factor in the relative productivity of the near-equatorial latitude band, should slow down, resulting in poor conditions at the low end of the food chain and in poor food densities for tuna larvae and early juveniles. Nonetheless, this is a period when the Pacific yellowfin and Pacific skipjack tuna populations, which spawn in the near-equatorial band (Cole, 1980; Forsberg, 1980), apparently experienced extended upward population trends.

Frigate mackerels (e.g., Auxis sp.) are small-sized, fast-swimming, voraciously feeding tuna-like fishes, which although not extensively fished, are apparently incredibly abundant in the tropical oceans (Richards, 1984; Fonteneau and Marcille, 1993; Colette and Aadland, 1996). They are likely to be major predators on young tunas. If poorly productive conditions during this period caused the local frigate mackerel populations, or whatever other species exert particular predation mortality on tuna early life stages, to collapse or, alternatively to shift their distributions away from the near-equatorial zone, this could perhaps have opened a sufficient "loophole" to have enhanced reproductive success of yellowfin and skipjack through this period.

POTENTIAL IMPLICATIONS TO THE MEDITERRANEAN SITUATION

The Mediterranean, of course, is characterized by fish species groups similar to those of the eastern Pacific: anchovies, sardines, large tunas, etc. Significant upwelling regions also exist within the Mediterranean, resulting in the sorts of "ocean triads" (Agostini and Bakun, 2002) that characteristically provide suitable reproductive habitat for pelagic spawning fishes. One wonders if the characteristic rather low productivity of the Mediterranean may represent a continuing "loophole" situation. Thus, if fish production in areas of the oceans where primary productivity is much higher than in the Mediterranean is not limited by food availability but by reproductive success, which in turn is limited by the impact of predators on larvae (which are more abundant in highly productive zones), it may not be so surprising that fish production in the Mediterranean may approach that in regions of higher productivity.

Note that even in the Mediterranean, tuna do not seem to seek out the most richly productive areas as sites for reproduction. Rather they seem to avoid the available "ocean triad" zones, and rather go to very poorly productive spots (such as the area near the Balearic Islands, etc.) for spawning. Moreover, recent surveys of tuna larvae made under the Spanish TUNIBAL Project have indicated that even near the Balearic Islands, the larvae are not necessarily found in the plumes of somewhat richer water identified in satellite ocean color imagery, but rather tend to be concentrated in the areas of clearest water situated between the richer plume zones (Garcia *et al.*, 2001).

Implications to empirical data analysis activities

Thus, in view of these considerations, it may happen that years when anomalously high productivity occurs in spawning regions, may be years of poor reproductive success rather than good reproductive success as one might otherwise expect. In analogy to findings in the Pacific systems, it may also be found that multi-year periods of steep trends in environmental characteristics, regardless of their direction, may benefit productivity of a variety of fishery resource species by opening "loopholes" in the fields of predation on fish larvae due to the fact that the predator populations may not respond to the changes as quickly and adaptively as mobile fish populations that can migrate to search out acceptable habitats, and then "explode" into new opportunities by virtue of their very highly leveraged reproductive mode.

It would be of interest to test for effects of regime-scale (decadal to inter-decadal scale) variability in the Mediterranean. In particular, prominent anomalies extending over the period from the early to mid-1970s to mid-1980s would be of great interest, in that this period seems to have synchronized marine population variability, which somehow appears to react in a way so to amplify more subtle signals of climatic variability occurring on these time scales (Hare and Mantua, 2000). Certainly, a phenomenon capable of measurably affecting the rotational velocity of the earth (i.e., the length of day) might be expected to also influence the Mediterranean area as it has apparently influenced other regions of the world's oceans.

Implications to fishery resource modeling

The "loophole" viewpoint is at odds with the assumption of rather stationary density-dependent population control underlying a large superimposed quasi-random "noise" component that has underpinned much of fisheries resource modeling activity over the past half century. It also suggests an additional aspect to modeling approaches which track trophic energy transfers among ecosystem components; to incorporate loophole dynamics, these approaches would need to somehow develop and incorporate modules that could account for trophic interrelationships impacting various early life stages of the same species that are represented in terms of adult biomasses.

Research opportunities

The potential value of organized comparative investigation of processes and mechanisms (both by analysis of available time series and by process-oriented studies where possible) in the two distinct, as well as distinctly different, spawning regions of North Atlantic bluefin tuna has been briefly mentioned in the Introduction. In addition, the rather separate sub-basins of the Mediterranean, each featuring rather distinct environmental settings (Agostini and Bakun, 2002) would seem to offer opportunities for addressing key issues in marine resource ecology as well as local issues of fishery resource management, biodiversity preservation, and ecosystem protection. The fact that sardines and anchovies appear not only to alternate in abundance in a similar out-of-phase pattern as do the very large oceanic populations of the Pacific and eastern Atlantic oceans, but to do so actually in rather precise interdecadal-scale synchrony with the other regions of the world (Pinnegar *et al.*, 2003; Bakun, 1996) suggests something common and very essential in the operation of these ecosystems that is as yet not well understood or appreciated.

Ecosystem time-series analyses in the Black Sea

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Human-induced factors such as eutrophication, heavy fishing, and the introduction of exotic species have been evoked to explain the Black Sea ecosystem changes in recent decades (Caddy and Griffiths, 1990b; Zaitsev, 1993; Prodanov *et al.*, 1997). However, having recognized that natural factors are responsible for the basic physical, chemical and biological processes in the sea, several authors have recently explored possible explanations based on natural abiotic and biotic factors (Niermann *et al.*, 1999; Ozsoy, 1999; Daskalov, 2002).

To elucidate the causes of the ecosystem changes, several questions must be asked, e.g. what are the relative roles of the natural and anthropogenic factors (including fishing pressure) for the observed patterns; how do the different scales of temporal change – seasonal, annual, decadal – affect productivity; are natural populations predominantly controlled by resource availability (bottom-up) or by predation/competition (top-down) factors; does the recent change in the Black Sea ecosystem result from transition between favorable and unfavorable environmental regimes?

In order to address some of these questions, the present paper explores the synergistic nature of the change by analysing multiple time-series of physical, biological and anthropogenic data. It attempts to identify long-term patterns, providing possible explanations for the changes, which occurred over the past few decades. The study explores different temporal scales: multidecadal, decadal, interannual and seasonal variations, revealing the crucial importance of the physical processes and climate change. Evidence of decadal regimes resulting in a rise in productivity in the 1980s is presented. Anthropogenic effects upon the ecosystem are linked to physical and biological factors.

Three types of time-series data were used in exploring the environmental variations: hydroclimatic, biological, and anthropogenic (see Appendix in Daskalov, 2003). The hydroclimatic series possessed the best temporal resolution (monthly data). These were derived from COADS (Woodruff *et al.*, 1987) together with published marine environment monitoring data (Appendix, Daskalov, 2003). Biological series were of generally lower quality than the hydroclimatic series (lower resolution, missing values), but were the best series available as indicators of the system’s change over time. It was difficult to describe anthropogenic influences by means of historical time-series, because in many studies only mean values, qualitative or semi-qualitative information were presented (e.g. Bologa *et al.*, 1995; Zaitsev and Mamaev, 1997). As with the biological series, the best available data were included in this study.

Changes in time-series data can result from a combination of the influences of different processes. Temporal patterns could contain signatures of global and local influences, long-term trends, low-frequency cycles, and seasonality (Durand and Mendelssohn, 1998). The original time-series can be decomposed empirically through a procedure of repeated fitting and the removal of components of different periodicity (Cleveland, 1993). The observed series Y_t can be represented as a sum of non-stationary, unobserved components: seasonal (S_t), non-linear trend (T_t), 1.. p oscillatory components ($O_{t1}..O_{tj}..O_{tp}$), and stationary residuals (R_t):

$$Y_t = S_t + T_t + \sum_{j=1}^{p} O_{tj} + R_t$$

Each component can be consecutively fitted and substracted from the series, the analysis continuing on the residuals (Cleveland, 1993). First the seasonal component is filtered out, followed by the long-term trend and oscillatory components. With all regular components being extracted, residuals must be stationary.

Repeated *loess* fitting was applied for visualizing and exploring the time-series. Locally-weighted regression or *loess* is a flexible non-parametric method for fitting curves or surfaces to data (Cleveland *et al.*, 1992). The goodness of the fit was evaluated using the approximate F-test (Cleveland *et al.*, 1992; Daskalov, 2003). Each *loess* fit was characterised by the approximate coefficient of determination (r^2) and equivalent number of parameters, which is analogous to the number of parameters in the ordinary linear regression (Cleveland *et al.*, 1992; Daskalov, 2003). A STL procedure (Seasonal-Trend decomposition based on loess, Cleveland *et al.*, 1990) was applied in modelling seasonality. After removing all regular components, residuals were tested for normality and trends.

Principal component analysis (PCA, Lebart *et al.*, 1995) was applied in order to explore long-term patterns in multiple series. PCA reveals the dominant correlation structure in data and reduces the number of variables to a few independents (orthogonal) principal components (PCs), which are linear combinations of the original variables. The newly derived PCs are non-correlated artificial variables accounting for the general long-term patterns in input variables. The initial variables are correlated to the PCs in that they share long-term patterns described by the PCs. PCA was applied to the period 1960-1993, for which there was best data coverage by all series.

Major patterns of variability were apparent on seasonal (for hydroclimatic series), interannual (~1-5 years), decadal (~10-12 years), and interdecadal (~20-30 years) scales. In the present paper, only long-term patterns were analysed. Seasonal and interannual patterns, as well as detailed loess, spectral, and correlation analyses have been presented elsewhere (Daskalov, 1998).

In Fig. 1 non-linear trends of the seasonal components fitted by STL (Cleveland *et al.*, 1990) of SST at Odessa (SSTO), and Batumi (SSTB), precipitation (PREC) and river run-off (RIV) are plotted. These plots were prepared by taking the values for the specific month from the extracted seasonal component of each time-series and account for the seasonal change (Daskalov, 1998). For example the SSTO series displayed increasing trends during the winter months (Dec., Jan., Feb., Mar.) and decreasing trends during spring-summer (Apr., May, Jun., Jul., Fig. 1). Similar trends were found in river run-off series (RIV, Fig. 1). The pronounced downward change in RIV during the 1950s and 1960s may reflect the artificial regulation of run-off started after the construction of the big dams on the rivers Dniepr and Dniestr (Daskalov, 1998).

In Fig. 2 non-linear trends fitted by *loess* are illustrated. The *loess* regressions were adjusted to decadal and longer-term variability, i.e. residual, seasonal, and interannual variations were filtered out from the fitted lines. There were significant negative linear trends for SST, wind, zooplankton, oxygen, and transparency data. The SLP, river inflow, HS2000 and most of the biological series exhibited positive trends. A decadal signal was very clear in most of the series, especially in SST, SLP, wind and run-off (Fig. 2a), the ctenophore *Pleurobrachia* and fish recruitment (Fig. 2b), and phosphorus, hypoxia and hydrogen sulphide (Fig 2c). Interdecadal (~20-30 years) regimes are distinguished in coastal SST data (SSTO, SSTB), biological, and transparency series.

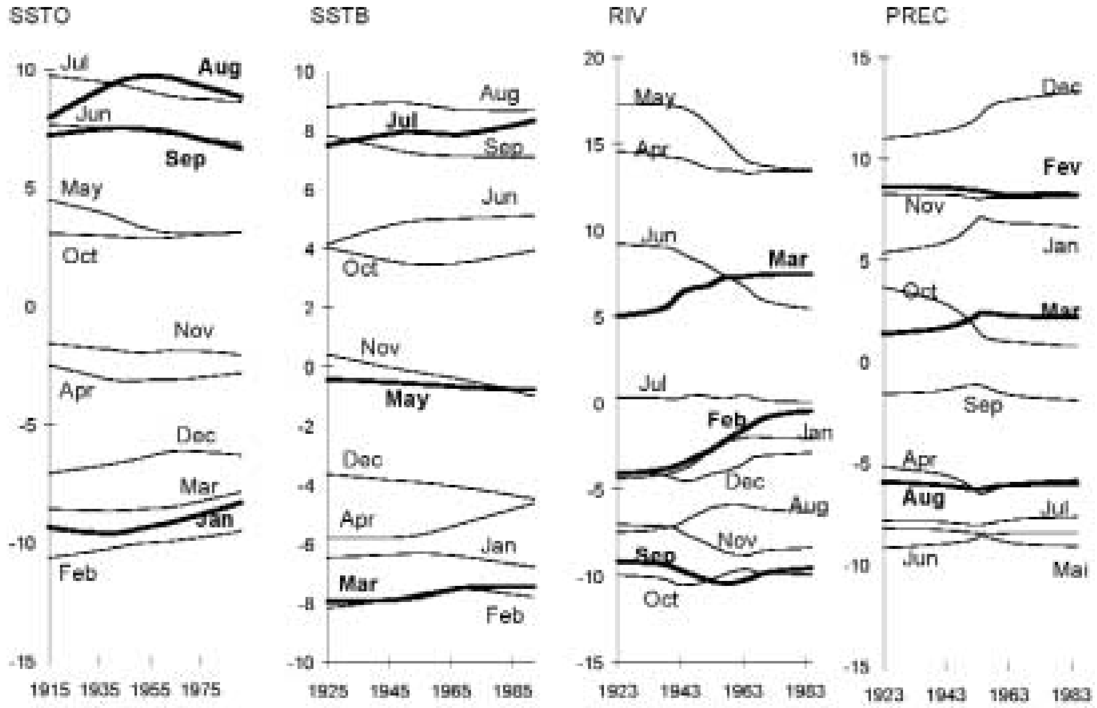

Fig. 1. Non-linear trends of the seasonal components of SSTO (SST at Odessa), SSTB (SST at Batumi), PREC and RIV fitted by STL (Cleveland *et al.* ,1990, see text for details)

Most of the results indicate coherent long-term patterns in physical, biological and anthropogenic series (Fig. 2). Temperature (SST) was positively correlated to zooplankton and the dinoflagellate *Noctiluca*, and negatively correlated to phytoplankton, *Pleurobrachia*, and fish. SLP was positively correlated to fish recruitment. Higher run-off (RIV) appeared to favour anchovy and whiting reproductive success (Daskalov, 1999). There were significant correlations between hydroclimatic and anthropogenic series: positive – SST with oxygen, hypoxia, transparency, and *Phylophora*; negative – SLP with hydrogen sulphide (HS150); negative – wind with hypoxia; positive – run-off with phosphorus input, hypoxia and hydrogen sulphide. Therefore the effects attributed mainly to anthropogenic impact also seem to depend strongly on natural forces. Phosphorus input clearly depends on the river inflow; hypoxia develops on a bulk of dead organic matter in stagnated (less aerated) water and it is related to run-off (nutrient and organic input) and stratification (run-off, SST – water density, turbulence – wind stress); hydrogen sulphide production occurring in anoxic conditions is influenced by the same factors as hypoxia. Comparing biological with anthropogenic series helped to elucidate the distinction between natural and human-induced effects on the ecosystem. Phosphorus input seemed to have a positive effect on phytoplankton, *Noctiluca*, anchovy and whiting, and a negative effect on *Pleurobrachia*. High phytoplankton biomass seemed to contribute to the oxygen deficit on the bottom (OX negatively, HYP positively correlated with phytoplankton). Hypoxia tended to negatively influence *Pleurobrachia* and sprat. *Noctiluca* abundance was positively correlated with P, and itself could be indicative of ecosystem degradation (Zaitsev 1993).

The principal component analysis (PCA) revealed the main long-term patterns in multiple time-series data. The first two PCs explained ~17% and ~14% respectively of the total variance in the data, whereas all other PCs explain less than 9% of the total variance. The first PC accounts for the decadal (~10 year) variation, displaying two and a half decadal cycles with respective maxima around the early 1970s, 1980s and 1990s (not completed), and minima around 1965, 1975, and 1985 (Fig. 2). These roughly correspond to decadal cycles in SST, wind, run-off, *Noctiluca*, phosphorus, hypoxia, and hydrogen sulphide: series that exhibited higher correlation with PC 1 (Figs 1 and 2). Decadal cycles inverse to the pattern in PC 1 (and correspondingly highest inverse correlations) were evident for SLP, *Pleurobrachia*, and sprat. The second PC was

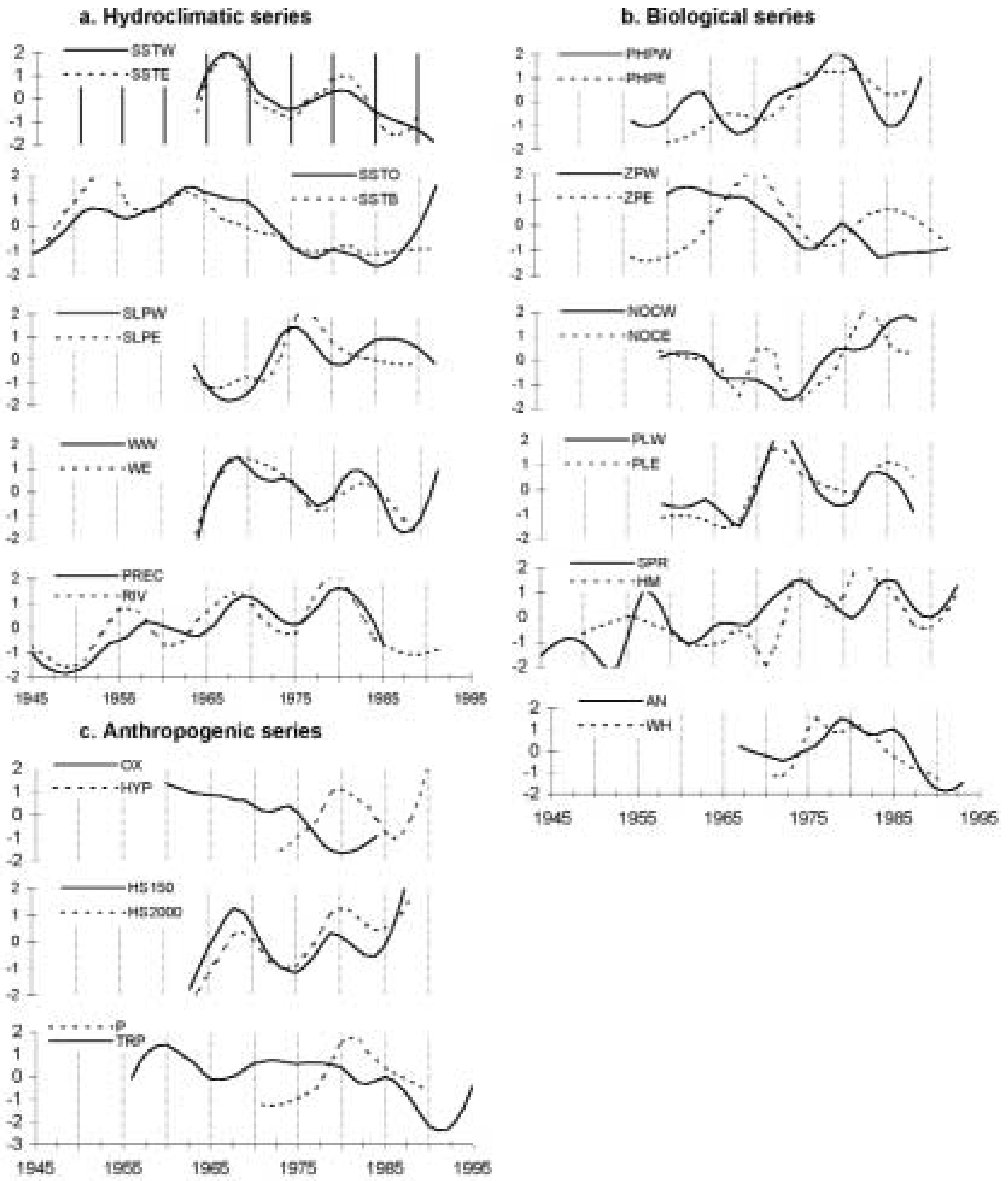

Fig. 2. Non-linear trends of selected time-series fitted by loess. Variables from different parts of the Black Sea are indexed as follows: SST : sea surface temperature, SLP : sea level atmospheric pressure, W : wind speed, PREC : precipitation, RIV : river run-off, PHP : phytoplankton, ZP : zooplankton, NOC : *Noctiluca scintillans*, PL : *Pleurobrachia pileus*, SPR : sprat, HM : horse mackerel, AN : anchovy, WH : whiting, P : inorganic phosphorus , OX : oxygen, HYP : hypoxia, HS : hydrogen sulphide, TRP : transparency. W, E, O, B at the end of the indexes denote West, East, Odessa and Batumi respectively (for full description of data see Daskalov, 2003).

positively correlated with SLP, RIV, phytoplankton, horse mackerel, anchovy, whiting, phosphorus and hypoxia; and negatively correlated with zooplankton, and *Pleurobrachia*. These were the series contributing to the greatest extent to the overall pattern in PC 2. The time trajectory of PC 2 accounted for the interdecadal (~20 years) variation, displaying one complete cycle starting in the late 1960s-early 1970s and ending by the late 1980s-early 1990s, with a maximum around 1980. The temporal pattern of this PC may illustrate a long-term regime shift in environment and ecosystem productivity. Correlations and hypotheses about underlying causality must be interpreted with caution: some of the series are too short, often of different time span, and may be strongly autocorrelated or have a trend over time caused by different processes. Final interpretation was based on evidence of multiple consistent patterns.

Consistency in hydroclimatic series revealed the importance of global climatic factors in influencing physical characteristics and circulation in the Black Sea. As the Black Sea is a virtually closed basin, such global influences are mainly attributable to atmospheric transfer or riverine inflow. Low frequency signals of similar periodicity (interdecadal, decadal, interannual) have also been found in other marine areas and their causes and propagation have been explained by ocean-atmosphere interactive processes (Polonsky and Voskresenskaya, 1996; White *et al.*, 1997). The main possible sources of such variability for the Black Sea are the atmospheric connections with the Atlantic (Polonsky *et al.*, 1997). The long-term trends in the time-series of phytoplankton, *Noctiluca*, *Pleurobrachia*, sprat, horse mackerel, anchovy and whiting accounted for a general increase in biological production during the 1970s and 1980s which could be related to variation in hydroclimate. A long-term decline in SST after 1965 may be responsible for increased upper layer instability and convection (most important in winter). This process intensifies divergence (upwelling) and mixing in the central zone and over the shelf (Ovchinnikov and Popov, 1987), leading to enrichment of nutrients in the photic layer. An increase in run-off, which peaked around 1980, may also have favoured increased productivity. By the end of the 1980s, the favourable conditions appear to have ended: run-off and wind forcing decreased, temperature increased. Zooplankton biomass was positively correlated with SST and exhibited an inverse trend with respect to phytoplankton and pelagic fish. This may be related to a temperature effect on zooplankton growth or caused by a trophic cascade effect of increased zooplanktivory by fish and gelatinous zooplankters (Daskalov, 2002). It was difficult to explain the massive phytoplankton blooms and the rise in small pelagic fish abundance during the 1980s solely by the influence of natural factors. After 1970, phosphorus discharge increased, correlated with the increased hydrogen sulphide content and inversely correlated with the hypoxia coverage (Figs 2c and 3).

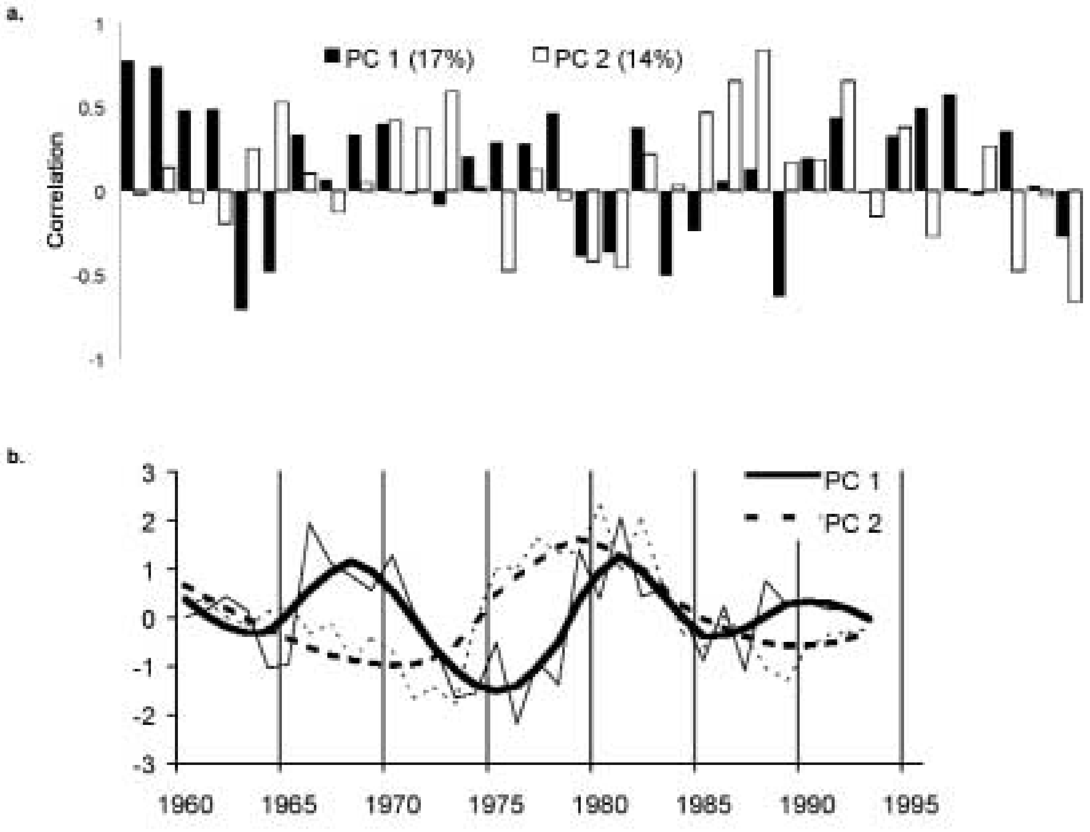

Fig. 3. PCA on hydroclimatic, biological and anthropogenic variables: a. Correlation of the input variable to the first two principal components (PC1, PC2), b. PC scores against time. Notations are as on Fig 1.

Phosphorus, hypoxia and hydrogen sulphide indices showed ~10 year variations similar to the run-off (Fig. 1). There was a significant positive trend in deep-water hydrogen sulphide content (HS2000), but not in hydrogen sulphide at 150 m (HS150). The deep-water hydrogen sulphide content (HS2000) is a more reliable index of hydrogen sulphide production, because in the deep anoxic zone the hydrogen sulphide is less disposed to oxidation. The other index (HS150) measures the hydrogen sulphide content at the break between the oxygenated and anoxic layers (the so-called oxygen deficit zone) and could be influenced by vertical circulation and penetration of oxygenated water. The positive trend in HS2000 seems to confirm the hypothesis of an overall increase in hydrogen sulphide production in the sea (Bryantzev *et al.*, 1988; Ilichenko and Sorokin, 1991).

Empirical analyses alone cannot reveal the causes of changes, but they do allow the formulation of hypotheses concerning the relationships between the abiotic environment, productive processes and population dynamics. The physical environment is recognised as the main factor driving biological productivity and influencing essentially all processes in the sea. Biological interactions and anthropogenic impact were responsible for another part of the observed variability in environmental series. The interaction between hydroclimatic, biological and anthropogenic factors generated synergistic responses by the marine ecosystem, resulting in temporal patterns studied here. The results given here can facilitate the integration of reliable environmental indices in the procedures of ecosystem-based fisheries modelling and forecasting.

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Use of Box-Jenkins models to analyse time series of fishery data in relation to environmental factors in the northwestern Mediterranean

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1. INTRODUCTION

1.1. Forecasting with statistical techniques

Apart from methods based on biological principles (e.g. VPA, yield per recruit, etc), a variety of statistical techniques have also been used to assess fish stocks. Explaining the variability of an observed time series and forecasting the future values of this time series is an important task in many areas, e.g. fisheries. The most common statistical methods to model and forecast fisheries are shown in the following table:

UNIVARIATE PROCEDURES	MULTIVARIATE PROCEDURES
Characteristics • Forecasts of a given variable are based on a model fitted only to past observations of the given time series. • Simple models • Often give forecasts which are better than multivariate models, but the fit is not very good.	**Characteristics** • Forecasts of a given variable depend at least partly on values of one or more other series (explanatory variables). • Complex models. • Often give forecasts which are no better than simple univariate models, but often give a better fit.
Models ARIMA (Box-Jenkins) models Extrapolation of trend curves Holt-Winters procedure Discounted least squares Bayesian forecasting Adaptive filtering Structural modelling Exponential smoothing “Naive” models.	**Models** Transfer function (Box-Jenkins) models Multiple linear regression Generalized linear models (GLM) Generalized additive models (GAM) Fuzzy Logic Harmonic regression Vector autoregressions Dynamic regression

There is no “best” forecasting procedure, but rather the choice of method depends on a variety of factors such as the objective in producing forecasts, the degree of accuracy required, and the properties of the given time series (Chatfield, 1984). Univariate forecasts are particularly suitable when there are large numbers of series to be forecast so that a relatively simple method has to be used. Multivariate models are appropriate to assess the effects of explanatory variables, but in many cases they do not provide better forecasts than univariate models : multivariate models need reliable forecasts of the explanatory variables, a prerequisite often not satisfied.

1.2. The utility of Box-Jenkins models

A large amount of data in the natural sciences occur in the form of time series, where observations are dependent and where the nature of this dependence is of interest itself (Box and Jenkins, 1976). The body of techniques available for the analysis of such series of dependent observations is called time series analysis. These methods take into account the lagged relationship of the observations, an important aspect that other models (e.g. linear regression) do not consider. Box-Jenkins methods are one of the most reliable methods for time series analyses (Box and Jenkins, 1976; Chatfield, 1984; Pankratz, 1991). These models may tell us something about the nature of the system generating the time series; they can be used for obtaining optimal (short and medium term) forecasts of future values of the series and can represent dynamic relationships between different time series. These models learn about the past history of a time series in relation to other variables to produce optimal forecasts. They are statistical, dynamic models that need to be updated continuously with the most recent collected data. They take into account the possible lagged relationships between variables when two or more variables are considered. Although linear modeling of time series is complex and requires a large expenditure of time and effort, it has made major progress with the appearance of new software (e.g. ForeTESS; Prat *et al.*, 2001), and generic linear Box-Jenkins models are now widely used. They are especially useful when time series are not dominated by trend and seasonality, i.e. when the irregular component of the time series is strong. Recently, a number of non-linear time series models have been proposed. Neural networks have also emerged as an alternative for non-linear process modelling.

The Box-Jenkins methodology has been most commonly used to model and forecast economic variables such as tourist numbers (Lim and Mc Aleer, 2002) or energy consumption (Gonzales-Chavez *et al.*, 1999). But they are also very useful to analyze fishery data – especially in those cases when biological data necessary to build classical models (VPA, yield per recruit, etc) are lacking. In fisheries, Box-Jenkins models have been used to model and forecast landings or catch per unit effort (CPUE), to analyze the dynamics of the fishery and the species (seasonality and trend in relation to the reproductive and feeding cycles and the behaviour of the fleet), to detect anomalies in the time series, and to evaluate the effects of environmental factors on fish landings or CPUE.

1.3. Preparation of data before construction of Box-Jenkins models

Box-Jenkins procedures apply to stationary series (time series with no systematic change in mean and variance) whose data are normally distributed. First- or second-order differencing (non-seasonal-regular and/or seasonal) usually remedies non-stationary mean and logarithmic transformation remedies non-stationary variance and also non-normal distributions of original data. Regular and seasonal differencing is usually required, because most fishery series exhibit quite strong trends and seasonality. The Box-Jenkins methodology requires complete data records and observations equally spaced in time. Time series should span more than 50 values, which is adequate for a proper time-series analysis (Pankratz, 1991). Of course, the quality of the data (fishery statistics, environmental factors, etc) is very important. Any biological characteristic may improve the models and the interpretation of the results (for example, the desegregation of time series of fish landings by fish size classes).

1.4 The different Box-Jenkins models and their application to fisheries

1.4.1 Univariate-ARIMA (Autoregressive-Integrated-Moving-Average) models

Univariate-ARIMA (Autoregressive-Integrated-Moving-Average) models are constructed using only the information contained in the series itself. Thus, models are constructed as linear functions of past values of the series and/or previous random shocks (or errors). Forecasts are generated under the assumption that the past history can be translated into predictions for the future. Box and Jenkins (1976) formalized the ARIMA modeling framework by defining three steps: identify the model, estimate the coefficients and verify the model. Identification of the number of terms to be included in the model is based on the examination of the autocorrelation (ACF) and partial autocorrelation (PACF) functions of the differenced, log-transformed time series. Estimation of the coefficients of the model is done by means of the maximum likelihood method (a non-linear method). Verification of the model is done through diagnostic checks of residuals (histogram and normal probability plots of residuals and standardized residuals). An important check of any model is to compare estimated with observed values. The forecasting ability of ARIMA models can be tested by applying the final fitted model to all available data but excluding the monthly data of the last year, which is used to compare with forecasts obtained for that year. Forecasting accuracy is higher for monthly than annual data (Stergiou *et al.*, 1997). The standard deviation and the Theil's U-statistic can be used to measure the accuracy of the ARIMA models obtained. Theil's U-statistic indicates whether or not the improvement achieved by using a sophisticated technique like ARIMA instead of using a simple naive model (a model which uses as a forecast at time $t+1$ the catch at time t) is worth in terms of time and cost involved (Makridakis *et al.*, 1983). $U>1$ indicates that there is no point in using ARIMA models while $U<1$ indicates that the ARIMA approach is better than the naive method.

The Box-Jenkins models provide additional information on fish catch time series structure and dynamics. It is often the case that a series contains a seasonal component and a trend. It is necessary to distinguish between these two attributes in order to get an adequate representation of the series. Apart from the seasonality there is also the trend. There are many types of seasonality and trend. Seasonality may be additive (the value for any given month is a given quantity over the annual mean) or multiplicative (the value for any given month is a percent over the annual mean). The multiplicative seasonality shows us whether the seasonal component in the time series is increasing or decreasing over time. The seasonality may have a regular component (recurring seasonal pattern at given months) and a stochastic component (changing over time: this often applies to biological variables). The first one can be removed simply by seasonal differencing while the second one must be removed using more complex techniques. Trend can also have a well defined, regular structure (that may be extracted fitting linear, exponential or damped models) or may have an irregular component (that needs to be extracted with more complex models). The biological interpretation of seasonality and trend is important to describe the dynamics of the fishery. The comparison between the seasonal patterns and trends in landings might be of interest in trying to identify important events on the level catch. Important catch declines of some fish species may be preceded and followed by a strong variation of their respective seasonal patterns, and thus might be used as a tool for predicting important negative changes in landings of a species (Lloret *et al.*, 2000). Complex techniques of seasonal and trend decomposition are: Census Method 1, "X-11" (Makridakis *et al.*, 1983; Makridakis and Wheelwright, 1989); TRAMO, SEATS, TRACE and SAGG (Prat et al, 2001), moving average smoothing (Box and Jenkins, 1976), weighted least squares smoothing, etc. Apart from seasonality and trend, there may be cyclic changes.

ARIMA models have been used worldwide to forecast the landings and catch per unit effort of many fish and invertebrate species (e.g. Jensen, 1985; Fogarty, 1988; Stergiou, 1989, 1991; Molinet *et al.*, 1991; Yoo and Zhang, 1993; Pajuelo and Lorenzo, 1995; Hare and Francis, 1995; Stergiou *et al.*, 1997; Downton and Miller, 1998; Lloret *et al.*, 2000; Pierce and Boyle, 2003). Seasonal models have been the most common due to the seasonal cycles of reproduction and recruitment and/or the seasonal dynamics of the fleet. ARIMA models have been also used to forecast production rates (Keller, 1987) and environmental factors such as water level of lakes (Irvine and Eberhardt, 1992), river runoff and rainfall (Fandy *et al.*, 1994), salinity in estuaries (Niu *et al.*, 1998) and sea water temperatures (Stein and Lloret, 2001).

1.4.2. Intervention analysis

Intervention analysis can be used to detect and quantify non-random changes in variables. Owing to lack of independence between successive observations, t-tests for equality of means could not be used to test for production shifts. Therefore intervention analysis is used to identify the significance, magnitude and form of structural shifts (interventions) of the time series. While the input of an intervention represents a pulse shift in a given month, the output or consequence of that event may be modeled in several ways. Thus, according to the output, two types of interventions are defined, pulse and step. A pulse intervention represents a temporary event that affects the level of the catch, and can be modeled as abrupt (i.e. a pulse intervention at $t=1$ shifts the level up or down only during period $t=1$) or delayed (i.e. a pulse intervention at $t=1$ causes a decreasing or an increasing response during periods $t+1$, $t+2$, $t+3$...). The first one is also called

Additive Outlier (denoted AO), the second one is also called Temporary-Change intervention (denoted TC). Step interventions may be thought as a permanent change in the level of a time series. They are also called Level-Shifts (denoted LS). By carrying out the intervention analysis we will not only obtain better models (estimated parameters will improve) and better forecasts (when the intervention occurs in the last values used to model the series) but also it will be possible to learn more about the time series under study (i.e. detect possible external events and try to explain them).

Intervention analysis has been used in fishery science to identify anomalies in the time series of landings or CPUE (see e.g. Hare and Francis, 1995; Downton and Miller, 1998; Lloret *et al.*, 2000). In the analysis of fishery data, we are often most interested in regimes that define points in time where major shifts occur in the catch history of a species. Thus, TC and LS are the most important interventions to be considered while AO interventions may be often disregarded because they might be a direct consequence of recording errors or anomalous fishing effort.

1.4.3 Transfer function models

Transfer function models are multivariate models that are constructed using the information contained in two or more time series. These models describe the time-lagged relationship between dependent and explanatory variables while taking into account the autocorrelation of the disturbance. The easiest models to build and interpret are the bivariate transfer functions, even though we may build multivariate transfer function models where several explanatory variables interact to affect the dependent variable. Multivariate models can usually be made to give a better fit to data than univariate ARIMA models, but this superiority does not necessarily translate into better forecasts, perhaps because multivariate models are more sensitive to changes in structure and because the computation of multivariate forecasts require the prior computation of forecasts of exogenous variables, and the latter may not be good enough (Chatfield, 1984). Transfer function models give inconsistent estimates of the coefficients when there is feedback from the output to the inputs, a problem that arises when there is an influence of the output on the inputs or when data are temporal averages (Pankratz, 1991). However, in fisheries, it is not reasonable to think that changes in catch or CPUE will lead to later changes a given environmental factor (there is no feedback). In addition to this, environmental data and CPUE are usually monthly averages, and only catch data are monthly aggregates.

The transfer function models have been often used in fishery science to determine the possible relationships between time series of recruitment or yield (catch and CPUE) and selected environmental variables over time, or during any critical phase of the species such as the reproduction season (see e.g. Quinn and Marshall, 1989; Kim *et al.*, 1997; Stergiou *et al.*, 1997; Tsai *et al.*, 1997; Downton and Miller, 1998; Lloret *et al.*, 2001; Pierce and Boyle, 2003).

2. SOME EXAMPLES OF BOX JENKINS MODELS TO ANALYSE FISHERY DATA IN RELATION TO ENVIRONMENTAL FACTORS IN THE NW MEDITERRANEAN

2.1. ARIMA models and intervention analysis

Time series modelling of landings in the northwestern Mediterranean Sea. By J. Lloret, J. Lleonart and I. Solé, 2000.

Univariate seasonal ARIMA and intervention models were developed to forecast monthly catches of 53 commercial species in the northwestern Mediterranean Sea, up to one year in advance. In general terms, there was good agreement between forecasts and observed catches of target demersal species (Fig. 1). By contrast, models fitted to non-target demersal species and pelagic species were unsatisfactory in terms of explained variability and predicting power. Large commercial size-classes were better explained than the small size-classes. Intervention analysis was used to identify the significance, magnitude and form of structural shifts (interventions) of the time series for each species. Most of the fitted interventions appeared in small commercial size-classes and indicated a decrease in the mean level of the catch (Fig. 2). Seasonality of demersal species caught mainly by trawlers, was mainly attributed to changing availability and recruitment (Fig. 3). By contrast, gear type explained the seasonal variation in landings of pelagic and some coastal species.

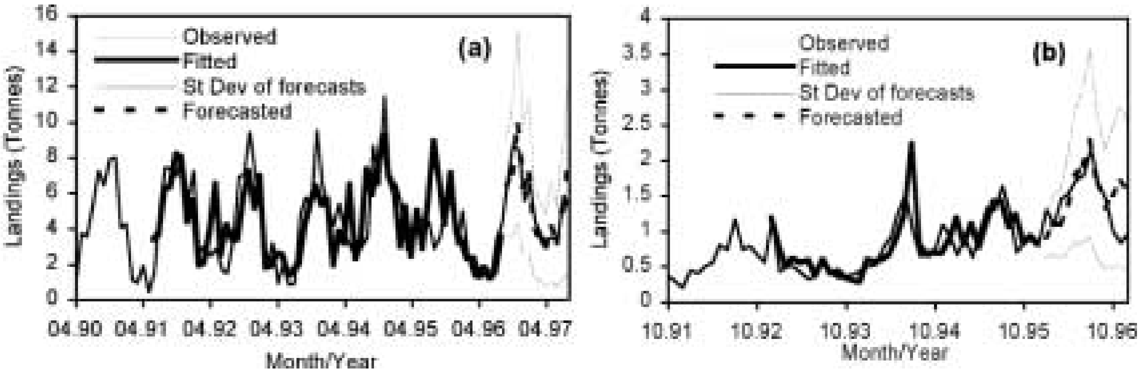

Fig. 1. ARIMA models: comparison between observed monthly catches of two species or groups of species together with fits (for all months used to construct the models) and forecasts (± standard deviation with 75% probability) predicted from those models (for the 12 following months). (a) *Trisopteris minutus capelanus*, (b) *Citharus linguatula* and *Lepidorhombus boscii*

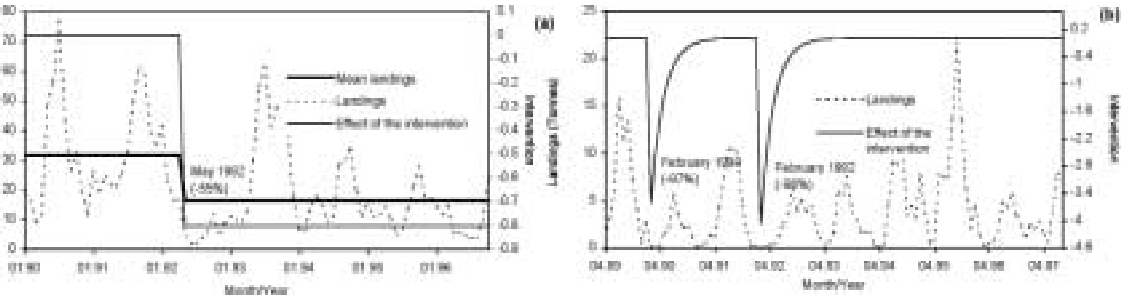

Fig. 2. Intervention analysis: (a) Level-Shift intervention in May 1992 for the small *Merluccius merluccius;* (b) Temporary-Change interventions in February 1990 and February 1992 for the small *Eledone cirrhosa*. The effect of the interventions and the mean catch before and after them are shown by straight lines. Timing of the interventions and deviation from the expected values, i.e. the resultant change in mean (in percent), are also shown.

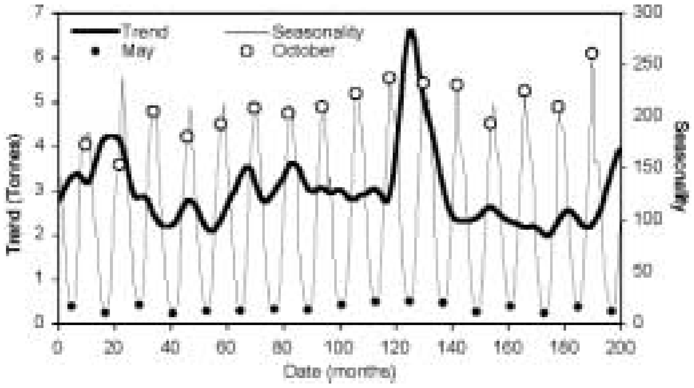

Fig. 3. Seasonality and trend: seasonal pattern and trend of catches of big Loligo vulgaris

2.2. Transfer function models

• *Fluctuations of landings and environmental conditions in the northwestern Mediterranean Sea. By J. Lloret, J. Lleonart, I. Solé and J.M. Fromentin, 2001.*

• *Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre River delta (northwestern Mediterranean). By J. Lloret, I. Palomera, J. Salat and I. Solé, in press.*

Transfer function models were used to study the influence of Rhône and Muga river run-off and wind mixing index on the productivity of several demersal, benthic and pelagic invertebrate and fish species in the Gulf of Lions and the Gulf of Roses (northwestern Mediterranean). Most of the monthly catches and CPUE of 13 studied commercial species in the coastal waters of the northwestern Mediterranean were significantly positively correlated with runoff of local rivers (Rhône and Muga) and the wind mixing index during the spawning season, with time lags of less than a year (transfer function analyses; Fig. 4). We used only the values of river runoff and wind mixing for those months when a species is reproducing and replace the values for the rest of the months by "zeros" that mean "no influence" in the models (comparing the environmental conditions only during the spawning seasons with the resulting landings or CPUE or the smallest commercial size classes, i.e. recruitment). The results showed that enhanced hydroclimatic conditions in the NW Mediterranean were favourable for the productivity of the fish and invertebrate stocks, suggesting the presence of linkage between recruitment of Mediterranean species and local (river discharges, wind conditions) and global (NAO) environmental conditions.

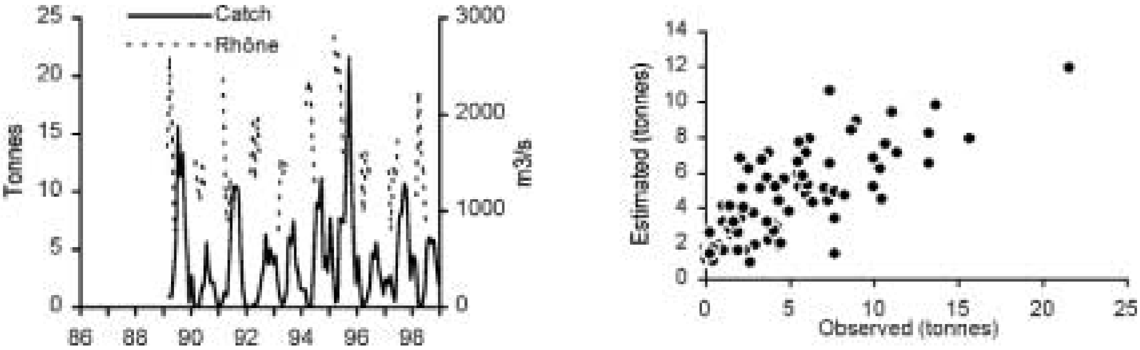

Fig. 4. Transfer function models: the time series of catch and of Rhône river runoff during the spawning season of Small *Eledone cirrhosa* (graph on the left), and the observed against the estimated yield from the transfer function model (graph on the right).

Transfer function models were also used to study the influence of Ebre river run-off and wind mixing index on the productivity of the two most abundant species of small pelagic fish exploited in waters surrounding the Ebre (Ebro) River continental shelf (northwestern Mediterranean): anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*). These environmental variables (river flow and wind) were selected because they are known to enhance fertilization and local planktonic production, thus becoming crucial for the survival of fish larvae. The results of the analyses showed a significant correlation between monthly landings of anchovy and freshwater input of the Ebre River during the spawning season of this species (April-August), with a time lag of 12 months (Fig. 5a). In contrast, monthly landings of sardine were significantly positively correlated with the wind mixing index during the spawning season of this species (Nov.-March), with a lag of 18 months (Fig. 5b). The results provide evidence of the influence of riverine inputs and wind mixing on the productivity of small pelagic species in the northwestern Mediterranean. The time lags obtained in the relationships stress the importance of river run-off and wind mixing for the early stages of anchovy and sardine, respectively, through their impact on recruitment.

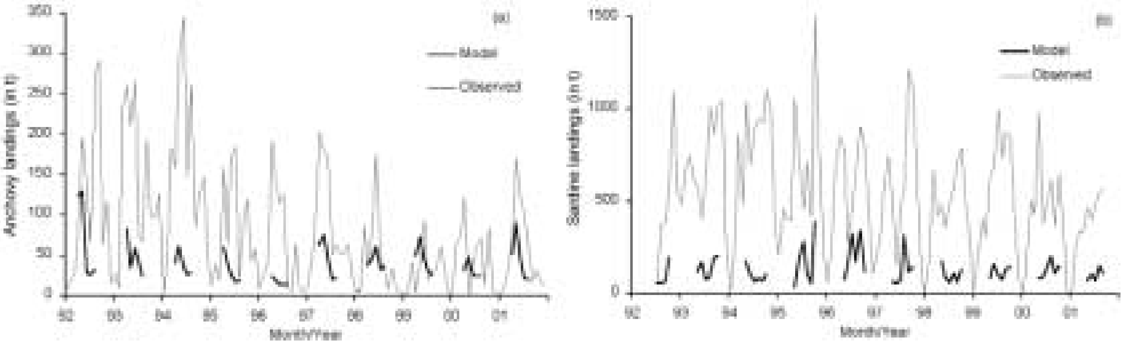

Fig. 5. Transfer function models: comparison between the expected landings from the models and the observed (actual) landings over the period 1992-2001: (a) anchovy and (b) sardine. Model values in (a) represent the contribution of the river outflow to the landings of anchovy 12 months after spawning, while in (b) represent the contribution of wind mixing to the landings of sardine 18 months after spawning.

A unifying topological framework to deal with scales, intensity and unusual, extreme events in biological time series

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INTRODUCTION

Considering the increasing evidence of the intermittent nature of both physical and biological patterns and processes in marine sciences, and the increasing awareness of the heterogeneous nature of plankton distributions from decimeter to millimeter scales, where the most ecologically relevant processes of viral infection, nutrient uptake, cell division and behavior occur, the ocean should be regarded as a “seascape” (Seuront *et al.*, 2003a), and should subsequently be topologically classified by analogy with landscape ecology. Seascape ecology nevertheless seems still in its infancy.

Recent theoretical and empirical developments, conducted both on turbulent energy dissipation rates and on the associated passive scalars distributions, have widely demonstrated the scaling and multiscaling properties of intermittent processes. In that way, one may note that the large numbers of modeling approaches which have been devoted to deal with the structure of turbulent flows only provided a description at a very limited range of scales. Indeed, Gaussian diffusion models or direct numerical simulations possess no way to change the scale upward or downward. It is natural, on the contrary, for multifractal processes. Moreover, Gaussian processes are determined by only two moments (i.e. the mean and the variance), while the first three moments of empirical processes are usually provided to characterize them. In the statistical framework of multifractals, we propose a more global approach since we provide all the moments (even non-integers), giving as much statistical information as the study of probability density directly.

On the other hand, the procedures devoted to test for independence between two processes, based on second order statistics analysis (i.e. correlation) become fallacious for intermittent non-Gaussian fields. It is then necessary to test for independence by studying joint moments of all orders. In addition, more recent procedures based on probability density functions examination do not deal with the multiscaling properties of intermittent fields.

In this paper, we briefly define the concepts and the importance of scales and intermittency in biological time series, and subsequently illustrate the scaling and multiscaling properties of natural biological and physical time series. We also describe the principles of an innovative objective technique for determining if two simultaneously recorded time series can be regarded as being independent or not (whatever the scales and the intensity), and for investigating the nature of their potential coupling. In particular, we stress that taking into account the intrinsic intermittent properties of biological ocean time series can provide new insights into our understanding of biological patterns and processes, as well as biophysical couplings.

SCALES IN BIOLOGICAL TIME SERIES

The geometry of shores, rocks, plants, waves, hydrodynamic flow, organisms trajectories and many other natural phenomena is important in different scientific disciplines, and each field tends to adapt specific concepts to describe the complexity of nature. Basically, ecological models often approach natural shapes as simple geometrical approximations. Lakes are approximated as circles, particles as spheres, patches as squares and rectangles, and trees as cones. Many patterns and shapes in nature, however, are so irregular and fragmented that they present not simply a higher degree but an altogether different level of complexity, as compared with Euclidean approximations. Curves, surfaces and volumes in nature can thus be so complex that classical measurement approaches become meaningless.

The term fractal geometry has been coined to characterize spatial or temporal phenomena that are continuous but, because of their complexity, not differentiable. Unlike more familiar Euclidean constructs, every attempt to split a fractal into smaller pieces results in the resolution of more structure. As a consequence, in fractal constructs the detail is similar to the whole, i.e. there is no characteristic scale. Fractal objects and processes are therefore said to display “self-invariant” properties, and can be further defined as being either “self-similar” or “self-affine”. Self-similar objects are isotropic (the same in all three spatial dimensions) upon rescaling, whereas rescaling of self-affine objects is direction-dependent (anisotropic). Thus, a trace of zooplankton motion in 3D space is self-similar, whereas a 2D trace, such as the plot of the x-coordinate of an organism’s movement as a function of time, is self-affine. Biological time series are thus self-affine processes.

Generally speaking, self-affine processes can be described using a variety of scaling techniques such as variogram or spectral analysis. The common feature of these techniques is to consider the dependence of a quantity Q (the variance and the spectral density for variogram and spectral analyses, respectively) to the scale l as a power law (i.e. scaling) relationship of the form $Q \infty l^{\alpha}$ where α is a characteristic exponent describing the scale-dependence of the process. Self-invariant patterns and processes can thus be described by a characteristic exponent, which can be viewed as a measure of complexity, or as an index of the scale-dependence. The scaling exponent, α, characterizes a range of scales over which similar patterns and/or processes are operating across that range of scales. One must nevertheless note that if there exists a critical scale beyond which a further increase results in a shift in the exponent, or a loss of scaling structure, this may define a transition zone where the environmental properties or constraints acting upon a given system are probably changing rapidly, between two different hierarchical levels in which different patterns and/or processes are operating (Fig. 1).

However, many patterns and processes are now widely acknowledged as being highly intermittent (i.e. characterized by a few “hotspots” dispersed over a wide range of low density areas) as the distribution of microscale fluctuations of turbulent kinetic energy dissipation rate (Fig. 2). In particular, there is a clear differences arising from the comparison of these intermittent patterns with standard fractal processes such as fractional Brownian motions, which raises the question of the reality of describing such processes using a single exponent in terms of fractals and scaling behaviour.

INTERMITTENCY IN BIOLOGICAL TIME SERIES

The concept of intermittency has been initially described in the framework of turbulence, where experimental records of the kinetic energy dissipation rate showed large fluctuations (bursts) possessing a spatial nested structure (bursts into bursts) instead of a steady, slightly variable and homogeneous behavior of the fluctuations (Fig. 2). It has thus been known for a long time that the assumption of a spatially uniform turbulent cascade is not satisfied for the incre-

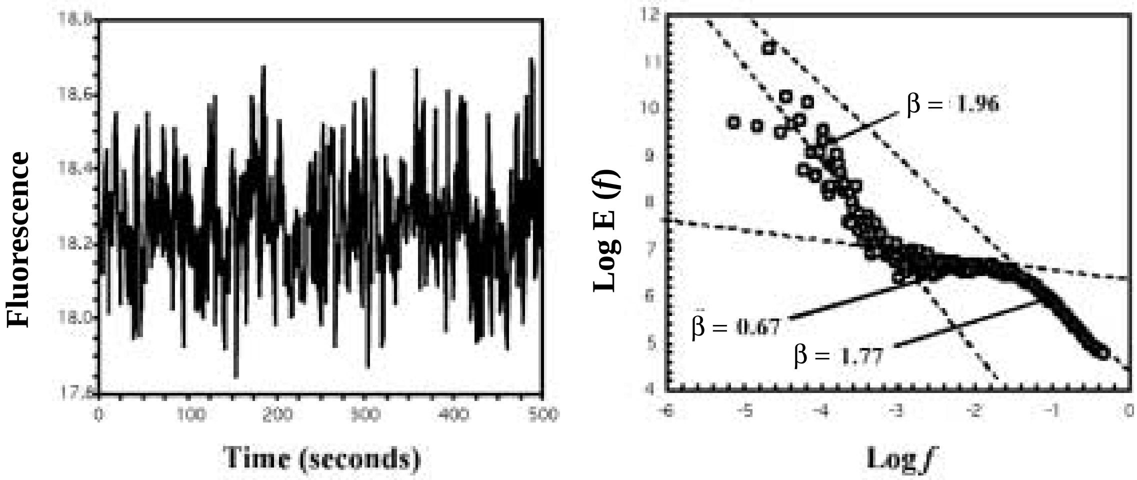

Fig. 1. Example of a time series of *in vivo* fluorescence and the result of its spectral analysis. The different values taken by the spectral exponent β are indicative of structural changes in the structure of fluorescence variability as a function of scale (adapted from Seuront *et al.*, 1999).

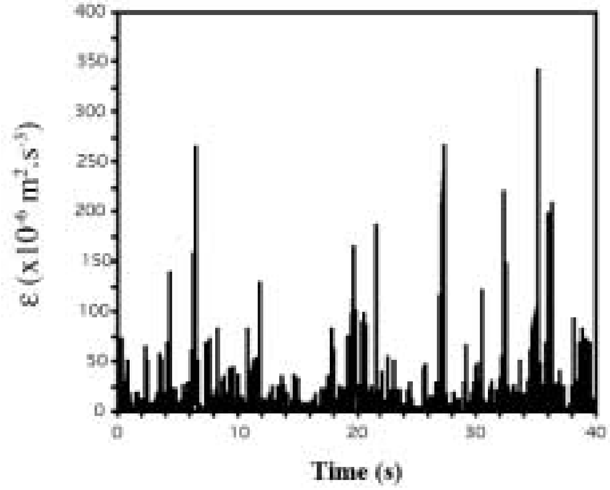

Fig. 2. Example of the intermittent character of the temporal distribution of the kinetic energy dissipation rate ε (adapted from Seuront *et al.*, 1999).

ments of turbulent velocity at distances in the inertial subrange or shorter, and that strong gradients are much more common that they would be for a Gaussian distribution. This means that most of the time, the gradients would still be of the order of their standard deviation, but that occasionally we should expect stronger bursts, much more often than in the Gaussian case. This is the phenomenon of intermittency that occurs at all scales.

This may be understood from a geometrical point of view, considering that the turbulent regions do not fill the whole space, but only a subpart, in a very irregular way. This picture of a non-space filling turbulence takes the intermittent nature of turbulence into account by assuming that subeddies in the inertial subrange are either “dead” (inactive) or “alive” (active), and leads to a (mono-) fractal description of turbulence. However, it is now known that both turbulent velocity and passive scalars fluctuations are intermittent in the sense that strong (i.e. ‘more active’) subeddies occupy tiny fractions of the space available. This leads to a multifractal description of turbulence, each intermittency level being associated with its own fractal dimension.

Practically, instead of considering the scaling relation $Q \infty l^{\alpha}$, we introduce the multiscaling of the statistical moments of order q of the fluctuations of the quantity Q as $\langle (\Delta Q_l)^q \rangle \infty l^{\varsigma(q)}$ where l is the spatial scale and the angle brackets “$\langle . \rangle$” indicate ensemble averaging.

For monoscaling (i.e. monofractal) processes, the function $\zeta(q)$ is linear: $\zeta(q) = q/2$ for Brownian motion, and $\zeta(q) = q/3$ for non-intermittent turbulence. For multiscaling processes, this exponent is non-linear and concave (Fig. 3a). More specifically, the low values of q characterize the weakest (and more frequent) fluctuations, while the high values of q characterize the highest and rarest fluctuations. The "distance" between monofractality and multifractality is then measured by the nonlinearity of the function $\zeta(q)$.

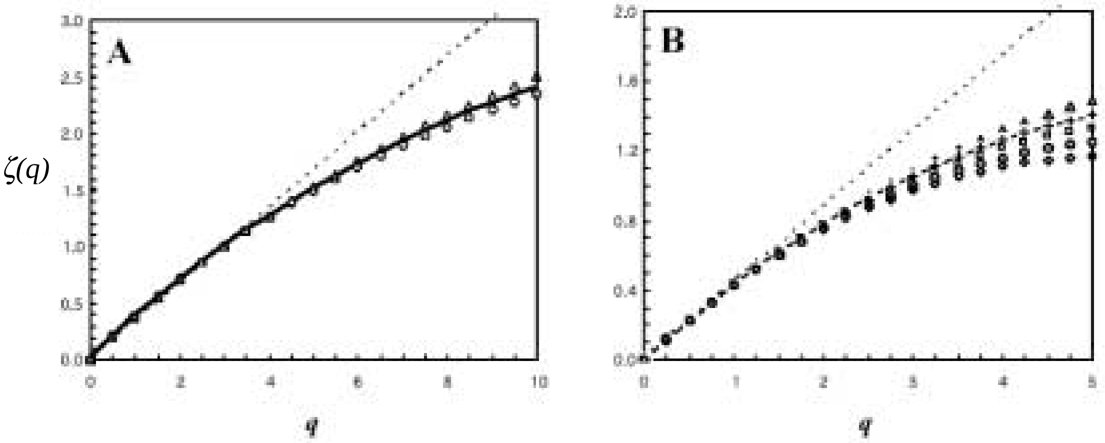

Figure 3. Comparison of (A) the empirical values of the functions $\zeta(q)$ estimated from grid generated turbulence (open dots), atmosphere turbulence (continuous curve) and ocean turbulence (open triangles), and (B) the empirical values of the functions $\zeta(q)$ estimated for temperature (continuous curve) and *in vivo* fluorescence for different values of the turbulent kinetic energy dissipation rate ε ($\varepsilon = 10^{-6}$ $m^2.s^{-3}$, rhombs; $\varepsilon = 5.10^{-6}$ $m^2.s^{-3}$, circles; $\varepsilon = 10^{-5}$ $m^2.s^{-3}$, squares; $\varepsilon = 5.10^{-5}$ $m^2.s^{-3}$, crosses; $\varepsilon = 10^{-4}$ $m^2.s^{-3}$, triangles). The nonlinearity of the function $\zeta(q)$ is indicative of the multifractal behavior of turbulent velocity, temperature and fluorescence. The linear curve expected in case of non-intermittent (i.e. monofractal) turbulence is shown for comparison (dashed line) (adapted from Seuront and Schmitt, 2001).

One of the major contributions of the multiscaling framework in our understanding of biological processes in the ocean might be illustrated comparing the multifractal structure of temperature and *in vivo* fluorescence, simultaneously recorded in the Eastern English Channel in different turbulent conditions. In the scaling framework of spectral analysis, the exponents β estimated for temperature and fluorescence were not significantly different from the theoretical value $\beta = 5/3$ expected in case of purely passive scalars advected by turbulent fluid motions. These results, fully congruent with previous studies conducted in the same area (Seuront *et al.*, 1996a,b, 1999, 2002), suggest an extreme similarity between the single scaling properties of small-scale temperature and fluorescence distributions. At this stage, phytoplankton biomass can then still be regarded as being a passive scalar. However, the functions $\zeta(q)$ obtained for temperature time series remain similar whatever the external hydrodynamic forcing (i.e. the values of the dissipation rate ε), while the nonlinearity of the functions $\zeta(q)$ characterizing fluorescence clearly increases when the value of the dissipation rate decreases (Fig. 3b).

The distribution of temperature then remains the same whatever the hydrodynamic conditions. This result is convergent with previous observations regarding the distribution of turbulent velocity fields (Fig. 3a; Seuront *et al.*, 2003b), and confirms the passive scalar behavior of temperature. On the opposite, the distribution of phytoplankton biomass is less intermittent, and closer to the one of temperature in high turbulent conditions (Fig. 3b). This suggests that phytoplankton cells behave more like a passive scalar under high hydrodynamic conditions, but exhibits very specific properties under lower levels of turbulence.

INTERMITTENCY AND COUPLINGS IN BIOLOGICAL TIME SERIES

Previous standard procedures devoted to test for independence between two given processes were generally based on second order statistics (i.e. covariance and correlation functions), even when they were conducted in scaling framework related to spectral analysis or geostatistical analysis. More recent procedures are based on the examination of probability density functions. The former are implicitly based on Gaussian hypothesis (uncorrelation implying independence), untenable in an intermittent framework characterized by a high-order statistical behavior. The latter do not deal with the intrinsic multiscaling properties of intermittent fields. Using an original procedure based on a high-order generalization of the correlation concept between two stochastic processes, or time series (Seuront and Schmitt, 2001), we illustrate how taking into account the intermittent nature of simultaneously recorded temperature and fluorescence time series can modify our understanding of biophysical couplings in the ocean. Briefly put, the main advantages of the Generalized Correlation Functions (GCF) and the Generalized Correlation Exponents (GCE) framework are the following (Seuront and Schmitt, 2001): (i) it makes no assumptions about the spectrum or the distribution of either data sets, (ii) it takes fully into account their intrinsic multiscaling properties, (iii) it may be used to provide much more fundamental relations between two patterns/processes, and (iv) it fully explores qualitatively and quantitatively the correlations of large and low fluctuations of both processes.

Now consider that the moments of order p and q characterize respectively the fluctuations of temperature and in vivo fluorescence. The Generalized Correlation Exponents, $r(p,q)$, obtained from the comparison of temperature and fluorescence time series recorded on different days remain close to zero, whatever the combinations of p and q and values (Fig. 4), indicative of the absence of any correlation. Alternatively, Figure 5 shows the GCE, $r(p,q)$, obtained for all the combinations of p and q and values with 0.1 increments, for temperature and fluorescence time series, simultaneously recording under three distinct levels of turbulence (10^{-4}, 10^{-5}, and 10^{-6} $m^2.s^{-3}$). It appears that the correlation between temperature and in vivo fluorescence fluctuations increases with hydrodynamic conditions, and is weaker, even nil, in low turbulent conditions.

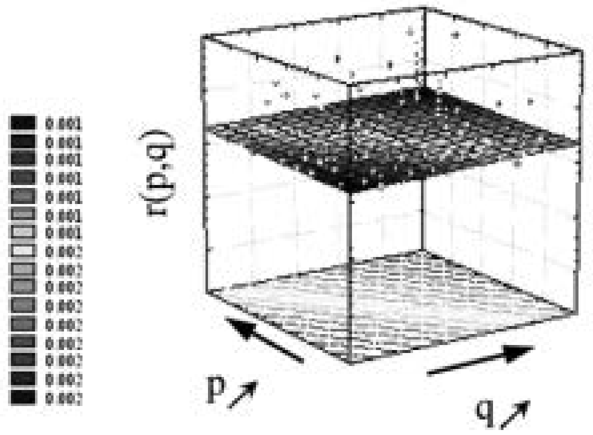

Fig. 4. The Generalized Correlation Exponents (GCE) $r(p,q)$, shown as a function of both p and q, which characterize *in vivo* fluorescence and temperature fluctuations, respectively. The function $r(p,q)$ is estimated here between time series of temperature and fluorescence independently sampled (adapted from Seuront and Schmitt, 2001).

We thus confirm here the increased physical control suggested under strong turbulent conditions from the analysis of the shape of the function $\zeta(q)$ estimated for temperature and fluorescence; see Fig. 3. On the other hand, the decorrelation between temperature and phytoplankton fluctuations under weak turbulent conditions suggests an increase in the biological contributions to the control of phytoplankton biomass distribution, and confirms previous observations (cf. Fig. 3). Phytoplankton distribution then appears independent of the temperature under the lowest turbulence levels investigated here, i.e. 10^{-4} $m^2.s^{-3}$ (Fig. 5a). More specifically, the shape of the function $r(p,q)$, indicates that large phytoplankton fluctuations are associated – under strong enough turbulent conditions –to weak temperature gradients, and conversely. This tendency seems to reflect findings of Desiderio *et al.* (1993); they observed the occurrence of 0.1-0.2 meter thick fluorescent layers just above local temperature gradients.

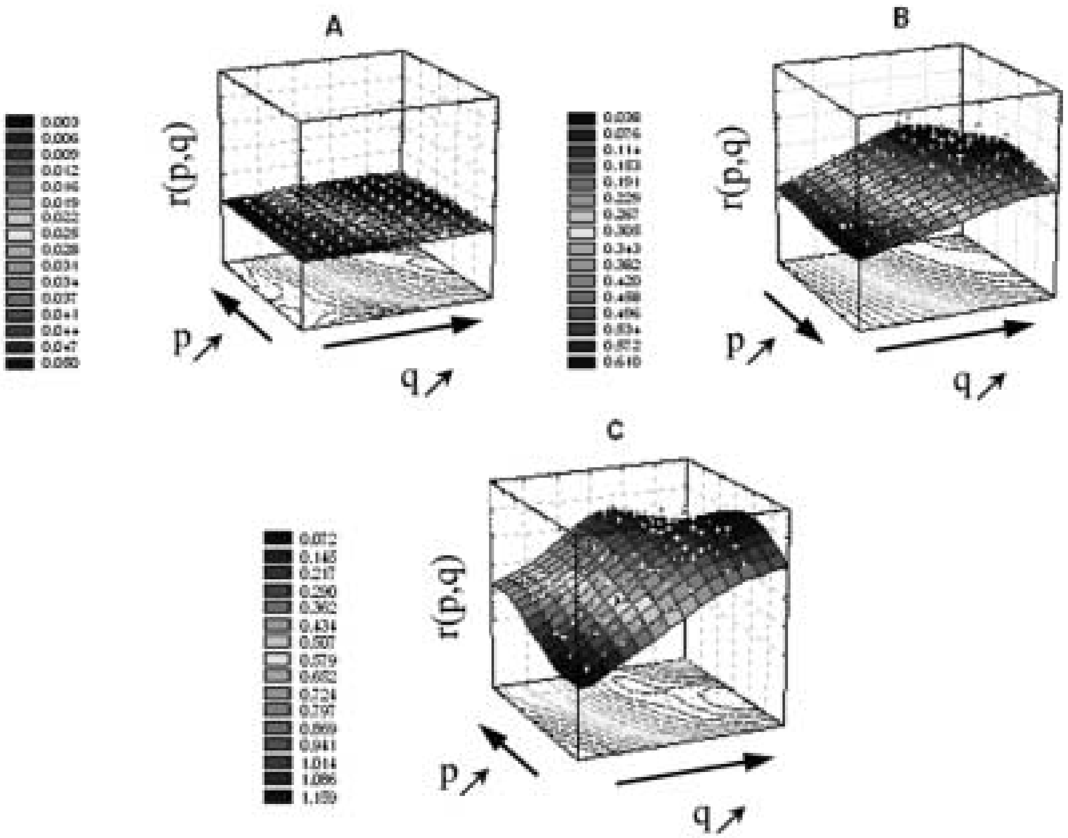

Fig. 5. The Generalized Correlation Exponents (GCE), $r(p,q)$, shown as a function of both p and q. Here the statistical orders of moment p and q characterize temperature and *in vivo* fluorescence fluctuations, respectively. The functions $r(p,q)$, correspond to two different levels of turbulence, i.e. $\varepsilon = 10^{-6}$ (A) and 10^{-5} (B) and 10^{-4} $m^2.s^{-3}$ (C) (adapted from Seuront and Schmitt, 2001).

CONCLUSION

Our results demonstrate that single scaling properties of temperature and phytoplankton would have erroneously led to conclude that the latter could be regarded as a purely passive scalar. However, investigations of their detailed variability in the multiscaling framework lead to consider that phytoplankton biomass presents very specific properties, depending on the intensity of local turbulent processes. This suggests a differential control of phytoplankton biomass distribution involving complex interactions between turbulent velocity fields, and the involved particles properties such as buoyancy, size, density or aggregative properties. In particular, this assertion is supported by the specific behavior of phytoplankton multiscaling properties under low turbulent conditions, suggesting the prevalence of phytoplankton cells specific properties on turbulent processes.

Finally, regarding the additional quantity of informations brought by the univariate and bivariate multiscaling procedures described here to our understanding of the structure of velocity, temperature and phytoplankton fluctuations, as well as the couplings between temperature and phytoplankton biomass, we claim, as already stressed elsewhere (e.g. Seuront *et al.*, 1999, 2002), that taking into account the reality of the intermittent nature of bio-physical microstructures could be the first step towards a general understanding of structures and functions in marine pelagic ecosystems. It has indeed been shown that the intermittent nature of turbulent flows and phytoplankton distributions could affect matter fluxes up to more than one order of magnitude (Seuront, 2001; Seuront *et al.*, 2001)

Finally, we emphasize that the a priori elevated cost associated with the use of the single and joint multiscaling tools outlined here in terms of algorithmic developments and computation time consumption will be easily overcome by the invaluable gain in emerging knowledge.

Linking the temporal variability in population abundance to the variability of community attributes

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Understanding the processes that govern the temporal variability of both populations and communities is one of the major challenges for ecologists. Using the data of a 30-year monitoring programme of macrobenthos species living on the tidal flats of the Wadden Sea, this paper examines cross-variability in species abundance and to which extent it is reflected in community attributes such as total benthic biomass.

It is a truism that community properties, such as total biomass or overall secondary production, reflect underlying population processes. Yet, it is also a self-evident truth that populations do not occur in isolation and population processes, for example birth or death rates, partly depend on overall community and ecosystem attributes.

Studies of the temporal variability of both population abundance and community properties have recently attracted renewed attention of ecologists. Understanding the connections between the two integration levels and how these interdependencies are reflected in the temporal variabilities at both levels, is one of the major challenges for ecologists.

A straightforward descriptive approach to link both levels is to define an aggregrate community property that is simply the sum of that property over all populations. For example, overall community biomass is the sum of all population biomasses. The (temporal) variability of a sum is given by

$$\mathrm{var}\left(\sum x_i\right)=\sum \mathrm{var}(x_i)+2\cdot\sum_i\sum_{j<i}\mathrm{cov}(x_i,x_j)\,.$$

When populations vary entirely independently, all covariances are zero, and the variance of the sum is simply the sum of the variances. Note that the coefficient of variation CV, which is defined by the square root of the variance divided by the mean, will then be much lower for the aggregate. If all species have the same CV, the CV of the aggregate will be $1/\sqrt{n}$ times smaller, where n is the number of species. The CV decreases in the same way as the variance of the mean decreases with the number of observations in simple random sampling. In ecology, this decrease of the variance of a community attribute with increasing species numbers is called the portfolio-effect, but it is not of our concern here. Here I am interested in whether or not the variance of the mean decreases more or less than expected on the basis of independent behaviour of the species. Focus is thus on the sum of all covariances: is that sum negative, zero or positive? This idea can be summarized by the index:

$$V = \frac{\mathrm{var}\left(\sum x_i\right)}{\sum \mathrm{var}\, x_i} \ .$$

Parallel fluctuations in species abundance, which will result in positive covariances and hence an index V larger than 1, may be caused by a similar response to external forcing functions, e.g. weather. An opposite response to environmental factors will result in negative covariances, and a V smaller than 1. On the other hand biological interaction processes such as competition and predation may induce negative covariances, whereas mutualism may reveal positive covariances. Hence one should not expect unambiguous answers on the underlying causes by studying the temporal covariance structure of a community.

A disadvantage of the index V is that it is dominated by the most abundant species (due to a variance/covariance-mean relationship). Alternatively one might look at the distribution of the Pearson correlation coefficients using all species pairs. Recall that Pearson's correlation coefficient is a scaled covariance:

$$r = \frac{\mathrm{cov}\left(x_1, x_2\right)}{\sqrt{\mathrm{var}\left(x_1\right) \cdot \mathrm{var}\left(x_2\right)}} \ .$$

MATERIAL AND METHODS

The data of a 30-year monitoring programme of macrobenthos species living on the tidal flats of the Wadden Sea were examined, tracking cross-variability in species abundance.

The index V and all pairwise Pearson correlation coefficients were estimated using (a) the raw species biomass time series and (b) reconstructed time-series after de-trending and removing the effect of the most important environmental variable, winter temperature.

The reconstructed time series were completed with the help of stochastic population process models in discrete time of the form:

$$R_t = R_m - \exp\left(-b_0 - b_1 X_t\right) + b_2 Z_t + \varepsilon_t \ ,$$

where the log reproductive rate at time t

$$R_t = X_{t+1} - X_t = \log\left(N_{t+1} / N_t\right)$$

is related to the previous log population biomass density X_t, an exogenous variable Z_t.(average winter temperature), and an independent, identically normally distributed error with zero mean et (see Van der Meer *et al.*, 2000 for further details). After fitting this model for each species, the reconstructed series were obtained by:

$$\log N_{t+1} = b_0 + \left(b_1 + 1\right)\log N_t - \overline{R}_t + b_2 \overline{Z}_t + \varepsilon_t \ .$$

Permutation tests (i.e., series were 1000 times reshuffled in a random order) were used for significance testing.

RESULTS

Using the original time series, the estimated index V equalled 1.7. Permutation test revealed a 95% interval ranging from 0.63 to 1.44. The average Pearson correlation coefficient equalled 0.10. Using the reconstructed series (see Figs. 1 and 2 for an example) the estimated index V was almost equal to one: V=1.1, and the average Pearson correlation coefficient was almost equal to zero, mean(r)=0.04. In many cases the reconstruction resulted in a change from a positive correlation to a correlation around zero (Fig. 3). However, a mean correlation coefficient of about zero does not necessarily imply that all series are independent of each other. Negative and positive correlations may have cancelled out, producing a mean around zero. I therefore looked at the variability of all estimated pairwise correlation coefficients in terms of the standard deviation. A set of 1000 permutations revealed a 95% interval for SD(r) ranging from 0.19 to 0.24. The estimated SD(r) using the reconstructed series equalled 0.29, pointing to the existence of some true negative and positive correlations.

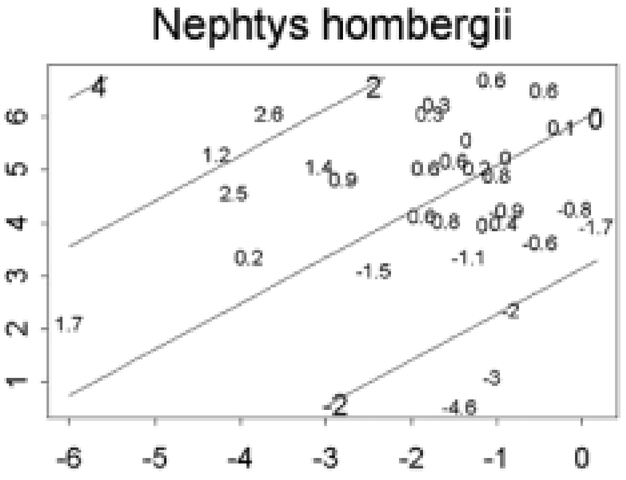

Fig. 1. Relation between the log reproductive rate (small figures give annual values, large figures and lines give model estimates) versus winter temperature (y-axis) and biomass density (x-axis) time for the polychaete worm *Nephtys hombergii.*

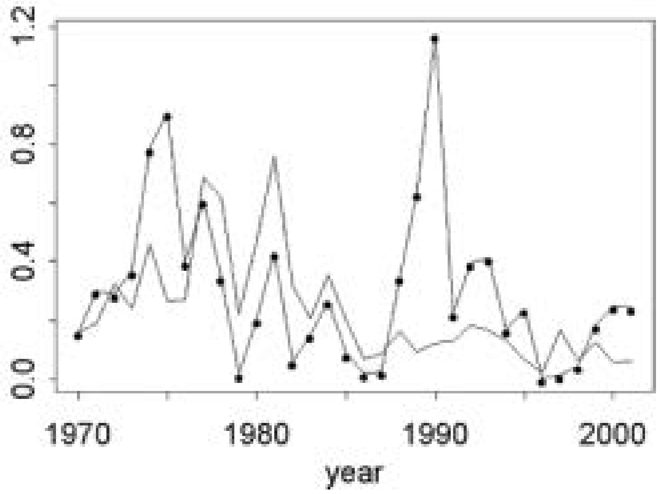

Fig. 2. Biomass density versus time for the polychaete worm *Nephtys hombergii* in original series (line with dots) and reconstructed series after detrending and removing the effect of winter temperature (line without dots).

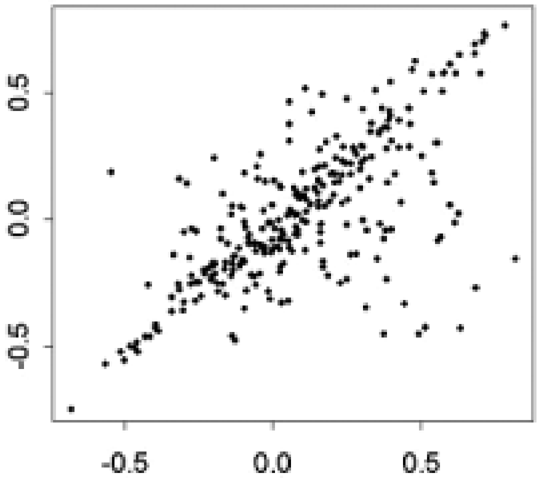

Fig. 3. Pairwise correlation coefficients using the original (x-axis) and reconstructed (y-axis) time series.

DISCUSSION

Studying the between-populations covariance structure using long term time series, as done here, might be a short-cut to get preliminary and rough ideas about the "connectivity" in a community. The example data that were used concerned short-living benthic animals in a coastal system,· most of them immobile and possibly dependent on more or less the same food source (many of them are filter feeders filtering edible particles from the water column). Hence, one could have expected that negative correlations would have predominated (if one species has for some reason a low abundance, another species might profit and attain high densities). This was not the case. Positive correlations were in the majority, although this predominance disappeared after correction for the most important environmental factor (winter temperature). This result does not rule out the possibility that intra-specific competition (which may, for example be a result of unexpectedly strong niche partitioning) is the predominating regulating force in this community.

I attempted to shed some light on the question of how strong are the links between populations in a real community. Are the time series of a single species and the fluctuations therein mainly the result of intra-specific processes and environmental factors operating in a density-independent way? Or do inter-specific processes (competition, predation, mutualism, ecosystem engineering) play a roles a well? This is hard to resolve particularly if available data are sparse and noisy.

Trends in sardine catches and “mare sporco” in the Adriatic

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Time series analyses of meteorological, oceanographic, and other kinds of geophysical data with annual values almost always yield a small number (usually only two or three in time series of the order of a century or so in length) of statistically significant multiannual signals. Similar results have been obtained too with many kinds of economic and biological time series (e.g., commodity prices, annual yields of fisheries, tree ring widths,...). Acceptance of these signals as real features of the temporal variability of these time series is reinforced by the fact that their periods are usually about the same in apparently independent series from all over the world, and that their phases appear to exhibit similarly intriguing (but often perplexing) relationships. Furthermore, since all these time series are “red”, meaning that power increases as recording periods lengthen, the few common signals present tend to bear the same power relations to each other. Most of the variance is at lower frequencies: commonly found signals are listed in Table I. The main signal found in time series around 100 yr long has a period near 18-19 yr, and is usually identified with the lunar nodal cycle of period 18.6 yr, or with the Hale solar cycle of 22 yr. A signal around 10-11 yr is also common, and attributed to the sunspot cycle (which varies between 6 and 14 yr, although the solar rotation rate is constant; Ulrich and Bertello, 1996). It is important to note that sources of error in time series which do not have narrow band line com-

Table I. Cycles which appear with high frequency in geophysical records. Quotations from Burroughs W.J., 1992.

name	period, yr	notes
Quasi-biennial oscillation, QBO	2.2-2.8	Stratospheric winds.
Sunspot cycle	≈ 11	Strong link with QBO; “*one of the strongest candidates for inclusion in a short list of confirmed cycles*”.
Nodal cycle	18.6	Most important multiannual lunar tidal component; evidence that it modulates weather is ubiquitous and “*appears to be formidable*”.
Hale cycle	22	Not easily distinguished from nodal cycle.
Gleissberg cycle	≈ 80	Strong in some long records (e.g., Central England Temperatures, Nile floods).
Suess or de Vries cycle	≈ 200	Found in auroral records, tree ring series, Scandinavian herring records,...

ponents increase variance over a broad bandwidth, so that the variance estimates at discrete frequencies in time series are minimal values. As an example of the ubiquity of the nodal signal, Robert Currie, who analysed thousands of time series worldwide using maximum entropy spectral analysis (MESA), and including about 14 600 United States rainfall records, found the signal in 10 200 of them (Currie, 1981; Currie and O'Brien, 1988). The same signal appears in records of sea surface temperatures, varves, river discharge volumes, sea level records, extent of sea ice, volcanic dust veil indices, tree ring widths, fish stock records, shellfish toxicity levels, dates of the vendange, and elsewhere.

Some of these records (air temperatures, rainfall, sea levels, tree rings) refer to precise localities, but others represent integrated data from areas of varying size; thus river discharge usually integrates the rainfall of an entire watershed, and fisheries yields often refer to management areas. This difference is important since only the former, when data from a geographical network of localities are available, can yield detailed spatial patterns. With a few exceptions, most of the information available from the marine environment, like fish catches, are in the second category, although this is now changing as coastal monitoring becomes more widespread.

Why is it then that studies of these cycles are so often marginalized (Burroughs, 1992)? Monthly tidal cycles (lunar), annual cycles (solar), and Milankovich cycles (orbital) are widely accepted as generating forces to which populations have adapted, but cycles which create forces on decadal or secular time scales are generally not. There are several reasons. The principal one is that the methods used are not always powerful enough to distinguish signals of similar period, such as the solar Hale and nodal cycles, and thus fail to provide unambiguous guides to the forcing involved; furthermore, information is degraded by using linear procedures to analyse nonlinear series, so that accurate identification of signal period and power content is not achieved, and phase data are lost. It is often difficult to persuade the sceptical mind that time series are not simply the products of "random noise". This stance usually fails to note that a "pure signal" such as a sine wave is almost no signal at all since it contains virtually no information; it only becomes music when subjected to frequency and amplitude modulation. The spectrum of a major or minor triad is mere noise in this view. Now however that the importance of tidal energy dissipation in the ocean has once more come to the fore (with the imprimature (!) of Walter Munk and Carl Wunsch, 1998; see also Wunsch, 2000), there is hope that these signals will receive more attention. It is also frequently demonstrated that signals emerge from artificial time series constructed with random numbers; this is not in doubt, but raises questions like why are signals of the same periods found in so many series, and is the central limit theorem an appropriate model for how the planet works. Rudnick and Davis (2003) who provide one of the most recent warnings against accepting multiannual signals end by writing: "*The climate record is replete with changes not easily explained as the Gaussian behavior of a linear process*". It is accepted here that nodal and solar forcing may eventually be shown to provide the forcing which generates the signals found in so many time series.

Figure 1 shows the discharge rates of some European rivers. The data have been smoothed with a low pass filter, and show remarkably clearly that most of the power lies in a frequency band around 20 yr, with some higher frequency modulation. Analysis shows that decadal and bidecadal signals account for a significant proportion of the variance in all these series. In an Adriatic context, looking at the curve for the Po River, we might anticipate for example that its plume had a more marked impact on the neighbouring coastal waters in the 1930s, and between about 1955 and 1965, than in the intervening years. A second obvious feature of these curves is that there are differences in the years in which the dominant signals reach their maxima and minima. These are due partly to the way in which the two signals sum, and also to phase reversals.

Figure 2 illustrates these phase reversals for another time series, the dates of the vendange for French wines from the late fifteenth to the twentieth century (1484 to 1977). The data are composite (several vineyards are combined to obtain a continuous series); the original dates were compiled by Leroy Ladurie (1983). The analysis is from Currie *et al.* (1993). We see that the nodal (here labelled luni-solar) and solar cycles both exhibit phase shifts (*) of 180 degrees, so that the maximum impact of the forcing is either in phase or out of phase with the epochs (⇑,⇓). The phase reversals occur at intervals of the order of a century or so, and provide evidence of

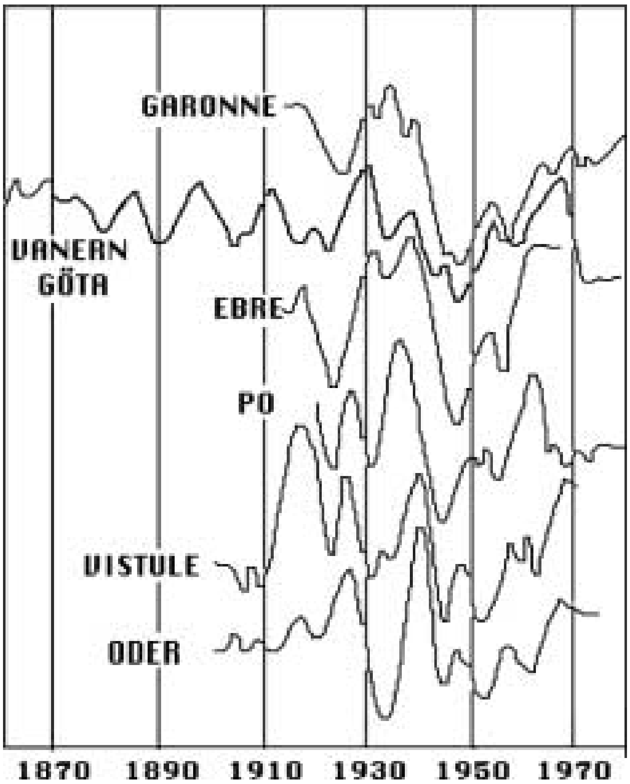

Fig. 1. Smoothed discharge rates of some European rivers (modified from Tardy, 1986).

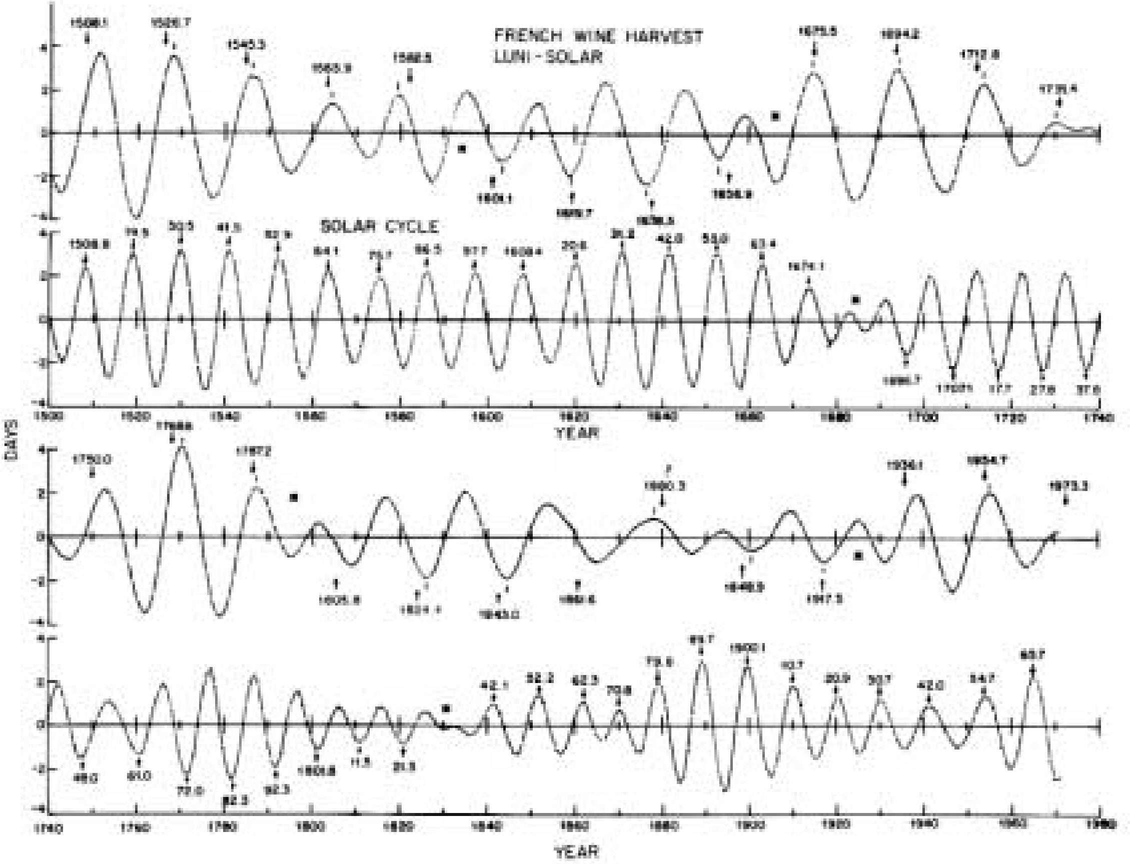

Fig. 2. Nodal (upper) and solar (lower) signals extracted by MESA from time series of dates of vendange in some French vineyards (data from Leroy-Ladurie, 1983; analysis from Currie *et al.*, 1993).

what signals engineers call a low frequency carrier. We can also see that the impact of the two signals increase to a maximum approximately midway between phase shifts, as expected if there is an underlying carrier. It is against this background that we can look at two sets of data from the Adriatic Sea, "mare sporco" on the one hand, and the records of the sardine fisheries.

The curious mucilaginous events known as "mare sporco" occur mainly along northern Adriatic shores from Istria to Rimini and Ancona, a distance following the coast of about 400 km. They parallel the saline front which hugs this coast. These have attracted scientific curiosity since at least the eighteenth century (Fonda Umani *et al.*, 1989), and unpublished records indicate that the phenomenon was known at least as far back as mediaeval times (Molin *et al.*, 1992). In fact, the antiquity of "mare sporco" is clear from historical documents which indicate that it had a significant impact on the cultural and social life of coastal communities in northeast Italy, mainly as a result of its occurrence being inimical to fishing, as various rites, supplications, and other customs attest.

Various attempts to account for "mare sporco" have been published, but no agreement on the mechanisms responsible has yet been reached. Both high and low nutrient availability have been invoked (Degobbis 1989; Vollenweider *et al.*, 1995; Tomasini 1996; Thornton *et al.*, 1999), as well as annual fluctuations in runoff and vertical mixing. Supic *et al.*, (2000) suggest that a strong countercurrent along the Istrian coast has been associated with "mare sporco" since 1966. Appeals to the availability of phosphorus, sulphur and calcium have been made. Flow of the Po River may be important, or perhaps is not. Whatever the causes of these events ultimately agreed upon, we do know that there was a long period, from around 1880-1905 until 1977-1997, when "mare sporco" was less widespread. But the 1920s and 1930s witnessed spatially restricted outbreaks off Rijeka (1929), Rovinj (1922) Trieste (1921, 1924, 1930) and Venezia/Choggia (1927, 1935, 1941). So there are weak hints of decadal scale fluctuations in the abundance of mucilage which may be related to discharge rates from the Po River, and a chance that secular trends might be identified with further archival delving.

A qualitative history of the fortunes of the sardine fisheries based on eastern Adriatic shores (that is, beyond the area influenced by "mare sporco"), which extends back to the early sixteenth century, was compiled by Zupanovic (1968); he also provided quantitative data from 1873 to 1960. Table II is translated from table IV (p. 468) of Zupanovic's monograph; it provides rough indications of whether the fishery was good or bad, and shows that these fortunes were in phase

Table II. periods of good and bad sardine catches in Japan and eastern Adriatic from Zupanovic (1968).

Years, AD	**Japan, *Sardinops***	**Adriatic, *Sardina***
About 1500 to 1600	catches increasing	good catches, especially from 1533 to 1588
1660 to 1730	good catches in Iyosi, from 1680 elsewhere too	good catches, especially after 1670
1716 to 1724	extremely good catches	extremely good catches, 1718 to 1725
1736 to 1789	poor catches, especially from 1768 to 1780	poor catches, 1730 to 1780 very poor at Vis and Hvar around 1775
1818 to 1859	good catches, especially around 1830	good catches, extremely good between 1830 and 1840
1870 to 1890	poor catches, very poor 1884 to 1888	poor catches except 1875 and 1876, extremely poor at Vis from 1878 to 1882
1917 to 1921	good catches in Japan Sea	good catches in Istria, 1919 to 1921
1923 to 1928	poor catches	poor catches
1929 to 1939	very good catches	very good catches
1941 to 1947	poor catches	poor catches, 1946 to 1948
1951 to 1957	poor catches, but better in northern part of Japan Sea	poor catches, but better in Istria, worse in Dalmatia and Montenegro

with a similar compilation concerning the Japanese sardine fishery, at least at this level of temporal resolution. Further details of this kind of synchronicity for the 1970s and 1980s are given by Bakun (this volume).

Figure 3 shows the numerical data of Zupanovic. This has been analysed using the wavelet method by Harald Yndestad, and the main results are shown in figure 4. There are three strong signals at 6, 18, and 55 yr, but no solar signal was identified. The phase of the 18 yr cycle shows maxima in 1908, 1925, and 1953, and minima in 1916, and 1942. There is also an obvious phase shift between 1880 and 1900. Thus the trends in this time series are of the kind seen in most of the records already briefly mentioned.

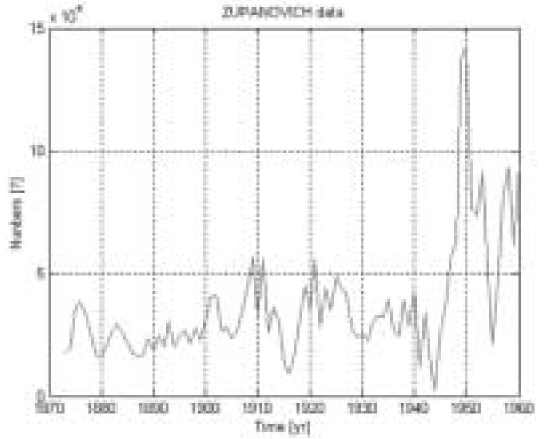

Fig. 3. Annual sardine yields from eastern Adriatic (Zupanovic, 1968).

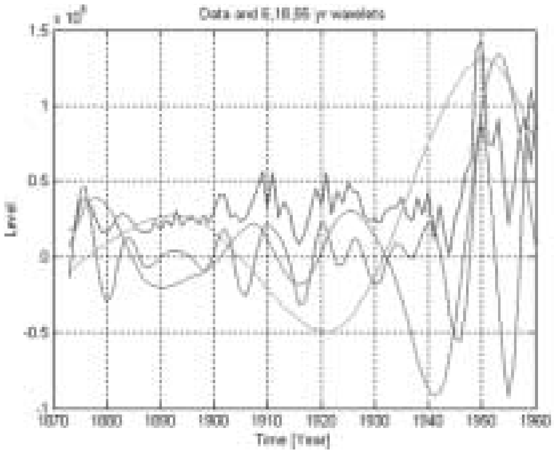

Fig. 4. Wavelet analysis of Adriatic sardine yield data: the annual catches and the 6 yr, 18 yr and 55 yr wavelets are shown. The analysis is by Harald Yndestad.

Ravier and Fromentin (2001) collected records of trap fisheries for bluefin tuna (*Thunnus thynnus*) in the Mediterranean and adjacent Atlantic, some of which extend back to the sixteenth century. With these records, they were able to show that there have been fluctuations in abundance on time scales of 100-120 years (fluctuations on this time scale can also be discerned in the vendange series of Fig. 2 above), and about 20 years, which together account for 45-80% of the variance. The trends on these time scales are synchronous at all locations, but the short term variability is only structured at scales less than 200 km. There were high catches in the years 1630-1650, 1750-1770, and 1870-1890, and low catches in 1690-1710, 1790-1810, 1910-1930.

The sardine data examined here suggest that patterns found in many geophysical and biological time series worldwide may be also characteristic of the Adriatic. The "mare sporco" data are too "thin" to judge in this context, but given that the countries bordering the Adriatic have rich historical resources which have so far hardly been exploited by marine ecologists, it seems possible that dedicated effort could turn up much more information with which to pursue such studies. Ravier and Fromentin have set a challenging standard for such studies of Mediterranean ecology.

System modeling of biological time series in the Mediterranean Sea

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The Mediterranean Sea represents a complex dynamic process. The paper describes a system modeling approach of how to start modeling this complex system. The method focuses on the importance of asking fundamental questions, modeling by general system theory and the importance of understanding the time variant properties statistics in time series.

INTRODUCTION

Time series from the Mediterranean Sea represent only small reflected indicators of what is going on in a complex dynamic system. When we analyze these time series, we have to understand the fundamental properties underlying the time series and the models that represent.

Thus in order to improve our understanding and our medium-term forecasting capacity, we need not only long time series, but also a deeper knowledge of the ocean dynamics, the influence of climate fluctuations, the eigen-dynamics of each species in the food-chain, the dynamic relation between the species, and the influence of catch.

There are no straightforward methods to solve this problem. In Norway there is a large research program under plan to understand the biomass dynamics in the Barents Sea (Svendsen, 2002). This approach is based on integrated dynamic models of the ocean, plankton, fish, and other predators, and biomass quota of landings. This author has worked on a different approach to solve this problem. Based on the idea that if the biomass dynamics is controlled by a fundamental deterministic cause, we may forecast future biomass fluctuations. In this case I have identified a relation between the 18.6 yr tide and the fluctuation of Northeast Arctic cod, herring and Barents Sea capelin (Yndestad, 2003a, 2003b).

While the Mediterranean Sea and the Barents Sea are clearly different ecological systems, there may be similarities in how to address the problem. This paper presents a set of questions and ideas that should be addressed before starting modeling the Mediterranean Sea ecology system.

MATERIALS AND METHODS

A first step in the analysis is to ask some fundamental questions :

1 - Is this a deterministic system?

2 - If it is deterministic, what is the fundamental drive behind the deterministic process?

3 - What is the reasonable time scale of a fundamental dynamic process?

4 - Is the biomass a stochastic stationary process?
5 - Is the biomass a time variant process?
6 - If it is a time variant process, what is a reasonable time of useful history data?
7 - Are fluctuations reflecting data noise or a fluctuating biomass?
8 - Is there a correlation between cause and effect in the food chain?
9 - What are the available data series?
10 - Is there a relation between a set of indicators?

General System theory

General System theory is a holistic approach of modeling biomass systems. System Architecture is a set of mutual related subsystems. A system S(t) may be represented by :

$$S(t) = \{B(t),\{S_1(t), S_2(t),,,S_n(t)\}\} \text{ Œ } w \qquad (1)$$

where $S_n(t)$ represents the n-te subsystem, B(t) represents the mutual binding between the subsystems and w is the purpose. A system element $S_i(t)$ may represent an organization from nature, a man made system, a substance, and any type of abstract organizations. The chosen system elements in the system S(t) are dependent on the system model purpose w. The binding B(t) may represent a force, a flux, or any type of relation that influences related system elements. A time variant binding B(t) will introduce a time variant and structural unstable system. Equation (1) indicates that science is dealing with concepts.

So, when “*testing ecological theories*” the ecological theories are dependent on the chosen elements in a system. An incomplete model will introduce noise or disturbance from an unknown source.

A subsystem $S_i(t)$ may be modeled by a new set of subsystems represented by the simplified architecture

$$S_i(t) = \{B_i(t),\{S_{i1}(t), S_{i2}(t),,,, S_{im}(t)\}\} \in w \qquad (2)$$

where $S_{im}(t)$ represents the im-te subsystem and $B_i(t)$ represents the mutual binding between the subsystems. The sub system $S_{im}(t)$ may be modeled by a new set of subsystems. A system model thus is dependent on the model system abstraction level. This means that the explanations of dynamics in nature are dependent on the integration of events in a system level. Equation (2) indicates that concept models are dependent on the abstraction level.

So, when “*testing ecological theories*” the ecological theories are dependent on the chosen abstraction level in a system.

The system dynamics

According to (1) and (2) we may expect a time variant binding B(t) between the system elements. This indicates we may expect
1 - a time variant stochastic system;
2 - time variant parameters in all models;
3 - no mean values in the system;
4 - no stationary biomass safe limits.

In a time variant system, the phase of dominant cycles are of most importance. The phase of dominant cycles may be studied by
1 - a wavelet spectrum analysis of time series;
2 - the relation between wavelet cycles in a mutual related system.

The driving force in the wavelet analysis can be estimated, then there is a possibility of long-term forecasting.

MODELING THE MEDITERRANEAN SEA

A simplified system model as shown on Figure 1 may represent the Mediterranean system. This system may be represented by the system elements

$$S_{Med}(t) = \{B_{Med}(t),\{S_{Climate}(t),S_{Ocean}(t),S_{Plankton}(t),S_{Biomass}(t),S_{Animal}(t),S_{Landings}(t),S_v(t)\}\} \in w \qquad (3)$$

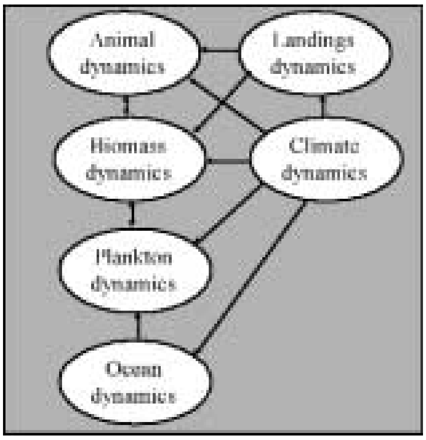

Figure 1. A simple Mediterranean system model

where $S_{Climate}(t)$ represents the climate system, $S_{Ocean}(t)$ represents the ocean system, $S_{Plankton}(t)$ represents the plankton system, $S_{Biomas}s(t)$ represents the plankton system, $S_{Animal}(t)$ represents the animal system, $S_{Landing}(t)$ represents the landing system, $S_v(t)$ represents disturbance from an unknown source and $B_{Med}(t)$ represents the mutual binding between the systems.

The objectives of the workshop included the applicationof time series to the testing ecological theories and to the improvement of short- and medium-term forecasting.

Testing ecological theories requires a holistic approach as described in Eq. (3). This implies that we must understand the dynamics of each system element in the system model (3), as well as the mutual dynamics controlled by the time variant binding $B_{Med}(t)$.

Short- and medium-term forecasting is dependent on
1 - the eigen dynamics in the system element;
2 - how the system is controlled by external system;
3 - the model abstraction level;
4 - sampling in time and space.

This means that we have a complex system, and we have to make some choices.

What are we looking for?

What are we looking for when we have a complex time variant system?

The answer is that we are looking for something deterministic in a time variant process.

More questions

When we are looking for something deterministic, it may be a good start to ask new questions about the system elements.

The climate dynamics

1 - Do we have some long climate indicator time series?
2 - Are there deterministic cycles in the climate indicator time series?

Ocean dynamics

1 - What are the large-scale circulation patterns, cycle time and cycle phase?
2 - What are the sub-basin scale circulation patterns, cycle time and cycle phase?
3 - What are the mesoscale circulation patterns, cycle time and cycle phase?
4 - What are the tide cycle time and cycle phase?
5 - Is there a vertical tide in the oceans?

Plankton dynamics

1 - What are the relations between plankton dynamics and ocean dynamics?
2 - What are the relations between plankton dynamics and climate indicators?
3 - What are the relations between plankton dynamics and seasons?

Biomass dynamics

1 - Why are there so many different species in the Mediterranean Sea?
2 - Why have the species a short life cycle time?
3 - Have most species the same spawning cycle time?
4 - Is there a relation between the species life cycle time and an ocean circulation cycle time?

Animal dynamics

1 - What are the relations between animal dynamics and biomass dynamics?
2 - What are the relations between animal dynamics and climate dynamics?

Landings dynamics

1 - What are the long history records of catch?
2 - What are the relations between long history records and climate dynamics?
3 - What are the official landing dynamics?
4 - What are the expected lading dynamics?
5 - What are the relations between landing dynamics and population dynamics?
6 - What are the indirect indicators of biomass catch?
7 - When we have some answers to these questions, the time has come to make an integrated-model.

DISCUSSION

Testing ecological theories needs a holistic view of the dynamic ecological processes on all levels. A holistic view of dynamic processes requires access to on a common pool of data. This means that marine scientists around the Mediterranean Sea must develop the sharing of data series.

The climate hypothesis

My analysis of biomass fluctuations in the Barents Sea has identified a relation between the biomass fluctuations, long-term tides and the Arctic climate. Time series presented on the workshop (Wyatt, this volume) indicated a fluctuation in the sardine biomass which had an opposite phase compared to biomass fluctuations in the Barents Sea. This indicates that the biomass growth in the Mediterranean Sea is controlled by deterministic climate fluctuations. A potential source of this climate fluctuation is reflected in the NAO winter index, which has an opposite phase in the Mediterranean Sea and in the North Atlantic Ocean. If this climate hypothesis is confirmed, the modeling of the Mediterranean Sea ecological system will be much simplified, and there would be no need for complex biomass modeling (Svendsen, 2003) as each biomass may be modeled by a climate driven model (Yndestad, 2003a, 2003b).

Application of a multivariate mapping method to detect changes and spatial-synchrony in phytoplankton composition at different temporal scales

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INTRODUCTION

Ecological time-series can serve several purposes: survey, better understanding of ecosystems dynamic, forecasting, etc. Ecologists are often interested in assessing cyclic patterns or interannual trends, identifying characteristic periods, detecting discontinuities, correlating variations in a series with changes in other series, formulating a forecasting model (Wyatt, this volume; Lloret, this volume). Analysis of time series reveals that ecological phenomena are largely influenced by geophysical rhythms, solar or lunar periods. This stage of observations and correlations is the first step to a better understanding of the changes, but when this framework of time-series analysis is applied to aquatic ecosystems, additional difficulties may arise, due to complex interactions between and within abiotic and biotic components. These interactions occur over a range of scales; interactions can be intense on certain scales and not on others. Consequently, the studies of scales in ecology are emerging and several techniques (semivariograms, fractals, multifractals…) are used to describe how patterns change across scales (Seuront and Schmitt, this volume). Other innovative approaches deal with the detection of shifts in the timing of recurrent events or in temporal and spatial associations (Beaugrand *et al.*, 2002). Indeed, changes in the phenology of the annual plankton successions have provided further understanding on the “phosphorus-phytoplankton paradox” in Lake Geneva (Anneville *et al.*, 2002a), underlined the influence of large-scale climatic changes in the dynamic of aquatic system (Straile *et al.*, 2003) and can serve as a basis to better understand recruitment fluctuations of fishes larvae (Nyberg *et al.*, 2001; Gerdeaux, in press).

Understanding the dynamics of aquatic communities at several scales requires multivariate statistical methods that treat several dimensions simultaneously. Souissi *et al.* (2001) recently proposed a multivariate mapping method that combines hierarchical clustering, Bayesian probability and the determination of species associations (Souissi *et al.*, 2001). The first applications of this method concerned the spatial mapping of fish assemblages (Souissi *et al.*, 2001) and phytoplankton associations (Ben Hamadou *et al.*, 2001).

We show in this paper that this method can be adapted to analyse long-term time series obtained from monitoring programs of water quality of lakes (Anneville *et al.*, 2002b). This paper provides two examples of applications through which we aim to illustrate the relevance of this method for the analysis of community changes and mechanisms underlying observed patterns. In the first example the method assesses temporal changes in phytoplankton composition of Lake Geneva. In the second example the method is deployed to analyse the spatial-coherence in phytoplankton changes in three neighbouring basins (Lake Walen and the two basins of Lake Zurich).

METHOD

Study sites

Lakes Geneva, Zurich and Walen are pre-alpine lakes located within a 200 km area and subject to similar meteorological influences. Long-term trends in water temperatures are similar, showing two coinciding periods: a cold one 1976-1987 and a warm one 1988-2000 (Fig. 1A). Lake Geneva is larger and deeper than Lake Walen and Lake Zurich, which is separated into two basins by a natural dam. The lakes are all monomictic and hardly ever freeze. However, mixing does not affect the entire column every year.

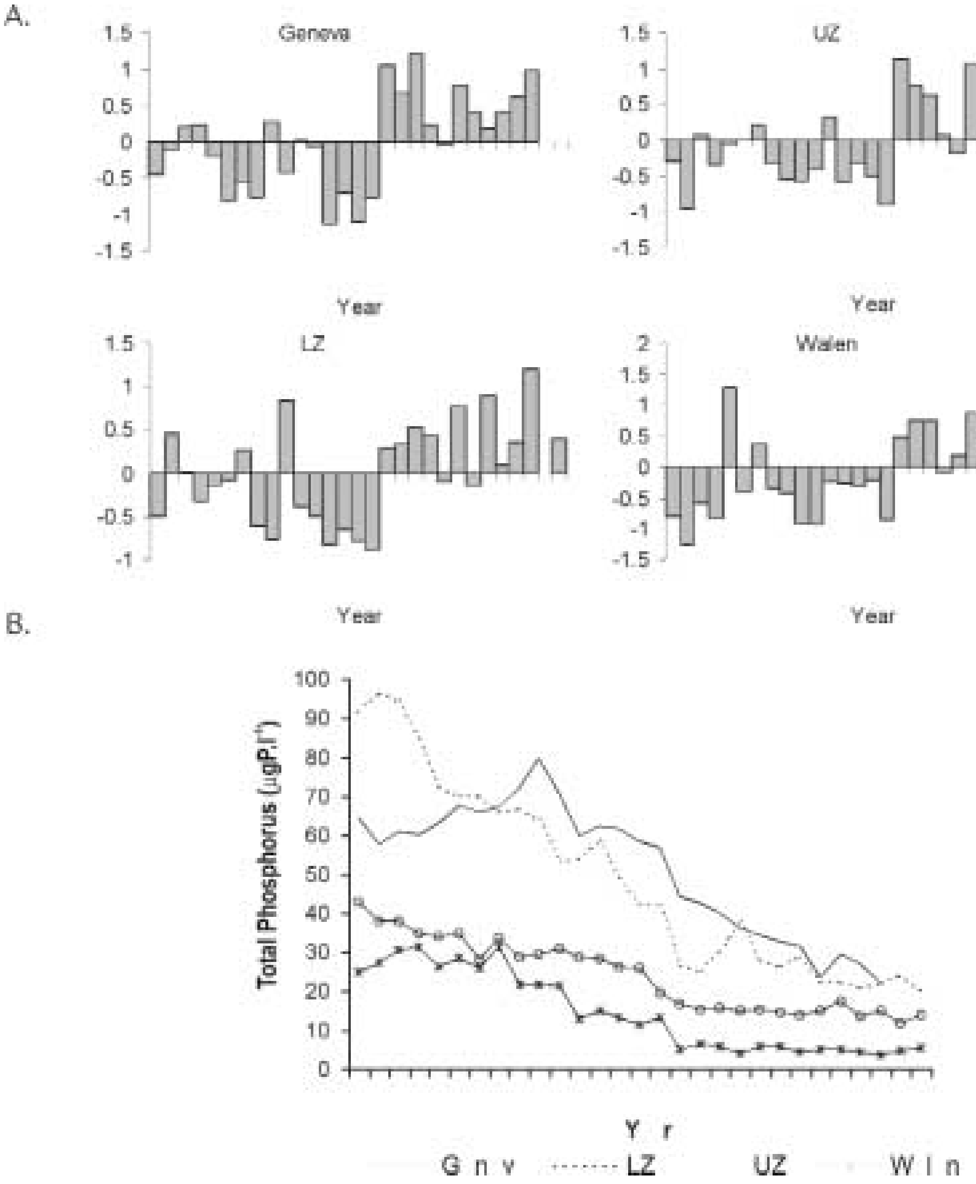

Fig. 1. **A)** Water temperature anomalies recorded in the upper 10m in: Lake Geneva, Lower Lake Zurich (LZ), Upper Lake Zurich (UZ) and Walen from 1974 to 2000. **B)** Long-term changes in total winter phosphorus concentrations in Lake Geneva, Lower Lake Zurich, Upper Lake Zurich and Lake Walen from 1974 to 2000.

These lakes have been under a long-term monitoring program since the beginning of 1970s. Local management measures have lead to declines in phosphorus concentrations (Fig. 1B). Phosphorus concentrations have been reduced by half, and these lakes now range from mesotrophic to oligotrophic states.

Data series of physical, chemical and biological parameters were available for all the lakes dating back to the ‘70s (Table 1). The sampling stations were all pelagic. In Lake Zurich, sampling occurred at two stations, one localized in the lower basin (LZ), the other in the upper basin (UZ). Physical and biological parameters were measured once a month in Lake Zurich and Walen. In Lake Geneva, sampling was performed once a month from 1974 to 1980 and then twice a month.

Table 1. Morphological attributes (area, maximal and mean depth), trophic state of the study lakes and years for which data on phytoplankton composition are available.

	Lake area (km^2)	**Max depth (m)**	**Mean depth (m)**	**Data available for the phytoplankton**	**Trophic state**
Lake Geneva	582	309	153	1974-2000	Eutrophic - Mesotrophic
L. Lake Zurich	65	136	51	1972-2000	Eutrophic - Mesotrophic
U.Lake Zurich	20	48	23	1972-2000	Mesotrophic - Oligotrophic
Lake Walen	24	145	103	1972-2000	Mesotrophic - Oligotrophic

In Lake Zurich and Walen, phytoplankton samples were taken in the first 20 meters (sampled at nine discrete depths between surface and 20 m) and average values of the uppermost 20 m are considered in this analysis. In Lake Geneva, water samples for estimating phytoplankton species and biomass were collected in the ten upper meters using an integrating device (Pelletier, INRA patent 1978). In all cases, phytoplankton identifications and cell counts were carried out in sedimentation chambers under an inverted microscope (Utermöhl, 1958). Species biovolumes were derived from cell numbers and mean cell volumes using geometrical models. The total biomass was then estimated by adding the biovolumes for each species, assuming a fresh weight of $1\ g \cdot cm^{-3}$. For spatial-coherence analyses in lake Zurich and Walen, the species were gathered by genera in order to homogenize the database and to reduce error in species identification.

2. General principle of the statistical method

The statistical method makes it possible to characterize phytoplankton assemblages and to compute the probabilities for given assemblages to occur. By keeping and mapping the information obtained at the sampling frequency time scale, it provides a new way of analysing temporal successions of these assemblages at both the annual and seasonal scales. The method has been described in detail elsewhere (Souissi *et al.*, 2001; Anneville *et al.*, 2002b). Here we give a brief summary.

In order to outline the pattern of taxa occurrences and minimize the noise generated by rare taxa, only the more frequent ones have been included in the analysis. The matrix is composed of the taxa as variable and the sample as object.

(a) A principal component analysis (PCA) was applied to the log-transformed data in order to obtain the multinormality required for the computation of the Bayesian probabilities.

(b) Hierarchical clustering, with Euclidean distances and flexible linkage was performed on the first axes of the PCA scores, which account for a great part of the total variance and fulfil the required multinormality condition for Bayesian probability computation (Souissi *et al.*, 2001).

(c) The probability that a given sample belongs to a specific cluster was computed for each sample. For the analysis of Lake Geneva´s time-series, the samples were reallocated when the maximum value of the conditional probability of a sample was obtained for another cluster. This analysis was performed for several successive hierarchical levels of the dendrogram.

(d) The advantage of using dendrograms is that different “resolutions” can be obtained from the dataset depending on the choice of cut-off level, i.e. the first cut-off level produces two clusters, the next level produces three clusters, etc. For each cluster of samples obtained at each resolution (cut-off level) a map of isoprobabilities is created for each lake. These maps describe the seasonal (on the abscissa) and interannual (on the ordinate) patterns of the probabilities of occurrence.

(e) After mapping the temporal patterns of the clusters the genera that best characterize each cluster were identified by using the indicator value index (IndVal) proposed by Dufrêne and Legendre (1997), as in the case of Souissi *et al.* (2001) and Anneville *et al.* (2002b). This index measures the specificity (measure of affiliation) and fidelity (measure of occurrence) of a taxa for a group. The taxa which best characterize a cluster are those which present a high IndVal. The set of taxa with the highest IndVal makes up a phytoplankton assemblage. To characterize an assemblage we retained the taxa with an IndVal above the arbitrary threshold of 25%. If a cluster has no indicator taxa with IndVal greater than 25%, this means that the phytoplankton communities in the samples making up this cluster were not sufficiently similar or specific to identify taxa with high fidelity and specificity indices.

At this stage, a phytoplankton assemblage then characterizes each cluster. The maps of isoprobabilities created for each cluster can be interpreted as a temporal map for the pattern of the corresponding phytoplankton assemblage.

RESULTS

Example 1. Phytoplankton succession in Lake Geneva: evidence for synergism between abiotic and biotic forcing

The hierarchical classification of samples produced a dendrogram and the level resulting in seven coherent groups of samples was chosen for the analysis. Indicator value indices for phytoplankton species were computed for the seven groups. Seven phytoplankton assemblages were thus identified. A phytoplankton assemblage is supposed to occur when it presents a greater probability than the other ones. Mapping their pattern of occurrence shows a seasonal dynamic which was characterized by the following sequence (Fig. 2): assemblage I (AssI) characterized by the diatoms *Stephanodiscus neoastraea*, followed by AssII characterized by species which are mainly nanoplankton and edible by the zooplankton. Then comes AssIII (the clear-water phase), which makes the transition to AssIV, which is characterized by a diversity of morpho-physiologic traits. Next comes AssV, which is characterized by mainly microplankton species whose morphometric characteristics limit their sedimentation or grazing losses, and finally AssVI or AssVII, depending upon the year.

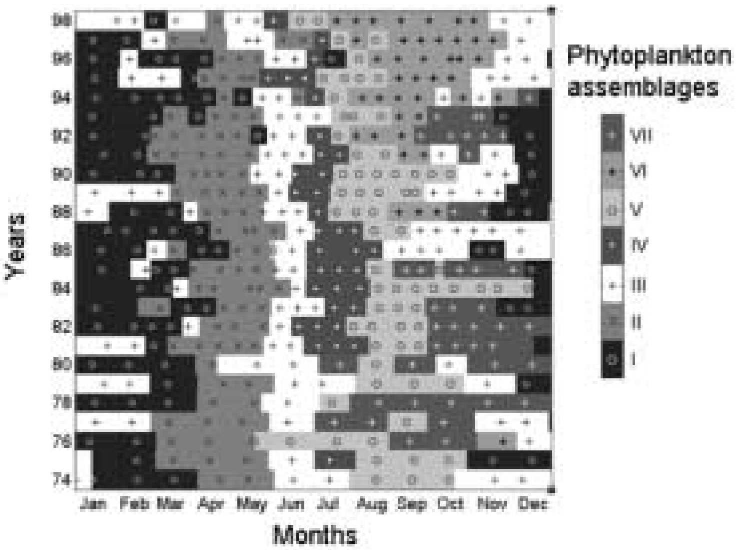

Fig. 2. Temporal map describing the seasonal (abscissa) and inter-annual (ordinates) phytoplankton assemblage successions in Lake Geneva. Each phytoplankton assemblage is represented by a grey level. A phytoplankton assemblage occurs when it presents the maximal probability (from Anneville *et al.*, 2002).

This sequence tended to recur over the 25-year period studied, but two major modifications of the general seasonal pattern stand out at the inter-annual scale (Fig. 3):

- We observe changes in the timing of occurrences: despite the low sampling frequency of the survey (one or two samples a month), AssII has been disappearing earlier since 1988, whereas AssV has been appearing earlier. The early disappearance of AssII and the appearance of AssIII as early as May, coincide with the milder winters and springs observed since 1988. Warm aver-

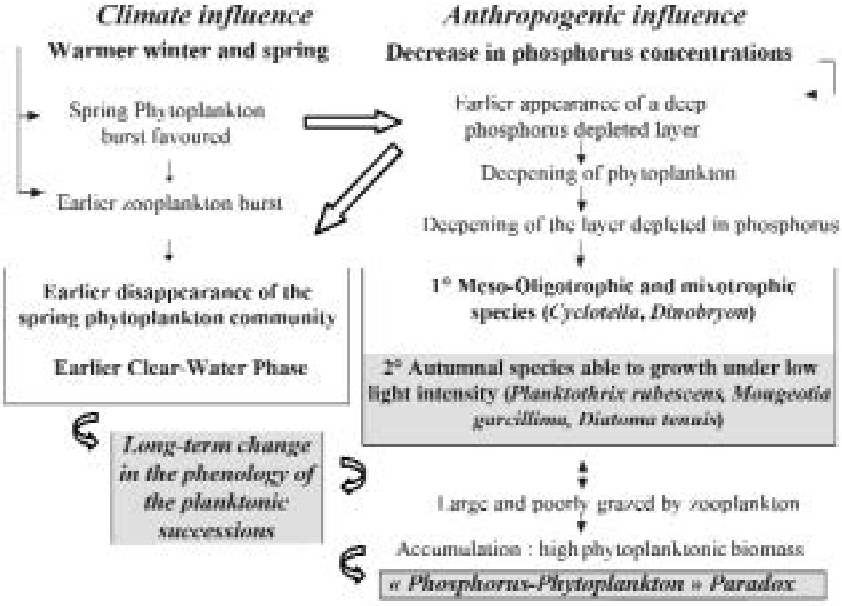

Fig. 3. Synthesis of the long-term changes observed in phytoplankton communities and conceptual schema for explaining long-term changes in the phenology of the successions and the maintainance of high phytoplankton biomass despite the decrease in P-concentrations.

age air temperatures are correlated with high values of the North Atlantic Oscillation index (NAO index), which also influenced water temperatures in several other European lakes (Straile *et al.*, 2003). Warmer winters and springs favor zooplankton growth. Indeed the date of the zooplankton burst appears to be closely correlated with the air temperature index ($p<0.001$). The date of the zooplankton burst is also correlated ($p<0.01$) with the last day with a phytoplankton AssII. Like in other European lakes (Straile *et al.*, 2003) changes in the timing of the clear water phase is thus the consequence of warmer winters and early spring meteorological conditions, which promote the development of zooplankton and enhance their grazing pressure (Fig. 3). Furthermore, the precocity in zooplankton burst is supposed to influence fish communities by enhancing the recruitment of spring haching species (Gerdeaux, in press).

- Since 1988, AssVI has become more frequent and colonizes the lake throughout summer. On the annual scale, AssV is thus being replaced by AssVI which tends to appear earlier and earlier. As a consequence, in the 1990s, the summer community was characterized from the month of July by a phytoplankton assemblage consisting of Diatoma tenuis, *Mougeotia gracillima* or *Planktothrix rubescens*, i.e. species that usually tended to be characteristic of the autumnal period and adapted to low light intensities. This “anomaly” coincided with the recent paradoxical increase in algae biomass despite a fall in phosphorus. The environmental parameter that distinguishes between AssV and AssVI is principally the depth of the DIP depleted layer. As a result of the synergism between the decrease in the loading of phosphorus into the lake and the high spring consumption favored by warm temperature, in the 1990s, the DIP depleted zone appears earlier and extends deeper in the water column (Fig. 3). Later, when the phytoplankton community is characterized by AssVI, the zone of severe DIP-depletion extends down to a depth of 30 m in summer. However, whereas DIP concentrations are very low in the surface water, they are still high in deeper layers, and local water mixing resulting from the breaking of internal waves is likely to supply the metalimnion with phosphorus. In such an environment, species localized in the water layer where there are episodic incursions from the deep richer layers may be able to gain some advantage. Indeed, as in other lakes in the process of oligotrophication, the actual trend in Lake Geneva is effectively a fast deepening of the phytoplankton. And, because light becomes a critical factor with increasing depth, in such an environment, the most appropriate adaptations are those of a good light-harvesting antenna and of an adaptive ability to increase the cell-specific photosynthetic capacity. Furthermore, since these species are large and not well grazed by the zooplankton, they can easily accumulate and lead to the high biomass observed last years (Fig. 3).

Exemple 2. Phytoplankton successions in Lake Walen and the two basins of Lake Zurich: Evidence for spatial-coherence

The first eleven cut-off levels of the dendrogram were retained for the analysis. A majority of phytoplankton assemblages can be detected in all three lakes. However, their probabilities of occurrence strongly differ between the meso-eutrophic (LZ) and the two meso-oligotrophic (UZ and Walen) basins. Information about the patterns of occurrence for each assemblage is provided by the temporal maps of isoprobabilities (Fig. 4). For each hierarchical level, the occurrence

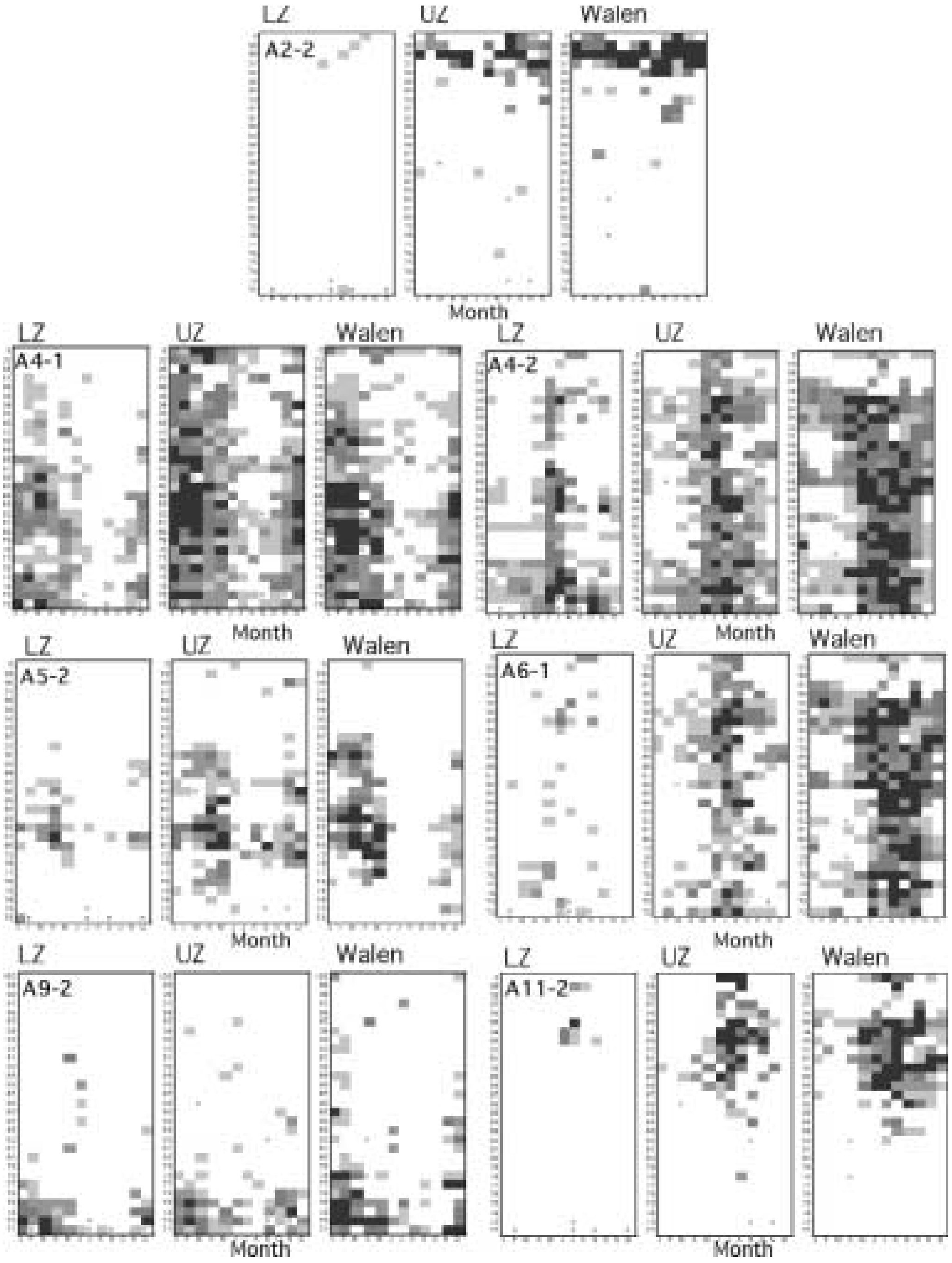

Fig. 4. Temporal maps of isoprobabilities describing the pattern of occurrence for phytoplankton assemblages A2-2, A4-1, A4-2, A5-2, A6-1, A9-2 and A11-2. In each map, the years from 1970 to 2000 are indicated along the ordinate and the months, from January to December, along the abscissa. The values of probabilities are represented by five classes from 0 to 1 by 0.2; the darker the pixels, the higher the probabilities.

of a phytoplankton assemblage is described via a probability value ranging from 0 to 1. Based on these probabilities, analysis of the temporal coherence is possible.

Most of the different phytoplankton assemblages described here display strong seasonal or/and interannual coherences in their pattern of occurrence among the lakes. According to the indicator species of the assemblages, the decrease in nutrient concentration appears to be a major factor of synchrony. Meteorological changes also have a synchronizing influence, at both the annual and inter-annual scales.

However, synchronous changes in composition do not necessarily imply the presence of the same phytoplankton assemblages. The temporal maps of assemblages show that synchronism can involve different genera (Fig. 5). Environmental factors first limit the composition to species able to inhabit a site. As a consequence, in neighbouring lakes influenced by similar large-scale factors, the evolutionary process can have different outcomes because of local physico-chemical and biological properties (Reynolds *et al.*, 2000). For instance, the middle of the 1990s was marked by changes in summer phytoplankton communities. Summers became characterized by A8-2 in LZ, whereas A2-2 appears in UZ and Walen. The appearance of these assemblages might be induced by a decrease in nutrient concentration, because the new assemblages are characterized by taxa that are more or less characteristic of oligo-mesotrophic waters. However, in LZ which is the more eutrophic, A8-2 additionally includes species (*Tabellaria, Fragilaria* and *Planktothrix*) able to tolerate low light intensities. The development of such taxa could be induced by a change in the vertical distribution of phosphorus and the presence of a metalimnic phosphorus-depleted layer while phosphorus concentrations remained high below the thermocline. Under such conditions species located at a deeper level, where light becomes a critical factor but where episodic incursions from deep, richer layers occur, might be able to gain some advantage due to their physiological ability to cope with low light intensity (Anneville *et al.*, 2002b).

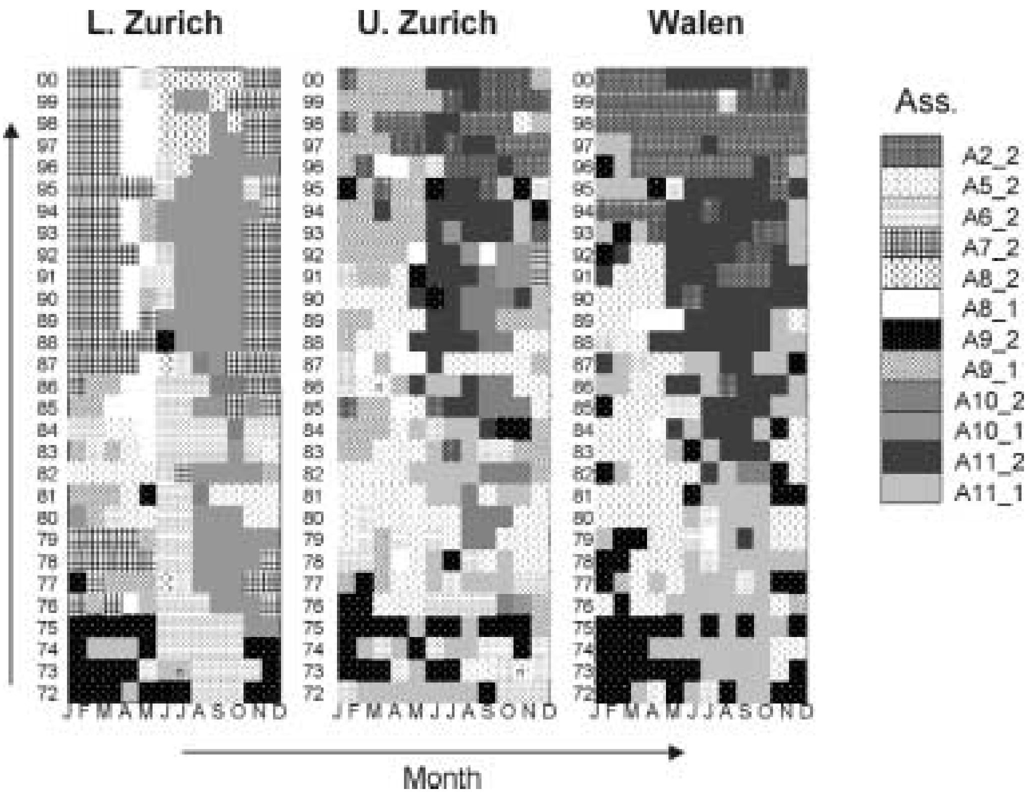

Fig. 5. Temporal maps of phytoplankton assemblage successions. Each phytoplankton assemblage is represented by a pattern. A phytoplankton assemblage occurs when it presents the maximal probability.

Such synchronism including different assemblages is also well represented at the annual scale, and a seasonal pattern involving different species assemblages can be drawn for each lake.

Phytoplankton species composition is often determined by a combination of several external factors. Consequently, environmental habitats of phytoplankton species should be regarded as a template of factors, in different environmental frames. Similar external large-scale drivers could thus place constraints on different resources and cause inter-lake differences in the best-fitted traits.

DISCUSSION

The eutrophication caused by excessive nutrients inflow into the lakes has been considered as one of the main ecological problems of the 20th century. During the past 30 years, loading from the sources of sewage and industry has been significantly reduced in Europe, North America and other industrial countries (Sas, 1989). As a consequence, phosphorus concentrations have substantially dropped in many lakes inducing significant changes in phytoplankton communities, which were usually at the origin of the problems. Meteorology also plays a major role in the dynamics of aquatic systems. Phytoplankton communities experience climate change indirectly through changes in lake level, ice-out time, stratification, nutrient inputs and zooplankton pressure (Straile *et al.*, 2003). These environmental changes affect species in many different ways, altering their productivity, their interactions with other species, behaviour and composition (Harrington *et al.*, 1999, Straile *et al.*, 2003). Understanding the combined effects of environmental drivers on species, communities and ecosystems is a key challenge for research management (Harrington *et al.*, 1999; Daskalov *et al.* this volume). Another challenge for research management concerns the understanding of temporal coherence (Magnuson *et al.*, 1990).

The usefulness of long time-series to achieve such goals is underlined by the present analyses. As quoted by several authors in this volume, long-term and comparative analyses of long-term dynamics can help obtain a more general understanding of changes with respect to external and internal drivers.

However, the observed variability of the system is conditional on the scale of description, and the scale of observation (spatial, monthly, annual, …) is generally deliberately chosen to elucidate key features of the systems. We should also recognize that changes are taking place on several scales at the same time. As a consequence, cross-scale studies appear to be important for the identification of the factors generating variability.

The method used in this paper presents an interesting tool to deal with this problem of scales and to analyse changes in biotic communities. The degree of morpho- and physiologic homogeneity within assemblages is still not clear (Zingone, this volume). However an approach based on species assemblages is theoretically interesting. Co-occuring species are supposed to share advantageous life traits which make them perform more effectively in the same environment. Consequently, changes in assemblages reflect changes in environmental parameters and consequent selection in favour to better-adapted species. Our results show that analyses of phytoplankton assemblages are a powerful way to detect spatial coherence in the phytoplankton community. While total biomass fluctuates without any synchronism, changes in assemblages occur at the same time.

Figure 3 illustrates how the complexity of the interactions within and between the biotic and abiotic components enhance the difficulty of distinguishing between climatic and anthropogenic induced forces. Long-term changes in phytoplankton communities appear as emerging from the collective behaviour of small scale changes promoted by the variation in environmental characteristic. Because communities show specific responses to environmental variables, changes not only affect the temporal association between species but also the interactions between different trophic levels. Temporal match of species occurrence with characteristic environmental conditions or with other species vary and this effect can spread to the upper trophic-layers (Gerdeaux, in press) and disturbs the functioning of the ecosystem (Straile *et al.*, 2003).

An ecosystemic approach that takes into account different components of the trophic level at different temporal scales appears to be more relevant for a better understanding of the dynamics of aquatic ecosystems and for developing the theoretical basis necessary to manage them. For future studies, it may be useful to know how changes in synchronization will affect population dynamics.

These latest remarks stress the need for maintenance of long-term physico-chemical and biological datasets and defining an appropriate sampling frequency which has to be high enough to deal with several temporal scales.

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How to use biological time series in Mediterranean ecosystem studies: can hydromedusae be indicator species ?

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INTRODUCTION

When looking into rational explanations for disturbances in an ecosystem we regularly try to get as many data as possible from historical databases, and, more often than not, we face the problem of incomplete data sets characterized by gaps in the information base.

One approach to identify patterns, regularities and irregularities is to focus on regions possessing extensive long-term research, documented in large number of published scientific papers. This is the case of the Adriatic Sea – especially its northern part – the focus of this paper.

The research of various aspects of the North Adriatic Ecosystem goes back to early modern oceanographic and marine biological investigations. Plankton research was very fashionable in the 19th and 20th centuries (Fonda-Umani and Specchi, 1979; Ghirardelli, 1983). Contributions from marine research expeditions such as R/V *R. Virchov* in 1909, 1911 (Neppi, 1912), R/V *Najade* in 1912-1914 (Neppi, 1922), R/V *Hvar* in 1948-1949 (Vucetic, 1963) were notable. In addition, a number of other research cruises took place in the Adriatic sea, although a large number of samples and biological material was were not examined and therefore potentially valuable information was lost (Mikus *et al.*, 1996).

TIME SERIES OF HYDROMEDUSAE

The first account of hydromedusae of the Adriatic Sea came from the Gulf of Trieste (Will, 1844). Further results originated mostly from the shallow north Adriatic, with a few investigations conducted also in deep waters of the middle and south Adriatic.

Claus (1877, 1880) has described medusan fauna with special reference to Aequoridae; Graeffe (1884) described medusan fauna and its development in the Gulf of Trieste; Stossich, (1885) gave a comprehensive account of coelenterata; Neppi (1912) published results from coastal and open waters of the entire Adriatic Sea; Neppi and Stiasny (1913) provided an excellent review of hydromedusan fauna of the Gulf of Trieste; Babic (1913) published results from the coastal waters of Kvarner region; Grobben (1915) and Neppi (1922) elaborated on medusae from open Adriatic waters; Pell (1938) elaborated on medusae from Hungarian expedition of R/V *Najade*; Babnik (1948) published results on the middle and south Adriatic. Since 1965 Benovic and collaborators have published a number of papers on systematics, distribution, abundances and vertical migration. The most comprehensive bibliography is given in papers of Benovic and

Bender (1987), Benovic and Lucic (1996) and Purcell *et al.* (1999). The most recent work of Benovic *et al.* (in preparation) will describe medusae in the middle and south Adriatic open waters.

DISCUSSION AND CONCLUSIONS

By quoting the entire list of published resources on hydromedusae in the Adriatic Sea we can clearly see that intensive research took place only during certain time periods, especially when large expeditions were organized. The historical record is therefore characterized by periodic publication of data collected for different aims, using different methods. The resulting record is so variable that the only consistent data that can be extracted through time are species names.

A comparative examination of records (Table 1) suggests that some inferences can be made about patterns of hydromedusan distributions. In the entire Adriatic Sea we recognize 66 species. There are differences between northern, middle and southern Adriatic populations. The indicator species are those that are present consistently through the time in a specific area and depths. Thus, their appearance in other regions probably indicates shift of water masses (Vucetic, 1969; Krcinic and Grbec, 2002). However, since the rare species appear very infrequently, it can be assumed that we missed them because of time gaps in research (Seguera-Puertas, 1992). An additional limitation of the intermittent hydromedusan record is that little or no evidence may be available around “bloom” events of various medusae.

Benovic *et al.* (1987) analyzed the hydromedusan fauna and environmental factors in the North Adriatic Sea. Based on comparisons of species composition from almost 100 years of research with recent data, they suggested that changes in environmental factors resulting from the discharge of terrigenous material by the northern Adriatic rivers probably caused changes in hydromedusan fauna and depletion of many species. In addition, they predicted that in the future environmental changes would take place on a large scale in the north Adriatic. Further papers (Degobbis *et al.*, 1995) dealing with blooms of plankton, mucilages and other disturbances in the North Adriatic that were published after 1987, confirmed those predictions.

Can a hydromedusa be an indicator species? Analyzing the list of species and trying to understand populations in different regions of the sea, Benovic and Lucic (1996) speculated about possible repopulations of the North Adriatic by species shifted from southern regions. Though some species appeared, they were in very small numbers, thus not having the potential to repopulate altered environment of the North Adriatic. These species can be considered as indicator species of some regions (Benovic *et al.*, in preparation), but they cannot serve as indicators of the entire environment.

In conclusion, studies of hydromedusae may be useful tools in Mediterranean ecosystem studies. However, only knowledge of entire populations can enable us to make predictions, even if weak and approximate.

Historical observations and knowledge about Hydromedusae of the Mediterranean Sea, as one of the oldest known marine ecosystems (Gili *et al.*, 1998), will contribute greatly to our current knowledge of hydromedusae, and their use as indicators. In all aquatic ecosystems, hydromedusae represent one of the oldest and most primitive of metazoan animal taxa (Buecher and Gibbons, 1999) : in their long time existence, they have developed populations that fit very specific niches in the vertical and horizontal sea horizons.

Table 1. Findings of hydromedusae of the Northern and Southern Adriatic Sea. Compilation of data from: **A**: Neppi, 1912; **B**: Neppi and Staisny, 1913; **C**: Neppi, 1922; **D**: Pell, 1938; **E**: Benovic, 1973; **F**: Benovic, 1976; **G**: Benovic and Bender, 1986; **H**: Benovic and Bender, 1987; **I**: Benovic and Lucic, 1995; **J & K**: Benovic and Lucic, 1996; **L**: middle and south Adriatic 2002 (see text). (**+** indicates northern Adriatic and ***** indicates southern Adriatic).

SPECIES **DATA**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
ANTHOMEDUSAE												
1. *Dicodonium adriaticum*		+			+							*
2. *Dipurena halterata*	+	+		*	+							
3. *Sarsia gemmifera*		+	*	*	+		+ *	+ *	+	+		
4. *Stauridiosarsia producta*		+			+							
5. *Ectopleura dumortieri*		+			+		+	+ *				
6. *Eucodonium brownie*	+	+	*		+							
7. *Euphysa aurata*	+*				+	*	+ *	+ *			*	
8. *Rhabdoon singulare*	+					*	+ *	+ *			*	*
9. *Corymorpha nutans*	+	+	*	*	+		+ *	+ *	+			*
10. *Zanclea costata*	+	+	*	*	+	*	+ *	+ *				*
11. *Cladonema radiatum*		+										
12. *Eleutheria dichotoma*		+										
13. *Cytaeis tetrastyla*	+		*	*	+							
14. *Oceania armata*			*	*			*	*				*
15. *Turitopsis nutricula*		+										
16. *Podocoryne carnea*		+	*		+							*
17. *Podocoryne areolata*		+						*				
18. *Podocoryne minima*					+		+ *	+ *	+	+		
19. *Podocoryne minuta*	+	+	*		+	*	+ *	+ *	+	+		*
20. *Rhatkea octopunctata*		+	*	*								
21. *Bougainvillia ramosa*	+*	+	*	*	+		*	+ *	+			
22. *Koellikerina fasciculata*			*	*								
23. *Lizzia octostyla*		+										
24. *Lizzia blondina*	+*	+			+			+				
25. *Thamnostoma dibalia*		+		*	+	*			+	+		
26. *Amphinema dinema*	+	+						+ *				*
27. *Leuckartiara octona*				*			*	+ *			*	*
28. *Merga tergestina*	+	+	*		+							
29. *Neoturris pileata*	*	+		*	+		+	+*				
30. *Pandea* sp.		+										
31. *Protiara tetranema*				*								
32. *Bythotiara murrayi*			*			*	*	*				

(Table 1: Cont.) **SPECIES** **DATA**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
LEPTOMEDUSAE												
33. Orchistomella graeffei		+										
34. Krampella dubia							*	+ *				
35. Laodicea ocelata							*	*				
36. Laodicea undulata	+*	+	*			*	*	*			*	*
37. Melicertissa adriatica			*									
38. Mitrocoma annae			*									
39. Octogonade mediterranea				*								
40. Obelia spp.	+*	+	*	*	+	*	+ *	+ *	+	+	*	*
41. Clytia hemisphaerica	+*	+	*	*	+	*	+ *	+ *	+	+	*	*
42. Eucope picta		+		*								
43. Eucheilota maasi		+		*								
44. Octophialucium funerarium						*	*					*
45. Eirene viridula	*	+				*	*	*	+	+	*	
46. Helgicirrha schultzei		+	*		+		+ *	+ *	+			*
47. Eutima gegenbauri	+	+	*		+		+ *	+ *				
48. Eutima gracilis	+	*	*				+ *	+			*	
49. Eutonina scintillans		+										
50. Tima luculana	+											
51. Aequorea aequorea		+		*					+			
52. Proboscidactyla ornata	+*	+	*									
TRACHYMEDUSAE												
53. Haliscera bigelowi												*
54. Geryonia proboscidalis		+	*									*
55. Liriope tetraphylla	+*	+	*	*	+	*	+ *	+ *	+	+	*	*
56. Aglaura hemistoma	+*	+	*	*	+	*	+ *	+ *			*	*
57. Arctapodema australis				*			*	*				*
58. Homoeonema platygonon			*	*								
59. Persa incolorata					+	*	+ *	+ *			*	*
60. Rhopalonema funerarium				*			*	*			*	*
61. Rhopalonema velatum	+*	+	*		+	*	*	+ *			*	*
62. Sminthea eurygaster			*	*		*	*	*			*	*
NARCOMEDUSAE												
63. Solmundella bitentaculata	*		*			*	+ *	+ *			*	*
64. Solmaris spp.	+*	+	*		+	*	+ *	+ *	+	+	*	*
65. Cunina globosa			*									*
66. Solmissus albescens			*	*		*	*	*				*
TOTAL SPECIES	**25**	**41**	**31**	**27**	**27**	**18**	**31**	**35**	**14**	**9**	**15**	**28**

Monitoring of coastal fishing communities along the eastern Adriatic Coast (1960-1995)*

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The coastal area of the eastern Adriatic is traditionally the most important fishing ground for small-scale fisheries. Of approximately 55 fishing gears known along the eastern Adriatic coast (Cetinic and Swiniarski, 1985) all of them are used in the coastal area, except otter-trawl, purse seine and pelagic trawl. The coastal area is also characterized by greater productivity rate compared to the open sea (coastal sea – gross primary production between 60 and 150 gC m^{-2} a year^{-1}, and open sea 55gC m^{-2} a year^{-1}), thanks to relatively small depths, vicinity of land and freshwater inflow (Buljan, 1964; Pucher-Petkovic, 1974). In this area an intensive fishing activity is performed. According to the estimated annual landings, about 60% of fish, crustaceans and cephalopods are fished in coastal waters.

1. MONITORING AREA

Monitoring of cephalopod, crustacean and fish communities along the eastern Adriatic coast were carried out in five Dalmatian areas: Kornati Islands, Split area, Mid-Dalmatian Islands, Palagruza Island and South Adriatic (Montenegro coast) (Fig. 1). Palagruza Island lies offshore, surrounded by the open sea and depth exceeding 155 m.

2. FISHING GEAR

Monitoring was performed by trammel nets (three-layer entangling nets) because of their great catch ability and small selectivity rate. Nets of the following basic construction characteristics were used: length 31-36 m, depth 1.3-1.5 m, external net panels ("popon") with 114 mm and internal net panel ("maha") with 28 and 32 mm mesh size. Experimental fishing was carried out with series of 10 or 11 nets tied together (total length approximately 310-360 m). Nets were commonly set at the bottom in the evening, at depths between 2 and 30 m, mostly to 15 m (80% of catches), and hauled the following morning (method of professional east-Adriatic trammel bottom set fishing).

3. TIME SERIES

Experimental trammel bottom set catches realized between 1960 and 1995 were the subject of our analyses. For the period between 1960 and 1964 the field and data published for the mid-Dalmatian area by Morovic (1965) were used. For other periods the data were obtained by the author's fieldwork. For catch analyses we did not have the year to year data nor the same time series of data for all the monitoring areas, so time series of data were somewhat different from one area to another (Table 1).

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* Rewiev based on results published in Morovic, 1965; Jardas and Pallaoro, 1989; Jardas *et al.*, 1988).

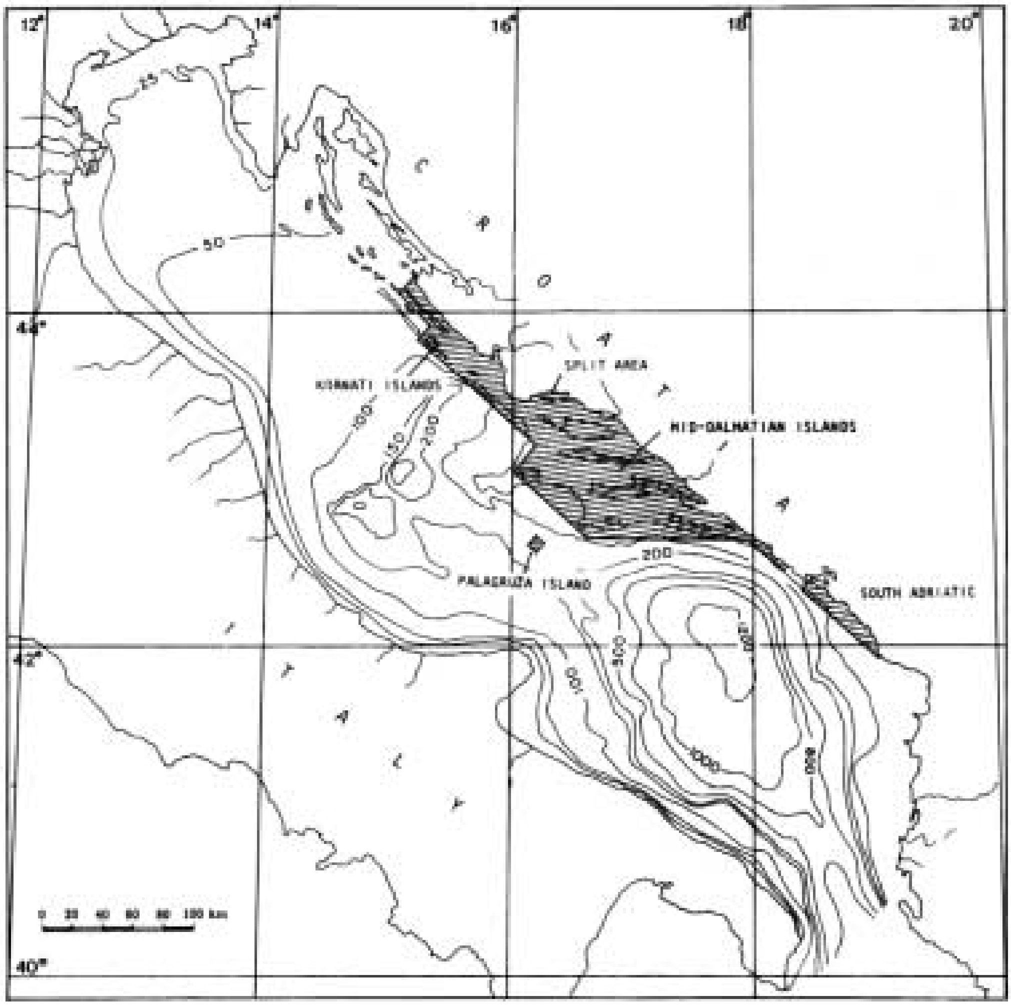


Fig.1. Monitoring area.

Table 1. Time series of data.

Monitoring area	Time series collected		
Kornati Islands	1960-1964	1977-1987	1990-1992
Split area	1960-1964	1977-1979	1990-1999
Mid-Dalmatian Islands	1960-1964	1971-1987	1990-1994
Palagruza Island	1961	1970-1971	1987-1995
South Adriatic (Montenegro coast)	-	1972	1987-1988

4. CATCH ANALYSES

Qualitative and quantitative structures of trammel bottom set catches as well as basic biometrical characteristics (TL in cm, W in g) of crustacean, cephalopod and fish species were analysed. All the data on the catch quantities were expressed as catch per unit effort (cpue, catch quantities per one standard net) in kg.

5. RESULTS

5.1. Changes in catch per unit effort (cpue)

During the thirty-five year period of the quantitative analyses of experimental trammel bottom set catches in the eastern Adriatic, considerable changes were recorded. The results revealed a decline in catch weight of fish and edible invertebrates. The extent of the changes is as follows:

Kornati Islands*:* During the first monitoring period (1960-1964) the cpue was, on average, 1.48 kg. In the following 1977-1987 period the average cpue dropped to 0.54 kg, to be maintained at the same level in the 1990-1992 period. With respect to the first records from 1960-1964, the average cpue decreased by 63.5%, or put in another way, it declined to not more than 36.5% of the initial cpue value (Fig. 2A).

Split area: The cpue steadily decreased in this area as well. Between the 1960-1964 and 1977-1979 periods, the average cpue fell from 0.95 kg to 0.50 kg, or by 47.7%, and between the 1977-1979 and 1990-1994 periods from 0.50 kg to 0.35 kg, or by 30%. The decline was 63.3% throughout the monitoring period (Fig. 2B).

Mid-Dalmatian Islands*:* Average cpue fell steadily from the 1960-1964 from 1.80 kg to 0.71 kg, or by 60.8%, in the 1971-1987 period. Between the 1971-1987 and 1990-1994 periods the catch further declined by 5.6%, i.e. from 0,71 kg to 0,67 kg. This decrease was 63.0% for the whole monitoring period (Fig. 2C).

Palagruza Island: During the past 28 years (1961-1995) similar changes occurred in the fish populations as in other monitoring coastal areas. In the 1961 the average cpue was 2.68 kg, then it fell to 2.18 kg in the second period (1970-1971) and to 1.47 kg in the third period (1987-1989) and finally it was 1.49 kg in 1995 (Fig. 2D).

South Adriatic: In 1972, when the monitoring of fish and edible invertebrates communities along the coast of the south Adriatic started, the average cpue was 0.57 kg. It declined to 0.43 kg, or about 25%, in 1987 (Fig. 2E).

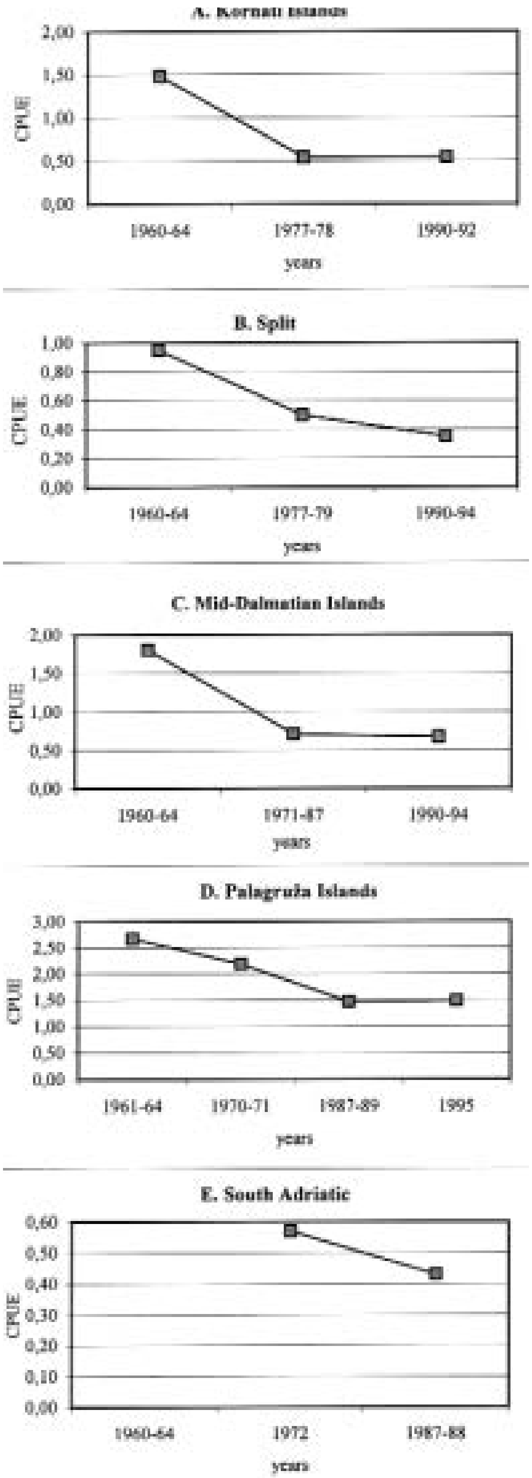


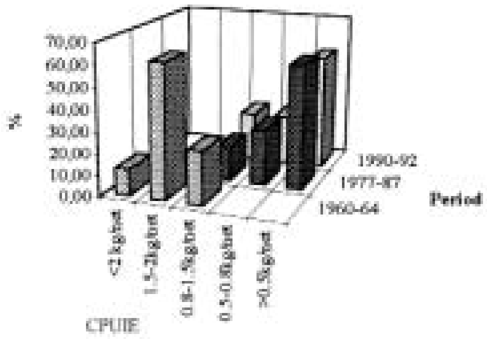
Fig. 2. Changes in quantity of trammel bottom set catches (expressed in cpue) in the eastern Adriatic coastal areas during the monitoring period.

5.2. Changes in the cpue categories

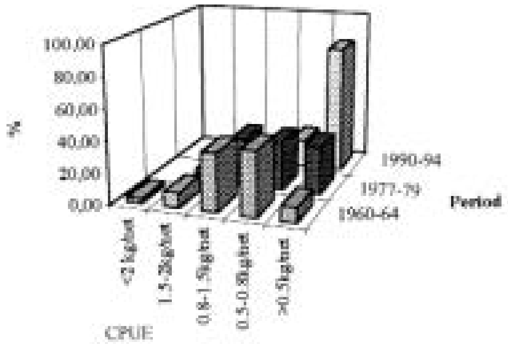
For the comparison of the state and changes in crustacean, cephalopod and fish communities in the mid-Dalmatian area between 1960 and 1964, Morovic (1970, 1971) established five cpeu categories: < 0.5 kg (very poor), 0.5-0.8 kg (poor), 0.9-1.5 kg (good), 1.6-2.0 kg (very good) and > 2 kg (excellent). We have applied the same cpue categories to compare frequency of occurrence during the monitoring periods. Higher cpue categories tend to be less frequent while lower cpue categories do increase in all monitoring areas for the period of investigation. The extent of the changes was as follows (Fig. 3):

Kornati Islands: Defined cpue categories showed obvious alternation in presence. In the 1960-1964 period 75.5% of cpue exceeded 1.5 kg (> 2 kg 12.5%, 1.6-2 kg 62.5%) and no average cpue was les than 0.8 kg. The cpue exceeding 1.5 kg disappeared in the following period with an apparent increase in cpue below 0.8 kg and with the dominance of cpue below 0.5 kg.

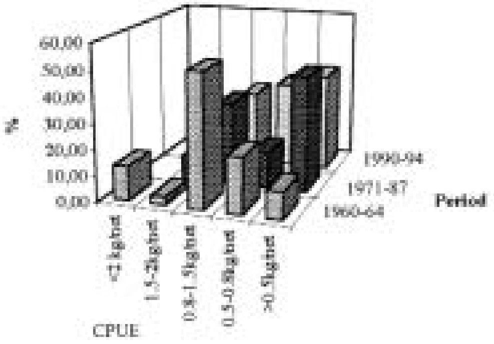
Kornati Islands



Split area



Midle-Dalmatian islands



South Adriatic

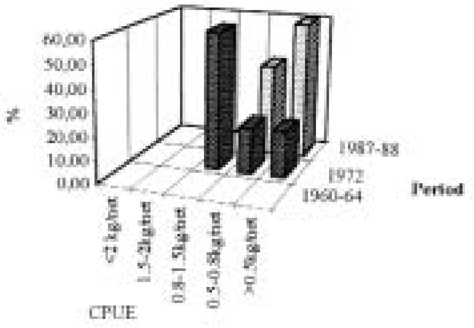


Fig. 3. Changes in presence of cpue categories in the eastern Adriatic coastal areas during the monitoring period.

Split area: Alternation in the presence of different cpue categories was notable in this area as in Kornati Islands area. In the period between 1990 and 1994 only categories from 0.5-0.8 kg and < 0.5 kg were present, while all other categories were completely absent. At the same time the cpue < 0.5 kg increased from 9.4% in 1960-1964 to 82.3% in the 1990-1994 period.

Mid-Dalmatian Islands*:* Again we can see a regular decline in the presence of “good” cpue. It is replaced by “poor” and “very poor” cpue. So the cpue categories of 1.5-2 kg and more disappeared in 1990-1994 and that of 0.8-1.5 kg fell from 51.6% in 1960-1964 to a low level of 28.6% in the 1990-1994 period. At the same time the cpue < 0.5 kg increased by 38.1% in 1990-1994 with respect to the 1960-1964 period.

South Adriatic: In 1972 there were no cpue categories exceeding 0.8-1.5 kg recorded in that area. In 1987-1988 the cpue of 0.8-1.5 kg also disappeared. At the same time the presence of 0.5-0.8 kg and particularly of <0.5 kg cpue categories increased from 20.0 to 40.0%.

5.3. CHANGES IN CATCH COMPOSITION

In the coastal waters of the eastern Adriatic five fish families prevail in the trammel bottom set catches: Scorpaenidae, Labridae, Serranidae, Sparidae and Mullidae. Changes in the presence of already mentioned families in the trammel bottom set catches are observed only in the area of Palagruza Island. Numerical and weight abundance of Labridae, Mulidae and Serranidae families in the trammel bottom set catches showed a tendency of slight decrease during the monitoring period, and Sparidae family a tendency of slight increase in both the numerical and weight abundance. Scorpaenidae, as the most abundant family in the trammel bottom set catches along the eastern Adriatic coast, in the monitoring period showed a tendency of slight increase in number on one hand, and slight decrease in weight on the other (Fig. 4).

Values of both numerical and weight abundance for all target fish families show notable variety from one period to another, which is probably a consequence of insufficiently large samples and, to a certain degree, of different seasons of sampling.

Trends of the numerical and weight abundance of target species (which are generally the

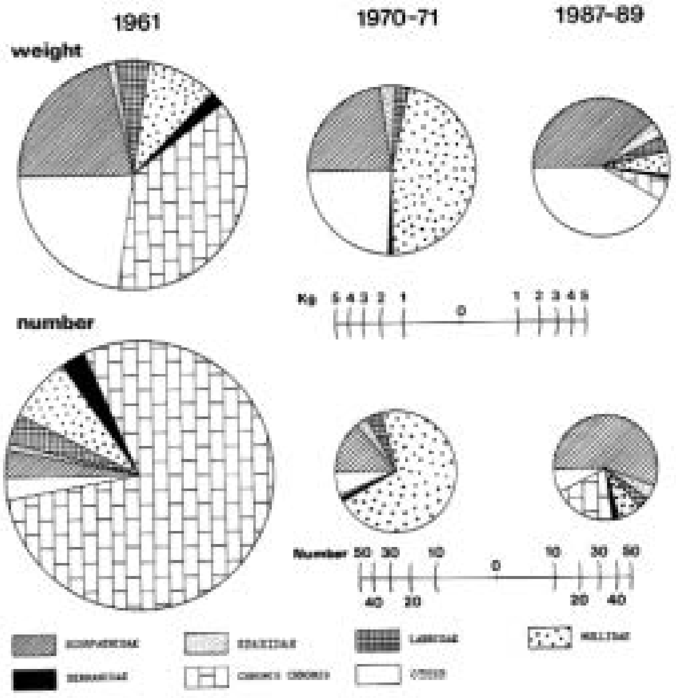


Fig. 4. Changes in presence of dominant fish families in trammel bottom set catches in the Palagruza Island area during the monitoring period.

most abundant in the trammel bottom set catches along the eastern Adriatic coast) in the catches between 1962 and 1993 are given in Figure 5. A trend of steady increases in both the numerical and weight abundance of the fish species *Scorpaena porcus* and *Symphodus tinca*, cephalopoda species *Sepia officinalis*, and decapod crustacean species *Maja crispata* was observed throughout the entire monitoring period. On the contrary, *Mullus* species (particularly *M. surmuletus*) and the cephalopod species *Octopus vulgaris* showed a decrease in both numerical and weight abundance.

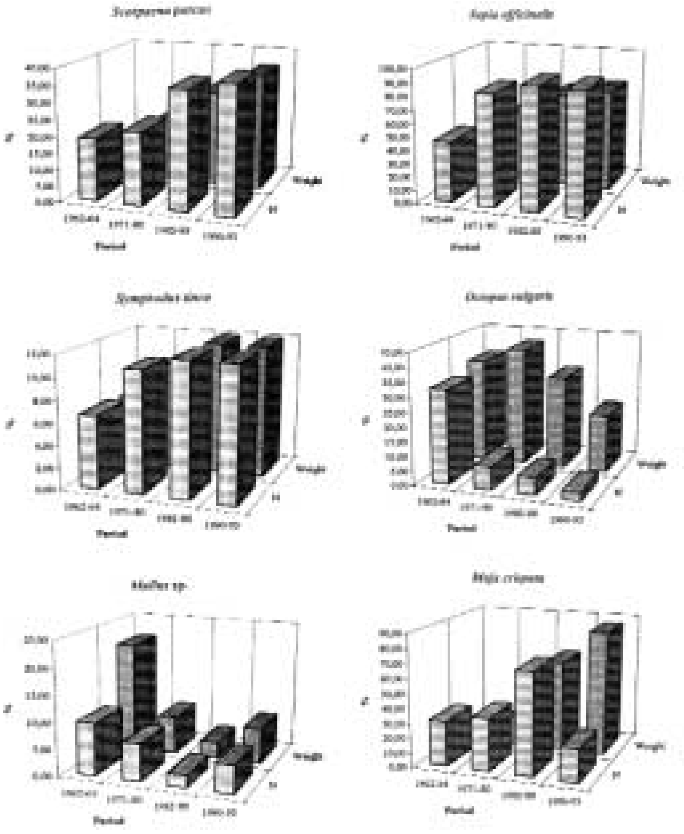
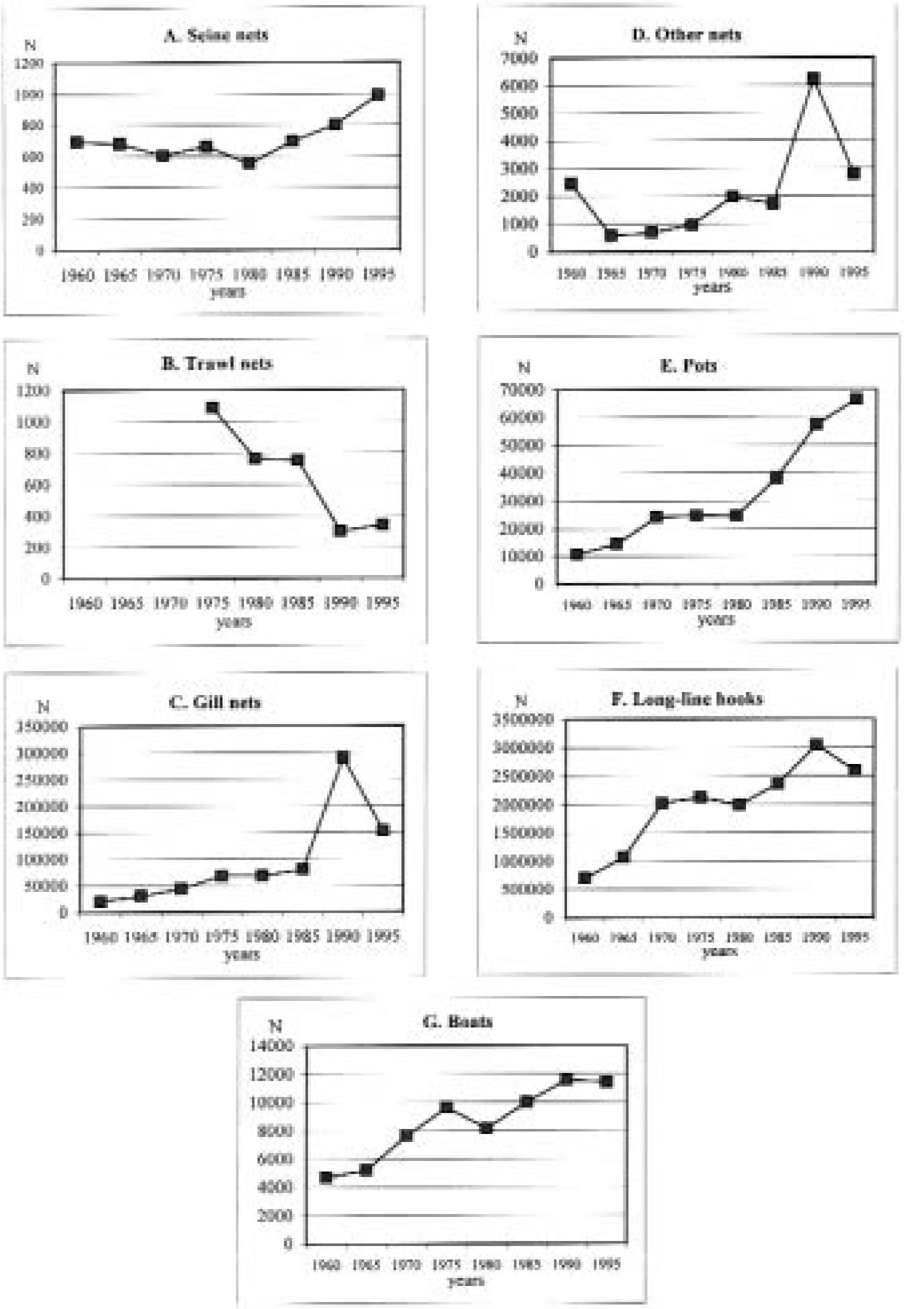


Fig. 5. Trend of the numerical and weight abundance of target species in the trammel bottom set catches in the eastern Adriatic coastal area during the monitoring period.

We believe that the observed changes are the result of long-time intensive exploitation, use of inadequate fishing gears, violation of legislation and poor implementation of legislation concerning the exploitation and protection of marine biological resources. Increasing marine pollution also has an effect : particularly evident in the vicinity of large urban and industrial centres, its influence on the coastal biological resources could not yet be adequately assessed. Growing intensity of exploitation in coastal waters, as the main cause of observed changes in the communities, is clearly shown by the statistics of fishing gears and small fishing boats for the 1960-1995 period (Fig. 6). For instance, the number of seine nets increased 1.4 time since 1960, gill nets 7.6 times (that of trammel nets alone 6.3 times), fish and crustacean pots more than 6 times, hooks of long-lines 3.7 times and fishing boats 2.4 times. Parallel to this obvious increase in fishing effort, quantities of catches of fish and edible invertebrates constantly decreased.



A. Seine nets

B. Trawl nets

C. Gill nets

D. Other nets

E. Pots

F. Long-line hooks

G. Boats

Fig. 6. Number of fishing gears and small fishing boats of small-scale fisheries in the eastern Adriatic coastal area in 1980-1995 period.

Can market prices and fishery landings data tell us anything about underlying ecosystems ?

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It is often difficult to assemble and maintain long time-series of biological data for a particular marine system since sampling programmes are costly and staff at marine institutes have to balance the limited time and resources available. Most fishery-independent survey time series do not extend back beyond the 1970s yet we are increasingly being asked to comment on the long-term impacts of climate change or increased fishing pressure.

Unlike biological data, historical records of financial transactions are commonplace and often meticulous. Ravier and Fromentin (2001) for example were able to reconstruct a 300 year (1650-1950) time series of Mediterranean tuna catches based on the records of bankers, financiers and tax collectors. Records of fishery landings and their market value have been collected systematically by local and national authorities for centuries and fish market prices often reported in trade newspapers. Thus, economic and commercial time series may represent a rich, and thus far largely neglected, source of useful data for biologists hoping to investigate long-term changes in marine ecosystems (e.g. Southward *et al.*, 1988; Alheit and Hagen, 1997).

Fishery scientists tend to take a rather short-term view of history (Pauly, 1995), referring only as far back in time as their biological sampling programmes will allow. However, a recent study (Myers and Worm, 2003) has demonstrated that populations of predatory fishes can decline by as much as 80% within the first 10-15 years of exploitation, and that the majority of fish stocks we see in the ocean today are at 10% or less of pre-industrial levels. Anecdotal and archaeological evidence suggests that in many cases fishes were larger in the past than they are today (Wing and Wing, 2001). Clearly fisheries scientists must begin to take a longer-term view and in order to do this they may need to embrace economic and commercial time series.

FISHERY LANDINGS DATA

Changes in the composition of landings often reflect changes in the structure of underlying fish communities (Pinnegar *et al.*, 2002). Since landings data are collected for fisheries throughout the world, these data have been widely used to assess the large-scale and long-term effects of fishing on community trophic structure. Pauly *et al.* (1998a) used aggregated landing statistics from the FAO, together with estimates of trophic levels for particular species derived from food-web models and demonstrated that the mean trophic level (TL) of global landings declined significantly and steadily since the late 1950s.

However, fishery landing data can reflect changes in gear technology, consumer preferences, management measures, and not only the abundance of species in the environment (Pinnegar *et al.*, 2003). It could be argued that fishery landings tell us more the financial pressures faced by fishermen than the state of underlying fish stocks.

THE MEDITERRANEAN

Based on FAO fishery and aquaculture landings data for the Mediterranean and Black Sea (FAO area 37), Pauly *et al.* (1998a) demonstrated that the mean trophic level (TL) declined by around 0.2 between 1950 and 1994. This finding prompted much interest (CIESM, 2000a) and debate (Caddy *et al.*, 1998) with regard to the future sustainability of fishing in this region. Stergiou and Koulouris (2000) demonstrated a similar trend for fisheries around Crete.

Caddy *et al.* (1998) and Caddy and Garibaldi (2000) raised several concerns about the approach used by Pauly *et al.* (1998a), and many of these criticisms have subsequently been addressed by Pinnegar *et al.* (2003). Rather than using the heavily aggregated fishery data available from the FAO, and the somewhat patchy trophic level data available from ecosystem models, Pinnegar *et al.* (2003) used detailed fishery landings data for the western Mediterranean (obtained from GFCM) together with locally-derived TL estimates from stable isotope analyses. These authors again found a significant decline in the mean trophic level of landings (Fig. 1a), and they also found that both fish and total landings had become more diverse over the 26-year period for which data were available (Fig. 1b).

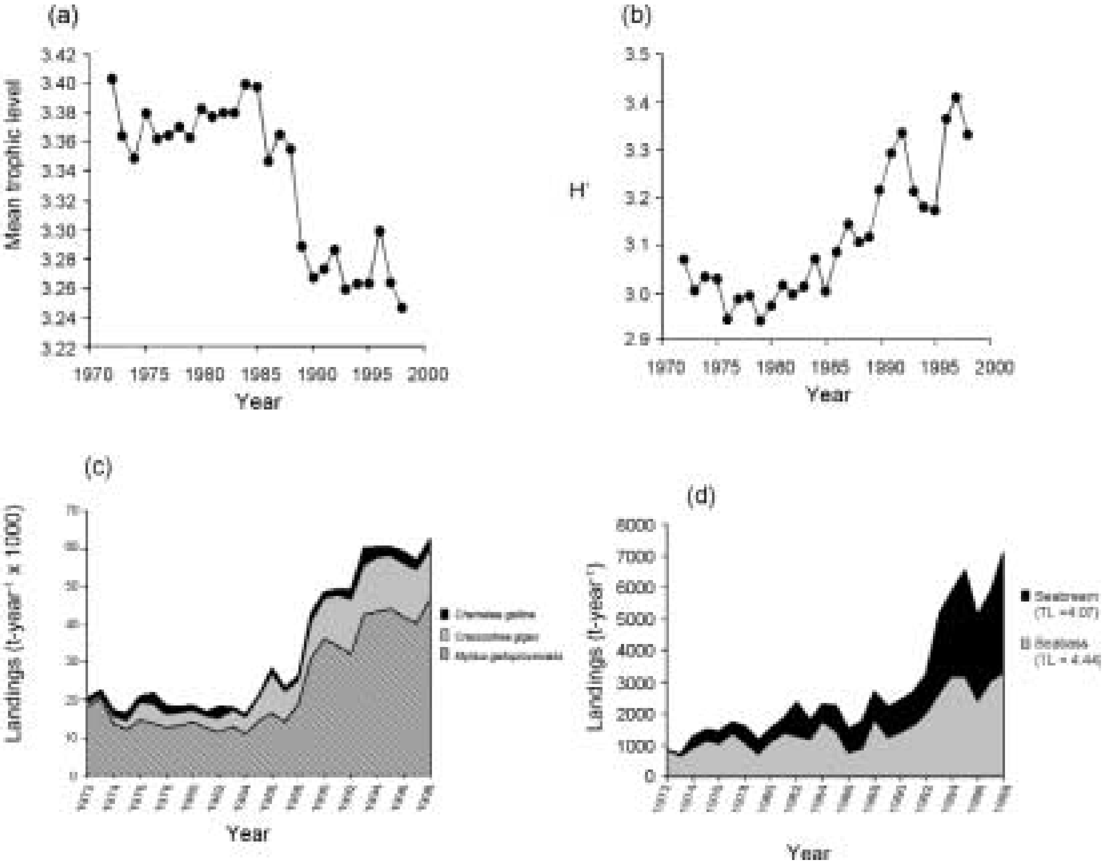

Fig. 1. Patterns of changing (a) mean trophic level in General Fisheries Council for the Mediterranean (GFCM) capture fishery and aquaculture landings, (b) Shannon-Weiner diversity (H') of fin-fish landings, (c) bivalve mollusc landings, (d) sea bass (*Dicentrarchus labrax*) and gilthead seabream (*Sparus aurata*) landings (trophic level (TLNi) in parentheses).

Aquaculture contributes a much higher share (~16%) of total production in the Mediterranean than is the case anywhere else in the northeast Atlantic (Symes, 1999). In their original assessment of trophic level decline, Pauly *et al.* (1998a) did not specifically account for the role played by expanding aquacultural production (capture and aquaculture landings were not separated in the FAO data at that time). Caddy *et al.* (1998) argued that a dramatic increase in the production of low trophic level bivalve molluscs (TL ~2.16) would be expected to artificially enhance the apparent "fishing down" of marine food webs.

Since the mid 1980s there has been a marked increase in the production of cultured molluscs in the western Mediterranean (Fig. 1c). When Pinnegar *et al.* (2003) excluded all aquacultural landings from their analyses, the apparent long-term decline in mean TL was much less marked (only 0.07 TL in 26 years) although still statistically significant.

Initially most fin-fish culture in the Mediterranean focused on grey-mullets (Pedini, 1996), species which naturally feed at relatively low trophic levels (e.g., Liza ramada, TL 3.24). However, seabass and seabream, which have dominated in recent years, are high trophic level species and Pauly *et al.* (1998b) suggested that the culture of high trophic level fin-fishes may in fact counter the "fishing down" of marine food webs apparent from landings data. When Pinnegar *et al.* (2003) excluded all clupeoids (which otherwise added noise to the data) from the analyses, a slight increase in the mean trophic level of fin-fish landings became apparent. This, together with a pattern of increasing fin-fish diversity (Fig. 1b), closely mirrored the period of expansion in landings of cultured seabass and seabream (Fig. 1c). No increasing pattern in mean trophic level or diversity was detectable when cultured fish landings were excluded.

In other areas of the North Atlantic, aquacultural production remains relatively small scale (e.g., the Celtic and North seas), and observed trends in the mean trophic level of landings are undoubtedly the result of changes in capture fishery landings (Pinnegar *et al.*, 2002; Jennings *et al.*, 2002). However, even here we must be cautious since it is possible that apparent changes in the composition of landings may be related to technical innovation and the development of new gears. The technological revolution of the 1950s and 1960s allowed large-scale, mid-water trawling and purse-seining by industrial fleets for the first time. This in turn has greatly increased the vulnerability of small pelagic stocks worldwide (Caddy and Garibaldi, 2000). In the Mediterranean, there has been a gradual disappearance of artisanal gear (trammel nets, bogue gillnets, long lines, hand lines, pots etc.), and a great expansion of semi-industrial trawling/seining (Bas *et al.*, 1985).

Fishery landings data are known to be notoriously unreliable and there are undoubtedly problems associated with both GFCM and FAO time-series. Landing figures are thought to be greatly underestimated in several Mediterranean countries where statistics are obtained from fishermen for tax collection purposes. It has been suggested that the most acute problems in the management of Mediterranean resources are the multispecificity of the catches and the lack of reliable official statistics (Papaconstantinou and Farrugio, 2000).

MARKET PRICES

Price differs markedly between fish species and reflects the supply available and/or the desirability of the product to the consumer. Thus live Maori wrasse Cheilinus undulatus sold to restaurants in Hong Kong fetch in excess 100 €/kg^{-1} but sandeels *Ammodytes* spp. caught in the North Sea industrial fishery are worth less than 0.1 €/kg^{-1} (Jennings *et al.*, 2000).

Prices carry information from consumers to suppliers regarding how much they are willing to pay for a given amount of product, and prices carry information from suppliers to consumers regarding how much can be produced or obtained from the environment at a given price. If consumers want more of a product than is being offered, they tend to bid up the market price to bring forth the additional supply (Ludicello *et al.*, 1999), hence we might expect the price of traditional target fish to increase as they become more and more scarce (see OECD, 1997).

Generally, large high trophic level fish species command higher prices at market than do small low trophic level fishes or invertebrates. Hence in Figure 2 on the Italian fish market, species such as *Lophius* spp. (Lo) and *Dentex* spp. (Dn), both top predators, command high prices but small-

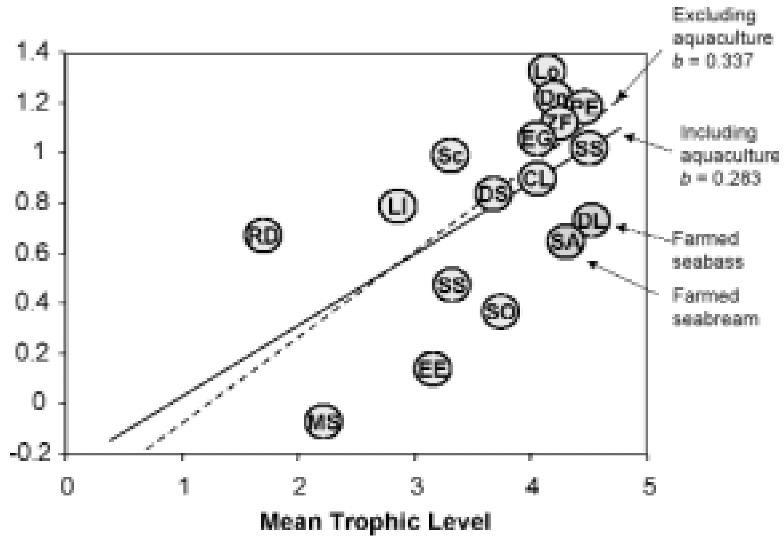

Fig. 2. Logarithm of seafood prices in Italy (January 2002) against mean trophic level (from Pinnegar *et al.,* 2003). Seafood prices from GLOBEFISH – European Fish Price Report. Solid line (slope = 0.283) is the regression including cultured fish species; dashed line (slope = 0.337) is the regression excluding cultured species. Key to species: Lo, *Lophius* spp; Dn, *Dentex* spp.; PE, *Pagellus erythrinus*; ZF, *Zeus faber*; EG, *Epinephelus guaza*; SS, *Solea solea*; DS, *Diplodus sargus*; CL, *Cheilidonichthys lucerna*; Sc, *Scorpaena* spp.; SA, *Sparus aurata;* DL, *Dicentrarchus labrax;* SO, *Sepia officinalis*; SS, *Scomber scombrus*; EE, *Engraulis encrasicholus*; Li, *Loligo* spp.; RD, *Ruditapes decussatus*; MS, *Mytillus* spp.

pelagic fishes such as *Engraulis encrasicholus* (EE) and *Scomber scombrus* (SS) or bivalve molluscs such as *Mytillus* spp. (MS) and *Ruditapes decussatus* (RD) fetch much lower prices per kg.

Since large top predators are usually the species most adversely affected by fishing, we might expect their prices to spiral upwards as they become scarce (i.e. their supply declines). Pinnegar *et al.* (2002) proposed a “relative price index” (RPI) to explore this effect, using the slope of the regression between price and mean trophic level. Here we refine this idea and offer a new but closely-related index which takes better account of annual inflationary price rises (Fig. 3).

The slope of the relationship between log price (in this case in €/kg) and mean trophic level (0.283 in Fig. 2) is used as an index (LRPI) for each year of the time series. If the LRPI levels

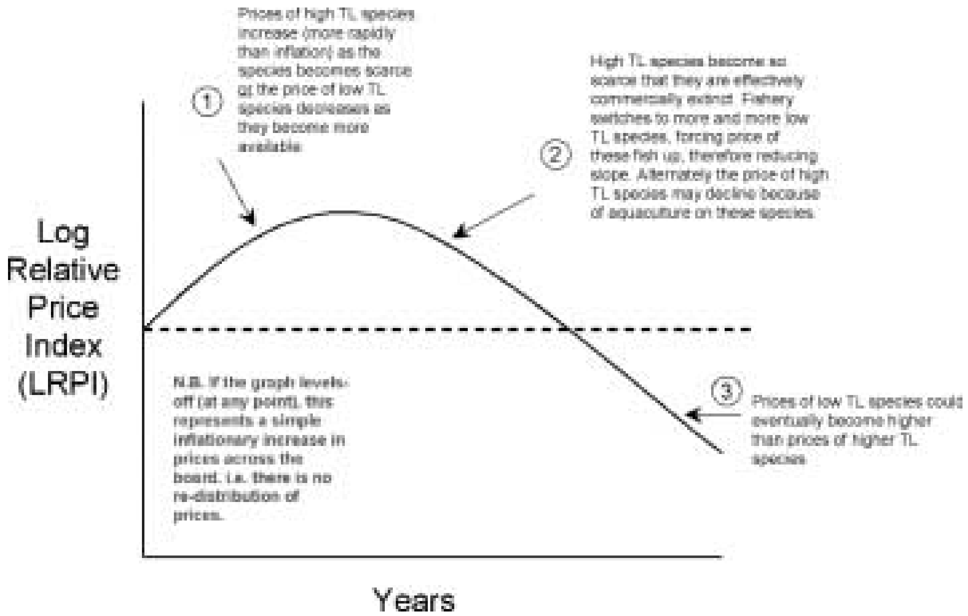

Fig. 3. Conceptual model illustrating how the log relative price index (LRPI) might develop over time, assuming increasing fishing effort.

off during any part of the time series, this infers that there has been no significant re-distribution of prices and that the price of each species has simply increased in line with inflation. By contrast, an increase in the value of LRPI would indicate either that the price of high trophic level species has increased (faster than inflation), or that the price of low trophic level species has declined (because technological advances allow fish to be caught more easily, or that they are more abundant in the environment). A declining value of LRPI would conversely indicate either that the relative price of high TL species has declined or that low TL species are becoming relatively more valuable (Fig. 3).

Here we have attempted to calculate the LRPI for a Mediterranean fishery, using Italian fish market price data (collated by the Istituto di Ricerche Economiche per la Pesca e l'Acquacoltura) together with trophic level estimates for 35 species from nitrogen stable isotope analyses (Pinnegar *et al.*, 2003). Between 1972 and 1980 the LRPI remained remarkably stable, indicating that the relative distribution of seafood prices did not change markedly. However, between 1980 and 1991, LRPI declined dramatically, indicating major re-distribution of prices, before assuming a new (but different) equilibrium thereafter (Fig. 4)

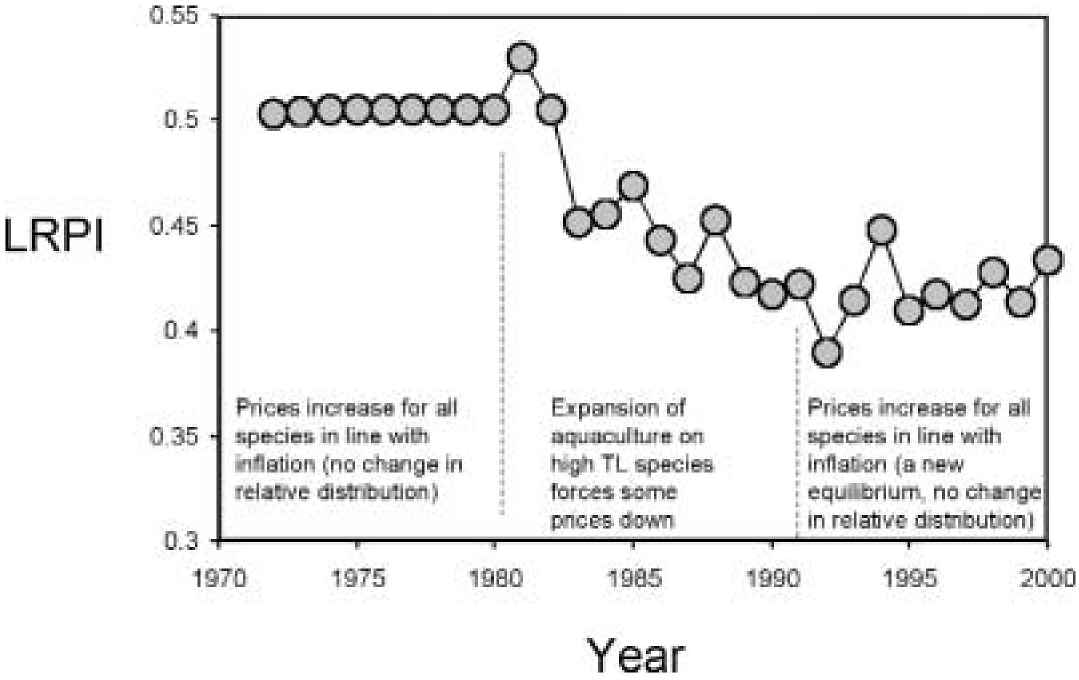

Fig. 4. Pattern of change in the price distribution of 35 species of fish over a 27 year time-series Italian fish markets, expressed as a "log relative price index" (LRPI). Prices expressed in € / kg.

One problem with the LRPI is that it may be skewed by the expansion of aquacultural production. Most fin-fish culture in the Mediterranean currently focuses on seabass (*Dicentrarchus labrax*) and gilthead seabream (*Sparus aurata*). In the wild, these species occupy a high trophic level and thus would be expected to command high prices at the fish market. Aquaculture has the effect of making fish more available and thus through the laws of supply and demand, results in lower than normal prices for these high TL species (Fig. 2). This in turn results in a less steep relationship than would be expected between TL and log prices (the LRPI in Fig. 2, excluding cultured species would be 0.337 as opposed to 0.283 including cultured species). Brigante (2001) demonstrated that the price of wild seabass and seabream in Italy has differed markedly from, and is significantly higher than, the price of farmed seabass and seabream (Fig. 5). Furthermore, it was shown that the price of farmed fish declined significantly between 1991 and 1998, and this resulted in a decline in the overall price of these species, as reported by IREPA (Fig. 6). This is almost certainly the main reason that we observed a decline in LRPI after 1980. Similarly, increased cage-culture of salmon (high TL species) has led to a global decline in salmon prices (OECD, 1997) and this may be one reason why Sumaila (1998) observed a decline in the global LRPI over the past 50 years.

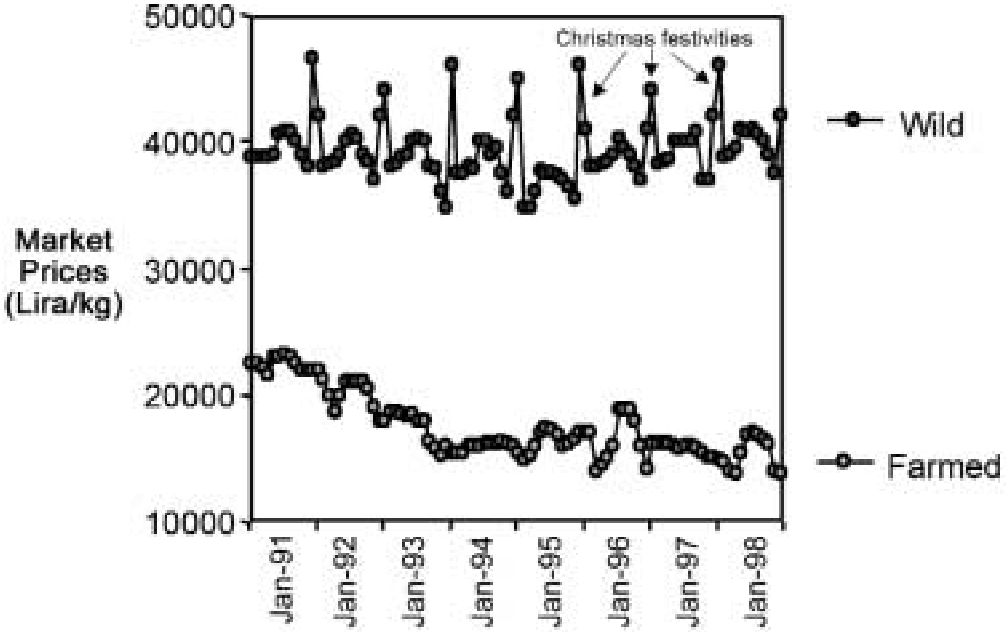

Fig. 5. Trend in the monthly prices of captured and farmed seabass on Italian fish markets (after Brigante, 2001). Prices in Lira/kg.

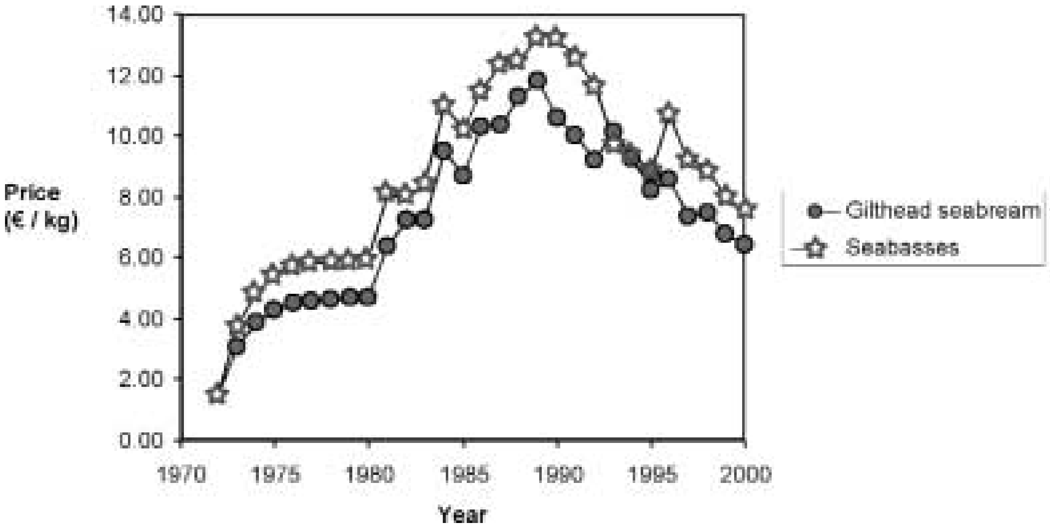

Fig. 6. Trend in the annual prices of seabass *Dicentrarchus labrax* and gilthead seabream *Sparus aurata* on Italian fish markets (data from IREPA).

In the past fish prices were largely governed by local patterns of demand and supply (e.g. cod and haddock in the U.K., Taylor, 1960), thus under these circumstances the LRPI would be a useful indicator of trends in the underlying ecosystem. With increasing globalisation however, prices (particularly of high value species) tend to reflect availability or scarcity on global markets. Asche, Bremnes and Wessells (1999) found that salmon prices were globally integrated, and that different salmon species (from the US and Norway) exhibited similar trends, irrespective of national boundaries. Hannesson (1999) reported similar integration among whitefish prices (e.g cod and haddock) across United States and European markets. Thus our conclusion must be that under certain circumstances (particularly for artisanal fisheries, selling catches locally) landings data and economic time-series may provide useful hints about the status of the underlying natural system. However where alternate means of supply are available (e.g. imports or aquaculture), the conflicting market pressures may greatly confound any trends which might be of use to biologists.

Long-term investigations of small pelagic fish in the Adriatic Sea

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INTRODUCTION

The most important small pelagic fish species in the Adriatic Sea are the sardine, *Sardina pilchardus* (Walb.), anchovy, *Engraulis encrasicolus* (L.), Atlantic mackerel, *Scomber scombrus* L. and chub mackerel, *Scomber japonicus* (Houtt.). They are migratory species, common and shared, rather widely distributed in the Adriatic sea (Fig. 1). They play a very important role in the economy of the eastern Adriatic Sea countries (Fig. 2), especially sardine and anchovy. During the 1950-2001 period sardine catches comprised more than 73% of the total pelagic fish species. Owing to the great economic interest of the eastern Adriatic Sea countries for the sardine, this species was subject of numerous studies, and this consequently resulted in long-term series data of this species.

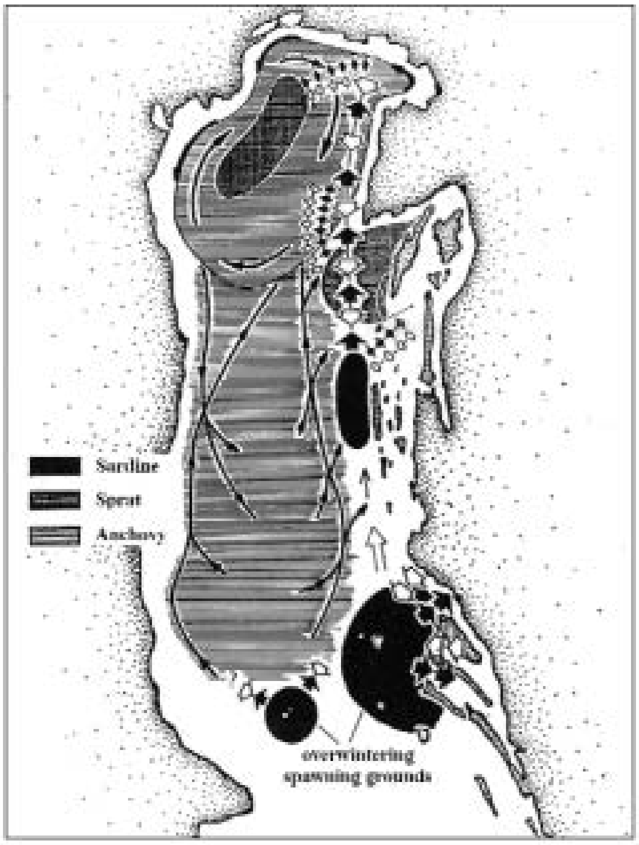

Fig. 1.Schematic presentation of sardine, anchovy and sprat migrations in the Adriatic Sea.

RESULTS AND DISCUSSION

Two subpopulations of the sardine inhabit the Adriatic Sea (Muzinic, 1954; Krajnovic, 1968, Krajnovic-Ozretic, 1975; Alegria *et al.*, 1986). Jabuka Pit is a geographical boundary between the areas of distribution of the sardine subpopulations (Muzinic, 1954; Alegria *et al.*, 1986; Sinovcic and Alegria, 1997). Sardine predominates towards the eastern part, whereas anchovy predominates towards the wester shore of the Adriatic Sea (Stirn

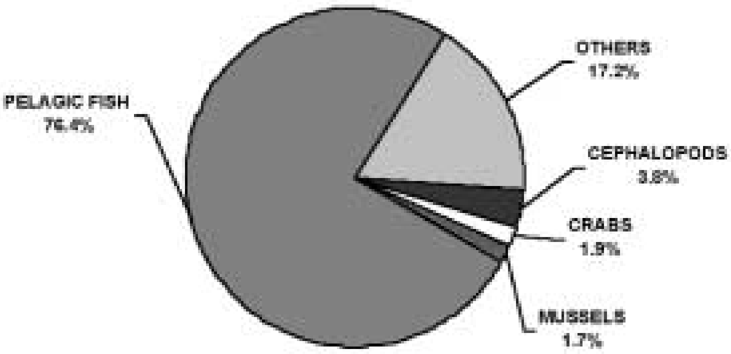

Fig.2. Percentual presentation of the total catch of various edible resources in the eastern Adriatic Sea (Croatia).

and Kubik, 1974; Muzinic, 1969, 1979; Gamulin and Hure, 1983). That is in accordance with the realised catches of these species in the countries along the western and eastern part of the Adriatic Sea (Anonymous, 1975-2000). Periods of the sardine fishery have alternated with those of anchovy fisheries (Fig. 3). Another antagonistic pair of fisheries is that of Atlantic mackerel and chub mackerel (Muzinic, 1979; Sinovcic *et al.*, 1991).

The most important fishery grounds of the small pelagic fish species in the eastern part of the Adriatic Sea is the south-western coast of Istra, off the Dugi Otok, Svetac-Vis-Bisevo-Jabuka, Susac-Palagruza islands area and Bar area. They are influenced to some degree by water masses inflow and outflow regimes between the Jabuka Pit as well as the southern Adriatic Pit and neighbouring regions, where upwelling conditions are evident (Regner *et al.*, 1987).

Historical records indicate that sardine in the eastern part of the Adriatic Sea undergone large fluctuations (Figs. 3-5), the cause of which have been the subject of many discussions. Zupanovic (1968) linked the periods with large quantities of sardine catches (which alternated with periods of extreme scarcity) with strong influence of inflow of the Mediterranean into the Adriatic Sea (years of ingression - Buljan, 1974) as well as with severe winters which produced intensive mixing of the sea water layers. Regner and Gacic (1974) connected the fluctuations of sardine catches with solar activity. Sinovcic and Alegria (1997) found that the highest sardine abundance index coincided with the years when high primary production and low temperature were recorded

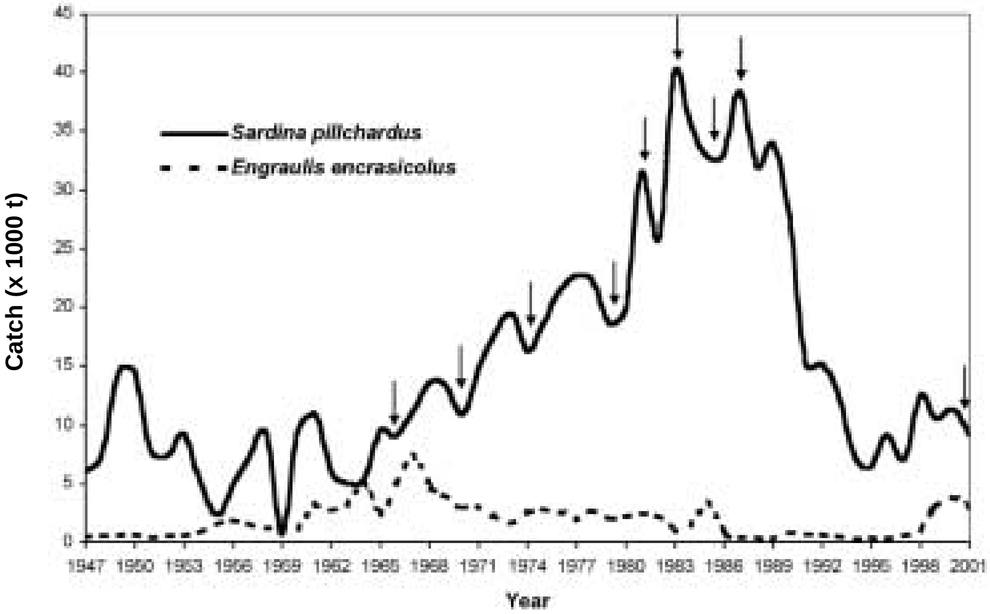

Fig. 3. Fluctuations of the sardine (___) and anchovy (- - -) catches in the Croatian part of the Adriatic Sea from 1947 to 2001. Arrows indicate the appearance of the sardine year class strength.

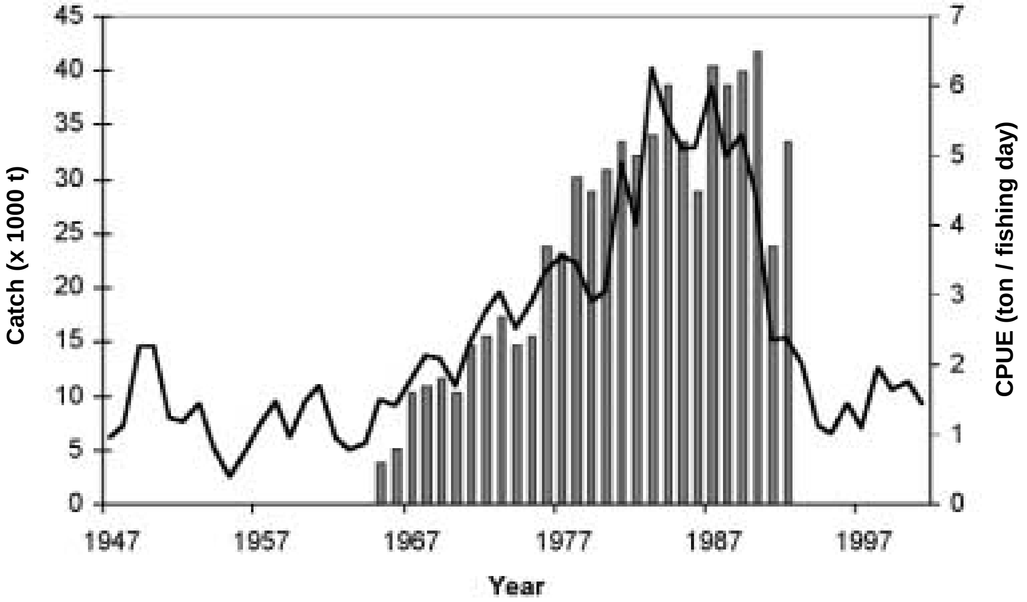

Fig 4. Fluctuation of the annual catches as well as the values of CPUE of the sardine in the Croatian waters of the Adriatic Sea.

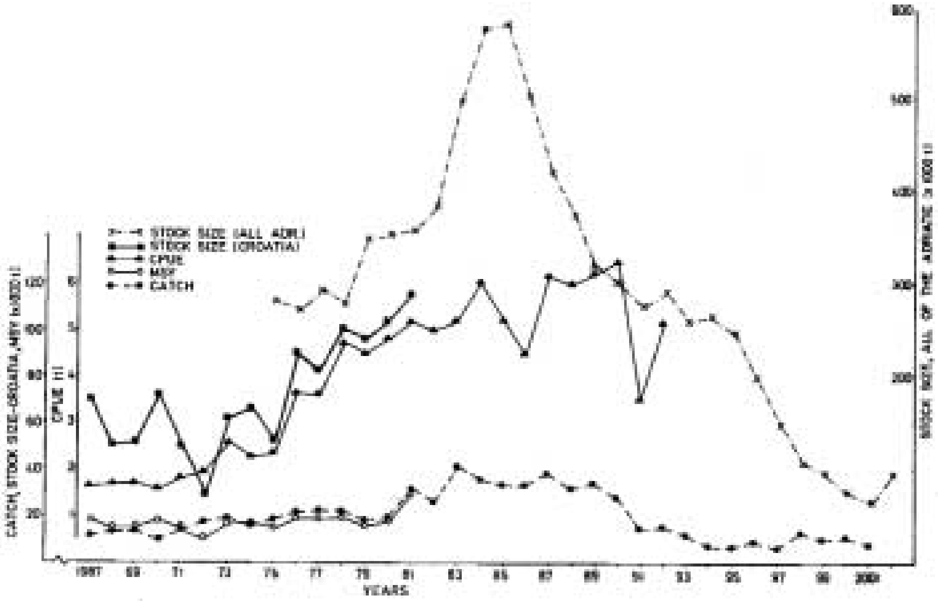

Fig. 5. Variations in sardine stock size, in all of the Adriatic Sea (Cingolani *et al.*, 2003), as well as sardine total catch, catch per unit effort (catch/boat/fishing day), stock size and amount of MSY in the Croatian waters of the Adriatic Sea.

during the period from hatching up to entering into exploitation phase. In any case, the fluctuations of the sardine catches reflect real fluctuations of the biomass (r = 0.85; Fig. 3.) and the recruitment. It is evident from Fig. 4 that the sardine catches increased a year or two after the appearance of a strong year class.

The sardine fishery was more prevalent during the spring and autumn period, with the highest value of abundance index in autumn and winter for all of the mean fishing grounds in the eastern part of the Adriatic Sea, except in the Susac and Palagruza fishing ground. In this area the abundance index was highest in winter (Alegria and Jukic, 1981; Sinovcic, 2001a). The anchovy fishery was more prevalent during the summer (Sinovcic, 2000, 2001b).

Periodically, after spawning, large amounts of sardine migrate toward the coast during the spring when the feeding conditions are much better compared to the open sea waters (Vucetic, 1955a,b, 1971, 1975). In the period of maturation (autumn), sardine create the denser aggregations and shoals and migrate towards the spawning grounds (Muzinic, 1950, 1952, 1954, 1973). During the migrations they support considerable fisheries (Zupanovic, 1955; Muzinic, 1969; Sinovcic, 2001a).

The richest sardine catches are realised in the years when masses of sardine migrate close to the shore. The years in which the large shoals remain in the open sea are considered as the poor years (Muzinic, 1979).

A poor period or sardine catch occured in the middle 1950s, a similar situation repeated recently (Fig. 4). The periods of high quantity catches of sardine are of extraordinary socio-economic importance. When sardine catches are low, regional economy and well-being of the population is heavily affected because the canning industry in the eastern Adriatic depends on the exploitation of the sardine.

Spawning stock biomass of sardine in the Adriatic Sea has considerably decreased since 1989. The size of the feeding area and the spawning ground location of this species probably changed with the stock size as well. There was prolonged recruitment failure since that period (Fig. 5). The last strong year class appeared in 1987, and after a large period of absence it appeared only last year (2002). Therefore we might expect higher catches in following years if overfishing of the juveniles does not occur.

Why biological time series require physical ones ?

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INTRODUCTION

The first studies on the general circulation of water masses in the Mediterranean began in the early 1900s (Nielsen, 1912), depicting a circulation smooth and stable along the slopes. Major revisions arose only in the 1980s, after the satellite imagery revealed upwellings, meanders and eddies, that is the mesoscale dynamics (see for instance Millot, 1985, 1987a; Le Vourch *et al.*, 1992). In the western basin, its role and consequences have been assessed with satellite observations that were later confirmed by *in situ* studies using a mesoscale-dedicated sampling strategy. Besides validating the use of satellite thermal images (SST: Sea Surface Temperature) to infer circulation features (Millot *et al.*, 1994, 1997) such a strategy has shown that mesoscale must be taken into account since it can impact the general circulation (e.g. Millot, 1987b; Millot and Taupier-Letage, 2003). The revised schemes for the western basin display meandering and eddying alongslope currents in a counter clockwise circuit (Millot, 1999). In the eastern basin, a major fieldwork effort (POEM) was carried out in the 1990s (e.g. Robinson, 1991; POEM group, 1992). The resulting representations of the surface circulation showed jets crossing the central part of the basin, instead of alongslope. It is worth noting that the southern parts from the Ionian to the Levantine sub-basins were not investigated, and that the sampling strategy was not adapted to assess the mesoscale (especially with a sampling interval too large, generally half a degree), which was then most likely to be deceiving. Another revisit of the surface circulation in the eastern basin has just been completed, based on the analysis of a ~4-year time series of SST images, which provide a synoptic view with a fine spatio-temporal resolution (~1 km, ~1 day). They show that the circulation is alongslope, as one might expect from the simple application of the Coriolis effect, and is affected by mesoscale dynamics. The resulting new scheme (Hamad *et al.*, 2003) strongly differs from that mentioned above, and shows a meandering and eddying alongslope circulation forming a counter clockwise circuit, which is confirmed by modelling work carried out in the LODYC (Alhammoud, 2003).

Correctly assessing the mesoscale dynamics is not only important for general circulation studies, it is also pivotal for biology. Indeed, at this scale the dynamical phenomena drive the biological ones, at least at the lower trophic levels, as shown on Figure 1 by the very close correlation between the dynamical signatures (as seen on SST images) and the biological ones (as seen on visible/"ocean colour" satellite images). Moreover, as the intensity of the mesoscale variability of the biological parameters is generally higher than the seasonal one, allegedly well-known, it is necessary to resolve the mesoscale to correctly ascribe the observed changes to a cause/process.

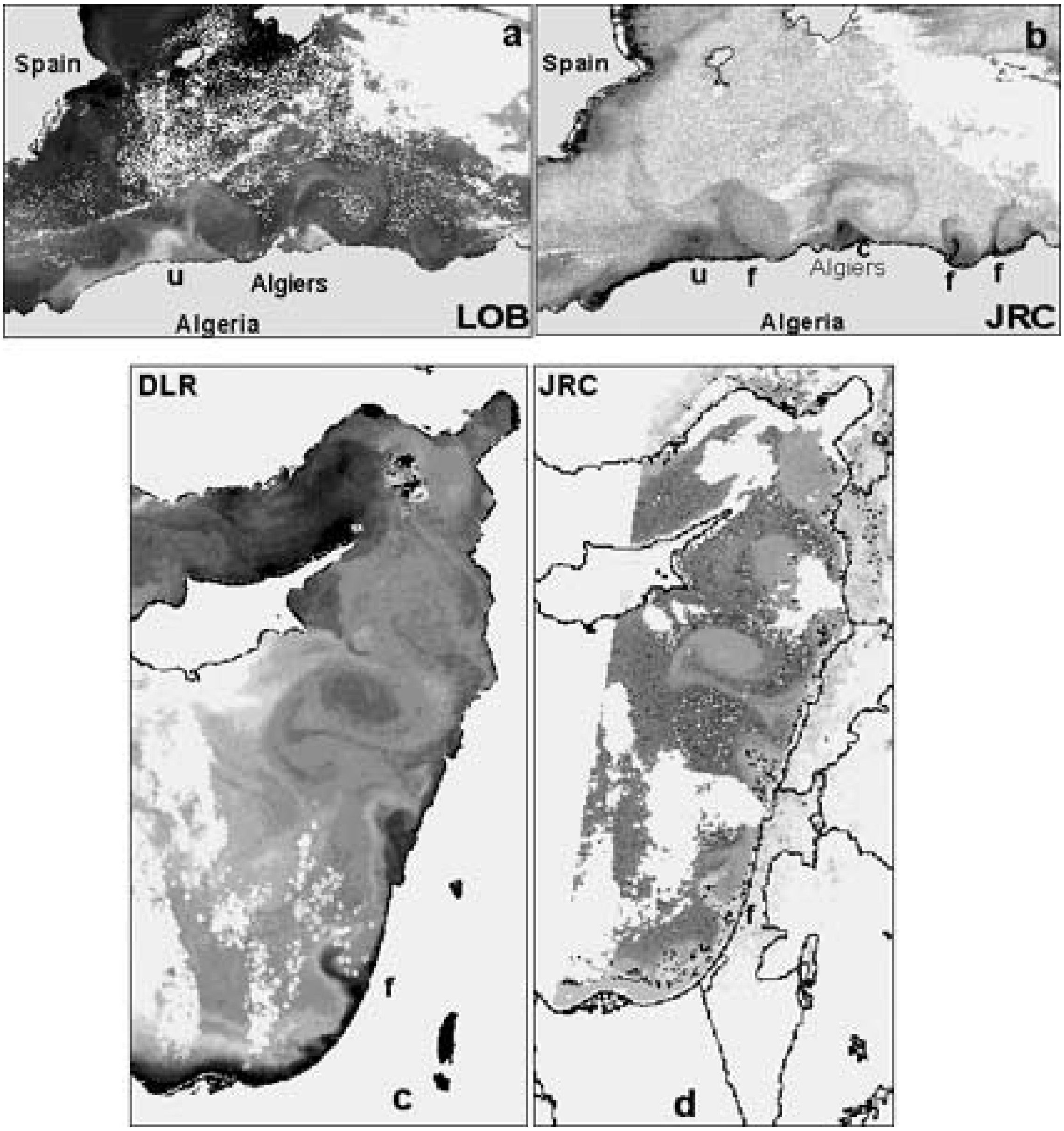

Fig. 1. SST (a, c) and surface chlorophyll concentrations (b, d) satellite images of the Algerian sub-basin on 19 July 1981 (top) and of the easternmost part of the eastern basin on 31 July 2001 (Middle-East, bottom). **a**: AVHRR image processed by LOB; **b**: CZCS image from JRC/Ocean project <www.me.sai.jrc.it/OCEAN/ocean.html>); **c**: AVHRR image (daily composite) from DLR <http://eoweb.dlr.de:8080/ servlets /template/welcome/entryPage.vm>; **d**: SeaWiFS image from JRC <www.me.sai.jrc.it/me-website/contents/shared_utilities/frames/archive_seawifs.htm>.

NB: in all images, temperature and chlorophyll concentrations increase from light to dark grey.

This requires at least acquiring biological and hydrodynamical parameters concurrently with a sampling interval adequate to resolve the important scales, or better, performing multidisciplinary and multiplatform experiments, fostering the use of satellite imageries and that of *in situ* autonomous instruments. In the following section, we will use examples from the one-year experiment ELISA (Eddies and Leddies Interdisciplinary Study off Algeria, see <www.com.univ-mrs.fr/ELISA>) which we conducted from 1997 to 1998 in the eastern part of the Algerian sub-basin.

We will first describe the main physical /dynamical phenomena that potentially translate into biological variability (with special emphasis on the mesoscale, which is generally less recognised), then we will suggest sampling strategies and list physical parameters that should be acquired in order to strengthen the interpretation of the biological time series.

VARIABILITY OF THE DYNAMICAL ENVIRONMENT AND POTENTIAL BIOLOGICAL CONSEQUENCES.

Although we do not focus herer on decadal scales, it is well-known that there are long-term hydrological trends in the Mediterranean (CIESM, 2002), which, in turn, are most likely to induce long-term changes in populations. Now, changes can also affect atmospheric forcings on a few-year timescale, leading to interannual changes in hydrology and circulation, as observed with the so-called "Transient" (CIESM, 2000b), or observed with the circulation pattern change in the western part of the Ionian sub-basin (Pinardi and Masetti, 2000; Hamad *et al.*, 2003). These scales will not be addressed here, as we rather focus on the seasonal and meso-scales.

The Mediterranean is an evaporation basin, so that less saline/lighter water enters at Gibraltar (Atlantic Water: AW, <www.ciesm.org/events/RT5-WaterMassAcronyms.pdf>). Schematically, AW flows counter-clockwise along the continental slopes to finally sink in the northern parts of both the western and eastern basins during the wintertime process of dense water formation. Characteristics of the AW circulation thus appear to be different in the southern and northern parts of both basins (more details on the comparison between the tow basins are given in Millot, 1992). The southern currents (which flow eastward) are unstable and meander, for some up to spawning anticyclonic eddies that propagate downstream at a few km/day, and/or can pinch off and drift offshore (Fig. 2). These eddies have spatial horizontal scales of 10s to several hundreds kilometres (up to diameters of ~250 km, in both southern sub-basins), and vertical extents ranging from hundreds to thousans of metres, down to the bottom (~3000m) as is now clearly demonstrated for the Algerian eddies at least (Millot and Taupier-Letage, 2003). Their temporal scales range from ~1 month to a few years (up to ~3 years observed in both western and eastern southern

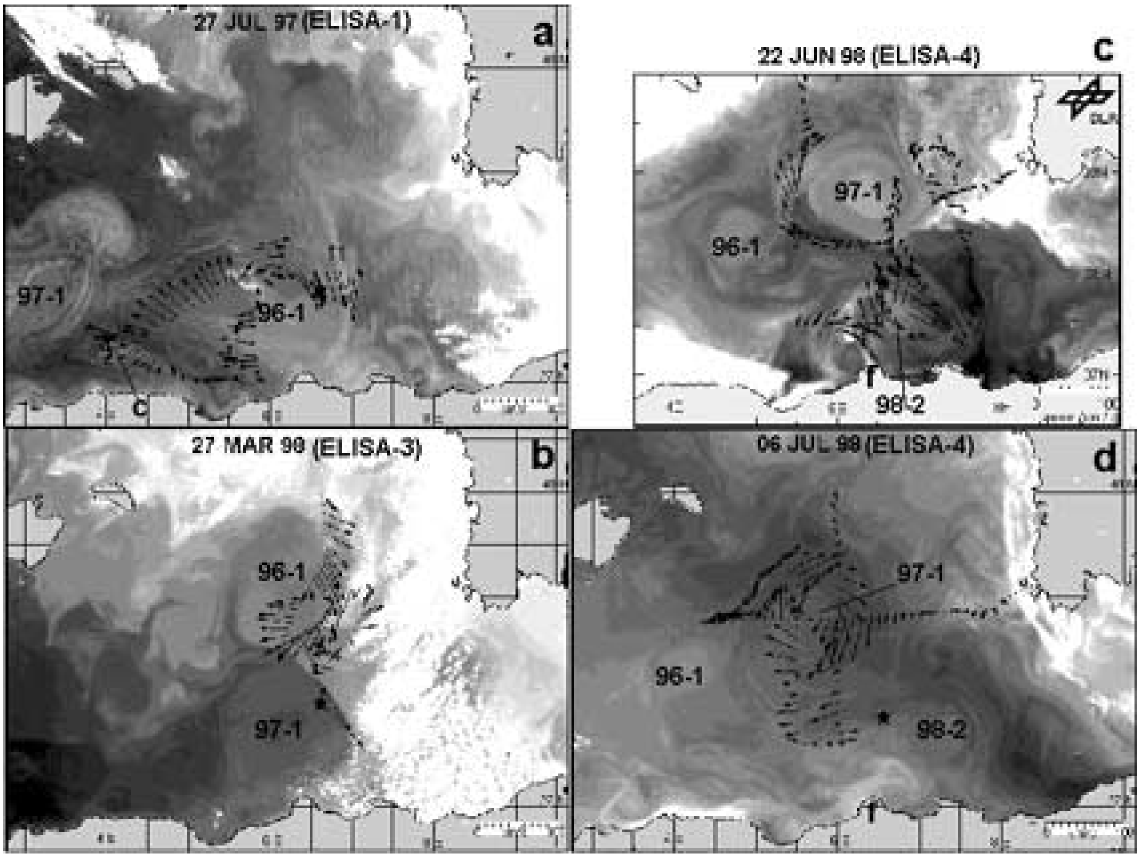

Fig. 2. A sub sample of the SST images time series, showing the successive positions of the Algerian eddies 96-1 and 97-1 from July 1997 to 1998. The arrows represent the mesoscale currents they induce (max ~1 knot), as sampled during the ELISA cruises with a shipborne ADCP. *: position of the mooring 8 equipped with 4 autonomous CTD/Fluorometers. Note the propagation, between 22 June and 06 July (~2 weeks) of the eddies along their general counter clockwise circuit in the eastern part of the Algerian sub-basin.

parts of the Mediterranean (Puillat *et al.*, 2002; Hamad *et al.*, 2003). Analyses of satellite images show that mesoscale activity is intense in nearly all parts of the Mediterranean (e.g. Le Vourch *et al.*, 1992; Millot *et al.*, 1994) and present all year-round, with a peak in winter in the northern parts (demonstrated at least in the western basin) in relation with the deep water formation process. The northern currents (that flow westwards) are less unstable. They mainly generate meanders which evolve into mesoscale eddies of relatively small scale only in the eastern basin (Hamad *et al.*, 2003). Both the southern and northern currents are, when roughly stable, "only" a few tens of km wide, so that sampling interval must be fine enough and adjusted to the physical phenomena expected to drive markedly the biological ones.

As it can be deduced from Fig. 1 and is shown on Fig. 2, the current does not flow smoothly along the coast: it is disturbed by eddies in a direction opposite to the general circulation (see Fig. 2a). Most of the gradients created are oriented cross-shore, with an offshoreward current (and upwelling) on the upstream (resp. shoreward and downstream) side of the eddy. Besides the temperature and salinity changes at the edges of the eddies, one must expect changes/ alternation of open-sea/saline/nutrient-depleted/low chlorophyll water populations with coastal/fresher/nutrient-rich/high chlorophyll ones as the eddies are passing by. This is clearly shown by the physical and biological time series collected during ELISA with four autonomous CTD/fluorometers fixed on top of one mooring (see location in Fig. 2) between 30 and 80 m (Fig. 3).

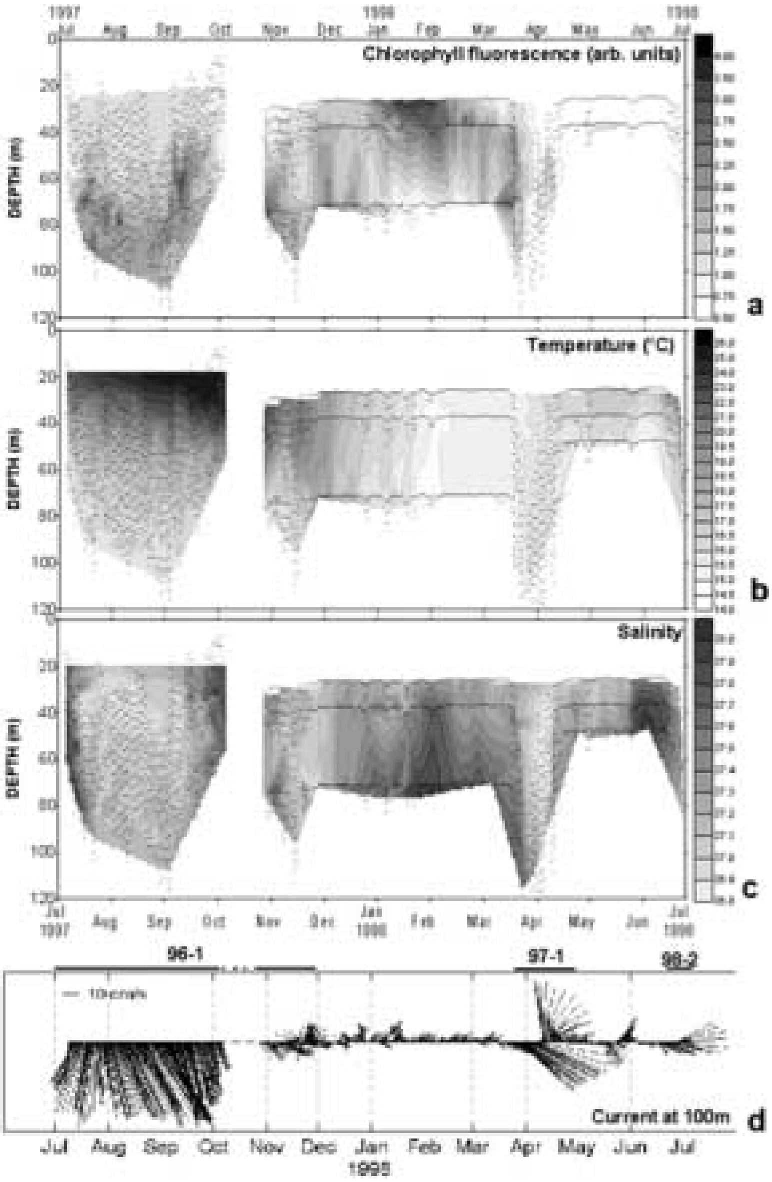

Fig. 3. The concurrent biological and hydrodynamical time series recorded during ELISA on mooring 8. **a**) chlorophyll fluorescence, **b**) temperature, **c**) salinity, **d**) current at 100 m (North points upward). The dots represent the immersions (subsampled) of the CTD/Fluorometers.

For what concerns the biological response of the eddies, the fact that they are anticyclonic is significant. Indeed, their dynamical structure is a depression (~150 m deep), so that, after the phytoplankton has depleted the nutrients from the euphotic zone, it cannot grow further as the deeper nutrient-rich water is kept below the euphotic depth. In the eddy 96-1, which was sampled in July 1997 close to the Algerian slope (Figs. 2, 3), the oligotrophy was as severe as in the eastern basin. When it was sampled in March 1998 offshore (Fig. 2b) it was there that the maximum integrated chlorophyll values were found (Taupier-Letage *et al.*, 2003). It has been shown for the Algerian eddies, at least, that their biological response depends, in a complex way, upon their history (age and trajectory), the season, their location and the dynamical environment (interactions with their parent current or with other eddies).

Interactions of meanders and eddies with other eddies or with coastline breaks can generate smaller-sized and shorter-lived features, such as cyclonic shear eddies “c” and/or filaments “f” in Figures 1 and 2. In the “c” sampled during ELISA -1 (Fig. 2a), the chlorophyll maximum concentrations reached ~ 8-10 mg/m3, when the maximum recorded during the seasonal bloom was ~1-4 mg/ m^3 (Fig. 3a).

Eddies can also disturb the general circulation for months, hence the local hydrodynamical situation. For instance, in 1984 close to Algiers (3°E), the huge eddy W (up to 250 km, Fig. 4) has been disturbing the alongslope flow of AW during 9 months at least, diverting it offshore so that colder (~ 17-18°C in summer) and fresher water reached the southern coasts of Mallorca (Taupier-Letage and Millot, 1988). Concurrently, along the Algerian slope downstream W, as long as the Algerian Current was diverted offshoreward there was no strong mesoscale activity, reducing drastically the number of associated upwellings. Most likely this specific situation, generated by mesoscale dynamics, had a time scale long enough to impact the food web and local fisheries.

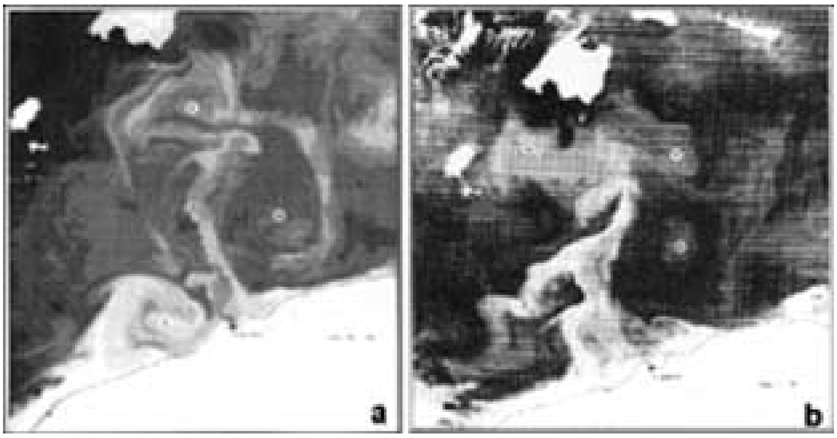

Fig. 4. The Algerian sub-basin in summer 1884: SST from 29 July (a) and 07 August (b) 1984 (from Taupier-Letage and Millot, 1988). The younger/smaller eddy c propagates eastward up to impinging on W, and disintegrates. On the other hand the eddy A succeeds in propagating around W.

Seasonal variations occur everywhere, and the season is probably the spatial scale that has focussed the most efforts for biological time series. Mesoscale variability is always superimposed on better-known seasonal varirability, and is likely to appear like “noise” to the untrained eye, and disregarded as such, so that in many cases the seasonal variability cannot be considered as well known. Now, as the biological variability associated with the mesoscale can be higher than the seasonal one, as shown above with the ELISA data, this argues for the adoption of a sampling interval resolving the local mesoscal. This should cover a few years at least, so as to get a biological time series describing seasonal cycles reliably, noting that seasonality for biology is not only that induced directly by the earth orbit. Seasonality for biology also results from seasonality in dynamics, as an indirect consequence of the earth orbit.

RECOMMENDATIONS FOR CONCURRENT TIME SERIES ACQUISITION

The quality of a time series depends first on the adequacy of its sampling interval with the spatio-temporal scales of importance. The analysis of satellite images time series (especially thermal, visible, altimetry) prior to the in situ data collection ensures that this condition is met. A second condition is the absence of gaps. To this all steps must be taken to decrease the enornous effort required for sampling, especially switching to autonomous sensors whenever possible, and to autonomous platforms whenever relevant. The quality of the interpretation of the biological time series requires the understanding of the dynamical environment (on a large domain) at least, and better, of the trophic conditions too. This can be achieved by analysing concurrent data sets such as satellite images, and acquiring concurrently basic parameters such as temperature and salinity, chlorophyll fluorescence, nutrients, ... If we take the example of the interdisciplinary ELISA experiment, we had a good a priori knowledge of the spatio-temporal scales and phenomena, gained from our previous analyses of the SST and ocean colour images. We combined a one-year network of nine moorings (3 to 5 currentmeters each, plus one equipped with four autonomous CTD/fluorometers) and four cruises (total ~100 days) year-round. We received the SST images in near-real time on board to track the eddies and associated phenomena, and thus decided about the most-adapted sampling scheme. About 250 casts were made along ~ 30 transects, with a sampling interval ranging from 5 to 14 km. During the first cruise the investigation of the eddy 96-1 was also carried out (team from Southampton Oceanographic Center) using a Seasoar device and a towed LHPR (Longhurst and Hardy Plankton Recorder). More than 500 SST images were analysed (Puillat *et al.*, 2002) to track the eddies and interpret the time series recorded on the moorings (Taupier-Letage and Puillat, 2001; Aubertin *et al.*, 2003) ... and of course processing is still going on, and will go on for a few more years yet!

Details on platforms and sensors can be obtained for instance on websites (<www.pml.ac.uk/globec/main.htm>, <www-ocean.tamu.edu/GOOS/goos.html>, <www.opl.ucsb.edu/tommy/pubs/hawaii01/dickey.pdf> and <www.bom.gov.au/OceanObs99/Papers/Send. pdf>). We will only list here what we consider as the most efficient platforms and strategies (i.e. requiring a minimal effort for a maximal understanding) to collect and/or improve biological time series.

• Satellites

Satellite images – mainly sea surface temperature (SST) and colour – easily provide essential information about the local spatio-temporal characteristic scales and the representativity of the sampling site. Time series of images provide a description of the evolution of the dynamical (SST) and biological (surface chlorophyll) phenomena, and allow targeted sampling to check hypotheses. Satellite images are also sometimes the only means to get information on the poorly known/sampled areas, such as the southeastern Mediterranean.

Whenever possible the in-depth analysis of the images times series must precede the start of any biological time series acquisition, so that i) the area/site most representative of the signal which is looked for is clearly identified, and ii) the observational effort can be optimised (i.e. larger adequate sampling spatio-temporal interval). Images should be used too in (near) real time to guide any shipborne additional complementary sampling. A posteriori, time series of images must be used to describe the spatial environment of the sampling site, to check its representativity, and to interpret the observed biological signal variability. Many satellites/sensors are available to back biological studies, the images processing is now much easier and faster, and their availability has improved as some can be obtained from the web for free. The images to be sought first are the thermal ones from AVHRR (Advanced Very High Resolution Radiometer, on board satellites NOAA, see <http://www.ipo.noaa.gov/>, since the SST they provide is representative of the temperature of the whole mixed layer as soon as waves mix the surface layer (which is most often the case). Then the visible “ocean colour” ones such as SeaWiFS, MERIS and MODIS (see <http://www.ioccg.org>) since they provide phytoplankton concentration distributions, integrated over a layer ranging from a few metres in very turbid waters up to several tens of metres in very oligotrophic (clear) waters. These medium-resolution sensors provide images with a ~1 km pixel on an area ~ 2000 km wide, at least once per day (i.e. any point of the Mediterranean is covered at least once per day). The analysis of images (cloud cover permitting) such as the

SSTs is relatively easy, as currents can be deduced intuitively, either by following the isotherm contours (e.g. rotation of currents associated with an eddy), or by tracking the displacement of a structure (e.g. progression of the tip of a tongue). Note that the visible images are also good tracers, although indirect, of the dynamics (of mesoscale dynamics on Figures 1b, d, and of seasonal dynamics on Fig. 5b). The analysis of time series of images provides the indispensable description of the spatio-temporal variability of the area at scales ranging from meso- to seasonal and interannual.

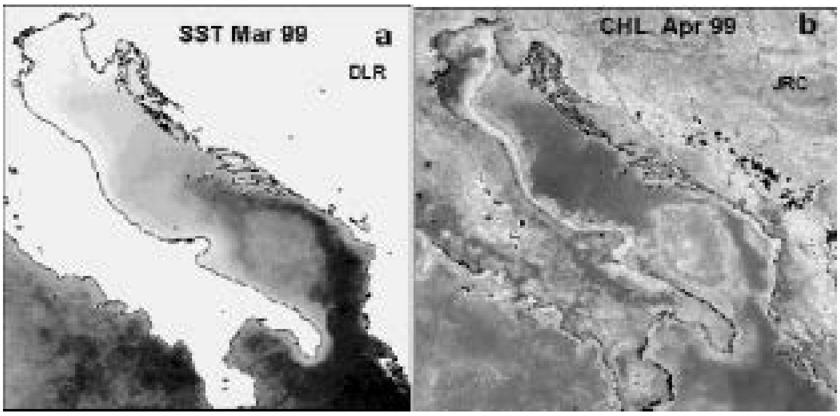

Fig. 5. Monthly composite images of **a**) STT for March 1999 (AVHRR from DLR) and **b**) surface chlorophyll concentrations for April 1999(SeaWiFS from JRC).

The critical gap is the availability of full resolution (1 km) products for end-users. As far as the AVHRR images are concerned, daily, weekly and monthly SST composites can be found (free) on the DLR server <http://eoweb.dlr.de:8080/servlets/template/welcome/entryPage.vm>. Daily composites are usually posted within a few days, so that they can be used to determine the hydrodynamical context in preparing a campaign at sea. As for the ocean colour images, the closer ones found on the web are the SeaWiFS images posted (free) on the JRC site <http://www.me.sai.jrc.it/>. There are daily, decadal and monthly composites at a 2-km resolution. Unfortunately there is a one-year delay (at least), and a few of the orbits only are processed, so that the daily coverage of the Mediterranean is incomplete. Full resolution data are available of course in archiving centres, but imply to undertake a large part of the processing chain, which is not within the reach of most end-users. Several projects process images at high resolution up to end-user products, however it is either for a limited duration or dedicated to a limited public. As several institutions across the Mediterranean have receiving stations, there should be a coordinated effort to cover the whole Mediterranean to ensure the availability of final products to end-users (possibly in near-real time).

• Moorings

Moorings provide a way to sample continuously and objectively with a temporal interval as fine as necessary, in an unattended mode and over a "long" period. Variations in time only are recorded, which provides an unbiased measure and is convenient to compare data with models (as opposed to drifters where variations in both space and time add). Technological progress has provided a great variety of autonomous sensors easy-to-use and relative cheap (at least as compared to the value of the information provided, and/or to the cost of hand-collected time series, and/or to the cost of a small ship). Basic parameters such as temperature and salinity must be acquired to provide the hydrological environment (autonomous CTD probes are now easy to use and cheap). Currentmeters are also easy to use, as well as the current profilers (ADCPs) that provide a description of the structure of the water column. Chlorophyll fluorescence is also a basic parameter to record. Several autonomous fluorometers have been developed and have been used (cf. Fig. 3a). However, for the bio-optical sensors (including cameras) in general there appear to be no fully satisfying solution to avoid biofouling on long-term deployments (1 year). Nevertheless this will not hinder bio-optical moorings in the coastal zones, as periodic operations for the maintenance of the sensors are easier to set up there. As for the biogeochemical sensors, it seems that the sensors developed up to now have sensitivity and detection limits not fully adapted to the (extreme) oligotrophic conditions of the Mediterranean. A 1-hour sampling interval provides a sound description of the mesoscale variability.

For biology the surface layer is critical. Collecting biological time series in that layer will be advantageously made, in regions where waves are not too high, with moorings equipped with surface buoys (this requires an efficient signalisation), thus allowing sampling up to the surface. In deep waters and in unprotected coastal zones and shelves, however, surface buoys will need to be relatively large. The corresponding price and required logistics are (too) high, so that subsurface moorings are preferred, which prevents from sampling the critical upper few tens of metres. During periods of strong current, the mooring head deepens as the drag on the mooring line increases. The drawback is that the immersion of the sensors is not constant, but the great advantage is that, during these periods, each sensor profiles a few 10s of metres, thus increasing the vertical resolution (see Fig. 3). A critical gap for the mooring strategy is the absence of device that allows profiling in the upper layer up to the surface (carrying thus only one set of sensors). One profile per day with a vertical step of 50cm in the upper 200m would provide an adequate resolution of the mesoscale variability.

It must be noted that a CIESM co-ordinated action to monitor the long-term hydrological trends in the Mediterranean has just begun this year, using small moorings to be recovered every one or two years (<www.ciesm.org/newsroom/2201.html>). This information will be very useful in the future for the interpretation of local biological time series.

• Shipborne

If the biological parameter constituting the time series requires a ship, a CTD should be systematically used (they have become cheaper and easier to use, some models work in stand-alone mode) to collect a water column profile. There is a great variety of sensors that can equip the CTD for chlorophyll fluorescence (high priority), dissolved oxygen, etc. However there is no profiling nutrient sensor on the shelf. A complementary structure-oriented sampling, as defined upon the (near)real time analysis of satellite images, will significantly improve the understanding of the distribution of the biological parameters.

Biological time series can also be collected along regular tracks, at regular intervals and over long periods, using autonomous instruments on board ferries. Collection of plankton has been carried out for a long time on ferries across the Channel with a LHPR, for instance. This is certainly a strategy to foster, as it is very cheap, the domain sampled is larger (the surface layer along the whole ship track, potentially the whole basin), the data set is homogeneous (the same track is sampled repeatedly), and the effort for sampling is extremely reduced (but full automation must be sought, as the intervention of a crew member cannot be envisaged on ferries). There is nearly no risk of data gaps due to bad weather, as a ferry must cross. And finally the issue of biofouling of sensors can be addressed properly as the opportunities for maintenance are frequent (regular port calls). Such a strategy is all the more valuable when the relationships between the surface and deeper layers are well understood. The use of a thermosalinograph (TSG) must be systematic, especially since Salat and Pascual (2002) have shown that a long-term hydrological trend could be extracted from the surface water temperature signal.

Such a project which will cover the the routes Marseilles-Algiers and/or Marseilles-Tunis is currently in its pilot-phase with the support of CIESM.

In conclusion, efforts must be made to develop the biological and biogeochemical autonomous sensors, to develop the availability of satellite final products, and, in some cases, to develop discussions and joint work between physicists and biologists.

Swordfish abundance trends in the Mediterranean

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INTRODUCTION

Swordfish (*Xiphias gladius*) is a large pelagic species of high commercial value heavily exploited in the Atlantic Ocean and the Mediterranean Sea. Past genetic studies indicate that there is practically no mixing between Atlantic and Mediterranean individuals and suggest that all Mediterranean individuals form a unique stock (Kotulas *et al.*, 1995).

Swordfish landings in the Mediterranean showed a strong upward trend from about 4,000 metric tons in 1976 to 20,000 tons in 1988. Since then, landings have fluctuated between 13,000 and 15,000 tons. Greece and Italy are among the most important swordfish producers in the Mediterranean and, in the latest years, account for about 50-60% of the total Mediterranean production. (ICCAT, 2003)

A preliminary assessment of the Mediterranean stock, carried out by the International Commission for the Conservation of Atlantic Tunas (ICCAT) in 1995, revealed that the stock might be close to over-exploitation (ICCAT, 1996). A more recent assessment based on Greek and Italian data suggested the presence of a rather stable situation in terms of mortality and recruitment (Tserpes *et al.*,. 2001a). However, the above assessments were not considered sufficiently reliable for an in-depth evaluation of the state of the stock, due to lack of detailed data from certain important fisheries and the short time-series of the available data. In any case, it has been pointed out that measures should be taken to reduce the proportion of juvenile fish in the catches, so as to help the rational management of the stock (Di Natale *et al.*, 2002).

For several marine species it is difficult to determine absolute population sizes, due to lack of sufficient fisheries and (or) survey data. This is particularly true in the case of the Mediterranean swordfish where fisheries time-series is short and information for several important fisheries is lacking. In such cases, relative abundance indices, such as the catch per unit effort (CPUE), can give important information on the stock size fluctuations by assuming that stock abundance is proportional to that index (Hilborn and Walters, 1992).

The present work attempts to investigate fluctuations in the abundance of the Mediterranean swordfish through the analysis of CPUE data derived from the main Greek and Italian fisheries exploiting the central and eastern part of the Mediterranean basin. Data have been analysed by means of commonly used Generalised Linear Modelling (GLM) techniques.

MATERIALS AND METHODS

The presently analyzed CPUE data were collected in the frames of past European and national projects and included spatial and temporal information on catch- effort for long-lines and driftnets, in as much detail as possible, i.e. on an individual boat trip basis. CPUE observations were expressed in terms of kg/1000 hooks for long-lines and kg/km of net for driftnets. Sampling, which was based on information from landings to pilot ports, covered the period 1987-2001 and included the main Greek and Italian fleets exploiting different areas of the central and eastern Mediterranean (Fig. 1).

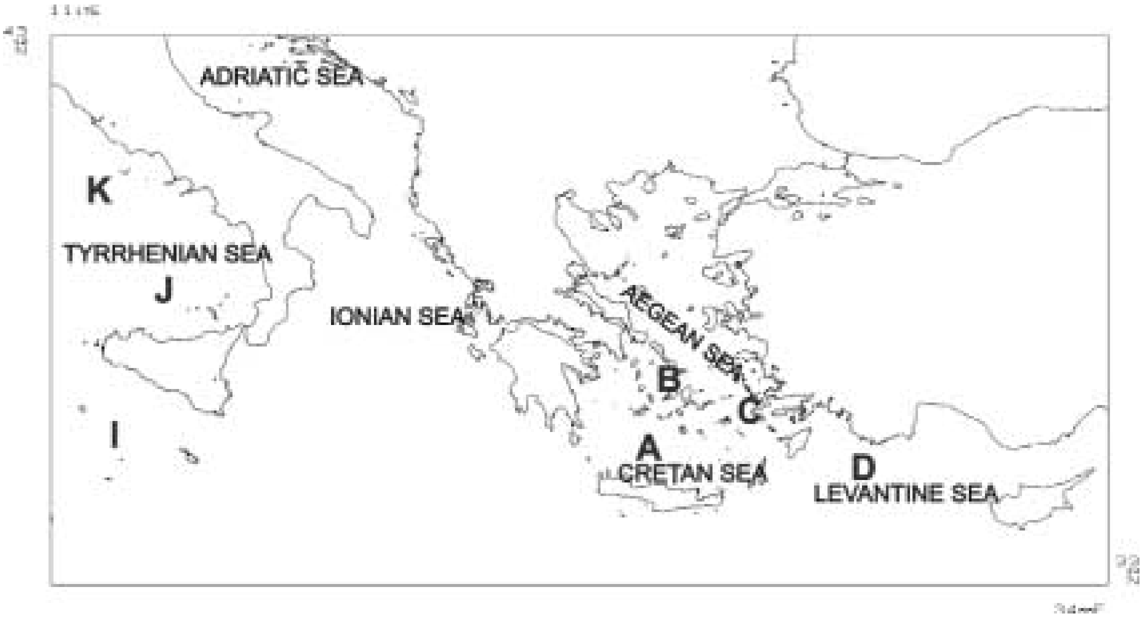


Fig. 1. Map of the central-eastern Mediterranean indicating the main areas exploited by the fleets studied. A = Cretan sea, B = Central Aegean, C = Southeastern Aegean, D = Levantine, I = Straits of Sicily, J = Southern Tyrrhenian and K = Central Tyrrhenian.

In the case of Greece, a total of 2,569 data records were analysed covering the period 1987-2001 with the exception of 1989, 1996 and 1997. Four fishing areas were considered: A = Cretan sea, B = Central Aegean, C = South-eastern Aegean and D = Levantine (see also Fig. 1). Observations covered the activities of the two main swordfish fleets operating in the country, the fleets of Kalymnos and Hania. Generally, catches of both fleets represent 50-70% of the total Greek production (Tserpes *et al.*, 2002a). These fleets mainly exploit the central, south-eastern Aegean Sea but occasionally extend their activities to the northern Aegean and Levantine basin. Fishing is carried out using drifting surface long-lines through February to September while is prohibited by law from October to January. In the last five years, the traditional long lines have been modified, resembling the ones used for the tuna fishery in the Atlantic. The modified gear, which is known as American-type long-line, is set deeper than the traditional one and uses fluorescent material to attract the fish. Catchability differences among the different long-line types were taken into account when creating the global data set. Specifically, observations from the American-type long-line were multiplied by 0.64 to reflect previously estimated catchability differences among gears (unpublished data).

In the case of Italy, a total of 2,500 observations from the Sicilian fleet were analyzed. The Sicilian fleet, which is the largest swordfish fleet in the Mediterranean, mainly exploits the Tyrrhenian Sea but occasionally expands its activities into a much wider area. It accounts for about 70% of the total Italian catch (Tserpes *et al.*, 2002). Available data covered the long-line and driftnet fishing activities (large mesh size net) carried out in the central and southern Tyrrhenian Sea, as well as, in the Straits of Sicily. The long-line fishery operates throughout the year but the main fishing season lasts from August to December while the driftnet fishing season lasts from April to August.

Regarding the long-line fishery, a total of 1,520 data records were analyzed, collected throughout the year from 1991 to 2001, with the exception of 1993 and 1996. Analysis did not include data from January and February as they were too scarce. Three fishing areas were considered: I = Straits of Sicily, J = South Tyrrhenian and K = Central Tyrrhenian seas (see also Fig. 1). A total of 980 observations from the Italian driftnet fishery that targets swordfish (large mesh size net) were available from 1990 to 2001 throughout the year. However, the regular activity is carried out from April to August and only data from those months were included in the analysis. Two fishing areas were considered: J = South Tyrrhenian and K = Central Tyrrhenian (see also Fig. 1).

CPUE data were analysed, separately by gear and country fleet, by means of Generalised linear modelling (GLM) techniques (McCullagh and Nelder, 1983). Based on the deviance residuals plot, models assuming a Gamma error structure with a log link function were found to be the most appropriate for all examined data sets. The models included year, month and area as main effects. It was preferred not to examine interactions terms incorporating the “Year” effect as this could bias estimates of annual trends (Ye *et al.*, 2001). Month-area interactions were included in the models in the cases where sampling coverage allow fitting of such a term. Model fitting was accomplished using the statistical package S-plus, following the approaches described by Venables and Ripley (1997).

Finally, in order to allow comparisons among fleets and gears and facilitate the identification of possible global trends, the estimated standardized indices for each fleet-gear combination were scaled to the corresponding average value for the years 2000-2001, and the resulted estimates were presented in a common plot. Furthermore, the scaled values were averaged to obtain a global scaled index of abundance.

RESULTS

Eastern Mediterranean (Greek long-liners)

The deviance residual plot did not demonstrate any outstanding feature suggesting that the model is inappropriate for the observations (Fig. 2). The model included only the main effects; the analysis of deviance table indicated that it explained 15.18% of the total variation. All factors were significant at the 95% statistical level.

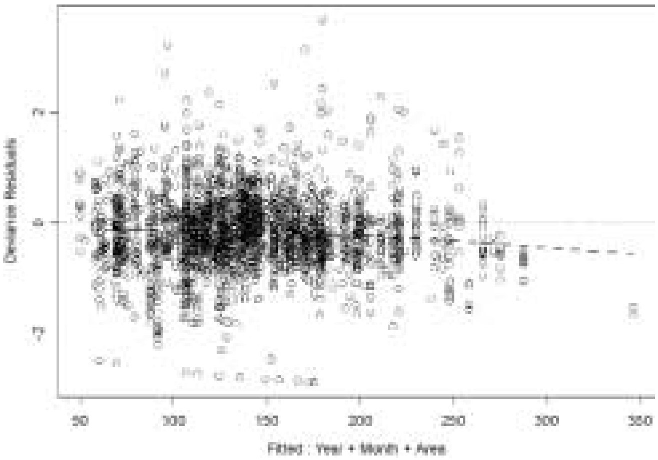
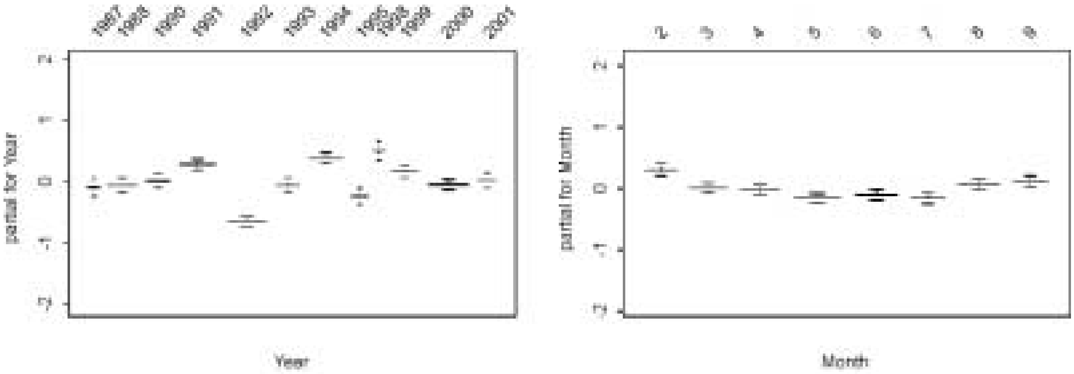


Fig. 2. Residual deviance of the generalized linear model fitted to Greek long-line data, plotted against predicted CPUE. The fitted line represents a locally weighted smoother.

The effect of the significant predictors on CPUE is shown on the y-axis for different values of the predictor (x-axis) (Fig. 3). CPUE levels do not show any particular trend among years while the beginning and end of the fishing season seem to be more productive. The standardised CPUE indices were calculated by predicting the year effects for area C in July; the values are given with associated standard errors in Table 1.



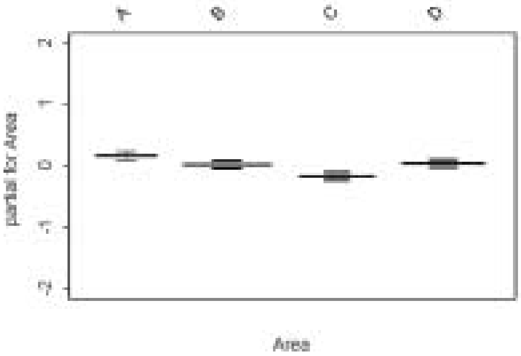


Fig. 3. Generalized linear model derived significant effects on CPUE index for the Greek long-line data. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors.

Table 1. Standardised abundance indices and the corresponding standard errors (s.e.) by year, gear and fleet. LL=Long-line, DN=Driftnets. Indices are expressed in terms of kg/1000 hooks for the long-lines and kg/km of net for driftnets.

	Greek LL		**Sicilian LL**		**Sicilian DN**	
Year	**CPUE**	**s.e.**	**CPUE**	**s.e.**	**CPUE**	**s.e.**
1987	86.85	8.35				
1988	88.88 7	63				
1989						
1990	95.78	7.38			6.19	0.50
1991	125.26	9.27	121.14	7.70	6.02	0.64
1992	49.73	3.75	109.73	6.77	10.14	0.62
1993	89.70	7.36			12.581.22	
1994	138.76	0.14	104.81	5.82	9.72	0.65
1995	74.78	6.56	132.15	7.66	14.59	0.90
1996					8.58	0.76
1997			87.79	5.76	15.45	1.37
1998	156.41 1	5.31	153.16	9.72	6.71	0.66
1999	111.93	9.19	164.83	9.08	8.67	0.84
2000	90.22	6.76	69.67	7.34	12.71	0.91
2001	96.64	8.41	113.73 1	1.02	10.77	0.85

Central Mediterranean (Sicilian long-lines)

A model, which included only the main effects, provided a good fit to the data as it was demonstrated by the deviance residual plot (Fig. 4). The analysis of deviance table indicated that it explained 24.02% of the total variation. All factors were significant at the 95% statistical.

The effect of the significant predictors on CPUE is shown on the y-axis for different values of the predictor (x-axis) (Fig. 5). The CPUE levels in 2000 and 2001 were among the lowest estimated, particularly that of 2000. The period July-October was the most productive and among

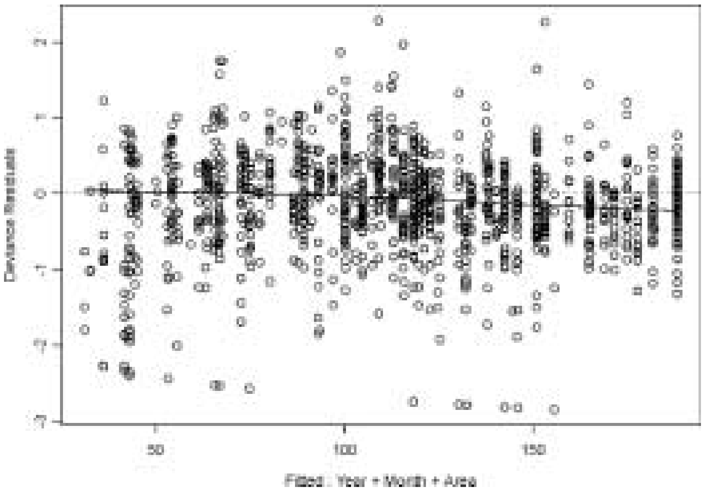
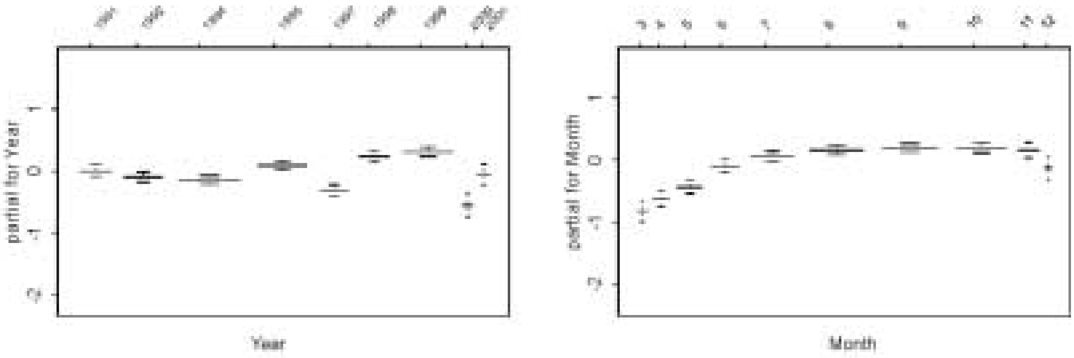


Fig. 4. Residual deviance of the generalized linear model fitted to Sicilian long-line data, plotted against predicted CPUE. The fitted line represents a locally weighted smoother.



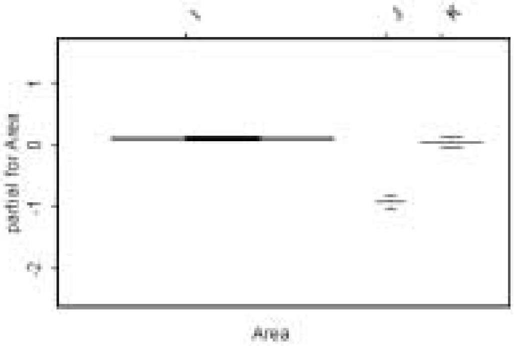


Fig. 5. Generalized linear model derived significant effects on CPUE index for the Sicilian long-line data. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors.

areas the higher levels were estimated for the Straits of Sicily. The standardised CPUE indices were calculated by predicting the year effects for area I in July; the values are given with associated standard errors in Table 1.

Central Mediterranean (Sicilian driftnets)

The deviance residual plot demonstrated that the model provided a good fit to the data (Fig. 6). The model included the main effects and the month-area interaction. The analysis of deviance table indicated that it explained 35.34% of the total variation. All factors were significant at the 95% statistical level.

The effect of the significant predictors on CPUE is shown on the y-axis for different values of the predictor (x-axis) (Fig. 7). Annual estimates do not show any particular trend. The months of

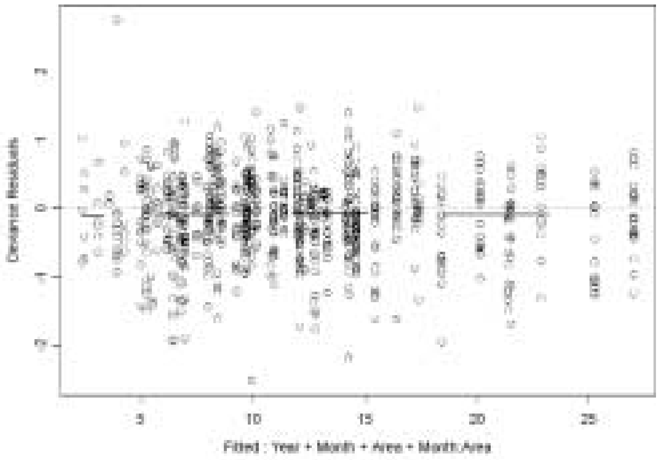


Fig. 6. Residual deviance of the generalized linear model fitted to Sicilian driftnet data, plotted against predicted CPUE. The fitted line represents a locally weighted smoother.

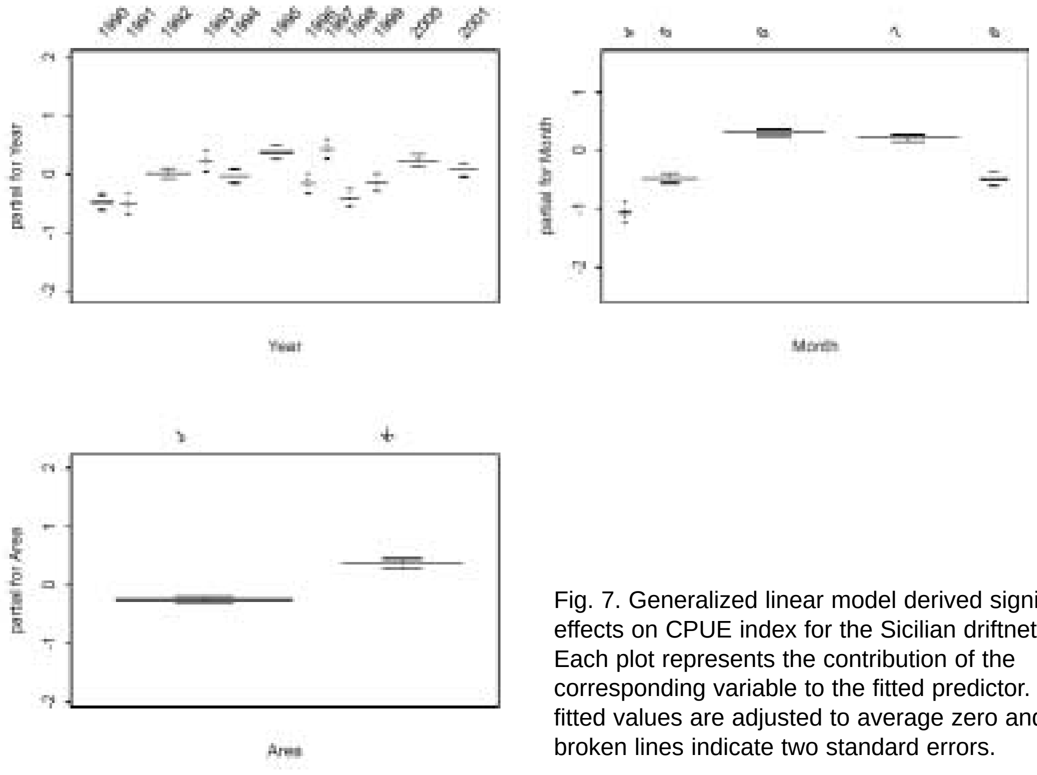


Fig. 7. Generalized linear model derived significant effects on CPUE index for the Sicilian driftnet data. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors.

June and July were the most productive and among areas the higher levels were estimated for the Central Tyrrhenian Sea. The standardised CPUE indices were calculated by predicting the year effects for area J in July; the values are given with associated standard errors in Table 1.

Gear-Fleet comparisons

Table 2 presents all standardised abundance indices scaled to the mean 2000-2001 value. The estimated values and the average scaled indices are plotted against year in Fig. 8. No particular trend can be seen, except perhaps for the presence of an overall peak every 3-4 years. Generally, the fluctuation patterns vary depending on the fleet and gear.

Table 2. Scaled standardised abundance indices (see text for details) by year, gear and fleet and the corresponding average values. LL=Long-line, DN=Driftnets.

Year	Greek LL	Sicilian LL	Sicilian DN	Average
1987	0.93			0.93
1988	0.95			0.95
1989				
1990	1.03		0.53	0.78
1991	1.34	1.32	0.51	1.06
1992	0.53	1.20	0.86	0.86
1993	0.96		1.07	1.02
1994	1.49	1.14	0.83	1.15
1995	0.80	1.44	1.24	1.16
1996			0.73	0.73
1997		0.96	1.32	1.14
1998	1.67	1.67	0.57	1.31
1999	1.20	1.80	0.74	1.24
2000	0.97	0.76	1.08	0.94
2001	1.03	1.24	0.92	1.06

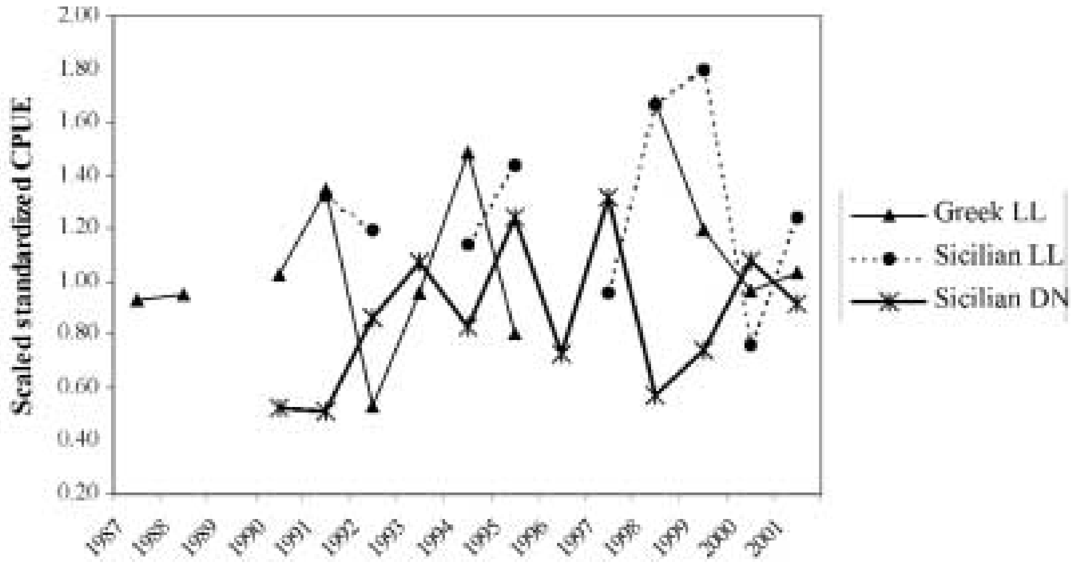


Fig. 8. Scaled standardized CPUE index by year for the examined fleets. LL=Long-line, DN=Driftnets

DISCUSSION

Catch-effort data have been successfully used to derive stock indices of relative abundance from different fisheries or survey data (Gulland, 1956; Kimura, 1981; Stefansson, 1996; Goñi *et al.*, 1999; Punt *et al.*, 2000; Walsh and Kleiber, 2001). However, the use of commercial CPUE data for constructing relative abundance indices requires correction to take into account various parameters, such as changes in fleet characteristics, which could affect the ability of vessels to catch fish (Hilborn and Walters, 1992; Kimura and Zenger, 1997). Corrections are also needed to account for changes in the exploitation patterns.

In the latest years GLM techniques have been widely used to examine various factors affecting catch rates of different commercial fisheries or for the analysis of experimental fishery survey data (Goñi *et al.*, 1999; Punt *et al.*, 2000; Walsh and Kleiber, 2001; Ye *et al.*, 2001; Tserpes and Peristeraki, 2002; Tserpes *et al.*, 2002b). In the present case we used them in order to identify the factors that influence catch rates and to estimate standardized abundance indices by year. Results indicated the presence of large fluctuations among years but failed to demonstrate the presence of any trend. A similar lack of trend can be also observed in the Italian, Greek and global Mediterranean swordfish landings over the latest years (ICCAT, 2003). Although the analyzed time series of data was short to allow identification of annual cycles, it seems that peaks in the overall CPUE index are observed every 3-4 years. Previous authors who modeled a time series of monthly Greek swordfish landings by means of ARIMA and X-11 models reported analogous cycles on the landings (Stergiou *et al.*, 2003).

The estimated standardized abundance indices by gear and fleet did not follow the same pattern over the years examined. This can be, at least partially, attributed to differences in the exploitation pattern of the fleets. Driftnet fisheries target older age-groups than the long-line ones, while there are also differences among the long-liners, as the Sicilians tend to capture more juveniles than the Greeks (Tserpes *et al.*, 2001b). Hence, the differences found in the CPUE pattern among gears and fleets may reflect real differences in the abundance fluctuation pattern among ages. Taking into account that the examined fleets exploit different areas, such differences may be also due to the presence of sub-stocks a fact that has been already speculated, based on preliminary findings of genetic studies (Kotulas, personal communication).

Our findings demonstrate that the patterns of the estimated monthly abundance indices differ among areas : in the summer months the relative abundance is increasing in the central Mediterranean and decreasing in the eastern. Taking into account that swordfish spawn in summer (Palco *et al.*, 1981), this finding may relate to spawning migration, as the presence of a spawning ground in the Straits of Sicily is known (Rey, 1988).

Under the scenario of a common Mediterranean stock and taking into account that the examined fleets have dissimilar exploitation patterns and exploit different areas, it is preferable to consider the mean scaled standardized estimates (see Table 2) as better representing the abundance variations of the stock.

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Revising paradigms and myths of phytoplankton ecology using biological time series

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Marine phytoplankton is deemed to be responsible of about 50% of the primary production on the planet, yet our knowledge of its biodiversity and ecology is limited, compared e.g. to terrestrial plants. Most of our ignorance stems from the great divergence between time and space scales over which most phytoplankton processes take place and the scales of our observations. As a result, a few paradigms are available that endeavour to account for time and space distribution of marine phytoplankton. These include, for example, the seasonal sequence of minimum and maximum abundances of the temperate latitudes, with the classical spring and autumn blooms (Sverdrup, 1953) and the temporal succession of life forms and species groups which exploit different conditions of turbulence and nutrient concentrations (Margalef, 1978; Smayda and Reynolds, 2001). In want of more precise information, these invaluable and stimulating contributions of enlightened ecologists are at times misused and applied to all kinds of situations, and often beyond the original ideas of their respective authors.

Time series of data offer a unique possibility to test a number of current views on phytoplankton ecology. Repeated observations over the years may indeed allow to discern between regular and exceptional events, changes and fluctuations, endogenous and exogenous regulation of the pelagic system, resulting in a better knowledge of both organisms and environmental variability. In this paper we provide evidence that several key questions on phytoplankton can be addressed using time series, based on a 15 yrs data set gathered at a coastal station 2 miles offshore in the Gulf of Naples (GON, Tyrrhenian Sea). Details of the methods applied and results of a first general analysis of this dataset can be found in Ribera d’Alcalà *et al.* (2003).

THE ANNUAL CYCLE OF PHYTOPLANKTON ABUNDANCE

Phytoplankton biomass in the GON shows three main periods of growth. A first increase is often recorded in February-March, much before the thermal stratification of the water column, that starts in late April. This anticipated biomass accumulation is probably allowed by stable meteorological conditions (Duarte *et al.*, 1999), which reduce vertical and horizontal dispersion. Annual peak values are generally attained in surface waters in late spring-summer, in stratified conditions, corresponding with the advection of nutrient-rich coastal waters (Ribera d’Alcalà *et al.*, 2003). Another increase is often recorded in autumn, which again is driven by stable weather conditions that allow the exploitation of nutrients of terrestrial origin (Zingone *et al.*, 1995). In all cases, a difference from classical paradigms exists not only in the timing of the blooms but also in the factors driving the biomass increase, i.e. nutrient sources, local circulation patterns and recurrent meteorological singularities. The seasonal pattern recorded in the GON could be a restricted phenomenon, being driven by the local variability of environmental parameters. However, some phases of autotrophic biomass accumulation in the GON are similar to those of other Mediterranean coastal areas (Duarte *et al.*, 1999) and, in the case of the winter bloom, possibly concern open waters too.

Interannual variability is clearly shown in our time series for cell numbers of total phytoplankton and single species (Fig. 1). A great limitation to the interpretation of this variability is constituted by the above-mentioned problems of time and space scales of sampling. Overall, it appears that phytoplankton cell numbers are increasing over the years despite a decrease in biomass (Ribera *et al.*, 2003). This apparent contradiction is explained by a consistent decrease in the average cell size of phytoplankton populations, with more frequent blooms of tiny species (e.g. *S. pseudocostatum*, *S. menzelii, Minidiscus comicus*) in recent years.

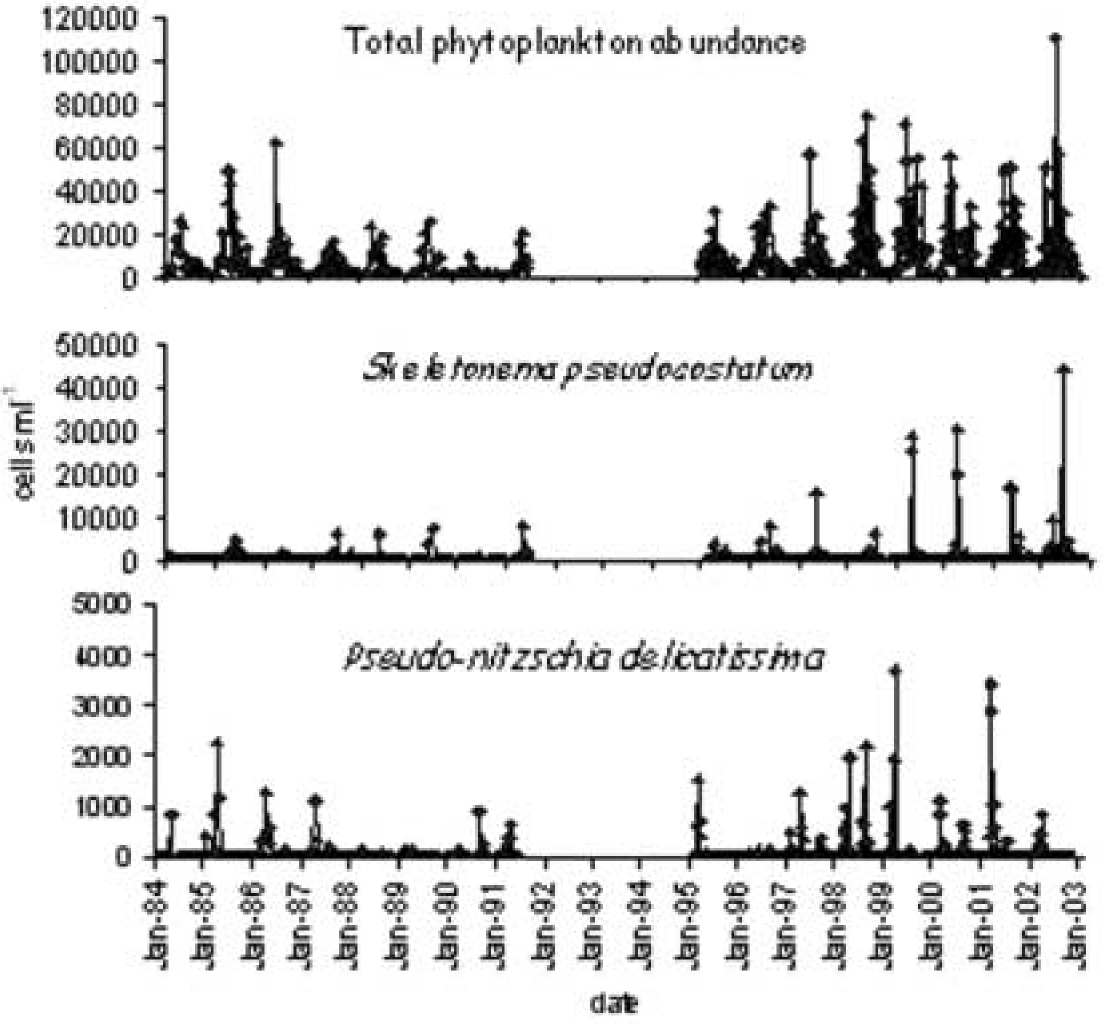

Fig. 1. Time series of cell numbers for total phytoplankton and two key species in the Gulf of Naples.

Diatoms are the most abundant microalgal group in the GON even during the late-spring summer maxima (Zingone *et al.*, 1995). This diverges from the paradigm of phytoplankton succession, which predicts motile species and dinoflagellates to dominate under stratified and nutrient-rich conditions, when diatoms would be sinking out of the photic zone (Margalef, 1978; Reynolds and Smayda, 1998). However, sinking as a passive and mandatory behaviour for diatoms is another myth of phytoplankton ecology: several papers have demonstrated a very active role of diatoms in controlling their buoyancy, as well as the ecological and evolutionary significance of sinking and floating (Smetacek, 1985; Villareal *et al.*, 1999).

PHYTOPLANKTON SPECIES ASSOCIATIONS: DO THEY REALLY EXIST?

There is a desperate need to reduce the complexity of phytoplankton data to a more simplified and manageable form for several reasons. The first is that noise deriving from redundant or scarcely significant information can hide the important signals. In addition, changes at the level of communities are deemed to be more significant than fluctuations of single species. Finally, mathematical models can generally handle only a limited set of information. For these reasons, stable species associations with similar "life-forms" and rules driving species assembly have been looked for in the apparent mess of field observations (Margalef, 1978; Reynolds, 1997; Smayda *et al.*, 2001). Freshwater phytoplankton provides examples of stable species assemblages that recur over the years and in different lakes under similar environmental conditions. These assemblages are composed of species sharing similar ecological requirements (Reynolds, 1997; Reynolds *et al.*, 2002) and can be considered as functional groups, i.e. "*a non phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors*" (Gitay and Noble, 1997).

Are these concepts also applicable to coastal marine phytoplankton ? Two different methods have been used in the analysis of the time series from the GON. One is a classical R-mode analysis based on a hierarchical clustering methods, the other is an asymmetric method (Dufrene and Legendre, 1997) which allows the identification of indicator species that characterize groups of observations (i.e. periods) obtained with a hierarchical classification of the observations. Results obtained so far show only few species recurrently occurring together, while the majority do not specifically characterize one or another species-groups or periods obtained, with discrepancies between the results of the two analyses.

These somewhat discouraging results may depend on a number of technical reasons. First, the nature of phytoplankton data, often having poor taxonomic resolution, is not optimal for sound statistics. In fact, an important, non quantifiable and variable fraction of the species in natural samples cannot be identified and counted with routine methods. In addition, it is more and more evident that one species name may hide a number of cryptic species, and that different life stages of one species may peak at different times. Besyonds these limitations, which should be common to all kinds of environments, the picture emerging from our data is very different from that of lakes (see e.g. Anneville *et al.*, this volume), where a template of environmental conditions determines an association to be present rather than another. In the coastal GON, stable associations cannot be recognised, since species group together in different ways over the years. In addition, co-occurring species often belong to distinct functional groups, e.g., non-motile, colony forming and silica-requiring diatoms, solitary and scarcely silicified diatoms, tiny autotrophic flagellates, mixotrophic species, fast-swimming dinoflagellates. It is therefore hard to believe that co-occurring species have the same ecological requirements, or that they are the result of a similar ecological response. More likely, members of distinct functional groups autonomously exploit different parts of the environmental spectrum. On the other hand, species apparently sharing similar ecological requirements (e.g. congeneric species) can thrive in different seasons, under notably different environmental conditions. The case of *Pseudo-nitzschia* species illustrated below provides a good example of the latter situation.

To explain the apparent difference between marine and freshwater phytoplankton, a condition closer to an intermediate level of disturbance (Reynolds *et al.*, 1993) can be hypothesized for marine coastal waters. This would keep the system far for equilibrium (Huston, 1979) and create conditions for the coexistence of a wider range of niches and for a higher functional diversity (Weithoff *et al.*, 2001).

IS THE SEASONAL PATTERN OF SPECIES OCCURRENCE DRIVEN BY ENVIRONMENTAL FACTORS?

Despite the weak results obtained with species associations, a rather high regularity in the occurrence of several species is observed over the time series from the GON. A clear example is provided by *Pseudo-nitzschia*, a genus that includes species producing Domoic Acid (DA), a potent neurotoxin. Two of the seven species identified in the GON, *P. galaxiae* and *P. multistriata*, have so far been proven to produce DA. *Pseudo-nitzschia* species from GON show distinct seasonal patterns of occurrence (Fig. 2). For example, *P. delicatissima* generally peaked in early spring ($\leq 3.4*10^6$ cells l^{-1}) and at times in autumn, *P. galaxiae* showed maxima in late spring and in summer ($\leq 9.3*10^6$ cells l^{-1}), while *P. multistriata* typically peaked in autumn ($\leq 2.1*10^5$ cells l^{-1}). These results reveal that species apparently very similar are adapted to thrive in different environmental conditions in terms of nutrients, water-column stability and light availability.

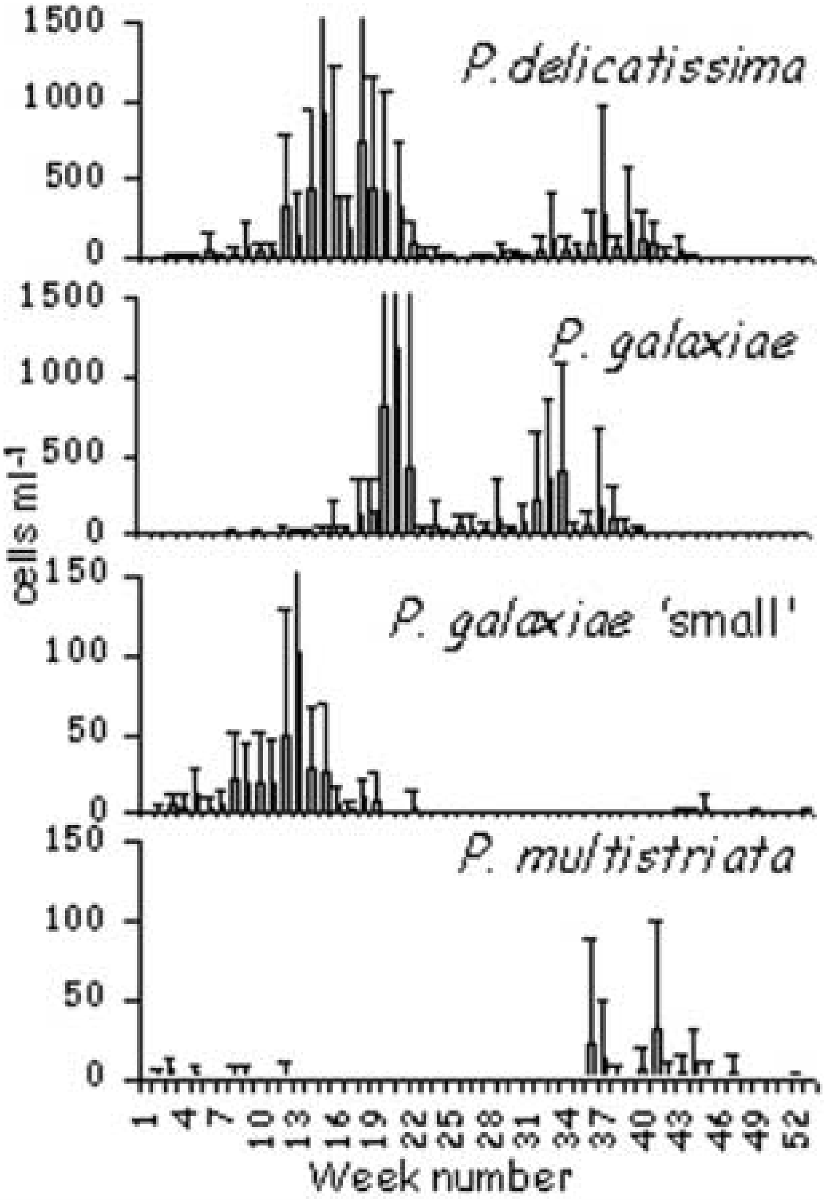

Fig. 2. Seasonality (weekly means) of some *Pseudo-nitzschia* species from the GON.

It is difficult to identify a set of environmental conditions which could drive the seasonal patterns of *Pseudo-nitzschia* species, due to the notable interannual variability of environmental parameters in the coastal GON. The regularity of the biological events in spite of the variability for environmental conditions would suggest an endogenous regulation in the timing of occurrence of these species, as well as of other recurrent species in the area.

A distinct and regular pattern of occurrence has also been detected for different life forms within a single taxon. Small, solitary cells of *P. galaxiae* peak in early spring, whereas medium to large sized specimens have blooms in late spring and/or in summer (Fig. 2). In diatoms, cell size decreases over the asexual part of the life cycle, therefore the smallest specimens represent the oldest populations. The separation of size classes over the year could be due to yearly synchronised sexuality, but could also represent a first step of niche partitioning over the time which might precede speciation.

The annual re-appearance of a species after months of no-show has often been explained with heteromorphic life cycles, characterised by the alternation of non motile stages resting in the sediments, which periodically germinate and seed plankton blooms. In the case of *Pseudo-nitzschia*, as for many other planktonic species, benthic stages have not been found so far. In this case, it is reasonable to hypothesise the existence of stages which are morphologically similar to the actively dividing population but functionally resting, which could be present in the water column at undetectable concentrations.

CONFRONTING DIFFERENT TIME SERIES: ARE ALL PHYTOPLANKTON SPECIES EVERYWHERE?

It has been recently hypothesised that, as compared to pluricellular organisms, aquatic microorganisms have a very low species diversity, despite a remarkable diversity at high taxonomic levels (Finlay, 2002). The absence of physical barriers in aquatic environments and the high cell numbers attained would favour the dispersion of these tiny organisms, resulting in very similar species compositions in ecologically comparable areas.

Skeletonema costatum is among the most popular marine weeds and, being recorded almost everywhere, would certainly support Finlays's theory. *S. costatum* is considered not only ecologically plastic, but also oportunistic, being able to thrive under different conditions, especially in eutrophic waters such as those of the Kastela Bay (Pucher-Petkovic and Marasovic, 1980).

In the GON, *S. costatum* is regularly recorded over the years, with peaks in summer. In the Adriatic Sea, *S. costatum* is instead the main component of the winter bloom (Totti, pers. comm.). These different patterns of occurrence on the two sides of Italy stimulated detailed investigations, leading to the conclusion that the species from the Tyrrhenian Sea is in fact *S. pseudocostatum* (Fig. 3) and the one from the Adriatic Sea is possibly a new species. In addition to this, we found

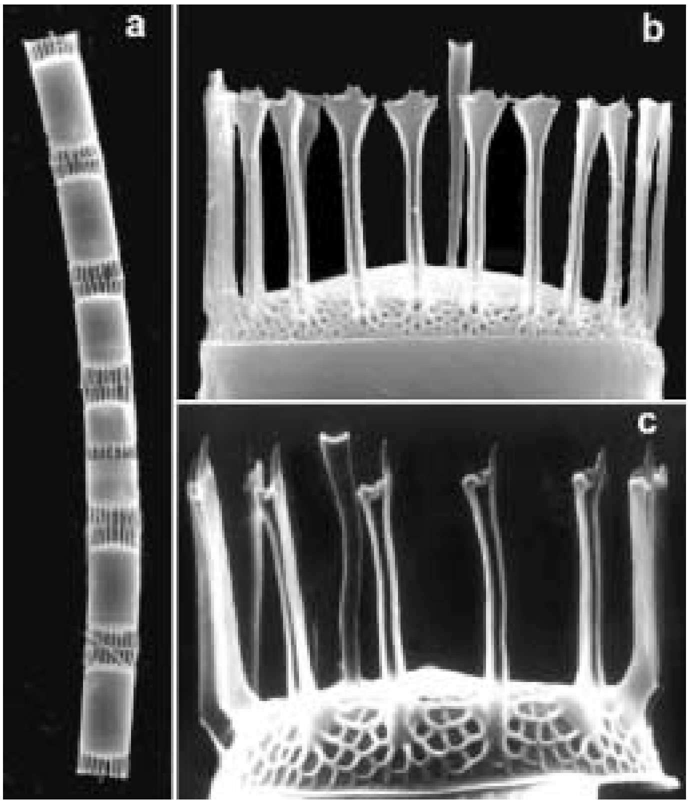

Fig. 3. *Skeletonema* sp. from the Adriatic Sea (a, b) and *S. pseudocostatum* (c).

at least another undescribed *Skeletonema* species in the GON, and discovered that several distinct species are commonly called *S. costatum* around the world (Sarno and Zingone, unpublished data). Instead of one plastic and ubiquitous species we are now confronted with numerous cryptic species that are probably distinct from the ecological point of view. These results challenge the idea of a few phytoplankton species distributed worldwide.

S. pseudocostatum and the Adriatic *Skeletonema* have been found in the GON and in the Adriatic Sea, respectively, but neither of the two has been found in the other area. This is not the unique case of a species present only in one of the two major Italian seas, which raises several questions on the biogeography of coastal phytoplankton species.

SPECIES FLUCTUATIONS AND INTRODUCTIONS

The genera *Skeletonema* and *Pseudo-nitzschia* offer also good cases of species appearance and disappearance. The toxic species *P. multistriata* has been detected in the GON only since 1995. Last summer, *Skeletonema tropicum* has appeared for the first time in the GON, reaching concentrations of $3.1*10^5$ cells l^{-1}. Man-mediated introduction e.g. via ballast waters is often advocated when a species is recorded for the first time somewhere. However, the name of *S. tropicum* evokes a possible role of climate change in favouring the widening of the geographic range of this species.

It could be worth understanding why the sudden appearance of a species generally receives more attention than a disappearance. There is no convincing explanation so far of why *Pseudo-nitzschia subpacifica* was common in our area in spring, but has never been recorded after 1987.

CONCLUSIONS

Time series of data can be used to shed light on phytoplankton ecology. Species seasonality, fluctuations and introductions can only be tracked with observations repeated over the years, which can also open the way to a reliable prediction of species occurrence and to a better management of coastal resources, e.g. in the case of harmful species. The analysis of a 15-year data set from the GON provides information useful to elucidate a series of processes currently on the stage of the scientific debate on marine phytoplankton. These include:

- the annual phytoplankton cycle, not always explainable on the basis of the classical paradigms;
- the relevance of species associations and functional groups;
- species-specific seasonal rhythms of occurrence, and the role of endogenous exogenous control in determining seasonal patterns;
- the role of life cycles in species seasonality;
- the evident and hidden diversity of marine phytoplankton and mechanisms of speciation;
- fluctuations in species abundance leading to community shifts and local extinctions;
- species introductions and range expansions, and their relations to man-mediated transport and climate changes.

Several of these issues require a combination of ad hoc field and laboratory investigations to be properly addressed. Yet long-term series remain a source of inspiration for focused research and a test bench for hypotheses and conceptual models. A further step is the contemporary analysis of parallel time series of biological observations, which can allow to detect common trends and separate them from local events. In fact, the comparison of the ecological behaviour of single species over their range of occurrence may be of great help in shedding light on endogenous versus exogenous control of phytoplankton distribution.