A minimal model of the variability of marine ecosystems

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Abstract

In marine ecology, population abundance time series often reveal patterns, such as decadal pseudo-cycles, on scales that make them difficult to mathematically characterize by means of conventional models based on functional responses. We propose here a simple non-deterministic model based on three strong ecological constraints, without any use of functional responses or external factors: (i) mass balance constraints between flows and biomass, (ii) a satiation constraint relating inflows and biomass and (iii) an inertia principle restricting the variation of populations of a given species according to its lifespan. This model reproduces in a robust manner observed patterns of variability and can be used to question the relevance of other modelling approaches of ecosystem dynamics with regard to determinism, constraints and stochasticity. Referring to a non-deterministic model without any functional relationships and environmental or anthropogenic forcing can help in avoiding misleading advice based on the belief that we can explain the causes of observed patterns, which may simply result from basic structural constraints within which the ecosystem functions.

Keywords Benguela ecosystem, constraints, indeterminism, interdecadal variability, null model

Introduction

Most marine ecosystems exhibit large interdecadal variability of biomass at intermediate trophic levels made up of small pelagic fish, which are characterized by low species diversity. This pattern can be expressed in terms of pseudocycles, which display a 'quasiperiodicity' (Turchin and Taylor 1992; Bakun 1996; Spencer and Collie 1997; Kendall *et al.* 1999). The average duration of a cycle varies from 10 to 80 years according to the species, and the coefficient of variation of this period is in the order of 30–50% for a given stock (Fréon *et al.* 2008). Similar variability patterns are observed in terrestrial ecology and parasitology (Turchin and Taylor 1992; Menu *et al.* 2002). In contrast, zooplankton data display a shorter variability over time and is at the interannual scale (see for instance series in Edwards and Richardson 2004; Montecino *et al.* 2006) whereas time series of abundance of top predators such as marine birds and mammals display more stable patterns or at least have fewer turning points (Sydeman and Allen 1999; Cury *et al.* 2000). This pattern extends to the wasp-waist hypothesis: in wasp-waist systems ample pseudocycles are observed at the intermediate trophic level whereas interdecadal variability is less at the lower and upper levels (Bakun 1996; Cury *et al.* 2000).

To explain the dynamics of such ecosystems and to generate this kind of variability, an approach using ecosystem models is usually adopted. These models are mostly based on functional responses, which deterministically relate food flows to populations (Yodzis 1994). Since the formulation of the Lotka–Volterra equations, based on a principle of mass action, more sophisticated functional responses have been proposed based on predator saturation effects (Holling 1966), or depending on prey or predator density (Arditi and Ginzburg 1989). Once these relationships have been specified, it is straightforward to express a differential equation or a finite difference equation and numerically solve it (Yodzis 1994). Identified functional relationships are convenient for the sake of generalization and for exploring how such interactions can generate

patterns similar to those observed in the field. Most models used in marine ecology are based on such assumptions; e.g. in the Ecosim model, a functional response is used which is based on the foraging arena hypothesis (Christensen and Walters 2004).

These modelling approaches raise several concerns and objections (Jost and Ellner 2000; Whipple *et al.* 2000), among which we emphasize the following. First, functional relationships are not fully supported by empirical evidence (Mitchell *et al.* 1992; Mittelbach *et al.* 1995; Jost and Ellner 2000; Hassel 2000); e.g. analysis of fish stomach contents reveal that diet does not always reflect preferred prey abundance or availability as was initially thought (Pinnegar *et al.* 2003; Trenkel *et al.* 2005). We will further discuss why this issue could lead to a debate similar to that in stock-recruitment relationships. Second, functional responses are not easy to define and justify in a multispecies context; emphasis is made on the relationship between a prey and its predator. To represent the ability of a predator to switch between several prey species, functional responses need to be reformulated (Chesson 1983; Post *et al.* 2000) to allow quantification but these new forms still have little empirical or theoretical justification. Third, resulting dynamics may generate unrealistic patterns of temporal variability, and this is a key issue because variability, which differs from uncertainty or imprecision, is identified as a major characteristic of ecological systems, and warrants dedicated research (Rothschild 1986; Spencer and Collie 1997; Grimm *et al.* 2005).

A crucial question is whether or not assuming a functional response prevents the variability inherent in the process from being examined in its own right. Indeed, intrinsic variability in the abundance of different components of an ecosystem, such as the one represented in the wasp-waist pattern, is not necessarily because of external factors such as climate change or anthropogenic forcing, but can be attributed to the complex internal dynamics of the ecosystem (Rothschild 1986). Although external forcing might explain some trend or act as a trigger, a large part of the variability is unrelated to

external forcing but is still essential to consider (Kolasa 2006). This point is particularly important in a context of the increasing use of ecosystem models for management (Wu and Marceau 2002; de Young *et al.* 2004), which requires that special attention be paid to model assumptions, particularly to the representation of the predation process, represented by functional responses.

Bayesian modelling (Punt and Hilborn 1997; Clark and Gelfand 2006) is a response to the last of the concerns listed, representing time series of observed abundance that result from stochastic processes. However, most Bayesian models still involve some type of functional response, and it is not clear how they address the previous concerns related to functional responses, either their nature or even their existence. The following remark of Koen-Alonso and Yodzis (2005) still applies to stochastic models:

> The functional response is a core structural feature of a trophodynamic model. Its precise mathematical form represents the researcher's view of the biological details of that particular predation process and profoundly affects model behaviour. In most cases, however, so little is known of these biological details that there is only weak evidence, if any, that points towards a given specific mathematical formulation. Under these circumstances, it is essential to avoid the temptation to assume some particular form for the functional response and proceed on that basis to get answers that are reassuringly, but meaninglessly, definitive. Rather, one needs to explore the range of behaviours that are consistent with what we do know about the system.

In this paper, we propose a direct approach to the issue of intrinsic variability, questioning the conventional assumptions on the nature of functional responses and the structure of variability. Instead of adding stochasticity to process models, we propose to add constraints to a totally non-deterministic model. This allows the interplay between the 'structural' and stochastic parts in stochastic models to be reconsidered, relaxing most of the hypotheses about them. We present a model of a marine ecosystem, avoiding any reference to functional responses and show that this model is able to reproduce patterns of variability of marine ecosystems as well as patterns related to diet/abundance or stock/recruitment relationships. In a context of increasing pressure on marine ecosystems because of over-exploitation and climate changes, where it becomes important to question the foundations of marine ecosystems modelling, we propose to use our non-deterministic model, not as an alternative model, but to question the causality schemes of more deterministic and predictive models, and to emphasize strong structural constraints within ecosystems.

Material and methods

Model

Our modelling approach consists of: (i) defining the structural part in terms of constraints instead of functional relationships; (ii) assuming no structure in the stochastic part and no associated probability function. The model is biologically constrained but its dynamics are largely non-deterministic; the modelled ecosystem evolves with no other rules than minimal and obvious constraints and, through many runs, the model explores possible solutions that can emerge.

In marine ecosystems, most of the mortality occurs at early life stages and thus the variability in the total biomass of a population is buffered by the number of year classes. Consequently, the biomasses of species with short life spans are more variable than those with long life spans. As a result, population series are obviously autocorrelated and furthermore the span of the autocorrelation is linked to the life span of the species (Spencer and Collie 1997). Thus, an immediate first step in modelling is to compare observed patterns with those generated by the most simple autoregressive process:

$$N_s(t+1) \in N_s(t)LN(0, \rho_s),$$

where $N_s(t)$ is the abundance of species s, $LN(0, \rho_s)$ is the log-normal distribution, with dispersion parameter ρ_s related to the lifetime of the species s (Table 1). This model reproduces patterns of variability observed in nature, especially for medium and high trophic level species, although the modelled patterns for species at low trophic levels display longer periods of autocorrelation than observed in nature (Fig. 1). However, as we may have expected, the model is totally unrealistic in terms of energy with the biomass of some prey species being zero or much smaller than that of their predator in many instances. At other times the model may predict no plankton whereas the fish may be highly abundant.

Table 1 Input parameters of a pelagic ecosystem model. These parameters have been derived from a simplified (9 functional groups instead of 23) version of the mass balance model of the southern Benguela (Shannon *et al.* 2004). We have proceeded in the following way. For all functional groups, biomass is the observed value. Trophic efficiency is the ratio (production/consumption). Metabolic activity coefficient is negatively related to trophic efficiency; inertia coefficient ρ_s is related to the lifespan l_s of a representative species of the functional group according to $\rho_s = 1 - (1 - 0.7) \, l_s$, satiety coefficient is half of the (consumption/biomass) coefficient. For phytoplankton, we have arbitrarily considered a relationship between nutrient intake (import) and an assimilation efficiency coefficient.

Species (s)	Nutrient intake (t km^{-2}) (I_s)	Biomass (t km^{-2}) $B_s(0)$	Efficiency (γ_s)	Metabolic activity (μ_s)	Inertia (ρ_s)	Satiety (σ_s)
Phytoplankton	3000.00	126.00	2.00	15.00	0.98	
Zooplankton		50.80	0.30	12.00	0.85	90.80
Anchovy		10.00	0.09	0.50	0.60	21.20
Sardine		9.00	0.08	0.20	0.50	15.40
Squid		3.20	0.10	0.10	0.70	8.30
Hakes		1.60	0.06	0.05	0.35	5.80
Birds		0.92	0.10	0.07	0.12	0.77
Seals		0.96	0.06	0.05	0.10	0.92
Whales		1.00	0.05	0.05	0.05	1.11

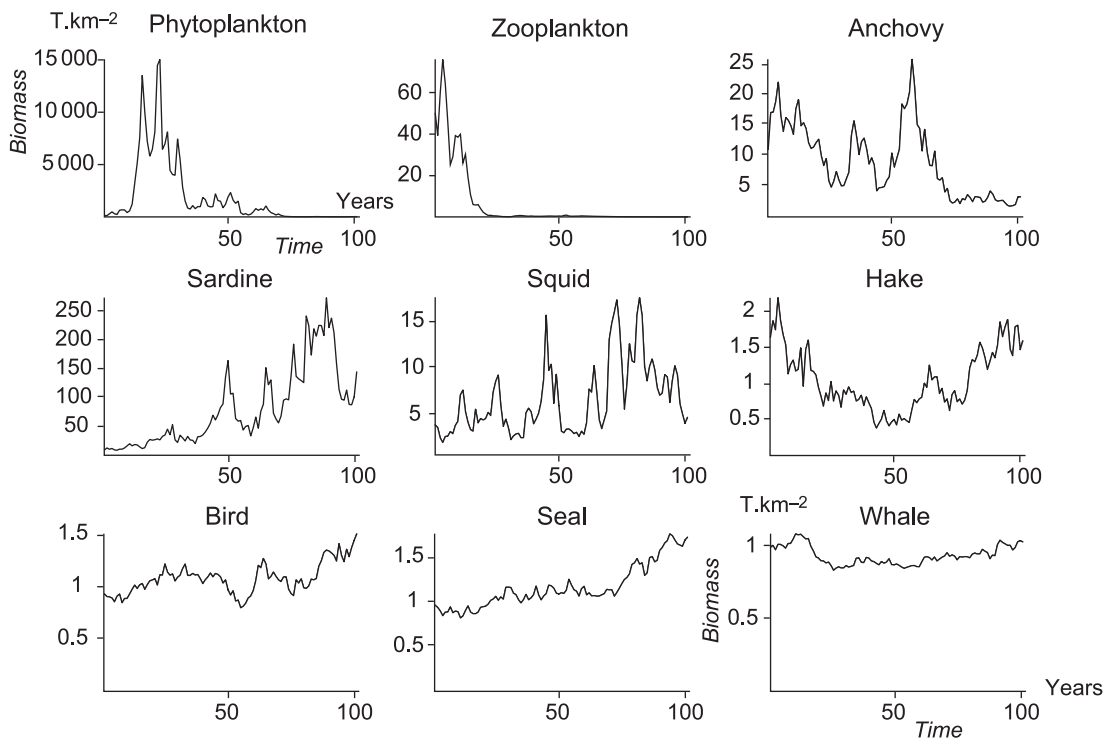**Figure 1** Autoregressive process given as $B_s(t+1)/B_s(t) \in LN(0, \rho_s)$: time series of simulated biomass dynamics over 100 years.

It is obvious that more constraints need to be included in the model.

To deal with these deficiencies we develop a model in which the dynamics are non-deterministic but this model is biologically constrained. Modelling assumptions are as follows. This second model, as in the first attempt, assumes that biomass changes are limited according to an inertia princi-

ple related to the lifespan of the species. In addition, the new model assumes that food ingestion is limited according to a satiation constraint determined by maximum stomach distension and a finite digestion rate. Third, the model uses a conventional mass-balanced equation relating flows and biomass of each species. Production, the part of ingested food which is transformed into the biomass of a species, is equal to the part of the biomass which is lost to the population by predation, or that is used for metabolic purposes such as respiration and calorific losses. We consider a recurrence mechanism in which a new state of the system at time $t + 1$ is randomly chosen from the set of feasible states, given the state of the system at time t, where a new state is said to be feasible at time $t + 1$ if three constraints are fulfilled: abundances at time $t + 1$ are such that (i) their variation with abundances at time t is limited by the inertia principle, (ii) flows fulfil the satiation principle and (iii) flows are mass balanced. The mathematical definition of this recurrence mechanism is given in the Appendix.

Material

To illustrate how our model applies to a simplified marine ecosystem, we use as input values and parameters, those that can be reasonably deduced from previous analyses of large pelagic ecosystems, such as from the southern Benguela ecosystem (Shannon *et al.* 2004). The simplified model developed here represents nine main compartments of this ecosystem: two groups of plankton species (phytoplankton and zooplankton), two species of small pelagic fish (anchovy, *Engraulis encrasicolus*, Engraulidae and sardine, *Sardinops sagax*, Clupeidae), two groups of piscivorous species (squid, *Loligo vulgaris*, Loliginidae and hake *Merluccius capensis and Merluccius paradoxus*, Merlucciidae), two groups of top predators (marine birds including mainly Cape gannet *Morus capensis,* Sulidae and African penguin *Spheniscus demersus,* Spheniscidae and Cape fur seal *Arctocephalus pusillus pusillus,* Otariidae) and finally a group of large zooplanktivorous cetaceans (whales with mainly the right whale *Eubalaena australis,* Balaenidae, humpback whale *Megaptera novaeangliae,* Balaenopteridae and the Bryde's whale *Balaenoptera edeni,* Balaenopteridae) (Fig. 2). Input parameters appear in Table 1. From this model, we are able to obtain an estimate of the connectivity of the network. This shows which predation links are possible, which are not, and gives a first estimate of the parameters needed to fulfil the model constraints.

Results

In this part, we have been guided by a pattern-oriented modelling approach (Grimm *et al.* 2005), which involves observing variability patterns in the data and then asking the model to reproduce them. We are not using quantitative measures of comparison between observed and simulated patterns. This is the objective of a separate, ongoing study, which will be published at a later date. Here, we refer mainly to simple, intuitive and relative descriptions of patterns of variability.
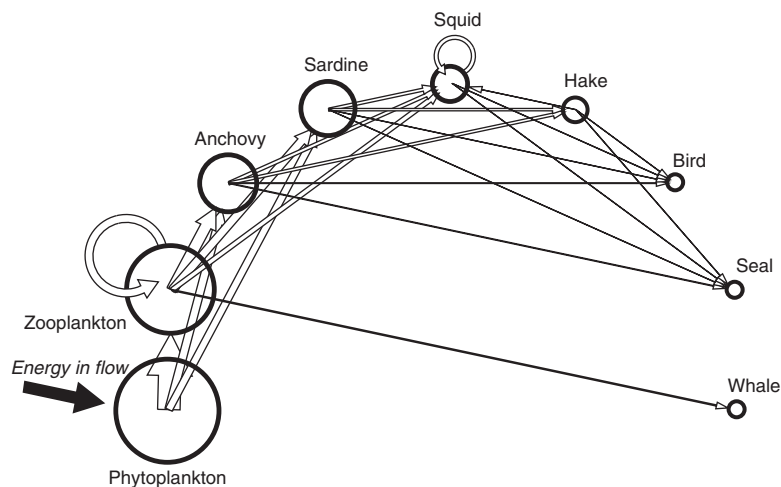

Figure 2 Structure of trophic flows in the null model considered here (the width of the arrows is proportional to the flux).
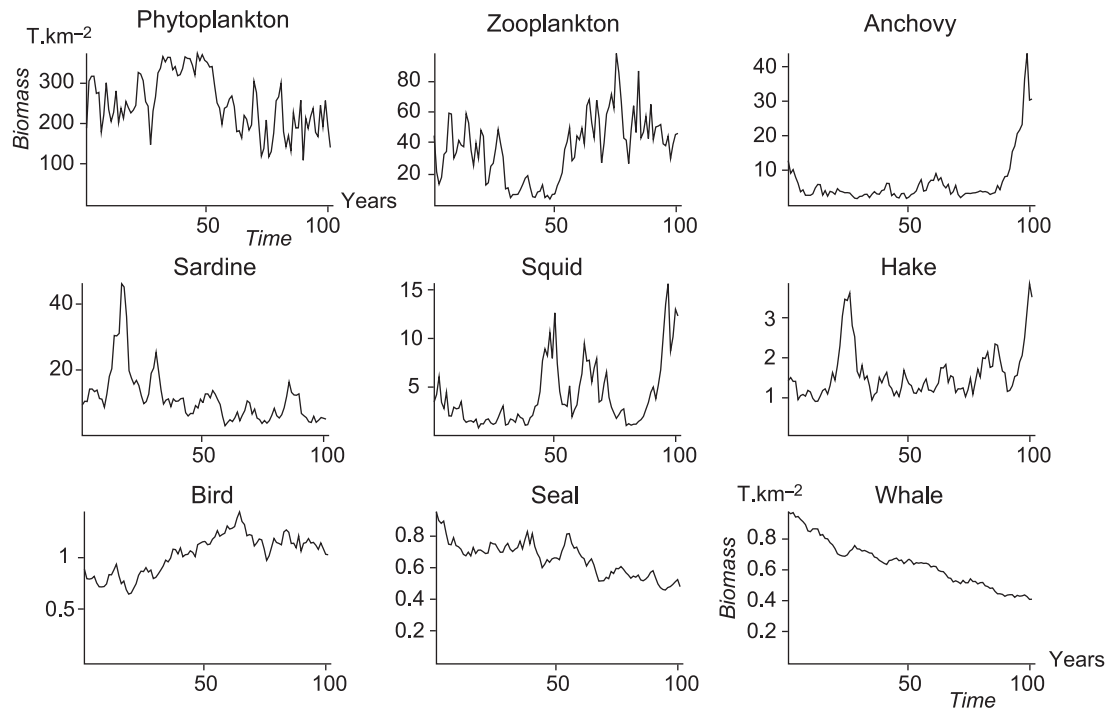
Figure 3 Simulated biomass dynamics over 100 years using the minimal model. Observe the variability patterns, especially the length of pseudocycles: no pseudocycles emerged for phytoplankton, zooplankton or whales; high-amplitude pseudocycles with peaks of high abundance lasting for several years emerged for anchovy, sardine and squid; decadal pseudocycles of moderate amplitude emerged for hake and birds.

Reproduction of pseudocycles

Running the model results in abundance series such as those depicted in Fig. 3. It appears that the model produces series with pseudocycles at intermediate trophic levels. For example, there are five to six pseudocycles for sardine, three for squid and three for hake. These cycles are a robust feature, common to all of the many repetitions simulated. According to the pattern-oriented modelling approach, the variability patterns observed in simulations need to be quantified. As we are interested in pseudocycles, we have performed a systematic analysis of the autocorrelations of the simulated abundance series. Figure 4 is an example of a given run where we observe cycles of different lengths, which seems to be more or less related to the trophic level or the lifespan of the species. For instance, phytoplankton and zooplankton display a 10-year cycle, anchovy a 40-year cycle and whales no clear cycle. But if we repeat the analysis and plot the mean values of autocorrelation coefficients, we obtain the results depicted in Fig. 5. The cycle duration increases systematically with increasing trophic level and life span, but by observing the variations of autocorrelations we conclude that, for a given species, the length of its cycle is highly variable, the pattern of pseudocycles of irregular lengths can be related to the species life span.

Reproduction of other patterns of variability

Another quantification of variability patterns is attempted by considering the variation and volatility of abundance series. Variation is defined as the ratio of the interquartile range to the median of the series. Volatility represents the ratio of short- to long-term variation (Fig. 6). Modelled abundance series from several 100-year simulations reveal that the model reproduces the wasp-waist pattern in a simple and robust manner (Table 2); variability is higher at mid-trophic levels. The indices of variation and volatility both indicate a dome-shaped pattern, with highest values at intermediate trophic levels. This could be a simple illustration of a wasp-waisted system (Bakun 1996).
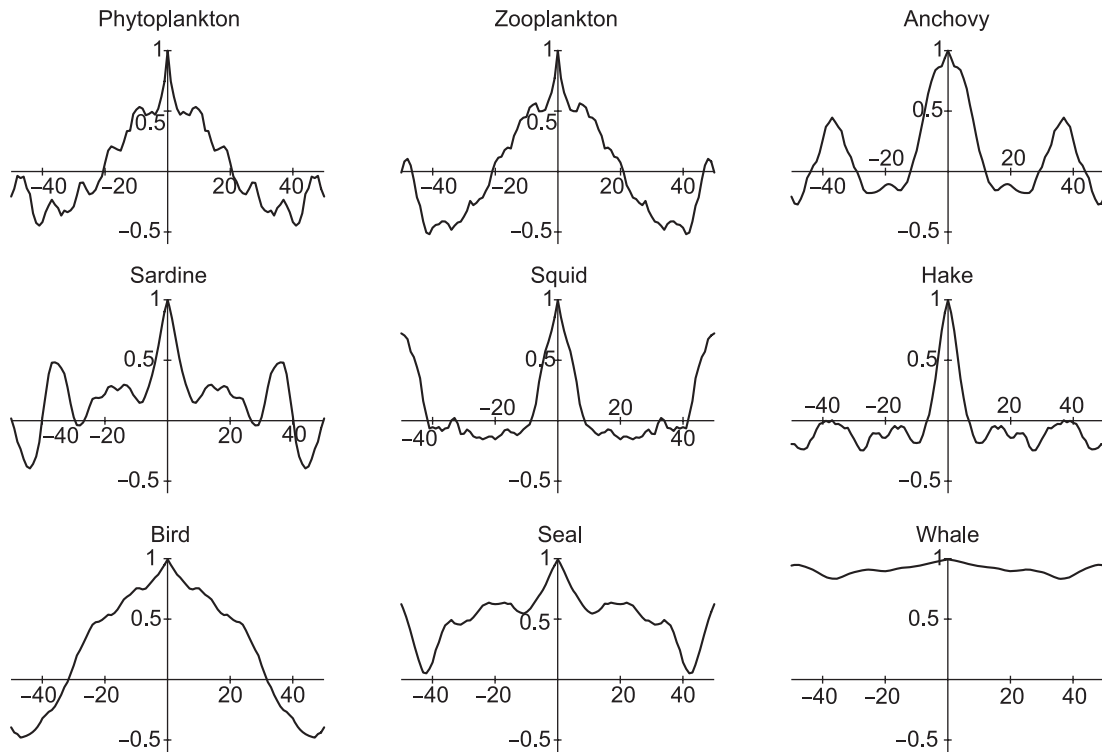
Figure 4 Autocorrelation series for a given run (time steps of the simulation on the *X*-axis; correlation coefficient on the *Y*-axis). An estimation of the cycle duration is provided by the lag associated with positive peaks, or twice the lag with negative peaks.

Reproduction of diet patterns

Let us examine now how the model reproduces other patterns of variability, such as those related to the relationship between diet and abundance. Simulated dynamics reveal no obvious functional response relating prey abundance to the diet of predators. Diet varies substantially at the interannual and interdecadal scale (Fig. 7) and is not or is only weakly related to the abundance of prey (Fig. 8). An exception among those relationships plotted may be that between hake and anchovy, where there is some indication that anchovy in the diet of hake increases linearly to a maximum. Overall though, these plots reflect what is observed in the analysis of diet variation, e.g. through the analysis of stomach contents of predators in relation to prey abundance (Sydeman *et al.* 2001; Pinnegar *et al.* 2003).

Reproduction of stock-recruitment relationships

From simulation results we can define a proxy for recruitment, which we compute as the variation of population biomass minus the annual metabolic activity or $R_s(t) = N_s(t + 1) - (1 + \mu_s)N_s(t)$. Simulated abundance series show weak positive stock-recruitment relationships for some species (anchovy, sardine), unclear relationships for some others (e.g. squid, hake) but that could be qualified as non-linear and compensatory according to the weak statistical criteria usually applied to qualify stock-recruitment relationships (Fig. 9). These patterns mimic reasonably well what is observed in published data and provide a specific insight into an old but still ongoing debate (Myers and Barrowman 1996): the model reproduces the ecosystem effects on recruitment and thus the stock-recruitment relationship emerges as a consequence of ecosystem functioning, not as a causal principle. We will return to this point later in the Discussion section.

Reproduction of correlations

Repeated simulations shed light on the significance of correlations observed in population dynamics, and underline the risk of taking into account spurious correlation when dealing with autocorre-
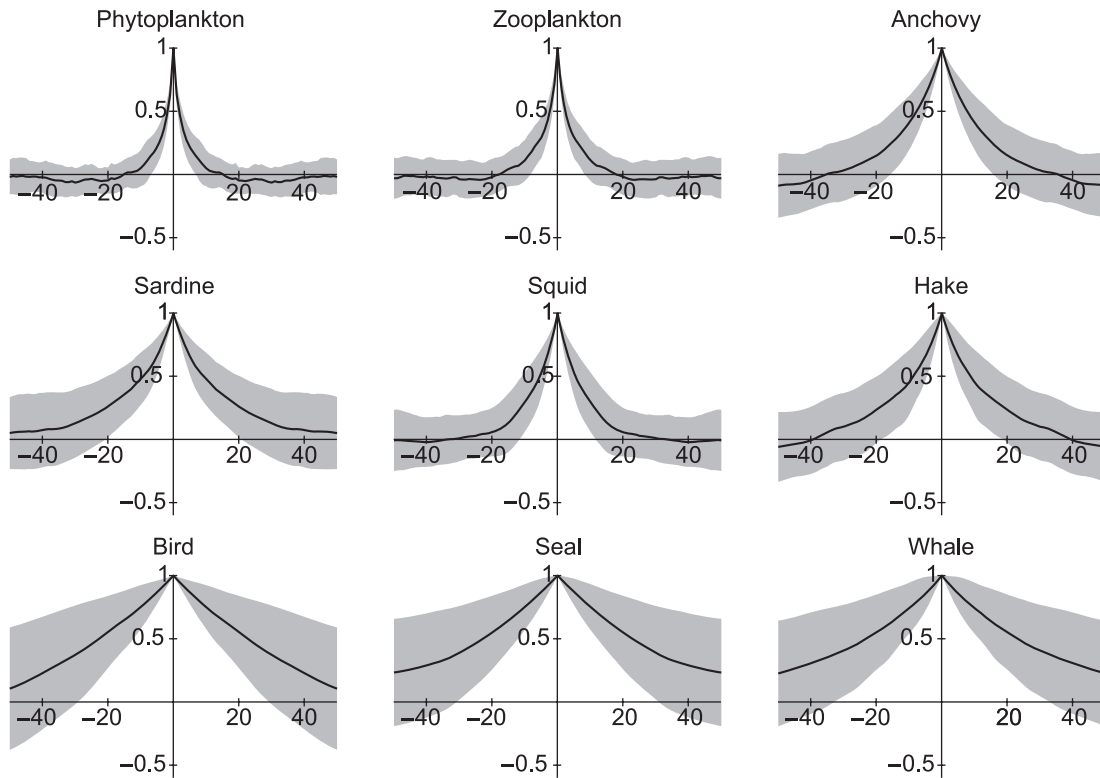
Figure 5 Mean (central line) and SD (shadow area, mean ± SD) on each side of the central line of autocorrelations, for a model experiment of 50 runs (same axis as in Fig. 4).

Table 2 Variability patterns in the simulated ecosystem (50 runs): average and SD (in parentheses) values of variation and volatility. For both parameters, a higher variability is observed at intermediate trophic levels.

	Variations	Volatility	Typical Trophic Level (TL)
Phytoplankton	0.346 (0.038)	0.456 (0.043)	1
Zooplankton	0.730 (0.220)	0.826 (0.065)	2.5
Anchovy	1.691 (0.986)	0.814 (0.063)	3.5
Sardine	1.722 (1.247)	0.694 (0.064)	3.0
Squid	1.502 (0.760)	0.967 (0.081)	3.8
Hakes	0.878 (0.442)	0.468 (0.034)	4.5
Birds	0.566 (0.422)	0.168 (0.012)	4.5
Seals	0.392 (0.204)	0.140 (0.007)	4.7
Whales	0.179 (0.098)	0.069 (0.004)	3.6

lated abundance series (Fréon *et al.* 2003). The abundance at intermediate trophic levels mimics the succession of regimes during which sardine and anchovy dominate alternately, as well as periods during which the abundance of both species are in phase or unrelated (Cury *et al.* 2000). Therefore, simulated time series of abundances for a given run appear to be significantly correlated. For example sardine and anchovy are sometimes positively and sometimes negatively correlated (Fig. 10). However, among cross-correlations corresponding to 50 runs of this algorithm, only the negative (and obvious) correlation between zooplankton and phytoplankton appears to be significant. Except for this pair, the mean values of correlations are always within the range [0.1, 0.15], and their SD are always greater than 0.4 (Table 3). As found in the case of the stock-recruitment relationships, regime shift and species alternation also emerge as a consequence of ecosystem functioning, not as a causal principle.

Discussion

So far we have identified variability patterns in the form of pseudocycles at mid-trophic levels, and designed minimal models and modelling experiments that reproduce them. The resulting simulations provide patterns characterized by variability,
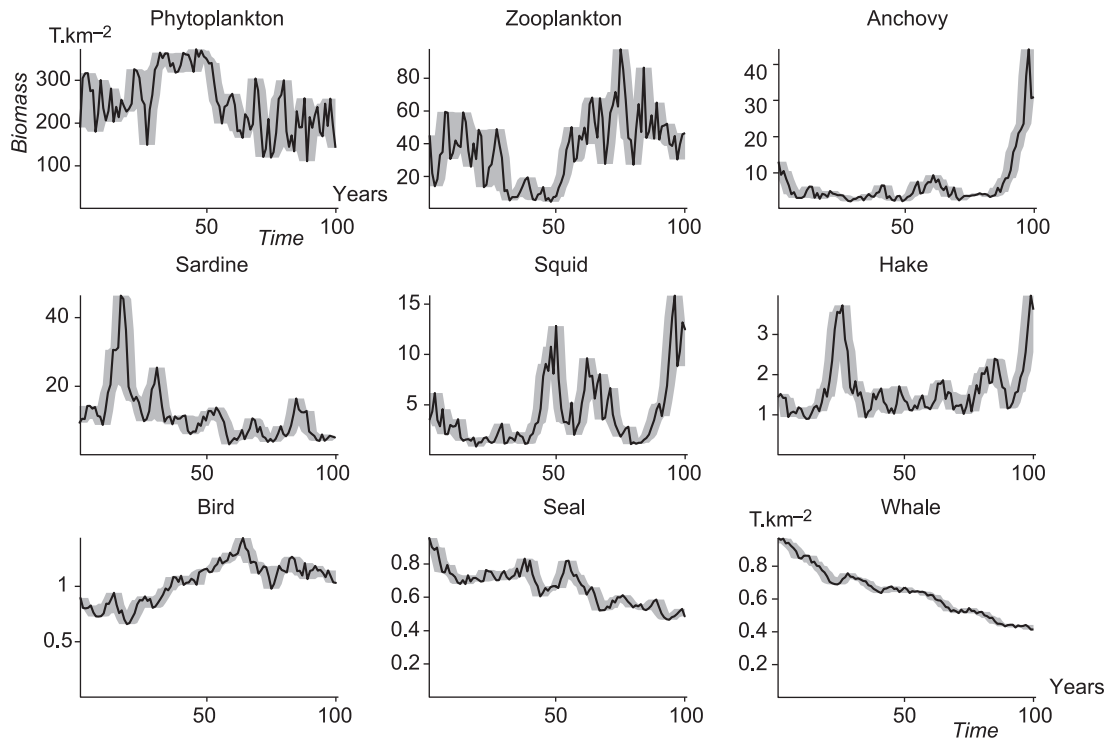
Figure 6 Volatility of abundance series superimposed on top of simulated biomasses (time steps of the simulation on the X-axis). Volatility is defined as $V(Y) = \sum_i V_i / \sum_i Y_i$, where $V_i = \max(Y_{i-4}, Y_{i-3}, \dots, Y_{i+3}, Y_{i+4}) - \min(Y_{i-4}, Y_{i-3}, \dots, Y_{i+3}, Y_{i+4})$. Volatility is the ratio of the 'snake' dark grey surface delimited by the series (central line) and the X-axis.

as shown in the section on reproduction of variability patterns, and unpredictability, as shown in the section dealing with the reproduction of correlations. Confrontation of model results with observations needs to be performed at the level of global patterns rather than at the level of individual data points, using a pattern-oriented approach (Grimm *et al.* 2005). In this case, it means describing samples of abundance time series according to their variability (such as the variation and the volatility described in the previous paragraphs), and then comparing the results with the simulated data. In this ongoing work, difficulties are encountered owing to the restricted length of the available series of observations.

Towards a null model approach

By envisaging beforehand the dynamics of a non-deterministic model, a number of frequently used models in marine biology and fisheries science can be revisited. By being very parsimonious in terms of assumptions but nevertheless reproducing realistic

patterns of variability, our modelling approach could help to define the framework of a null model approach (Harvey *et al.* 1983; Gotelli 2000, 2001) for marine ecosystems. This places a particular emphasis on differences between the consequences of type I and type II errors. Under type I error one would accept a deterministic model employing functional responses when a non-deterministic model, not using functional responses would perform equally well. Under type II error one would be rejecting a deterministic model when the non-deterministic approach is not appropriate. The latter underlines the need for a relevant method for comparing models; how do the results of a tested model compare with those of the null model? How models should be compared in terms of: (i) their ability to reproduce variability patterns using generic criteria, which are applicable to many situations, (ii) pertinence, which implies that they perform significantly better and (iii) efficiency by which we mean being parsimonious? This questions the true reasons for the observed variability; is a deterministic model right for the correct reason, or does it just reproduce the observed data because
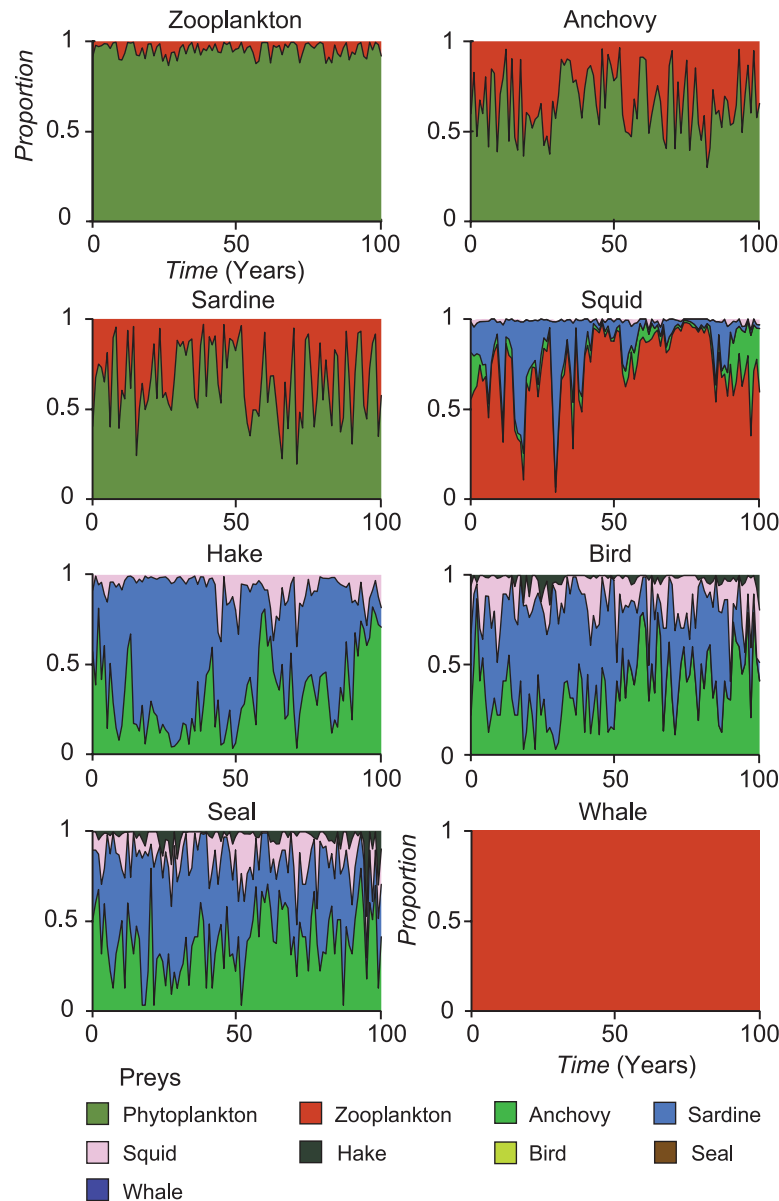
Figure 7 Diet composition dynamics (one single run of 100 years) for all model compartments. This figure also shows the connectivity of the network and its variability in time.

deterministic relationships have been selected to mirror with the main features of the structural constraints? We make explicit in the forthcoming paragraphs how our approach could provide new insights to old questions in marine ecology.

What if the null model approach had been applied to stock-recruitment relationships?

The most famous example of a functional response in marine ecology is that of the stock-recruitment relationship proposed to enable fisheries management through the exploitation of production models (Ricker 1954; Beverton and Holt 1957). The stock-recruitment relationship is indeed a relationship between a stock and a flow. Myers (2000) compiled a database of fish abundance data for about 700 populations; for many of them the stock/recruitment scatter plot is presented, together with the curves of the mathematical relationships devised either by Beverton and Holt (1957) or by Ricker (1954), which are supposed to fit them, and which
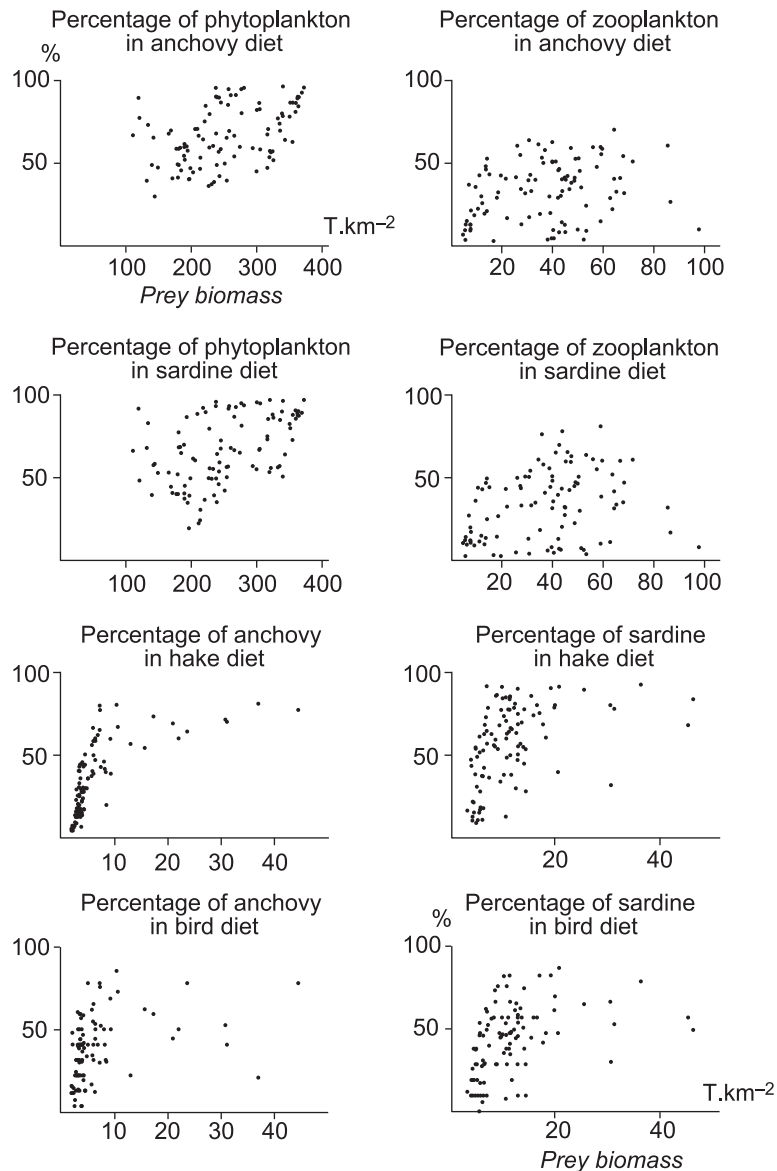
Figure 8 Simulated diet/abundance relationships. Captions indicate the name of predator species followed by the name of one of the major prey species for a predator. The *Y*-axis represents the proportion of prey in the predator diet and the *X*-axis represents the abundance of the prey species. These graphs show the absence of, or at most weak functional relationships (e.g. very weak relationship in the case of anchovy and sardine diets), between the diet composition of predator and the abundance of their prey.

are subsequently used to feed production models. The fits appear to be extremely poor for a large number of these data series, summarized in the words of Walters and Martell (2004) as: *a frightening shotgun scatter of points*. This lack of fit was mentioned in the pioneering work of Beverton and Holt (1957) and Cushing (1971) and has been recurrent in subsequent studies, which is worrying

as it represents a major flaw in subsequent modelling steps. This lack of fit has been explained as being caused by external factors such as the length of the available time series or the range of stock abundances (Myers and Barrowman 1996), measurement errors in both recruitment and spawning stock (Walters and Ludwig 1981; Myers and Barrowman 1996) or the failure to take account
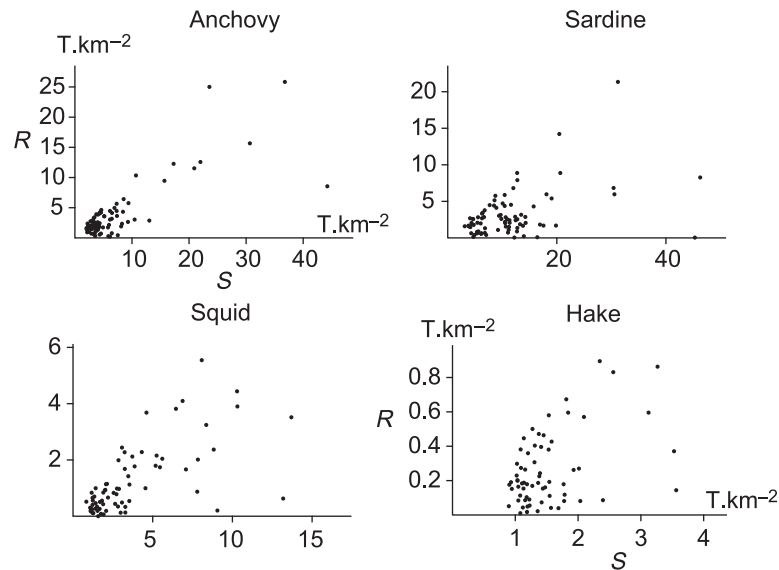
Figure 9 Examples of stock-recruitment (S, R) relationships using the variation of population biomass minus the annual metabolic activity as a proxy for recruitment: $R_s(t) = B_s(t + 1) - (1 + \mu_s)B_s(t)$.
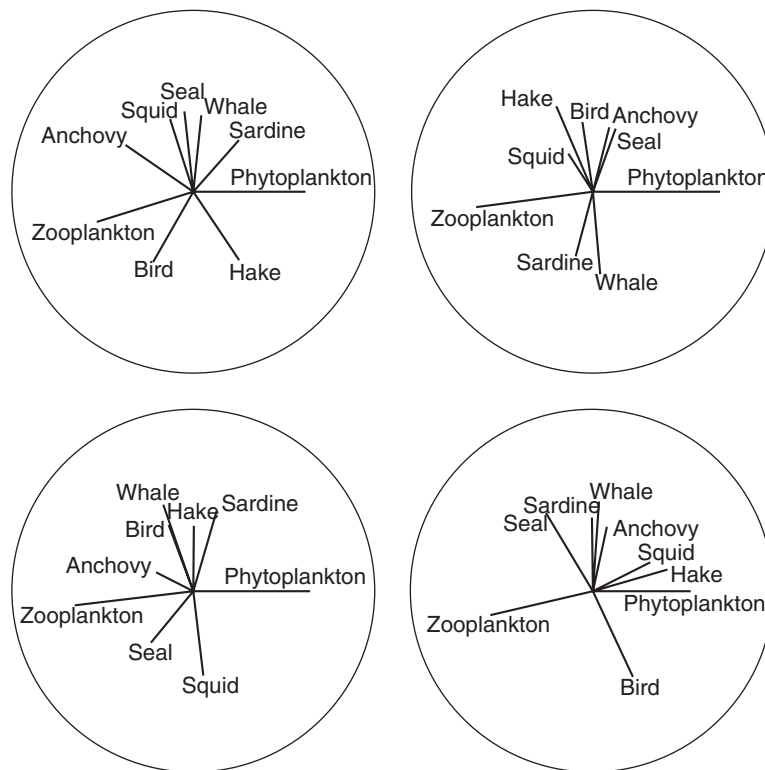

Figure 10 Circles of the correlations observed for four different runs of the model. Species close to each other are positively correlated; species diametrically opposed are negatively correlated and orthogonal species are uncorrelated. The contribution of the species is proportional to the length of the associated radius. Within each individual run, many correlations are significant. Almost every individual run allows reconstruction of a plausible theory of functioning. When analysed globally, species interactions differ from one run to the other and it is not possible to see the emergence of a unique functioning pattern.

Table 3 Cross-correlation between abundances per model compartment: mean and SD (in parentheses) of correlation coefficients resulting from 50 runs.

	Phytoplankton	Zooplankton	Anchovy	Sardine	Squid	Hake	Birds	Seals	Whales
Phytoplankton	1.00 (0.00)								
Zooplankton	-0.84 (0.05)	1.00 (0.00)							
Anchovy	-0.02 (0.16)	-0.16 (0.19)	1.00 (0.00)						
Sardine	0.02 (0.19)	-0.01 (0.23)	-0.15 (0.27)	1.00 (0.00)					
Squid	0.03 (0.16)	-0.10 (0.18)	0.02 (0.24)	-0.01 (0.27)	1.0 (0.00)				
Hakes	0.03 (0.14)	-0.07 (0.17)	0.15 (0.34)	-0.01 (0.30)	-0.01 (0.24)	1.00 (0.00)			
Birds	0.01 (0.19)	-0.03 (0.24)	-0.03 (0.38)	-0.03 (0.36)	0.04 (0.27)	-0.13 (0.36)	1.00 (0.00)		
Seals	-0.01 (0.20)	0.02 (0.22)	-0.04 (0.31)	0.01 (0.33)	-0.02 (0.24)	-0.02 (0.35)	0.09 (0.43)	1.00 (0.00)	
Whales	0.01 (0.19)	-0.02 (0.21)	0.01 (0.31)	0.02 (0.37)	0.02 (0.26)	0.02 (0.34)	-0.01 (0.45)	-0.03 (0.42)	1.00 (0.00)

of climatic effects (e.g. Lasker 1978; Zebdi and Collie 1995; Zheng 1996). Recent findings suggest that we should focus on the 'variability patterns' of the stock-recruitment relationship. For example, Myers (2001) showed that recruitment variability generally increases at low population sizes for species with higher fecundity, for populations at the edge of their range and in regions with less oceanic activity. Walters and Martell (2004) have addressed the contradictions; obviously there is no evidence to support the hypothesis of a compensatory stock-recruitment relationship, however the scientists who claim this argument also promote a conventional management policy that is based on the stock-recruitment relationship! Type I error would have resulted in overconfidence in single-species management, whereas managing the stock according to constraints imposed by the ecosystem would have been more appropriate. Conversely, type II error would have prevented efficient single-species management. The approach leads us to ask whether overconfidence in the ability of the models to adequately represent exploited marine resources has contributed to the failure of fisheries management worldwide, by magnifying postulates and preconceived assumptions (Larkin 1996; Mace 2001; Mullon *et al.* 2005).

The null model approach applied to ecosystem models

The desire for finding a deterministic functional relationship, despite a profound lack of concrete evidence, is recurrent. We propose that using functional responses in the present ecosystem trophic models raises similar questions to those of the debate that took place several decades ago on the use of the stock-recruitment relationship. The situation is indeed controversial. Although several specific examples exist to support the hypothesis of functional responses, there are many examples contradicting their existence. The response of a fish predator to the abundance of its prey is often far from being conclusive. On the Georges Bank, Link and Garisson (2002) showed that the diet of piscivorous species varied substantially from 1977 to 1998. In all the six species studied, the proportion of at least one major fish prey varied from zero to at least one-third of the diet over the period, despite the 3-year averaging of the data; these shifts in diet matched the major changes in prey abundance, especially for herring, *Clupea harengus harengus,*

Clupeidae, so supporting the hypothesis of a functional response. In contrast, the following examples do not support the functional response hypothesis. Bax (1998) reviewed similar examples of interannual variability in predation. Barents Sea cod (*Gadus morhua*, Gadidae) predation on capelin (*Mallotus vilosus*, Osmeridae) varied from 0.4 to 1.2 times their own biomass between 1984 and 1985 and this was attributed to a greater overlap between the two species (Mehl 1989) and to the arrival of a strong year class of cod that grew big enough to eat larger capelin. Changes in cannibalism by cod in the Baltic Sea fluctuated between 100 000 t in 1979–80 and around 1000 t in subsequent years according to cod abundance (Sparholt 1994). Bax (1998) reported profound modifications in predation on fish eggs and larvae by other fish species or by the same species, which were not mainly related to relative abundance of predator and prey. Recently, in the Celtic Sea, Pinnegar *et al.* (2003) did not find evidence for density-dependent feeding by predators on several species. The observed shifts in predator diet can be due to changes in their prey abundance but also to large-scale oceanographic variability that impact predator–prey interactions through predation or competition (Mehl 1989; Bax 1998).

These observations all lend support for the use of a null model, a model that does not assume any functional response relationships but rather allows functional responses, such as stock-recruit relationships, to emerge from simplified descriptions of ecosystems that attempt to capture the patterns we observe, without imposing a structure in them. Nonetheless, there are limits to this approach as demonstrated here when we used a very simple model (Fig. 1) but did not consider using it as a null model because of its obvious trophic inconsistency. Instead we propose to use as a null model our minimal model that incorporates a deterministic relationship between metabolic activity and biomass (see Appendix). This illustrates the incremental character of the null model approach.

We summarize what we may learn from experiences based on a null model approach in the context of ecosystem modelling: (i) accepting a deterministic model when it is appropriate would facilitate the development of ecosystems models; however, (ii) accepting a deterministic ecosystem model when a non-deterministic model is appropriate would lead to over-confidence in ecosystem management, to the risk of reacting too late to structural ecosystems changes; (3) rejecting a deterministic model when it

is not appropriate would contribute to the progression towards ecosystem management defined in terms of constraints and of critical thresholds. This is emphasized on the internal variability of ecosystems; however, (iv) rejecting a deterministic model when it is appropriate would mean missing the opportunity of efficient ecosystem management based on the control of its dynamics.

Indeterminism vs. constraints

These remarks shed light on a situation in which, despite repeated recommendations (Hilborn and Walters 1992; Schnute and Richards 2001), fisheries biologists still mostly use deterministic models, both for exploratory and management purposes (Walters and Martell 2004). Moving towards ecosystem-based fisheries management by recognizing interactions between exploited as well as non-exploited species operating as part of the whole ecosystem, may further exacerbate this problem (de Young *et al.* 2004). We believe that the approach proposed here, leading to emphasis being placed upon the reference points identified from the analysis of structural constraints and their associated thresholds can be regarded as an alternative to a more conventional management principle, based on target reference points (Mullon *et al.* 2004; Cury *et al.* 2005). Critically questioning the fundamental assumptions and hypotheses underlying our models should be central when elaborating management options, for terrestrial as well as marine ecosystems (Ostrom *et al.* 2007). This emphasizes the importance of considering constraints in ecosystem models, following one of the main recommendations of Popper (1962): 'Every ''good'' scientific theory is a prohibition: it forbids certain things to happen. The more a theory forbids, the better it is'. Addressing clearly the possibility or the impossibility of a deterministic explanation for the underlying dynamics of marine ecosystems could contribute to improve communication between scientists, fishermen and managers. It could be easier to find an agreement on states to avoid rather than on states to reach, and then on constraints effectively determining the dynamics of a marine ecosystem.

Acknowledgements

References

Arditi, R. and Ginzburg, L.R. (1989) Coupling in predator–prey dynamics: ratio-dependence. *Journal of Theoretical Biology* **139**, 311–326.

Bakun, A. (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. California Sea Grant College System, University of California, La Jolla.

Bax, N.J. (1998) The significance and prediction of predation in marine fisheries. *ICES Marine Science Symposium* **55**, 997–1030.

Beverton, R.J.H. and Holt, S.J. (1957) On the dynamics of exploited fish populations. *Fisheries Investigations, London* **II**, 1–533.

Chesson, J. (1983) The estimation and analysis of food preference and its relationship to foraging models. *Ecology* **64**, 1297–1304.

Christensen, V. and Walters, C.J. (2004) Ecopath with ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**, 109–139.

Clark, J.S. and Gelfand, A.E. (2006) A future for models and data in environmental science. *Trends in Ecology and Evolution* **21**, 375–380.

Cury, P., Mullon, C., Garcia, S.M. and Shannon, L. (2005) Viability theory for ecosystem approach to fisheries. *ICES Journal of Marine Resources* **62**, 577–584.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre-Teichmann, A., Quiñones, R.A., Shannon, L.J. and Verheye, H.M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in ''wasp-waist'' ecosystems. *ICES Journal of Marine Science* **57**, 603–618.

Cushing, D.H. (1971) The dependence of recruitment on parent stock in different groups of fishes. *Journal du Conseil International pour l'Exploration de la Mer* **33**, 340–362.

Edwards, M.E. and Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **7002**, 881–884.

Fréon, P., Mullon, C. and Voisin, B. (2003) Investigating remote synchronous patterns in fisheries. *Fisheries Oceanography* **12**, 443–457.

Fréon, P., Bouchon, M., Mullon, C., Garia, C. and Ñiquen, C. (2008) Interdecadal variability of anchoveta abundance and overcapacity of the fishery in Peru. *Progr. Oceanogro.* doi: 10.16/j.pocean.2008.10.011.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621.

Gotelli, N.J. (2001) Research frontiers in null model analysis. *Global Ecology and Biogeography* **10**, 337–343.

Grimm, V., Revilla, E., Berger, U., et al. (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* **310**, 987–991.

Harvey, P.H., Colwell, R.K., Silvertown, J.W., et al. (1983) Null models in ecology. *Annual Review of Ecology and Systematics* **14**, 89–211.

Hassel, M.P. (2000) Host–parasitoid population dynamics. *Journal of Animal Ecology* **69**, 543–566.

Hilborn, R. and Walters, C.J. (1992) *Quantitative Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall, New York.

Holling, C.S. (1966) The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* **48**, 1–86.

Jost, C. and Ellner, S. (2000) Testing for predator dependence in predator–prey dynamics: a non-parametric approach. *Proceeding of the Royal Society of London B* **267**, 1611–1620.

Kendall, B., Briggs, C.J., Murdoch, W.W., et al. (1999) Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* **80**, 1789–1805.

Koen-Alonso, M. and Yodzis, P. (2005) Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1490–1512.

Kolasa, J. (2006) A community ecology perspective on variability in complex systems: the effects of hierarchy and integration. *Ecological Complexity* **3**, 71–79.

Larkin, P.A. (1996) Concepts and issues in marine ecosystem management. *Review in Fish Biology and Fisheries* **6**, 139–164.

Lasker, R. (1978) The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. *Rapports et Procès Verbaux du Conseil International pour l'Exploration de la Mer* **173**, 212–230.

Link, J.S. and Garrison, L.P. (2002) Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fisheries Research* **55**, 71–86.

Mace, P.M. (2001) A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish and Fisheries* **2**, 2–32.

Mehl, S. (1989) The Northeast Arctic cod's consumption of commercially exploited prey species in 1984–1986. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **188**, 185–205.

Menu, S., Gauthier, G. and Reed, A. (2002) Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. *Journal of Applied Ecology* **39**, 91–102.

Mitchell, P., Arthur, W. and Farrow, M. (1992) An investigation of population limitation using factorial experiments. *Journal of Animal Ecology* **61**, 591–598.

Mittelbach, G., Turner, A., Hall, D., Rettig, J.E. and Osenberg, C.W. (1995) Perturbation and resilience, a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* **76**, 2347–2360.

Montecino, V., Strub, P., Chavez, F., Thomas, A., Tarazona, J. and Baumgartner, T. (2006) Chapter 10: Biophysical interactions of eestern South America. In: *The Sea XIV: The Global Coastal Ocean, Interdisciplinary Regional Studies and Syntheses* (eds A.R. Robinson and K.H. Brink), Vol. 12. Harvard University Press, Cambridge, pp. 329–390.

Mullon, C., Cury, P. and Shannon, L. (2004) Viability model of trophic interactions in marine ecosystems. *Natural Resources Modelling* **17**, 27–58.

Mullon, C., Fréon, P. and Cury, P. (2005) The dynamics of collapse in world fisheries. *Fish and Fisheries* **6**, 111–120.

Myers, R.A. (2000) The synthesis of dynamic and historical data on marine populations and communities; putting dynamics into the ocean biogeographical information system (OBIS). *Oceanography* **13**, 56–59.

Myers, R.A. (2001) Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science* **58**, 937–951.

Myers, R.A. and Barrowman, N.J. (1996) Is fish recruitment related to spawner abundance? *Fisheries Bulletin* **94**, 707–724.

Ostrom, E., Janssen, M.A. and Anderies, J.M. (2007) Going beyond panaceas. *Proceedings of the National Academy of Sciences* **104**, 15176–15178.

Pinnegar, J., Trenkel, V., Tidd, A., Dawson, W. and du Buit, M.H. (2003) Does diet in Celtic sea fishes reflect prey availability? *Journal of Fish Biology* **63**, 197–212.

Popper, K. (1962) *Conjectures and Refutations: The Growth of Scientific Knowledge*. Basic Books, New York.

Post, D.M., Conners, M.E. and Goldberg, D.S. (2000) Prey preference by a top predator and the stability of linked food chains. *Ecology* **81**, 8–14.

Punt, A. and Hilborn, R. (1997) Fisheries stock assessment and decision analysis: the Bayesian approach. *Review in Fish Biology and Fisheries* **7**, 35–63.

Ricker, W.E. (1954) Stock and recruitment. *Journal of Fisheries Research Board of Canada* **11**, 539–623.

Rothschild, B. (1986) *Dynamics of Marine Fish Populations*. Harvard University Press, Cambridge.

Schnute, J.T. and Richards, L.J. (2001) Use and abuse of fishery models. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 10–17.

Shannon, L.J., Christensen, V. and Walters, C. (2004) Modelling stock dynamics in the southern Benguela ecosystem over the last twenty five years. *African Journal of Marine Science* **26**, 179–196.

Sparholt, H. (1994) Fish species interactions in the Baltic Sea. *Dana* **10**, 131–162.

Spencer, P.D. and Collie, J.S. (1997) Patterns of population variability in marine fish stocks. *Fisheries Oceanography* **6**, 188–204.

Sydeman, W.J. and Allen, S.G. (1999) Pinniped population dynamics in central California: correlations with sea surface temperature and upwelling indices. *Marine Mammal Science* **15**, 446–461.

Sydeman, W.J., Hester, M.M., Thayer, J.A., Gress, F., Martin, P. and Buffa, J. (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California current system. *Progress in Oceanography* **49**, 309–329.

Trenkel, V.M., Pinnegar, J.K., Dawson, W.A., du Buit, M.H. and Tidd, A.N. (2005) Spatial and temporal structure of predator–prey relationships in the Celtic sea fish community. *Marine Ecology Progress Series* **299**, 257–268.

Turchin, P. and Taylor, A.D. (1992) Complex dynamics in ecological time series. *Ecology* **73**, 289–305.

Walters, C.J. and Ludwig, D. (1981) Effects of measurement errors on the assessment of stock-recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 704–710.

Walters, C.J. and Martell, S.J.D. (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton, New Jersey.

Whipple, S.J., Link, J.S., Garrison, L.P. and Fogarty, M.J. (2000) Review of models of predator–prey interactions and fishing mortality. *Fish and Fisheries* **1**, 22–40.

Wu, J. and Marceau, D. (2002) Modeling complex ecological systems: an introduction. *Ecological Modelling* **153**, 1–6.

Yodzis, P. (1994) Predator prey theory and management of multispecies fisheries. *Ecological Applications* **4**, 51–58.

de Young, B., Heath, M., Werner, F., Chai, F., Megrey, B. and Monfray, P. (2004) Challenges of modelling decadal variability in ocean basin ecosystems. *Science* **304**, 1463–1466.

Zebdi, A. and Collie, J. (1995) Effect of climate on herring (*Clupea pullusi*) population dynamics in the northeast Pacific Ocean. *Canadian Special Publication in Fisheries and Aquatic Science* **121**, 277–290.

Zheng, J. (1996) Herring stock-recruitment patterns in the North Atlantic and Northeast Pacific oceans. *Fisheries Research* **26**, 257–277.

Appendix: Mathematical formulation

The model is mathematically defined as follows. Assuming that production is proportional to inflow, the mass-balanced equation for a species is:

$$\gamma_s(P_s + I_s) = O_s + R_s + Y_s, \qquad (1)$$

where P_s is the biomass of the prey consumed by species s, I_s are other nutrients, γ_s is the assimilation efficiency, O_s is the biomass of the species consumed by its predators, Y_s is the caught biomass and R_s are other losses of species biomass, mainly through metabolic activity, respiration and deaths that are not from predation. Denoting X_{rs} as the predation of species r by species s and assuming that the metabolic losses are proportional to biomass: $R_s = \mu_s B_s$, where μ_s is a metabolic activity coefficient, one obtains the mass balance relationship:

$$\gamma_s\left(\sum_r X_{rs} + I_s\right) = \sum_r X_{sr} + Y_s + \mu_s B_s, \qquad (2)$$

which relates flows and biomass for all species. This equation is the basis of most mass-balanced models of marine ecosystems. Reversing the mass balance equation results in:

$$B_s = \left[\gamma_s\left(\sum_r X_{rs} + I_s\right) - \sum_r X_{sr} - Y_s\right]/\mu_s \qquad (3)$$

meaning that constraints of somatic maintenance allows for the consideration of biomass as resulting from excess between assimilated inflow and outflow.

Assuming that the ecosystem is $B(t) = \{B_s(t)\}$ at time t we denote the following constraints.

– *Inertia constraint:* Relative biomass changes are limited, in a specific way for every species; this is expressed as $|B_s(t+1) - B_s(t)| \leq \rho_s B_s(t)$, where coefficients ρ_s are related to life span or age at maturity of the species s. ρ_s is greater for short-lived species with high turnover rate.

– *Satiation constraint:* There exist trophic flows $\{X_{rs}\}$ are such that $\sum_r X_{rs} \leq \sigma_s B_s$.
– *Mass balance constraint*: Previous trophic flows $\{X_{rs}\}$ are such that mass balance equation is satisfied: $\gamma_s(\sum_r X_{rs} + I_s) = \sum_r X_{sr} + Y_s + \mu_s B_s$.

A state is said to be feasible at time $t+1$ if these three constraints are fulfilled. We consider $A(B(t))$ the set of all admissible states. The dynamics are represented through the recurrence mechanism.

1. Set $t = 0$ and consider, from previous estimation or modelling attempts, a state $B(0) = \{B_s(0)\}$. It is assumed to satisfy mass balance and inertia constraints.
2. Randomly choose a state X in the set of admissible states: $A(B(t))$.
3. Set $B(t+1) = X$ and $t \rightarrow (t+1)$. Go to step 2.

More precisely, we performed random selection as follows. We note that, according to the 'reverse' mass balance equation (2), flows determine biomass and that the relationship between flows and biomass $X = \{X_{rs}\} \rightarrow B(X) = \{B_s\}$ is linear, thus flows $\{X_{rs}\}$ at time $t+1$ must be such that $X_{rs} \geq 0$, and if $X = \{X_{rs}\} \rightarrow B(X) = \{B_s\}$, then $|B_s(t+1) - B_s(t)| \leq \rho_s B_s(t)$ and $B_s(t+1) \geq 0$. We denote K to be the set of such flows. Then state $\{B_s(t)\}$ at time t and constraints on flows determine minimum m_s and maximum M_s possible values for biomass of all species at time $t+1$; these values are computed using linear programming methods; e.g. $M_s = \max < B(X), U_s >$ for $X = \{X_{rs}\} \in K$, where $U_s = (0, 0, \ldots, 1, 0, \ldots)$. $B = \{B_s\}$ is randomly chosen in the hyper cube $\prod_s [m_s, M_s]$ until it satisfies all constraints. There exists $X \in K$ such that $B(X) = \{B_s\}$. Finally we randomly choose n vectors, $X \in K$, such that $B = B(X)$ and compute their mean. For this purpose, we solve n linear programmes $\max < X, V >$ for $X = \{X_{rs}\} \in K$, where V is random.