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Variability of species' roles in marine communities: change of paradigms for conservation priorities

Abstract The structure and organisation of aquatic communities, moulded in each environment by combinations of abiotic factors, recruitment and productivity rates, rely upon a network of both pairwise and transitive interactions among organisms. In many cases, a few strong interactors drive basic ecological processes by playing a leading role in channelling the available resources. Among these, keystone species may control the outputs of local biodiversity through large indirect effects, disproportionately large relative to their abundance. Functional roles are not fixed labels, and species interactions have variable outputs in both time and space: also, in spite of a growing literature on species interactions, terminology is often poorly applied. This leads to the loss of the informative value of concepts, like the keystone species, which might represent useful trade-offs between science and environmental politics. Species' roles are often used to set taxonomic conservation priorities, although this might even be regarded as unethical, ecologically wrong, or in disregard of the evolutionary meaning of species coexistence and interaction. A re-assessment of species' roles is given here, attempting to highlight their limits and applicability. Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at http://dx.doi.org/10.1007/s00227-001-0769-2.

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Introduction

A prerequisite to understanding the functioning of a community is the compilation of taxonomic inventories, providing morphological and dimensional snapshots of community structure (May 1988). A simple list considers species as equivalent units, but, in the real world, each species is characterised by the ecological role(s) that individuals play. A species' role is defined by its effect on the distribution and abundance of other species in the community (Sutherland 1978). A species' impact on its community is determined by the relative importance or strength of links in interaction webs, represented by any subset of species consistently connected by trophic and non-trophic interactions. Species interaction occurs either by pairwise, physical contacts (direct interactions) or by indirect, transitive relationships among three or more species (e.g. trophic cascades, competition for food) (Wootton 1993). Both types have comparable effects on community structure (Schoener 1993; Menge 1995a).

In intertidal systems, Menge (1995a) identified nine general types of indirect trophic interactions ("interaction chains"), with the "keystone predation" model as the commonest one (35% of all cases).

Keystone species are regarded as extremely important for conservation purposes: they have been (conceptually) sustaining communities since Paine (1966, 1969) first suggested their existence. The message was clear-cut: not all species are equal in contributing to community architecture. Abundant (dominant) species are like columns; they are important because they give support to a community, and they are easy to detect because their presence is very evident. Other species are important because, despite their relatively low abundance, they sustain the community by keeping its diversity high (Barbault et al. 1991; Bond 1993; Mills et al. 1993). These are keystone species, small elements sustaining complex ecological buildings, with the strongest interaction linkages within the community. In its original

definition, a keystone predator (KP) controls potentially dominant species, which would otherwise monopolise a given community, keeping diversity low. In this sense, keystone predation affects community diversity as a type of intermediate disturbance (Paine and Vadas 1969; Levin and Paine 1974; Paine 1977; Connell 1978; Fox 1979). The keystone-species (KS) concept soon became a paradigm in community ecology (Mills et al. 1993); however, it was too widely extended and, as a result, was criticised for its (acquired) ambiguity (Strong 1992; Mills et al. 1993). This led to redefinition of a keystone species as "one whose impact on its community is large, and disproportionately large relative to its abundance" (Power et al. 1996), so explicitly excluding "structural" and other dominant species. The original KS concept applied to predators that increased diversity (Paine 1969), whereas its expanded definition covers also the possibility of effects leading to a decrease in biodiversity (electronic appendix 1).

The ecologists' frenzy to coin new words stimulated Paine (1996) to issue a new commandment – "Thou shalt not commit jargon" – but its following, unfortunately, was ineffective and did not prevent confusion. In fact, the keystone attribute was (and, paradoxically, it still is) unsuitably applied to ecological dominants (see for instance, Kawasaki 1993; MacIsaac et al. 1995; Olesen 1995; Hacker and Gaines 1997; Khanina 1998; Hall-Spencer and Moore 2000). These organisms are "key species" (sensu Odum 1971). Some of them, due to their bio-architectural complexity (e.g. plants, corals and other less-known, reef-building invertebrates), can be better defined as "structural" species, hosting a variety of "interstitial" species within the bio-construction (Barbault et al. 1991; Huston 1994).

Application of the keystone label to species other than predators led also to proliferation of subterms (electronic appendix 1), each referring to the specific (or "proximate") mode of action or behaviour. In aquatic environments, carnivores, herbivores, parasites and pathogens are often recognised as keystones in consumer–prey interactions, but a number of species functioning as "ecosystem engineers" (Jones et al. 1994, 1997) were also shown to have keystone effects. These species were defined as "habitat modifiers" (Mills et al. 1993), because they modify the chemical and/or physical features of their environment (e.g. sediment enrichment by infaunal annelids: Levin et al. 1997). Other roles, such as "keystone mutualists" (Mills et al. 1993), are known from terrestrial ecosystems, but they have never been demonstrated for aquatic systems.

Role variability

Choice of spatial and temporal scales affects our interpretation of species' roles. If Paine's (1966) mussels had been perceived as a structurally important species (as they are), their starfish predator would have been regarded as a disturbance preventing development of both mussel beds and the associated community. Surely, *Pisaster ochraceus* enhances diversity among large sessile species by removing mussels. At the same time, however, it decreases diversity of small epibiotic species on *Mytilus* shells, of small "interstitial" species living among mussels and of symbiotic species living within the mantle cavity of the bivalves (Lohse 1993; see also Underwood 2000).

A difficulty in the identification of keystone roles is that the linkage or interaction strength among organisms is variable and not fixed in space and time (electronic appendix 1). The redefinition of the term keystone species (Power et al. 1996) required low relative abundance; thus, a species may play or not a keystone role according to changes in its own population density. Furthermore, the interaction effect of KS may vary according to environmental conditions, prey life history and resource availability. In some cases, keystone roles are played under high turbulence conditions, whereas community regulation is gradually driven under "diffuse" control of keystone guilds, when water movement is slower (Menge et al. 1994; Robles and Robb 1993).

Prey recruitment may affect keystone *status* of predators in opposite directions. Keystone predation by lobsters (Robles 1997) and sea stars (Menge et al. 1994) is effective at sites with high prey (mussels) recruitment. On the contrary, sea otters feeding on sea urchins act as keystones only when sea urchin recruitment is low, predating over every size class of prey. At high sea urchin recruitment, otters predate mostly on large prey items and discard small ones, which already have a strong impact on the algal community (Estes and Duggins 1995). Released from otter predation, sea urchins increase their feeding rates and shift their diet from drifting fragments to settled algal sporelings; as a result, they reduce algal covering (Harrold and Reed 1985). On coral reefs, the impact of *Diadema antillarum* on encrusting algal communities is different according to the side of the coral colony where the sea urchin grazes. On upper sides, the sea urchin preferentially feeds on algae with high overgrowth ability, thus acting as a typical keystone consumer, whereas, under corals, the sea urchin feeds mostly on weak competitors, having low overall impact (Jackson and Kaufmann 1987).

On a time scale, a species might exert a keystone role by population pulses, like those outbreak species with large impact, such as *Acanthaster planci* (Birkeland and Lucas 1990; Boero 1994). Episodic population blooms of a strong predator – which, due to its temporary abundance, cannot be labelled as keystone – can control potentially dominant species. However, the average abundance in time of the predator is low, so that it might be recognised as a KP if the concept were to be widened to cover community history. In this sense, the understanding of community dynamics and species' roles may require knowledge of present and past interactions (Hughes 1989).

Chains of interactions of several "critical" species may even bootstrap or counteract impacts of different

keystones. In several ecosystems, humans are candidates as top diversity depressors (Duran and Castilla 1989; Vitousek et al. 1997). The devastating fishery of *Lithophaga lithophaga* (endolithic date mussels) causes dismantling and denudation of large bottom areas on Mediterranean shallow rocky shores (Fanelli et al. 1994). Here, two species of sea urchins (*Paracentrotus lividus* and *Arbacia lixula*) heavily graze on newly settled recruits of almost every sessile species. They also act as biodiversity depressors (Fanelli et al. 1999), preventing restoration of the original epibenthic community by feeding on propagules from nearby unexploited areas. Therefore, damaged areas are blocked for tens of years in a semi-denuded state (barrens). However, at nearby sites, where date mussel fishery is low or absent, benthic communities flourish, with high coverage and diversity values. Here, sea urchin density is much lower, and it might be controlled by a predator starfish (*Marthasterias glacialis*) or by fishes (Sala 1997). As a result, a chain of predator species with high-impact and opposite roles (man and sea urchins vs. sea star and fish guilds) might control large-scale patchiness of areas affected by date mussel fisheries (Fanelli et al. 1999).

Identification and measurement

Several authors (Menge et al. 1994; Power et al. 1996) questioned the possibility of a priori identification of KS without field measurements of species interactions, since the array of keystone roles could hardly be framed by shared attributes or characteristics. In some cases, KS effects are well recognised, but keystone-specific features may not be fully perceived (Mittelbach et al. 1995). Menge et al. (1994) listed some frequent, but not constant, properties of KP in intertidal systems: preferential predation on competitive dominant prey, high mobility, and wide foraging ranges. As a starting point, a keystone control may be hypothesised to act in those high-energy systems where long-lived prey species are present but not dominant. KP-intertidal systems seem shaped by coupling of top-down controls and bottom-up influences (Bustamante et al. 1995; Menge 1995b). Paradoxically, the only shared feature in KP systems is associated with prey, namely high production, sustained by high resource availability and high recruitment. Such generalisations are not applicable to all KP systems (see next section), and keystone roles can be played through mutualistic relationships or habitat modifications in systems with no high-energy features. Hence, keystone roles do not always seem to be predictable but, instead, are more easily detectable by a posteriori inference.

Each species' importance can be graded according to its role in the community. This led to the introduction of the concept of community importance (Mills et al. 1993) for a given species as "the percentage of other species lost from the community after its removal". Dominant species (and, especially, structural dominants) are easily identified as important, whereas "importance" is less evident for KS. However, labelling a species as "more important" than other ones induces a related question: how much "more"? How can we quantify and compare interaction effects? A posteriori attempts to answer these questions can be obtained by comparing community performances (including effects of both direct and indirect interactions) before and after dramatic changes in abundance of one of its component species.

Differences in species composition can be explained on historical or geographical bases (e.g. mass mortalities, sharp fluctuations, immigration, etc.), or by accidental introduction of allochthonous species, or by controlled perturbation of experimental subsystems (Power et al. 1996). Manipulation of target species abundance – through complete removal, introduction, or density changes – may give experimental evidence of species' roles by measurements of interaction effects. This is possible by application of quantitative indices of changes in species abundance (electronic appendix 2). Among these, the index of per capita interaction strength (PCIS) measures the effect of individual interactions (Paine 1992). The community importance index (CI) weighs the overall effect of target species abundance on measurable properties of the community (Power et al. 1996). The CI index is closely related to the PCIS index, both measuring changes in systems examined before and after experimentally induced variations in target species abundance. Both provide evidence of strong interactor effects, and their use may be combined to reveal keystone-suspected or keystone-cryptic roles.

The choice and/or application of CI versus PCIS indices are based on both experimental design (e.g. single species vs. guild removal, species introduction) and the species involved. The CI index is commonly used to measure a species' impact (or "effect strength", Menge et al. 1997) by its complete removal from a community. The PCIS index is usually referred to simplified experimental arenas, where only selected important components can interact at different relative densities. The CI index may be more indicative than the PCIS index of the overall impact of a species over the community, by incorporating effects of all possible direct and indirect interactions. However, simplified subsystems used for the PCIS index computation allow scoring linkage strengths of target species without environmental noise (Power et al. 1996). Furthermore, changes due to smaller variations in population densities than the complete removal of a target species can be measured. This aspect may be particularly important when the keystone role is spatially and temporally context dependent. The PCIS index is highly applicable for interaction analysis of nonmodular species (usually dominant in both intertidal and in soft-bottom, subtidal habitats). It is, however, inefficient for species the individual numbers of which are hardly recognisable or manipulated, as in the case of modular organisms (usually dominant in hard-bottom, subtidal habitats). An extension of the PCIS index measures the per population interaction strength (PPIS) to average inter-individual variability and to measure

the global effect at the population level (Navarrete and Menge 1996).

The CI, PCIS and PPIS indices, however, can be measured for selected species or subsystems with few, strong interactors. The number of manipulative treatments required to investigate the roles of all components in complex communities would be too high to be practicable (Wootton 1994a).

Laska and Wootton (1998) reviewed theoretical and operational frameworks for interaction-strength measurements. They stressed the importance of combining observational approaches (reducing number of experiments to be performed), experimental analysis by pulse experiments (Bender et al. 1984) and dynamic multiple regressions (Wootton 1994a,b; Pfister 1995; Chase 1996). Berlow et al. (1999) used both simulated and published data to test the applicability of CI and PCIS indices and two other commonly used empirical measures of the importance of consumer–prey interactions (i.e. the raw difference between treatments and the limitation index according to Osenberg and Mittelbach 1996). All explored indices provided useful but complementary information about species' impacts on their communities, and the authors highlighted conditions under which each index can be most usefully applied. The CI and PCIS indices, for instance, perform best in experiments with community at or near equilibrium, or to measure long-term results.

Cryptic interactions, such as intraguild predation (Holt and Polis 1997), can affect interpretations of experimental results. The statistical technique of path analysis may overcome the difficulty of performing a large number of experiments to infer which interactions may be important or not (Wootton 1994a,b), measuring both direct and indirect interaction strengths. However, Smith et al. (1997) showed that experimental perturbation could not be omitted in generating interpretable results from path analysis, suggesting that long-term experiments are necessary to reveal indirect pathways with different time lags. On the other hand, Menge (1997) recognised that in rocky intertidal webs almost every direct and indirect effect appears just after 20–40% of the experimental length (ranging 2–31 months).

Meta-analyses, combining results from independent studies, are receiving growing interest in community ecology. They can synthesise and compare patterns of effects, such as interaction strengths, assessed under different circumstances (Gurevitch et al. 1992; Arnqvist and Wooster 1995; Goldberg et al. 1999). The success of this technique, however, requires definition of a suitable metric common to many studies, a difficult task often requiring specification of a biological model (Osenberg et al. 1997).

Jordán et al. (1999) proposed an "a priori" approach to detect species with the highest keystone potential within an interaction web dominated by trophic links. Their keystone index is the number of species supposed to go to secondary extinction following a removal event (electronic appendix 2).

How many keystones are there?

In spite of the popularity of the concept and of its bearing on conservation activities, the list of species demonstrated to play keystone roles is still short. Many examples of proposed keystone roles lack strong experimental evidence (Underwood 2000). This might be due to the variability of functional roles: a species might be a keystone at a certain population density and a catastrophe at another one (Birkeland and Lucas 1990; Boero 1994; GESAMP 1997).

The list of keystone species is so short that we should conclude that they are not very important in contributing to overall marine diversity. Most communities seem to thrive without them. However, is it truly so? Maybe keystones are easily identifiable in environments where interactions persist in time, like the intertidal investigated by R.T. Paine. What about planktonic communities, which cannot be investigated without disrupting the arrangement of their components? Plankton communities are surely more important than intertidal ones, and if they were not regulated by keystone controls, they would represent a sharp restriction to the generality of the concept. Several studies on the relationships between gelatinous zooplankton and fisheries are demonstrating that jellyfish can exert heavy predation on fish populations, being responsible for much larval mortality (Purcell 1989; Purcell and Grover 1990; GESAMP 1997). Jellyfish predation can be hypothesised to play a keystone role, providing greater availability of resources to less competitive fish species, otherwise overwhelmed by potentially dominating ones. However, gelatinous zooplankton usually undergoes outbreaks (like nearly all plankters), and its keystone role might be only played in pulses, or at a regional scale. This is hardly demonstrable, since plankton cannot be caged, and any manipulation might alter environmental conditions so much as to make the experiment misleading.

In freshwater plankton, daphnids have been regarded as keystone species, because of their importance for the community structure and dynamics beyond their biomass effect (Gaedke and Straile 1998), even during population blooms. Vertical migration of two daphnid species is the main process lowering the predatory biomass effect, and assigning keystone status to the guild of smaller subpopulations grazing on the epi-limnetic community. Nevertheless, vertical migration implies turnover of actively grazing subpopulations, and the overall effect is strictly related to the period of daphnid dominance among plankton grazers. Therefore, the keystone status hardly fits the daphnid guild, notwithstanding its key role for limnetic food webs.

Keystone predation envisaged adult predators feeding on adult prey, with a tendency to disregard species' life cycles. Supply-side ecology recognised the importance of life cycles in explaining community architecture and composition, and such appreciation might be now transferred to keystone predation. Larval and juvenile mortality is the main controller of species abundances in

most environmental situations. The main predator of a commercial fish is possibly not a bigger fish eating adults, but rather a small planktonic predator (often neglected by plankton studies due to its negligible biomass) eating fish larvae (Purcell 1989; Purcell and Grover 1990). The concept of meiofauna bottleneck (Zobrist and Coull 1994) follows the same rationale: macrofaunal juveniles, falling within the size range of meiofauna (being thus labelled as temporary meiofauna) are heavily predated by permanent meiofauna. Predation on benthic juveniles (following predation on planktonic larvae) determines the architecture of macrobenthic communities. The meiofauna, in this case, can be hypothesised as a keystone guild, as well as gelatinous zooplankton in the water column. Meiofauna might also exert predatory effects on plankton communities. Indeed, many coastal plankters have benthic resting stages that represent a reservoir of potential biodiversity (Boero et al. 1996; Marcus and Boero 1998) which will be realised at their activation. Benthic cysts of many plankters are wrapped by protective envelopes and contain living matter with, presumably, high-energy contents. Many members of permanent meiofauna have mouthpieces and pharynxes that allow them to pierce their prey and suck its content. Cysts of plankters are in the billions in marine sediments, such an abundant food source is probably used by a group of taxa (permanent meiofauna) having all the features to exploit it (Marcus and Boero 1998; Pati et al. 1999). Such a possibility has never been investigated, but natural history suggests that, for instance, dinoflagellate outbreaks might be controlled by a blend of loriciferans and tardigrades! Similarly, bioturbation by burrowing macrofauna can affect both the abundance and the distribution of benthic resting stages (Marcus and Schmidt-Gegenbach 1986). The macrofauna can impact the viability of planktonic copepod resting eggs either by downward transportation (Albertsson and Leonardsson 2000) or by direct, physical interaction (Albertsson and Leonardsson 2001). In fact, the deposit feeder *Monoporeia affinis* (Amphipoda) may reduce up to 60–70% the recruitment of *Eurytemora affinis*, the commonest calanoid in the northern Baltic Sea, by feeding on, or damaging early developmental stages (late embryos or newly hatched nauplii). This case represents the first experimental evidence of a (keystone) benthic control on a pelagic system: the amphipod might not have a relevant role for its own benthic community, but it may significantly influence the dynamic output of zooplankton communities.

Rare species and evolutionary roles

Very few marine environments, if any, have been thoroughly explored in their biodiversity at a species level. Current species lists are very incomplete and reflect partial taxonomic expertise. The concern for biodiversity conservation focuses on a few charismatic species (generally either vertebrates or large and coloured invertebrates) and disregards what represents the bulk of biodiversity at a species level: a host of inconspicuous rare species. Rarity can be either soffusive (when species are rare at some place and common at some other), or diffusive (when species are rare wherever they occur) (Schoener 1987). Soffusive rarity applies to species living at the edge of their preferential distribution. Conservation of such peripheral populations is not worth much action, since such populations probably just represent sinks, collecting several propagules from distant source populations. Diffusive rarity represents a different situation. According to some theories on viable population size, diffusive rarity reflects some sort of hopeless state! A local or even regional species list, however, usually comprises a few common species and a host of taxa that have been found just one or two times in decades or even centuries. These might have passed unnoticed to unskilled researchers, but chances are good that they are simply very rare. Boero (1994) argued that very small populations might represent the last representatives of a declining species, or the first representatives of an emerging one, or, finally, the normal abundance in a given time window. Over time, passage through periods of abundance and rarity might be a common speciation trend, as postulated by the "flush and crash" speciation model (Carson 1990; Boero 1994). Within this framework, rarity is a common state in the life of many species that, when rare, play almost no ecological role, although they play a potential evolutionary role. They are the insurance for the continuation of biological diversity and, at least some of them, will take the place of the species that are common now. Focusing conservation on abundant, charismatic, or keystone species represents an action linked to present-day ecological conditions, disregarding the evolutionary potential of rare species!

Conclusions

In spite of some scepticism toward the operational value of the keystone species concept (Mills et al. 1993; Hurlbert 1997), no convincing reason for its dismissal is evident. Operational definitions of keystone species cannot be used to compare properties of different ecological systems. It is meaningless, for instance, to argue whether a starfish is more or less keystone than a whale. On the contrary, a worthwhile task is to measure the functional role of each species within its own community, identifying processes and patterns most influenced by its presence (e.g. production, species richness, etc.).

A long way is still to be travelled before the intricacies of ecological relationships will be properly understood, even as mere natural history observations. The structure and functioning of biological communities depend upon multiple combinations of prevailing factors. A list of factors should comprise environmental (climatic and edaphic) variables, autochthonous (self-supply) and allochthonous (supply-side) recruitment rates (Connell 1985; Gaines and Roughgarden 1985; Sutherland 1990),

and productivity rates (Menge and Olson 1990; Menge 1992; Wootton and Power 1993). Changes in interaction webs (e.g. strength and type of interactions) affect resulting community dynamics. These changes may lead to expected results when attributable to dominant species, which can be easily identified and monitored. However, unpredictable dynamics may arise from changes in interaction webs due to KS extinction. Biodiversity and ecosystem conservation strategies should consider the (community) importance of recognising keystone roles of single species or guilds. Identification of opposite effects of KS or any other "high-impact" species (biodiversity enhancers vs. depressors) may lead to development of different strategies for biodiversity conservation. According to the identified role, such species could be subjected to opposite population controls (protection vs. demographic restraint). Nevertheless, protection of "spotlighted" keystones cannot have priority by default, since the functional role is spatially and temporally context dependent, cryptic and rare species playing different roles at different times and places. Dominant, structural species (e.g. sea grasses), and other strong interactors as well, may have community importance and PPIS values comparable to those of keystones. Furthermore, even weak interactors may play an important role in maintaining landscape-scale diversity when their effects are strongly context dependent or highly variable in sign or magnitude (Berlow 1999). In these cases, average impact data may not reflect broadscale signals, which can be locally strong, whereas extinction of such "weak" interactors may alter natural communities by magnifying spatio-temporal variation in community structure. These findings challenge the view that research and management should be focused on species exhibiting a strong impact on their community and support previous criticism of the redundancy concept (see electronic appendix 1). Nevertheless, fragility may be higher at focal points in any community structure, and ecosystem processes may flow through bottlenecks that are worthy of keen attention by ecologists and conservation biologists. In any case, a common glossary is a prerequisite to progress in the understanding of ecological functioning and in the management of natural resources, and to highlight risks related to the loss of crucial species.

Evolutionary roles are played, not only by species with a relevant ecological role, but also by species that every ecologist would disregard due to their negligible contribution to the functioning of the present-day community. However, these species represent a potential for future communities. We cannot decide what species are important and what are not, since we cannot predict the course of evolution. Ranking species according to their role implies that if some species are important, others are less important and expendable. Denying this paradigm does not mean that it is irrelevant to disentangle ecological complexity so as to understand species' roles. However, the view of biodiversity in terms of services to the biosphere, availability of products, aesthetic values and eco-ethical implications (Kinne 1997) suggests that the value of species is linked to our welfare, and that some species are more important than others. This view has a political bearing and helps to convince people that biodiversity is important. When set into an evolutionary framework, however, these arguments lose their intellectual impact and simply become anthropocentric and, thus, of limited value.

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