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Defining keystone species in European regional seas: what are the candidates for the Mediterranean?

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Abstract

Within the DEVOTES project a comprehensive catalogue of potential keystone species covering all the European regional seas and a wide range of habitats and biotic groups has been produced. The Mediterranean sublist included 129 species/groups with representatives from all the biological components considered in the study. The choices were mainly based on expert opinion (55%) and published work (30%), with a smaller percentage derived from models (15%). Among the potential keystone species for the Mediterranean, 55% are benthic invertebrates, 20% are macroalgae and 10% are fish. Most are engineer species (42%), the rest being habitat forming species (29%) and predators (28%).

Keywords: biodiversity, MSFD, habitat forming species, engineer, predator

1. Introduction

Biological diversity is a key factor and central descriptor for ecosystem health and resilience; thus scientists are engaged with the task to provide biodiversity assessments, at various scales. In assessing biodiversity it is important to note that while all species contribute to biodiversity, some species may be more important than others owing to their interactions and notable effects on other components of the community. Paine (1969) coined the term “keystone species” to describe the significance of a predatory starfish of a rocky shore community; when present in the community, the starfish kept it stable with 15 species, while its absence led to a poorer community of only eight species due to uncontrolled mussel growth (Paine, 1969). Ever since, the term has been loosened, broadened, reviewed and re-categorised. According to MARBEF (Marine Biodiversity and Ecosystem Functioning EU Network of Excellence), a keystone species is a species that has a disproportionate effect on its environment relative to its abundance (http://www.marbef.org/wiki/Keystone_species). Such species affect many other organisms in an ecosystem and determine biodiversity both qualitatively and quantitatively. By analogy to the role of a keystone in an arch (the arch collapses without it), an ecosystem may experience a dramatic shift if a keystone species is removed, regardless of its small percentage contribution in the ecosystem in terms of abundance or biomass.

Despite the fact that the term is extensively used nowadays, our knowledge on keystone species and how we identify them is still very limited, in particular with regard to marine communities. Yet with the urgent need to protect, monitor and sustainably use our seas, important species such as keystones, or potential keystones, need to be systematically identified and monitored, from at least a precautionary point of view.

As part of EU FP7 DEVOTES Project (DEvelopment Of innovative Tools for understanding marine biodiversity and assessing good Environmental Status), a comprehensive catalogue of potential keystone species was produced (Smith et al., 2014a,b), covering a wide range of habitats and all the MSFD regional seas (North East Atlantic, Baltic, Mediterranean, Black Sea) and the Norwegian Sea. The overall aim for compiling this catalogue was to define when keystone species are important for assessing biodiversity, and the possible production of an operational metric. In this study we highlight the catalogue’s main outcomes related to our regional sea, the Mediterranean.

2. Materials and methods

For the DEVOTES task of listing keystones in European Seas the definition of keystone species has been loosened so that more potential species could be included. Therefore, we decided to include and distinguish between the following types: 1) keystone predator (based on the MARBEF definition); considering other species that may have impacts on biodiversity (2) habitat forming species, i.e., structural species that form complex and often extensive habitats (e.g. seagrasses, coral reefs, mussel beds), and (3) engineering species that increase living space or affect processes. It is worth noting that though most habitat forming species listed in the catalogue are characteristic species of habitat types under several habitat classification schemes (e.g. EUNIS, the European Nature Information System), it was not our purpose to especially consider and include such species/groups.

The DEVOTES Keystone Catalogue is a simple Excel file consisting of single row entries for individual keystone species and a number of column categories of information on the proposed species to complete. Some categories were restricted to a specific drop-down list (e.g. species primary impact, size class, habitat type), while others were for free entries (e.g. species common or scientific name, description of importance). The entries were broken down into eight broad category groups: (i) Data Input identifier, (ii) Keystone, (iii) Importance, (iv) Habitat, (v) Region, (vi) More than one entry, (vii) Source and (viii) Notes section. These broad categories were then divided into more detailed individual categories in single columns (e.g. Habitat category was divided into two columns, Habitat types and MSFD habitats). The master catalogue was compiled from the regional project participants' contributions and suggestions from non-partner experts. Once the catalogue had been finalised, a meta-analysis of the data was undertaken for summarising results over broad categories, e.g. number and type of keystones by habitat type or MSFD region. For the present study, the subset of data regarding the Mediterranean Sea was treated separately.

3. Results

Among the 210 species and 19 groups included in the DEVOTES Keystone Catalogue as potential keystone species of European seas, more than half, specifically 129 species/groups, are proposed from the Mediterranean Sea, with all biological components considered in the analysis having representatives. Benthic invertebrates account for 55% of the reported Mediterranean species/groups (68 species and 5 groups), while macroalgae contribute with 20% (25 species and 1 group) and fish with 10% (11 species and 2 groups) (Fig. 1a).

A total of 54 proposed keystones were considered to act as engineers, 37 as habitat forming species, 36 as predators, while two were thought of having multiple roles in their ecosystems, namely *Posidonia oceanica* (engineer and habitat species) and *Caretta caretta* (predator and habitat species) (Fig. 1b). More than half of the proposed keystones (72) are believed to have promoting role in their communities, 45 are reducers, and four could have both roles depending, for example, on region or keystone type. For eight species the experts were unable to define their primary impact (Fig. 1c).

Most of the proposed species (55%) were DEVOTES partners selections based on their knowledge and expertise, while 30% of the potential Mediterranean keystones were suggested after consulting the literature (scientific papers, reports, books, etc). A smaller percentage (15%) was identified as keystones, mainly major groups (e.g. zooplankton, sharks, cephalopods) from Ecopath with Ecosim model outputs (Christensen et al., 2004; Libralato et al., 2006) (Fig. 1d).

Benthic invertebrates comprise most of the potential keystone species in the Western Mediterranean and the Aegean and Levantine MSFD subregions, while in the Adriatic and the Ionian and Central Mediterranean subregions both benthic and macroalgae species predominate (Fig. 2).

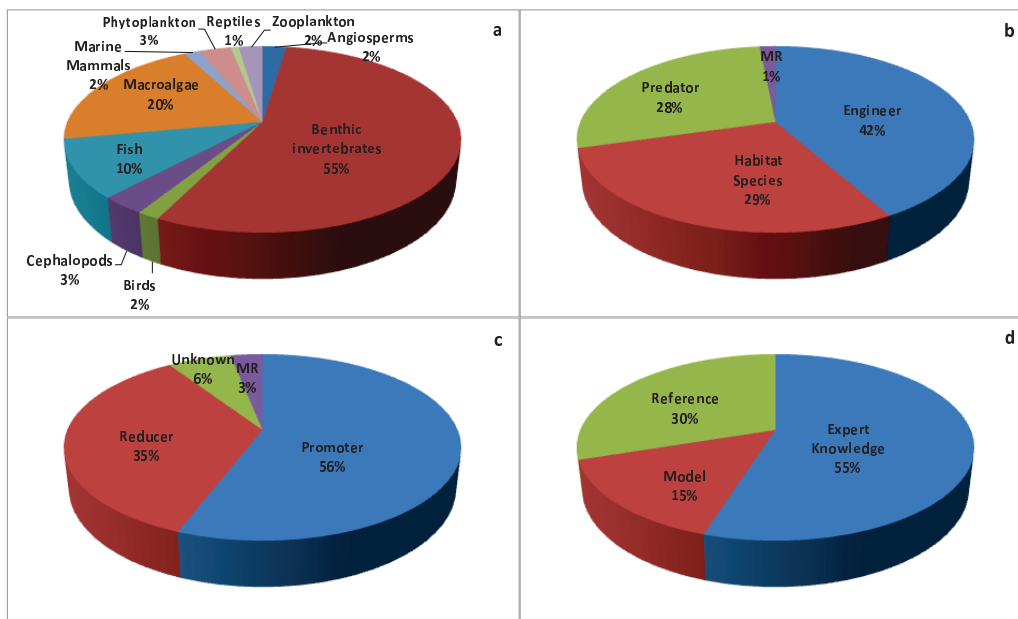


Fig. 1. Percentage of potential keystone species for the Mediterranean Sea by (a) Biological Component, (b) Keystone Type, (c) Primary Impact and (d) Source of Information.

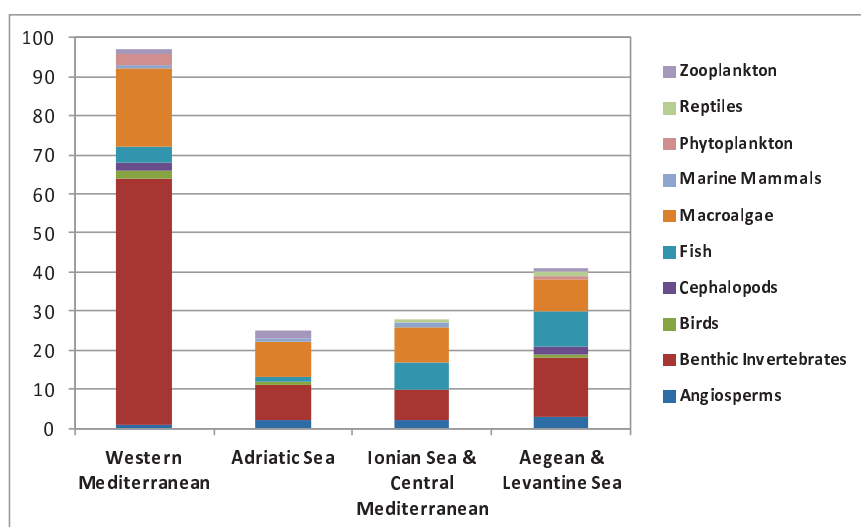


Fig. 2. Number of species per major biological component and Marine Strategy Framework Directive subregion.

The high number of benthic invertebrate keystones from the Mediterranean includes several components: polychaetes, classified as engineer species that act as promoters (e.g. *Ficopomatus enigmaticus*, *Hydroides dianthus*); engineer bivalve species that act either as promoters (e.g. *Chama pacifica*) or reducers (e.g. the invasive *Mya arenaria*); echinoderm species considered predators with a reducing (*Echinaster sepositus*) or unknown effect (*Ophiothrix fragilis*); sponge species considered as biodiversity promoters either as habitat forming (e.g. *Crambe crambe*) or engineer species (e.g. *Cliona celata*).

Among the 26 macroalgae keystones reported from the Mediterranean the association of *Phymatolithon calcareum* and *Lithothamnion coralloides* that form widespread maerl beds is included. These formations are considered promoting habitat species. Several invasive alien

macroalgae are also reported in the catalogue (e.g. *Acrothamnion preissii*, *Caulerpa taxifolia*), all of which are considered reducer engineers (outcompete native species for space and light and finally dominate). In the Western Mediterranean 9 macroalgae species are proposed as keystone habitat species with promoting role. The same stands for *Cystoseira amentacea* and *C. tamariscifolia* reported from the eastern Mediterranean.

A total of 13 fish species/groups spanning a wide range of habitats in the Mediterranean are predators that mostly have a reducing effect, although a few, such as *Merluccius merluccius*, are believed to have a promoting primary impact. Among the proposed fish species are also included the invasive aliens *Siganus luridus*, *S. rivulatus* and *Lagocephalus sceleratus*.

4. Conclusions/Discussion

With the wide keystone definition used for compiling the DEVOTES keystones Catalogue, more species and their impact on marine communities and ecosystems could be considered. This led to an extensive list consisting of species that fall within almost all marine biological components and habitats. Undoubtedly, that was expected, as it is widely recognised that keystone species occur in all major ecosystems and at any trophic and biological component level (Power et al., 1996).

There is an apparent emphasis in the DEVOTES list of Mediterranean keystones towards more benthic invertebrate species (55%). Benthic invertebrates encompass a diversity of taxa and guilds, which may have a variety of roles in the marine ecosystems, from foundation and habitat forming species, to bioconstructors, herbivores and top predators; hence, their high selection as potential keystone species.

The catalogue is seen as a good start to producing a list of up-to-date potential European keystone species, which could be reviewed and refined further. Reviewing and discussing the catalogue entries have already raised interesting questions and stimulated discussion between DEVOTES scientists. Among the issues we need to tackle are those regarding species dominance, context-dependency, habitat-specificity, spatial and temporal scale, suitability of keystones as biodiversity/status metrics.

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