

Episodic Events: Their Relevance to Ecology and Evolution

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With 7 figures

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Abstract. An episodic event can be one of the many "episodes" forming a normal flow of related events. But it can also be an "incident" interrupting a trend and initiating a new one. Appreciation of contrasting meanings of apparently identical categories of phenomena is familiar to evolutionary biologists who, for instance, envisage evolution as the result of both gradual and punctuated events. Seasonal plankton blooms (both normal and noxious), species outbreaks, mass mortalities, and human predation are taken as examples of "episodes" that can influence and/or modify what we perceive as "normality". Recruitment is another example of an episodic event heavily conditioning both community structure and function, as recently highlighted by the so-called supply-side ecology. The reductionistic study of ecology, more linked to thermodynamics than to history, allowed the formulation of general ecological laws which, however, stem from the laws of thermodynamics. The totalizing value of such laws blurs appreciation of heterogeneity and change, so that many ecologists tend to be rather conservative, using a concept like "conservation" as an absolute paradigm to follow and to consider "change" as an *a priori* negative phenomenon. Episodes can have a "conservative" or "innovative" meaning, and are the driving force of the history of life. Their importance is recognized mainly when dealing with the history of organisms (evolutionary biology), whereas the assemblages of organisms (*i.e.*, communities) are too often described and interpreted in an ahistorical context or in a too narrow time frame. Recognition of the importance of history in ecology (evolutionary ecology) can lead to a better understanding of environmental dynamics, albeit restricting the supposed predictive strength of ecology, a science timely integrating the reductionistic-thermodynamic approach with the holistic-historical one.

What is an episode?

The words "episode" and "episodic" have different and somewhat conflicting meanings. An "episode" can be one of the parts of a play, whereas "episodic" refers to something incidental, which could be outside an expected chain of events.

The history of life on Earth consists of many episodes which saw living beings evolve from the simple organisms of the Archeozoic to the complex organisms that inhabit the planet today. The link between the episodes in the history of life resides in the common language (the genetic code) with which all living beings transmit the information planning them.

All events that occurred during the history of life are thus episodes of a single play. This is the view of gradualist evolutionists, who view evolution as an uninter-

rupted chain of small modifications that led, in the long term, to enormous modifications. Some evolutionary biologists, however, proposed a saltational view of evolution, which sees microevolution (the normal flow of episodes in a play) as unlinked from macroevolution (the episodic appearance of big changes) (ELDREDGE & GOULD, 1972) (Fig. 1). Even an enormous number of small changes should not produce any modification in the body plan (bauplan) of a lineage, whereas major modifications, like those required for a bauplan shift, require great changes, beyond the sum of little changes.

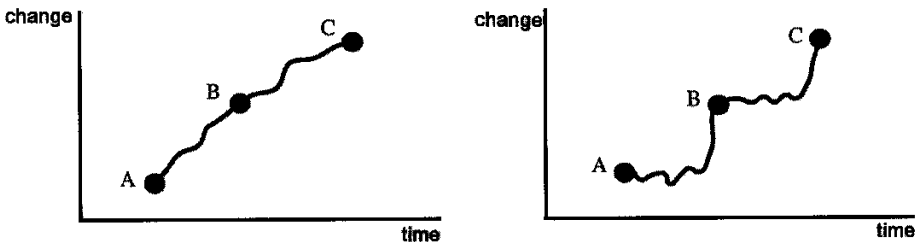


Fig. 1. Left: the pattern of evolution of a lineage consisting of three taxa (A, B, C) interpreted in the light of phyletic gradualism. Right: the pattern of evolution of the same lineage in the light of punctuated equilibria.

A bauplan change is a change of paradigm and its occurrence is, by definition, a catastrophe.

The existence of episodes of gradual modification is not in contradiction to episodic events of big change; the two possibilities are not mutually exclusive.

This is clarified, within the framework of evolutionary developmental biology, by the theory of the morphogenetic tree (ARTHUR, 1988): during ontogeny, the importance of modifications is maximal in the zygote and steadily decreases while passing from the zygote to the adult. A small modification in the first stages of development will lead to a big modification of the adult, with the possible saltational evolution of new bauplans, whereas a modification in the last stages of development will lead to gradual variation within the same bauplan. Species number in the millions, whereas just five kingdoms exist and living phyla (that is bauplans) add up to 92 (MARGULIS & SCHWARTZ, 1988). Abrupt change usually leads to malfunctions in the system, and homeostasis (or stabilizing selection) is there to avoid such changes. But in rare cases the modification can be fruitful and real novelties can appear.

The first representative of a phylum, for instance, is necessarily a new species (Fig. 2). Phyla are not established by independently formed classes, orders and families which, having reached a certain degree of differentiation, suddenly gather to "become" a phylum. In other words, to be sound taxonomic units, phyla must be monophyletic. The "episode" of speciation leading to a new phylum requires enormous modification of the representatives of a single ancestral species. Taxa ranked lower than phylum derive from splitting of the descent of the first representative of the new phylum. After the "accident" leading to a bauplan shift, regularity is restored by reiteration of what was accidental in the first place.

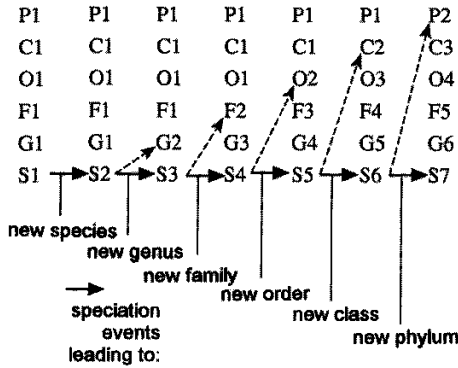


Fig. 2. Speciation events leading to differently ranked taxa, according to the amount of change involved. Each time a new higher taxon is formed, all lower taxa are automatically formed.

This has some bearing also in ecology, since the environments of our planet are characterized by the presence of living beings. The changes (i.e., evolution) of organisms, on one hand, affect their environment which, on the other hand, is the driving force of evolution (LAMOTTE & BLANDIN, 1985). Ecology and evolutionary biology deal with patterns and processes occurring over different time scales.

Time scales

Ecologists usually deal with short time scales compared with those of evolutionary biologists (especially palaeontologists), but environmental changes are forcing them to examine the past to determine if today's developments are "abnormal", or are part of a normal series of events occurring within wide time frames. Historical records show that climate has always been changing, and climate change effects are becoming a great issue of ecological research. Meteorologists, the students of climate features, contributed to the development of chaos theory by explaining the impossibility of precise long-term weather forecasts (e.g., LORENZ, 1963). Chaotic systems, contrary to stochastic systems, are deterministic, but the possibility of predicting their behaviour is limited to the short term, long-term predictions being intrinsically impossible. A chaotic system is very sensitive to initial conditions: a small difference in initial conditions leads to gradual divergence from a definite pattern, so that two systems can start to behave similarly but might end up behaving in a completely different way. General weather forecasts on the order of months are possible but, from year to year, cold or warm seasons might start earlier or later, or be hotter or colder, than usual. When considering the importance of weather in the quality of the environment, we are already in a difficult position if we intend to make precise forecasts about the future of communities or ecosystems. It's easy, for instance, to forecast the occurrence of a spring bloom of phytoplankton in shallow coastal waters, but it is more difficult to forecast its exact onset or the main species for that year. Easy (imprecise) long-term predictions are trivial, difficult (precise) long-term predictions are impossible. Many ecological models, built with sophisticated mathematical tools, usually end up formalizing what we could express with a verbal model

as a trivial prediction. For instance, we can say that the number of prey (*e.g.*, phytoplankton) influences the number of predators (*e.g.*, grazing zooplankton) and that the number of predators, in turn, influences prey number, and so on, so that we can expect a shift in the fluctuating abundances of prey and predators. The precision of such general assumptions is rather loose. If it were not, we could predict species abundances just by drawing data at a given moment and by applying some nicely built equations to such data. The real world is much more complicated. The number of interconnected variables in such a system is so great that no algorithm can contain it, which may allow precise long-term predictions. The level of indetermination of mathematical models is, in the long term, as high as that reached by using "common sense" and "intuition".

Environments are thus likely to be chaotic systems, often allowing short-term predictions but making long-term predictions impossible; these properties are being investigated by theoretical ecologists, but it is too early to express a judgement on the efficacy of this approach (see HASTINGS *et al.*, 1993 for a review).

The tendency to make predictions in ecology derives from the notorious *physics envy* affecting biologists at large. Thermodynamics is thus taken as the model to conform with in the effort to explain how environments work. This attitude led to a wealth of research on energy fluxes, based on precise measurements of energy flows and allocations. The progress of ecology due to such views has been and still is great; it has liberated ecology from too descriptive an approach, projecting it to the understanding of environment function. Unfortunately, however, the enormous number of variables involved in ecosystem analysis makes ecology more similar to microphysics than to thermodynamics. The principle of indetermination (we cannot know the exact linear momentum of a subatomic particle while also knowing its exact position) is paramount in microphysics but is nonsense if applied to the bodies considered by ballistics or astrophysics. Microphysicists are somewhat "proud" to make imprecise predictions and their "laws" are statistical. Biology is at the opposite end of microphysics within the spectrum of complexity considered by the empirical sciences but, just as microphysics, is largely "indeterminate", at least in the range of precision allowed to macrophysics.

History

The reason for this indetermination in the biological sciences resides not only in the number of variables involved, but also in the fact that biology (and ecology, since Earth environments are characterized by biological components) is a historical science (MILES & DUNHAM, 1993), and no historian would ever dare to attempt historical predictions! But a historian, like an ecologist, can describe historical events and try to understand what caused them and what their occurrence caused. Some regularities (patterns) can be identified, so that one can say that given a certain situation it is probable that another one or, as more often happens, a set of other possible situations will follow (see VERMEIJ, 1987). Ecologists should learn to accept history and must stop feeling uneasy if they are unable to make precise forecasts. Imprecision is an intrinsic property of ecology. If we tend to present our science as a discipline that can produce precise forecasts of the *if... then* type, we will do a disservice to ecology, to the commissioners of our research, and to ourselves.

The history of life is characterized by a succession of events that occurred in a random way yet obeyed rigid constraints (Fig. 3). It lacks directionality in the sense that the history of life does not follow a predetermined pattern. Since living beings transmit information from generation to generation, this information would flow unmodified if there were no accidents along its route. Evolution is strictly linked to change, so that episodic events leading to changes which overcome some constraints (attractors) are probably instrumental in determining world's makeup. Historical events leading to novel types of environment organization could be:

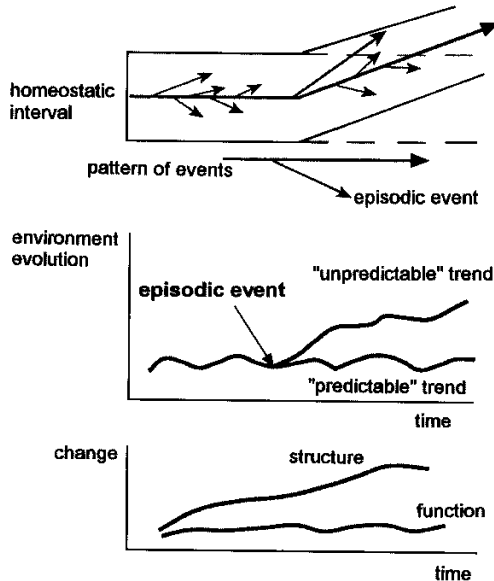


Fig. 3. Top: the flow of events determining the features of environments. When a change exceeds the homeostatic interval of the system, the features of the system, and its evolution, will be changed. Middle: environment evolution is predictable if environments remain stable and the events of the past are repeated with little change; episodic events of big change determine unpredictable patterns of environment evolution. Bottom: the functional stability of environmental systems is determined by strict functional constraints, but the same functions can be performed by a vast array of structures. Functional and structural stability are uncoupled.

- changes in species composition of communities (due to immigration of exotic species or to local extinction by emigration or terminal extinction);
- changes in the features of species (due to extinction by speciation or to fragmentation by allopatric or sympatric speciation);
- changes in climate (due to shifts in season occurrence, or to changes in the features of seasons);
- changes in the contribution of the species to the biomass of the community (due to rare species becoming abundant or to abundant species becoming rare).

The list of events leading to community change could be much longer, but the aforementioned ones are sufficient to show that the science of ecology cannot ignore the science of evolution.

Ecology and evolution

CHARLES DARWIN can be considered as the first modern ecologist, and "On the origin of species by means of natural selection, or the preservation of favoured races in the struggle of life" (DARWIN, 1859) is recognized as one of the most important books dedicated to ecology (see MCINTOSH, 1985). Darwin was aware of the importance of the environment in the evolutionary process. However, modern ecologists (and especially marine ecologists) and evolutionary biologists followed separate paths. Reductionism pervaded both evolutionary biology (with a tendency to interpret evolution as an essentially genetic phenomenon) and ecology (with a tendency to interpret the environment as an essentially thermodynamic system). Of course this vision is too extreme, and many steps (*e.g.*, LOEHLE & PECHMANN, 1988) have been made in these last decades to re-build a bridge connecting two disciplines which, in the mind of DARWIN, were the same thing.

It is increasingly evident that the functioning of an environmental system is strictly related to its history and to the history of its components. It is paradoxical that the presumed holism of thermodynamic ecologists, discarding structural diversity as "noise" and focusing on the functioning of black boxes, is turning out to be a somewhat reductionistic approach: structural complexity is "reduced" to functional simplicity, with lack of appreciation of the role of diversity in environmental systems. It is paradoxical, again, that many theoretical ecologists are now concerned about diversity (*e.g.*, MAY, 1988), whereas the success of their disciplines contributed to the disappearance of the expertise in recognizing diversity: nowadays taxonomists belong to an "endangered species".

The orgy of "unity" in the biological sciences saw the homologation of all biological phenomena to few paradigms of extreme reductionism. Stimulated by physics envy, molecular biology from one side, and system ecology from the other, reduced life to a series of standardized processes explained by a few more or less elaborated reactions. "Diversity" is now perceived as a primary feature of living systems, and the "unity" of life (evident from a functional point of view) is just one side of the coin. The outcome of such new attitudes is a renewed sensitivity towards species, not linked to romantic environmentalism, but to the recognition of the reservoir of diversity stored into the species pool of a community.

For too long a time knowledge about the species forming a community has been regarded as redundant, especially for practical reasons. The main goal of applied ecology, in fact, is claimed to be the understanding of how environments function in order to manage them. Management more and more entails restoration of a situation compromised by various types of impacts. A holist-thermodynamic ecologist can identify a malfunction in a black box, but the identification of the relationship between the malfunction and the malfunctioning structure is indispensable in attempting to fix the system (BOERO, 1990; 1994). Environments, however, are peculiar "machines" since they evolve while continuing to function.

Within the scenario depicted above, episodic events can be viewed as extremely important in shaping organisms, communities, and environments. The following examples will substantiate some aspects of the role of episodic events in marine ecology.

Noxious algal blooms and supply-side ecology

It is a rule, at temperate latitudes, that coastal waters are characterized by a spring bloom of phytoplankton. Such a bloom is usually the basis for a subsequent zooplankton bloom. Sometimes, instead of the usual species (often diatoms), other forms dominate, such as dinoflagellates. These protists produce toxins and their abnormal growth can severely alter coastal communities. In areas such as the Mediterranean, noxious blooms are "episodic" events which occurred several times in the past but are now causing great concern because they seem increasingly more frequent than before, heavily affecting both tourism and fisheries. Furthermore, the abnormal population growth of diatoms can cause noxious blooms due to mucus production (hyperscums or mucilages) or, simply, due to oxygen consumption deriving from the decomposition of the dying organisms when the bloom is over. Jellyfish have also recently undergone noxious blooms in the Mediterranean Sea.

Understanding the mechanisms leading to noxious blooms is of great interest, and research in this sense has been and still is widely commissioned, and carried out (*e.g.*, COLOMBO *et al.*, 1992; VOLLENWEIDER *et al.*, 1992). Some researchers retain human activities as responsible for blooms, others recognize a role of human activities but point out that noxious blooms also occurred occasionally (episodically) at a time when humans were less active than today.

In spite of disagreement about human responsibilities, most ecologists envisage an abnormal increase in the quantity of nutrients in the water column as the cause of noxious blooms. Nutrients are always required for any kind of bloom: they are necessary . . . but not sufficient! Most species of "protistoplankton" spend the adverse season in form of cysts that can remain suspended in the water column (such as the coccolithophorids) or sink to the bottom and become part of the sediments. This kind of life cycle is well known for diatoms, tintinnids, and dinoflagellates. Even zooplankters, such as copepods and medusae, have many species with resting stages. The biology of such life cycles is known to algologists and zoologists, but its importance is widely underestimated by ecologists (see BOERO, 1994 for a review).

Nutrient-oriented ecologists maintain that a bloom originates from the reproduction of few plankters which remained active in the water column during the unfavourable season. Some plankton is always present in the water column, but plankton composition is not always stable (plankton is a category, not an individual). The small quantity of plankton present in the adverse season cannot always be invoked to explain the plankton bloom in the favourable season, since not only species abundance but also species composition is different in the various seasons. Many species usually disappear completely from the water column during a certain period of the year. So, apparently, blooming species "come from nowhere", at least for nutrient-oriented ecologists. The occurrence of a bloom requires the fuel (nutrients) but also the "seeds" that will initiate the process. Such seeds are cysts, and the outcome of a bloom, especially the first spring bloom, depends on cyst availability when nutrient availability is optimal for population growth.

Increasingly, the type of blooms is felt to be linked to small shifts in the onset of both warm and dry seasons, and of cold and wet seasons. Species could alternate in being favoured by the beginning of the good season, for example via a mechanism proposed by BOERO (1994) and summarized as follows:

The life cycles of seasonal organisms (such as the vast majority of plankters) are characterized by the presence of resting stages (planktonic and/or benthic). The activation of such resting stages is endogenous (diapause) or exogenous (dormancy). Endogenous activation is regulated by circannual clocks. The abundance of a species should be linked to the relationship between the time of resting stage activation and the onset of the favourable season (Fig. 4). Potentially competing species do not have identically tuned circannual clocks, so that they can alternate in their contribution to the biomass, this being regulated by seasonal variability (Fig. 5).

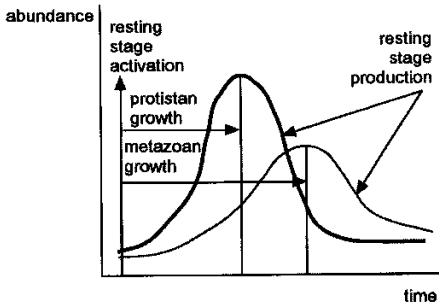


Fig. 4. Schematic representation of phyto- and zooplankton blooms in the light of resting stage availability. The time shift between phyto- and zooplankton blooms is also due to the different growth rates of protists (phytoplankton) and metazoans (zooplankton) (after BOERO, 1994).

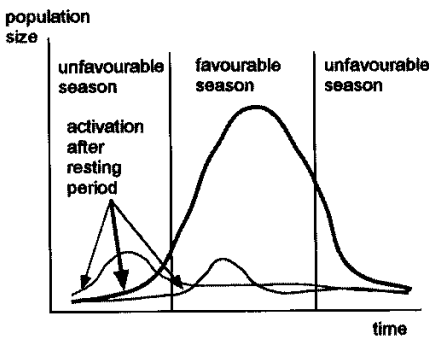


Fig. 5. Three species with differently tuned internal circannual clocks regulating the onset of their activity at the beginning of the favourable season. The species with an early-tuned clock (in respect to the onset of the favourable season for that year) will find an unfavourable situation and will be represented by few specimens. The species with a correctly tuned clock will take advantage of the favourable season and will be represented by many specimens. The species with a late-tuned clock will be outcompeted by the former species and will be represented by few specimens (after BOERO, 1994).

The explanation of plankton dynamics with the supply of resting propagules fits perfectly into supply-side ecology (GAINES & ROUGHGARDEN, 1985; LEWIN, 1986a), a model focusing on the importance of recruitment for community ecology; this approach has been widely overlooked by benthos and plankton ecologists. The presence of a community is due to the conditions determined by both biotic and abiotic factors, but its persistence depends on successful recruitment, allowing replacement of the individuals that, sooner or later, will die. Such recruitment is usually not linked to what happens in that community, since the propagules produced locally will be removed by currents: settling propagules will be supplied by adjoining communities (Fig. 6). As remarked by GROSBERG & LEVITAN (1992), the importance of recruitment has been widely recognized by fisheries ecologists since the beginning of the 1920s, but has been underestimated by other marine ecologists.

In the light of supply-side ecology, an event influencing the success of recruitment can show its effects much after its occurrence, so that the causes of an

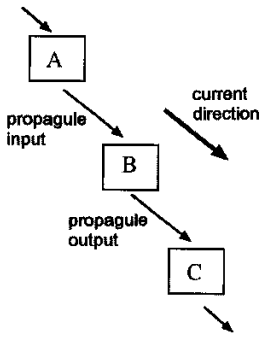


Fig. 6. According to supply-side ecology, the persistence of the features of the communities at site B depends on propagule supply from site A, whereas the propagules produced at site B contribute to the communities of site C.

"abnormal" situation can be easily overlooked. Multiple causality is paramount in ecology (PIANKA, 1992), and focusing on certain important causes (*e.g.*, nutrient availability) can lead to a neglect of other equally important causes (*e.g.*, propagule availability).

Episodic events such as shifts in both the periodicity and the quality of seasons, a phenomenon that we know as climate change, can dramatically change community composition and affect the functioning of whole ecosystems.

Mass mortalities

Blooms could be classified as mass recruitments and usually involve seasonal species with short life cycles. A bloom of seasonal organisms is invariably followed by a mass mortality. Cohorts are sharply distinct in seasonal organisms with a single generation per year, especially when the adverse season is spent as resting stages and there are no overlaps between subsequent cohorts, or there are many "generations" mainly due to rapid reproduction. We are not alarmed by mass mortalities of bivalve molluscs whose shells become stranded in enormous numbers at the end of the favourable season, and we are even less alarmed by the mass mortality of phyto- and zooplankton at the end of their blooms.

When mass mortalities affect perennial organisms, our attitude is different. If a species becomes part of a landscape for a long time, its presence is perceived as normal and its disappearance is seen as a catastrophe.

Mass mortalities can be generalized, affecting entire communities (*e.g.*, STACHOWITSCH 1984), or can affect single species (*e.g.*, GAINO *et al.*, 1992). Community mortality is usually linked to deterioration of abiotic conditions (often caused by biotic factors). A noxious algal bloom, for instance, can cause severe oxygen deficiency, followed by mass mortality at the community level. El Niño events cause temperature increases that can lead to local extinctions (GLYNN & DE WEERT, 1991).

The environment as a whole, however, may show no signs of "sufferance", and just one species may die out. Such events usually pass unnoticed, the only recorded cases being those of species of direct or indirect economic interest. In recent years mass mortalities have been observed (though not always recorded) for seagrasses, commercial sponges, coral-reef scleractinians, gorgonians, bivalves, sea urchins, and sea squirts. Many of these are long-lived organisms, a constant feature of their local environment. Usually such mass mortalities do not lead to the local extinction

of the species. The majority of the specimens die, but after some time the declined population re-establishes to almost normal densities. Such mortalities are often caused by disease, possibly linked to overcrowding. Other causes can also be postulated. A single episode of massive successful recruitment, for instance, could lead to the establishment of an exceptionally high number of larvae, followed by an abnormal increase in the abundance of a single species. Such an event should cause the "filling" of the environment by a single cohort and, at the end of the life span of its individuals, a real one-species mass mortality would become apparent. Its causes, however, should be linked to the former mass natality. Of course this is merely one possible scenario, and it is entirely plausible that populations might undergo mass mortalities for reasons unlinked to a former event of particularly successful recruitment.

In the long-term, species abundances are never constant and, from the study of the fossil record, it is normal that dominating species in a certain period were rare or absent before and became rare or absent again later.

Rarity

Modern ecology has its roots in cold-temperate regions, where diversity is not as high as at tropical latitudes, so that the importance of diversity was initially underestimated. Cold-temperate forests can be identified by the presence of few key species, whereas this is impossible for an equatorial rain forest. In the sea the situation is rather similar, and the number of species tends to increase while passing from the poles to the equator, at least in coastal waters. At every latitude, however, there are usually few abundant species and a host of less abundant (rare) species. The key species are considered as the backbone of the community (and they actually take on that role in a given period of the history of that community), whereas ecologists usually considered the rare ones as a nuisance. Their presence is a noise that has to be (conceptually) eliminated in order to obtain a clear picture of a situation which, otherwise, would be overwhelmingly complicated.

In a static situation this is certainly true. These rare species are inconsequential to the structure and function of that community. They are merely "tolerated" and survive because their requirements are minute compared with those of the dominating species: they are not "serious" competitors.

But "normality" is not eternal. Mass mortalities of the past, in which dominating species became extinct or almost extinct over a relatively short period, opened space for other species which, from rarity, suddenly came to play a primary role in the structure and function of communities in which, a short time earlier, they had the status of "tolerated" players.

Some of today's rare species will be the backbone of future communities: lacking perception of the importance of dynamic diversity is potentially very dangerous, especially when any deviation from a given set of initial conditions is *a priori* viewed as a negative event. As suggested by BOERO (1994), it is conceivable that the total biomass of an environmental system remains somewhat constant, but that species vary their contribution to total biomass in time, undergoing cycles of rarity and commonness (Fig. 7).

More and more evolutionary biologists accept pre-adaptation, together with adaptation, as a basic rule in evolution. The meaning of adaptation is the object of

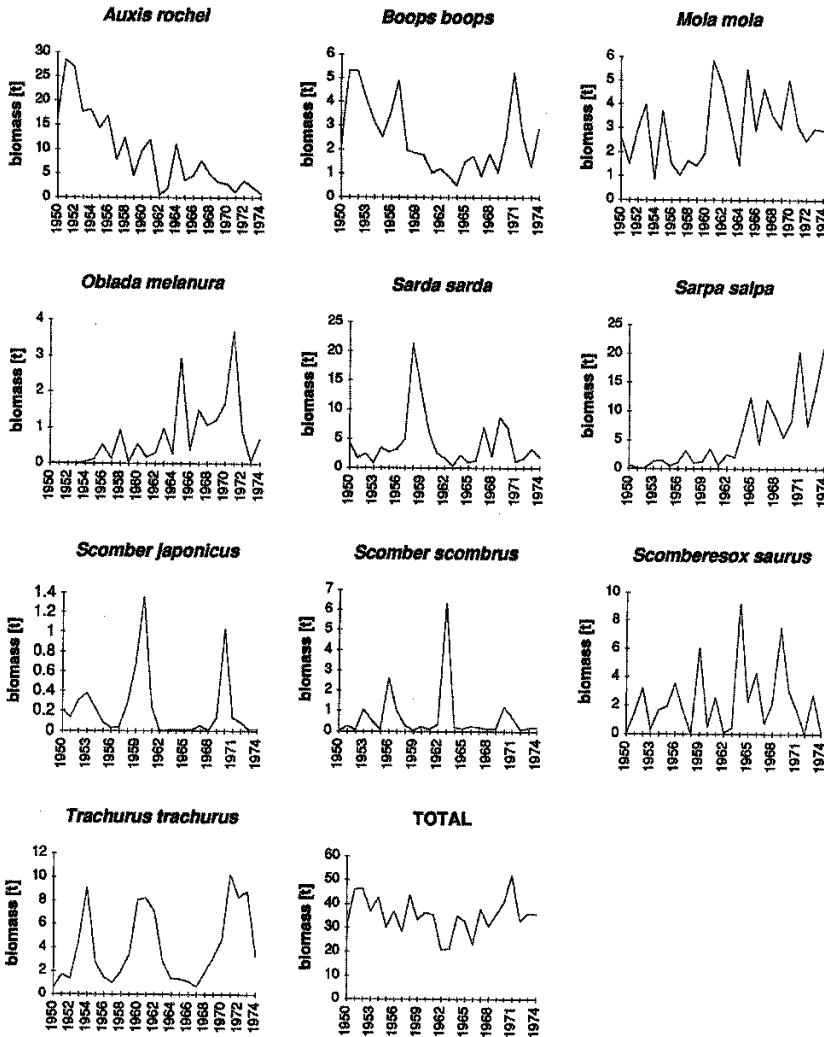


Fig. 7. Twenty-five years of catches of a fixed fishing net operating at the same location throughout spring and summer near Camogli (Ligurian Sea) (BOERO, unpubl. data). Total catches are relatively constant, whereas the contribution of the main species is varied in the long term.

long-lasting debate (BRANDON, 1990). A successful species is obviously adapted to common circumstances and can easily outcompete other species less adapted to these conditions. If the quality of the environment changes gradually, a Red Queen game can be played, with species changes following environmental changes (VAN VALEN, 1973). This requires high variability of the species and genetic propensity to change. With species selection, on the other hand, evolutionary biologists regard species, and not genes, as units of selection (VRBA, 1984). This shift in the target of selection generated heated discussions among evolutionary biologists, even though natural selection can be expected to act at all levels. Severe conditions will probably select at the specific level, favouring some species at the expense of

others, whereas less strict requirements will select within the same species, so that certain genetic makeups will be favoured at the expense of others. As a matter of fact, ecologists, with the principle of competitive exclusion, have formalized a concept that is very near to what evolutionary biologists call "species selection".

The action of a particularly efficient predator, especially when its evolution occurred elsewhere and its introduction into a community is abrupt, could cause the extinction of particularly "weak" prey species or of poorly competing predators; this would fall within the framework of species selection. *Homo sapiens* is one of the most rapidly evolving species, especially because its organic evolution is coupled with cultural evolution. The impact of humans can thus be considered as the cause of many "events" that are deeply affecting the global environment.

Human predation

Not long ago humans killing specimens of other species could be considered as predators and their impact could be studied as any other kind of predation (*e.g.*, KINGSFORD *et al.*, 1991). Usually, prey and predators are parts of a coevolved system with autoregulative properties. Human cultural evolution, however, is proceeding at too a fast pace to allow coevolution of prey, so that the impact of "inventions" might constitute episodes that can lead to the disappearance of prey species and even of their environment. The invention of SCUBA, for instance, made visually-oriented underwater "predation" easy, with the possibility of precise prey identification.

In the Mediterranean Sea, SCUBA diving is extensively used for many purposes, including collection of boring date mussels (*Lithophaga lithophaga*): SCUBA divers break the rocks with special sledge-hammers to extract the molluscs. This fishing activity has an even greater impact on the benthic communities covering the rocks inhabited by date mussels. All sessile organisms are eradicated during date mussel collection, and the exploited rocks remain completely bare (RUSSO & CIOGNA, 1991).

Two surveys carried out in 1990 and in 1992 along hundreds of kilometres of the Salento Peninsula (Apulian coast, SE Italy) showed that date mussel collection is active along the whole inspected shore and that the destruction of rocky bottoms has not slowed over the period 1990-1992 (FANELLI *et al.*, 1994). Professional divers operate methodically, exploiting a site until a given spot becomes unprofitable, then passing to the adjoining spot.

Five years of observation of damaged sites showed that recolonization of bare areas does not occur: sea urchins are extremely abundant and their grazing seems to play a central role in such recolonization failure: the absence of a dense covering of the substrate apparently offers good feeding opportunities to sea urchins, which may feed unselectively on newly settled organisms. Sea urchins are well-known "important species" in preventing the development of benthic communities (ELNER & VADAS, 1990) and their outbreak along the Salento Peninsula has been favoured by human predation. Their abundance is low in well structured communities, whereas it becomes abnormally high on bare bottoms where they can feed unselectively on settling propagules.

Due to the extremely low growth rate of date mussels and to the recruitment failure possibly caused by sea-urchin grazing, both *Lithophaga* and the whole benthic community can be considered as nonrenewable resources. Human predation in this case involves exploitation of a resource patch of limited size. The theory of optimal foraging

(STEPHENS & KREBS, 1986) envisions two possibilities for predators once a given portion of the available resource has been consumed: a drastic reduction of the collecting effort (in number of collectors) and/or a change in the exploited area. But there is a third possibility: an increase in predation efficiency. Since 1991, in fact, professional date mussel fishermen are using small underwater vehicles, thereby reducing the search effort and further increasing exploitation of easily accessible sites. Clearly, such a rapid evolution of the predator is not followed by an equally rapid evolution of the prey (and of its environment), which, therefore, is liable to local extinction.

Date mussel fisheries, followed by sea urchin grazing, are rapidly transforming hundreds of kilometres of the Salento shallow rocky coasts into a desert, and it is possible that in a short time this destructive activity will affect other portions of the Mediterranean coast.

A single destructive event, such as date mussel extraction, can heavily condition the underwater landscape, with a drastic change in the features of benthic communities.

Conclusion

Episodic events are the salt and pepper in the history of life on Earth. It is because of them that evolution proceeded at a pace that caused so many changes in the way life is organized.

This does not mean that every change is to be greeted as a positive event, especially when it is caused by humans. What pollution and human predation do to the environment need not to be stressed further here. On the other hand, even abrupt interruption of traditional human activities can severely change local communities (DURAN & CASTILLA, 1989), being comparable to abrupt removal of a keystone predator coevolved with the other members of the community. Conservation biologists tend to be "conservative" and to uphold as negative every change affecting the environments they are entrusted with managing. Historical records, however, allow a more optimistic outlook on the future of some communities undergoing rapid change: attempts to actively prevent change could even be a source of instability for such communities, whereas, as suggested by LEWIN (1986b), "change promotes stability".

The role of history in ecology is being increasingly underestimated: long-term surveys are being abandoned, and studies are to yield rapid results, with no attention to temporal variability. Reductionism is also prevailing in the time scales chosen to analyze a given situation.

The trendy field of biodiversity (*e.g.*, WILSON & PETERS, 1988) is, however, drawing attention to topics that will eventually lead to appreciation of historical patterns in ecology and to investigation of the processes that made them develop in a given way. This will further stress the importance of episodic events, not as freaks in a pre-determined flow of events, but as steering forces in an indeterminate (even if constrained) scenario.

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