A comparison of terrestrial and marine ecological systems

John H. Steele

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

I review here the differences between temporal variability in terrestrial and marine environments and consider how this external forcing may affect population fluctuations in the two systems. The internal dynamics and community responses are expected to differ significantly with marine populations more likely to show longer term changes between alternative community structures.

THREE essential features are used for conceptual or numerical models of natural systems: (1) a high order of nonlinearity, (2) large variability in the forcing functions and (3) a wide range of space and time scales. It is impossible to combine all three in any single model, so major simplifications are introduced. I discuss here the effects of variable frequency of forcing, regarding atmospheric and oceanic physical variations as the input and corresponding population changes as output. Two simple models reproduce some, but not all, of these input/output relations and may contribute to our understanding of the differences in response of marine and terrestrial ecological systems to these parameters.

Physical systems

The separation of 'noise' from 'signal' in terms of temporal variation corresponds to the distinction between predictable and unpredictable fluctuations in the physical environment. If regular diurnal, lunar and seasonal cycles are removed, there is a large residual variability which can be considered as inherently unpredictable in a strictly deterministic sense. White noise, defined as constant variance per unit frequency, is the statistically simplest and theoretically preferred form to describe this variability[1]. (The total variance of white noise defined in this way is unbounded as frequency (f) tends to infinity. One must assume a cut-off at high frequencies which corresponds technically to instrument response time; conceptually it is assumed that the world is predictable on very short time scales.) Is white noise an appropriate representation of variability, particularly on the longer inter-annual or decadal time scales?

For terrestrial environments, temperature records and other data analysed in terms of their variance spectra[2] show (Fig. 1a) that white noise is an adequate representation down to frequencies of ~0.02 yr^{-1}. For time scales longer than 50 yr, the variance increases significantly and the spectrum becomes 'red' (by analogy with the spectrum of red light), but the use of white noise can be appropriate for simulation of the random forcing of terrestrial ecosystems up to several decades.

The marine environment is very different. Long-term temperature records from the deep ocean[3] show a spectrum where the variance increases continuously from hours to years with, approximately, variance (v)/unit frequency proportional to f^{-2}. Records of sea-level changes have been maintained for longer periods[4] and are an index of general changes in temperature, ocean circulation and density structure[5]. At much longer (geological) time scales, there are general relations between temperature and sea level[6-8] so that the spectrum from geological data can be plotted together with the instrumental measurements (Fig. 1b). There is a gap at 10–1,000-yr, but interpolation would give a spectrum that decreases continuously with f.

Should one expect marine spectra to be red over the entire time range from days to millennia? A simple stochastic model of the forcing of an ocean by atmospheric white noise[9] shows that the much longer time scales of heat transport and transfer
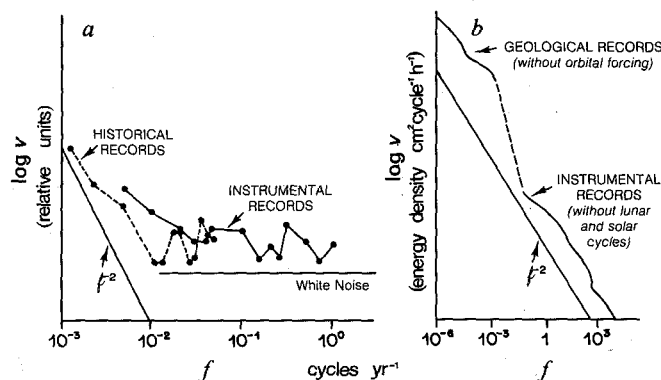

Fig. 1 Frequency spectra of variance for a, atmospheric temperature in England (redrawn from US National Academy of Science Report[2]) and b, sea level combining instrumental[4] and geological[6] data (J. Imbrie, personal communication).

in the ocean, ≤1,000 yr, can produce a red spectrum in the ocean's response so that $v \propto f^{-2}$ is an appropriate index for those external factors perturbing marine ecosystems. Again, there are technical and conceptual problems for the integrated variance over the whole frequency range. The total variance is bounded as f tends to infinity, so that the 'terrestrial' problem does not arise and the marine world is predictable at small time scales. But as f tends to zero, the total variance is unbounded, which no ecological system could assimilate. Thus, at very long time scales the system is inherently unpredictable and must be considered in the evolutionary, rather than the ecological, context; this brings into consideration questions such as 'punctuated equilibria'[10]. It is of interest also to ask whether the appearance of red noise in the atmospheric records at 50–100 yr is a reflection of the close coupling of the air and sea systems at and beyond these scales.

Ecological systems

Examples of relatively long-term population changes in terrestrial systems[11] show the variety of patterns involving persistence, cycles and trends. It was concluded that 'nearly all natural populations are characterized by patterns of change that keep their numbers within bounds. . . . only a minority of populations fluctuate so wildly that an equilibrium level is not obvious' (ref. 11).

Where very large changes do occur at fairly regular intervals (Fig. 2), it is assumed normally that internal features of the ecosystem dynamics are responsible. For example, the spruce budworm cycle of tree growth and defoliation[12] is assumed to have two equilibrium states, where the 37-yr-cycle is determined by tree growth rates and the rapid jump between states depends on the fast reproductive rate of the budworm. Climate variation does not seem to be significant.
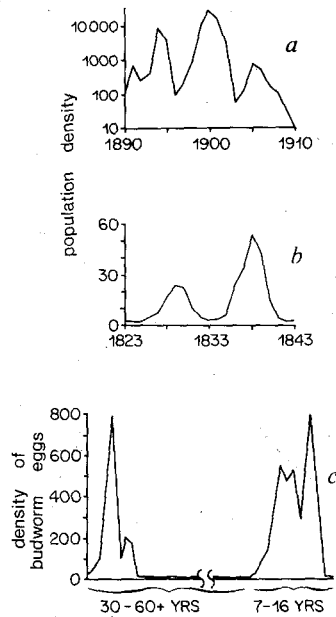
Fig. 2 Population changes in terrestrial species that show evidence of cyclical response: a, moth, *Bupulus*[11]; b, Arctic lynx[11]; c, spruce budworm[12].

Long-term information about marine ecosystems is dependent mainly on data from pelagic fish populations[13]. The longest records, covering 2,000 yr, are from fish scales in sediments off southern California[14]. A major feature is the relatively regular appearance and disappearance of sardines about every 70 yr, but these sediment records also show the continuous presence of anchovy and hake. From commercial fisheries there is historical evidence for the appearance and disappearance of breeding stocks of species such as herring (Fig. 3), mackerel and pilchard[15] over relatively large regions. In recent years, heavy fishing has altered the magnitude of population changes but maintained the rough periodicity of 50–100 yr[16]. In one case[15] where long-term data are available on community structure, many other species also changed whereas essential nutrients remained nearly constant (Fig. 3).

Historically, therefore, many pelagic stocks display marked fluctuations between states of high and low abundance. These alternative abundance levels may be regarded as two different equilibrium conditions, but the jumps between the two states are not considered in terms of the internal dynamics. They are connected usually to longer-term climate trends[11], although there are no simple relations between the physical and biological changes.
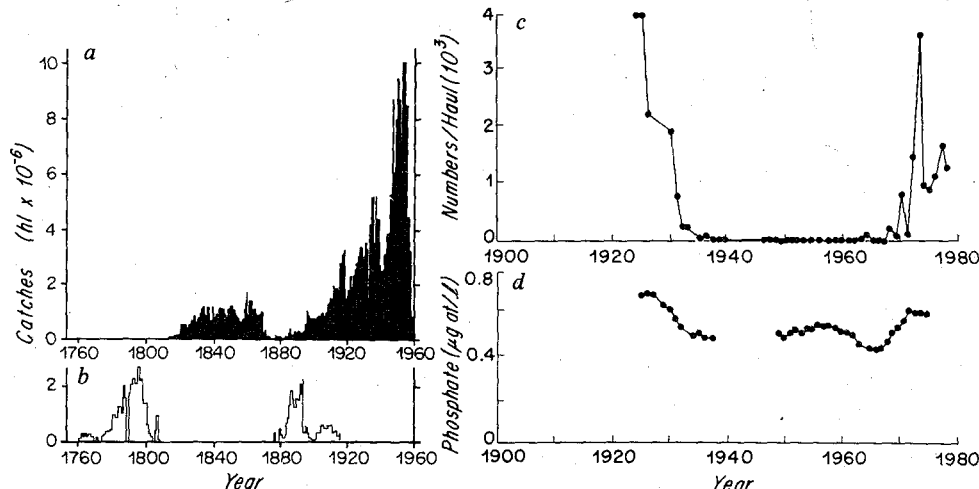
Theoretical models

To illustrate the relation between internal, biological, rates of change and external forcing at different frequencies, consider the response of a simple system with two equilibrium states $x = \pm 1$ subject to perturbation at a range of frequencies[17] (analysis provided by Dr Donald Ludwig).

$$\frac{1}{r}\frac{dx}{dt} = \begin{cases} -x+1 \\ -x-1 \end{cases}$$

where r is the response rate and the waiting time between switches has an exponential distribution with mean q^{-1}.

If $q \ll r$, the probability is overwhelming that x will be near $+1$ or -1. Thus the stationary distribution is peaked at both ends of this range (Fig. 4a). If $q \gg r$, the two dynamics are united and effectively $dx/dt = -rx$, where the most probable state (Fig. 4b) is between the equilibrium positions. If $q = r$, the distribution is uniform and the time sequence would be roughly and irregularly cyclical. More generally, if $q = 0(r)$, then the solution depends on the exact form of the system rather than only on the existence of two equilibrium conditions (Fig. 4c).

This model describes the essential response of systems with two equilibria to particular frequencies of stochastic variation. But the external environment contains random fluctuations at such a wide range of frequencies that both responses (Fig. 5a, b) may be expected to occur. Thus the quantitative distribution of the variance is highly significant. If we assume that the effects for terrestrial and marine systems will depend on the character of the physical frequency distributions, then the general qualitative response of these systems could be inherently different.

For marine systems with the ecological effects of variability proportional to the physical relation derived earlier, one would expect the system to be dominated by the lower frequencies. In consequence, the expected distribution (Fig. 4a) is similar to that derived from some of the long-term pelagic fish stock records. For terrestrial systems, equal weight would be given by white noise to the very different responses in Figs. 4a, b, so no conclusions would emerge about the character of the expected distributions. The output would depend on the internal dynamics of the system and the system could display persistence, cycles or occasional abrupt change. The evolution of system structure would tend to lead to the first category[11].

This very simple model has the advantages of analytical tractability and apparent generality. More complicated models contain specific descriptions of ecological relations and usually require numerical solution, particularly with stochastic inputs. One such model for a population (P) will be used here to illustrate the possible responses when red or white noise is applied over a range of frequencies[18].

$$dP/dt = P(1 - P/b) - cP^2/(1 + P^2)$$

combines a logistic growth with sigmoidal-shaped predation;

Fig. 3 Changes in marine species: a, Norwegian herring fishery[16]; b, Swedish herring fishery[16]; c, *Sagitta elegans* in English Channel[15]; d, winter phosphate concentration in English Channel[15].
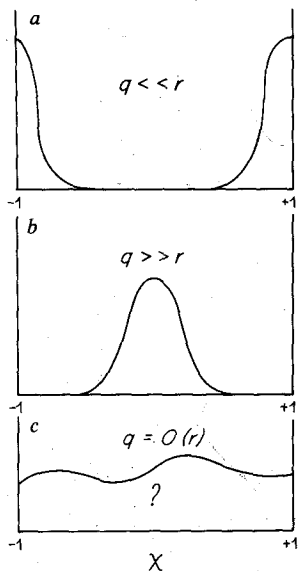
Fig. 4   Response of a two-equilibria system to stochastic forcing at frequencies: a, much less than and b, much greater than the intrinsic response rate of the system. c, Indeterminacy of the system when the rates are comparable.

Fig. 5   Response of P to stochastic forcing by red noise (a) and white noise (b) (see text for details).

b is carrying capacity; c is mortality rate. The general applicability has been reviewed[19] and used in specific applications for the spruce budworm[12] and for marine plankton[20]. For appropriate values of b and c the system has two equilibrium states; by varying c stochastically across these states, time sequences in the response of P are generated for different frequency ranges of red and white noise[18].

For red noise applied to the coefficient over a frequency range f to $30 f$, the system changes from a single to a double equilibrium condition at a value of $f = 0.015$ (in arbitrary units; Fig. 5a). For white noise with the same total variance in c and the same value of $b (= 10)$, the system does not begin to depart significantly from a single equilibrium state until $f = 0.003$ and then the response is highly irregular (Fig. 5b). For a time scale in years then, with red noise, the system would jump regularly when the longest period reached 70 yr. With white noise, however, the comparable forcing period is ~300 yr, but the system would then fluctuate irregularly at much shorter time scales. Thus, with the same model there are very different characteristic responses when the system is subject to external forcing by white and red noise typical of terrestrial and marine environments. Do physical fluctuations have a direct effect on the two types of systems in proportion to their physical amplitudes? Or do the mechanisms within the system accept, modify or eliminate the effects of this variability?

Discussion

Should comparisons of ecosystems include both terrestrial and open-sea examples? There is considerable interest and controversy about general ideas, such as resilience[21], which presuppose the concept of multiple equilibrium states with stochastic forcing. In one example, the concept of multiple equilibria is rejected but very limiting criteria are imposed: "We will deal only with the question of whether, under the same climate regime, populations are stable or persistent in the face of discrete, punctuated disturbances"[22]. Such criteria are not merely restrictive, but eliminate major features of both domains and, especially, the differences between them.

The inherent 'climate' of the ocean is unlike that of the land where the assumption of constant variance is acceptable up to periods of ~50 yr. In the sea, short-term variability is damped out by the very large heat capacity of the ocean. But in turn this large thermal capacity and the long period exchange rates between deep and near-surface waters (in the order of 10^2-10^3 yr) leads to relatively large-amplitude changes at long time
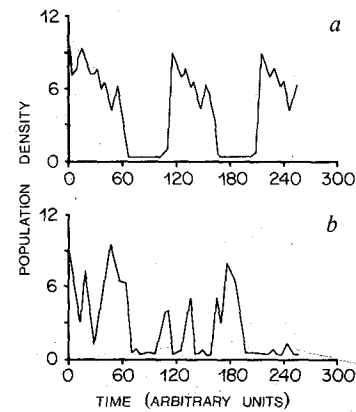
scales. Simple models can demonstrate the very different responses to these alternative forms of variability and some of the features of the two systems might be explicable in terms of differences in forcing by external physical factors. On the much longer (evolutionary) time scales, the terrestrial and marine ecosystems could develop and adapt differently in relation to their particular environmental structure.

The dominance of poikilotherms in the marine environment even at higher trophic levels is an obvious consequence not only of the much lower absolute range in diurnal and seasonal cycles, but of the smaller variability at short and medium time scales. There is little need (or opportunity) for individual pelagic organisms to create their own internal or immediate environment, unlike their terrestrial counterparts (including, in evolutionary terms, the marine mammals). At the population level, successful reproduction depends on a combination of physical dispersal and relatively predictable food cycles. Energetically and behaviourally, this is a preferable solution to close supervision and feeding of the young. From fish recruitment data there is little if any relation between stock size and recruitment on a year-to-year basis and the early life processes are decoupled from the adult state. This strategy is very different from that of most terrestrial populations, particularly vertebrates.

These differences in strategies make it difficult to relate concepts derived from terrestrial ecology to marine populations. For fish populations, the decoupling of larval and adult phases with their very different feeding and mortality patterns makes the r-k concepts inapplicable, even though the logistic relation may still be a useful simplification. Similar mathematical expressions for population growth or mortality may be derived from quite different ecological assumptions.

A simple definition of an ecosystem[1] is of an isolated community, uniformly unvarying in space, with time the only dependent variable. This definition is difficult to apply on land and even more difficult in the sea. The assumptions in this definition allow average food web and energy flow diagrams[23], but they fail completely to explain the switch[24] from one structure ('herring') to another ('haddock').

The two environments also have different spatial characters. Physical dispersion in the sea can blur the boundaries between regional systems and recruitment failures in one region may be reversed in suitable conditions by passive input from neighbouring breeding stocks. Similar processes on land usually require active migration between discrete locations. Further, the patchiness in marine organisms, combined with dispersion, may provide stabilizing mechanisms[25] mathematically similar to the functional responses in terrestrial animals[26,27], but with a different behavioural and energetic basis.

A 'terrestrial' system where environmental variability is large at both short- and long-term periods could be expected to

develop mechanisms internal to the system which would cope with short-term variability and in so doing, would minimize also the effects of longer-term variations. Such assumptions about internal mechanisms combined with relative immobility lead easily to the ecosystem concept with the emphasis, mathematically, on regulatory formulations independent of external variability. In 'marine' systems, less robust internal processes are needed to handle the smaller amplitude variability at short periods commensurate with the life span of the organisms. The possible absence of such mechanisms, combined with increasing variance with period, can mean that marine populations or ecosystems not only have different ways of dealing with short-term variance but also will respond differently at longer time scales. The dominant processes of numerically large larval reproduction, combined with extensive potential dispersal, means that replacement species may be available always. Thus deterministic ecosystem concepts and models are not so easily applicable.

On this basis, one should expect the internal dynamics and structures of marine and terrestrial systems, particularly at the higher trophic levels, to differ in significant ways in response to the temporal character of each physical environment. This does not mean that comparisons cannot and should not be made. Populations and communities face the same general requirements of long-term survival and evolution in the context of unpredictable environments. The concept of persistence within stochastically-defined bounds[22] demands explicit attention to the time (and space) characteristics of the variability. The fundamental differences in the two 'climates' should lead to significantly different types of system and so provide better tests of general hypotheses about resilience, food web dynamics and other ecological concepts.

1. May, R. M. *Stability and Complexity in Model Ecosystems* 2nd edn (Princeton University Press, 1974).
2. U.S. Committee for the Global Atmospheric Research Program *Understanding Climatic Change: A Program for Action* (National Academy Press, Washington, 1975).
3. Wunsch, C. *Evolution of Physical Oceanography* (eds Warren, B. A. & Wunsch, C.) 342–374 (MIT, Cambridge, 1981).
4. Munk, W. H. & Cartwright, D. E. *Phil. Trans. R. Soc.* **259**, 533–581 (1966).
5. Chelton, D. B., Bernal, P. A. & McGowan, J. A. *J. mar. Res.* **40**, 1095–1125 (1982).
6. Shackleton, N. J. & Opdyke, N. D. *Quat. Res.* **3**, 39–55 (1973).
7. Fairbanks, R. G. & Matthews, R. K. *Quat. Res.* **10**, 181–196 (1978).
8. Hays, J. D., Imbrie, J. & Shackleton, N. J. *Science* **194**, 1121–1132 (1976).
9. Lemke, P. *Tellus* **29**, 385–392 (1977).
10. Gould, S. J. & Eldredge, N. *Paleobiology* **3**, 115–151 (1971).
11. Pimm, S. *Food Webs* (Chapman & Hall, London, 1982).
12. Ludwig, D., Jones, D. D. & Holling, C. S. *J. anim. Ecol.* **47**, 315–332 (1978).
13. Cushing, D. H. *Climate and Fisheries* (Academic, London, 1982).
14. Soutar, A. & Isaacs, J. D. *Fishery Bull. Fish Wildl. Serv. U.S.* **72**, 257–275 (1974).
15. Southward, A. J. *Nature* **285**, 361–366 (1980).
16. Devold, F. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.* **154**, 98–108 (1963).
17. Slatkin, M. *Ecology* **59**, 249–256 (1978).
18. Steele, J. H. & Henderson, E. W. *Science* **224**, 985–987 (1984).
19. May, R. M. *Nature* **269**, 471–477 (1977).
20. Steele, J. H. & Henderson, E. W. *Am. Nat.* **117**, 676–691 (1981).
21. Holling, C. S. *A. Rev. Ecol. Syst.* **4**, 1–23 (1973).
22. Connell, J. H. & Sousa, W. P. *Am. Nat.* **121**, 789–824 (1983).
23. Steele, J. H. *The Structure of Marine Ecosystems* (Harvard University Press, 1974).
24. Steele, J. H. *Applied Biology* **4**, 103–140 (1979).
25. Steele, J. H. *Oceanus* **23**, 3–8 (1980).
26. Holling, C. S. *Mem. ent. Soc. Can.* **45**, 1–60 (1965).
27. Hassell, M. P., Lawton, J. H. & Beddington, J. R. *J. anim. Ecol.* **46**, 249–262 (1977).

ARTICLES

Targeting of a foreign protein to chloroplasts by fusion to the transit peptide from the small subunit of ribulose 1,5-bisphosphate carboxylase

Guido Van den Broeck, Michael P. Timko*, Albert P. Kausch*, Anthony R. Cashmore*, Marc Van Montagu & Luis Herrera-Estrella

Laboratorium voor Genetica, Rijksuniversiteit Gent, B-9000 Gent, Belgium
* Laboratory of Cell Biology, The Rockefeller University, New York, New York 10021, USA

Chimaeric genes can be constructed which fuse the transit peptide of a small subunit of the chloroplast-located ribulose 1,5-bisphosphate carboxylase with a bacterial protein. The fusion protein is translocated into chloroplasts and cleaved in a similar way to the small subunit polypeptide precursor.

CELLS of eukaryotes contain distinct subcellular compartments (organelles), delimited by characteristic membrane systems, which perform specialized functions within the cell. In photosynthetic leaf cells of higher plants, the most conspicuous organelles are the chloroplasts, occurring in a semi-autonomous fashion within the cell and containing their own genetic system and protein synthesis machinery, but relying on a close cooperation with the nucleo-cytoplasmic system for their development and biosynthetic activities[1]. Most chloroplast proteins are encoded in the nuclear DNA and are the products of protein synthesis on cytoplasmic ribosomes, many as soluble precursors[2–9] of higher relative molecular mass (M_r) which are then translocated through one or both of the plastid envelope membranes, processed and assembled into their final organellar compartment or holoenzyme complex. *In vitro* reconstitution experiments using isolated chloroplasts have demonstrated that the uptake and processing of >100 nuclear-encoded, cytoplasmically synthesized precursors by chloroplasts occurs by an energy-dependent[10], post-translational mechanism[6,10–17].

The most extensively characterized of these nuclear-encoded chloroplast proteins is the small subunit (SS) of ribulose 1,5-bisphosphate carboxylase. This polypeptide is synthesized on free cytoplasmic ribosomes as a precursor of M_r 20,000 with an amino-terminal extension or transit peptide of $M_r \sim 5,000$–6,000 (refs 6–7, 9). During or immediately after import of the precursor into the chloroplast, the transit peptide is proteolytically