DEVOTES

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Development of innovative tools for understanding marine biodiversity and assessing good environmental status

WP 6 | Deliverable 6.1

Report on identification of keystone species and processes across regional seas

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Abstract

In managing for marine biodiversity, it is worth recognising that, whilst every species contributes to biodiversity, each contribution is not of equal importance. Some have important effects and interactions, both primary and secondary, on other components in the community and therefore by their presence or absence directly affect the biodiversity of the community as a whole. Keystone species have been defined as species that have a disproportionate effect on their environment relative to their abundance. As such, keystone species might be of particular relevance for the marine biodiversity characterisation within the assessment of Good Environmental Status (GEnS), for the Marine Strategy Framework Directive (MSFD).

The DEVOTES Keystone Catalogue and associated deliverable document is a review of potential keystone species of the different European marine habitats. The catalogue has 844 individual entries, which includes 210 distinct species and 19 groups classified by major habitat in the Baltic Sea, North East Atlantic, Mediterranean, Black Sea (EU Regional Seas) and Norwegian Sea (Non-EU Sea). The catalogue and the report make use/cite 164 and 204 sources respectively. The keystones in the catalogue are indicated by models, by use as indicators, by published work (e.g. on traits and interactions with other species), and by expert opinion based on understanding of systems and roles of species/groups. A total of 74 species were considered to act as keystone predators, 79 as keystone engineers, 66 as keystone habitat forming species, while a few were thought of having multiple roles in their marine ecosystems. Benthic invertebrates accounted for 50% of the reported keystone species/groups, while macroalgae contributed 17% and fish 12%. Angiosperms were consistently put forward as keystone habitat forming and engineering species in all areas. A significant number of keystones were invasive alien species.

Only one keystone, the bivalve *Mya arenaria*, was common to all four EU regional seas. The Mediterranean Sea had the largest number of potential keystones (56% of the entries) with the least in the Norwegian Sea. There were very few keystones in deep waters (Bathyal-Abyssal, 200+ m), with most reported in sublittoral shallow and shelf seabeds or for pelagic species in marine waters with few in reduced/variable salinity waters. The gaps in coverage and expertise in the catalogue are analysed at the habitat and sea level, within the MSFD biodiversity component groups and in light of knowledge and outputs from ecosystem models (Ecopath with Ecosim).

The understanding of keystones is discussed as to when a species may be a dominant or keystone with respect to the definition term concerning 'disproportionate abundance', how important are the

‘disproportionate effects’ in relation to habitat formers and engineers, what separates a key predator and key prey for mid-trophic range species and how context dependency makes a species a keystone. Keystone alien invasive species are reviewed and the use of keystone species model outputs investigated. In the penultimate sections of the review the current level of protection on keystone species and the possibilities for a keystone operational metric and their use in management and in GEnS assessments for the MSFD are discussed. The final section highlights the one keystone species and its interactions not covered in the catalogue but with the greatest impact on almost all marine ecosystems, *Homo sapiens*.

Contents

1. Introduction

Marine scientists are continually being asked to provide information to managers and policy makers to support them in making decisions on the preservation of diversity and ecosystem integrity (Borja *et al.*, 2010). In assessing biodiversity it is important to note that some species may be more important than others. All species contribute to biodiversity by their presence (in the sense of increasing species richness), but some are notable for the effects and interactions, both primary and secondary, that they have on other components in the community, and therefore their presence or absence has a disproportionate effect on the biodiversity of the community as a whole (EASAC, 2009). In biodiversity assessments and particularly under the Marine Strategy Framework Directive (MSFD, 2008/56/EC (EC, 2008)), it is worthwhile to highlight or focus on these species and to track them in indicators for Good Environmental Status (GEnS).

1.1. Defining Keystones

MARBEF, the Marine Biodiversity and Ecosystem Functioning EU Network of Excellence, has defined a keystone species as a species that has a disproportionate effect on its environment relative to its abundance. Such species affect many other organisms in an ecosystem and help to determine the types and numbers of various other species in a community (http://www.marbef.org/wiki/Keystone_species). The role that a keystone species plays in its ecosystem is analogous to the role of a keystone in an arch - the arch collapses without it. Similarly, an ecosystem may experience a dramatic shift if a keystone species is removed, even though that species was a small part of the ecosystem by measures of biomass or productivity. Paine (1969) developed this concept from experimental work on rocky shore communities, where a stable community of 15 species existed with the presence of a predatory starfish. If the starfish was removed, mussel growth was uncontrolled, leading to a mussel-dominated community comprising of only eight other species. Marine keystone species are commonly apex predators in areas controlled by top-down forces, where the predator controls the prey (often herbivores) which otherwise act as dominants, thereby exerting strong effects on community structure (Konar, 2000). A rise and fall in the keystone abundance can cause a cascading effect on its prey, their food species, and ultimately the entire food chain. It has been wryly noted that a keystone is not recognized as a keystone until the effects of its absence become evident. A well-observed and commonly cited example of a keystone is that of the sea otter living around the Pacific Rim. The sea otter is the keystone species that maintains the population of otherwise dominant sea urchins at levels that maintain the kelp forest in good condition (the kelp forest is a high biodiversity habitat). Removal of the sea otter results in overgrazing by the dominant urchin and barren seabeds (Estes and Palmisano, 1974) or, as has been noted since the recovery of sea otters after being hunted for its fur, that kelp forests have (re)developed in areas where they are present (Estes *et al.,* 2010).

Since Paine's original work, familiarity has led to broader definitions and Mills *et al.* (1993) re-categorised keystone species into five types, examplarising the diversity of keystone effects. These include keystones in all biospheres, not all relevant to the marine world. They reviewed/defined:

- Keystone predator: predator controlling the density of other types of ecologically significant prey species;
- Keystone prey: able to maintain its abundance in the face of predation, normally high reproductive rate;
- Keystone mutualists: animals that are significant factors in the persistence of plant species – otherwise known as mobile link pollinators and seed/spore dispersers (terrestrial ecology);
- Keystone hosts: the other side of the mutualist link; those plants that support generalist pollinators and those fruit dispersers that are considered critical mobile links;
- Keystone modifiers: species that have activities that greatly affect habitat features without necessarily having direct trophic effects on other species. Mills *et al.* (1993) included habitat builders as well as urchin grazers in this category.

Power *et al.* (1996) partially in response to the Mills *et al.* (1993) tried to clarify and develop the concept further with an operational definition of keystone species through strength of effect (Community Importance) and more recently this has been married to Species Interaction Strengths (Berlow *et al.*, 2004). It was felt that through misapplication and questionable redefinition, ecologists and conservation biologists had obscured the meaning of the term keystone species. In the marine environment Power *et al.* (1996) were able to review information on 14 species/groups including predatory starfish, snails, fish, seabirds and sea otters, krill and amphipod eating whales, and herbivorous sea urchins and fish (the study actually covered, terrestrial, freshwater and marine environments). This demonstrated the presence of keystones in a variety of ecosystems at many trophic levels. The studies reviewed were experimentally based (predator removal), historical reconstructions (whale/krill), or comparative studies (predator re-introduction, e.g. sea otters) on relatively high profile species (easily observed). They also considered the identification of keystones by their traits (e.g. high consumption, active/mobile, small abundance/biomass, preferential prey) and the traits of their prey (propensity to form dominant populations), but could not consistently distinguish systems with keystone interactions, believing that context dependency needed to be considered and that keystones only play keystone roles under certain conditions. Obviously even at this stage almost 20 years ago and 30 years after the formulation of the keystone concept, it was seen to be a complex issue.

Menge *et al.* (2013) have more recently reviewed and considered keystone species. They have tried to separate keystone species from other closely related types of species, including 'key-industry species' (Elton 1927: single species of animals supporting a large number of consumers e.g. copepods, anchovies), foundation species (Dayton, 1972: critical species which define much of the structure of the community, including species that create or maintain habitats – engineering species, e.g. American beaver or kelp forests) and keystone processes (or critical processes, primarily abiotic processes or environmental stresses that control ecosystems, e.g. storms, waves, movement of substrata). In clarifying some of the terminology, Menge *et al.* (2013) define species in communities as:

- Keystone species: consumers having a disproportionately large effect on communities and ecosystems;
- Strong interactors (critical species): species having a large effect on species with which they interact;
- Weak interactors: species having little effect on other species;
- Dominant species: strongly interacting species that owe their influence to their high abundance;
- Key-industry species: prey that support a large group of consumers.

The identification of keystone species remains very difficult and to date there is only a limited set of clear cut examples; and although the original concept came from the marine world, much of the follow-up has been in terrestrial and freshwater systems. Keystone identification is laborious without the use of removal/exclusion experiments (Paine's starfish), well-documented historical data on species removals/recoveries (e.g. beavers, sea otters, bison), or predictions based on population, community, traits and patterns (Menge *et al.*, 2013).

A keystone species might not be keystone in all environments and conditions. This has been highlighted as context dependency, normally considered where abiotic factors hold a controlling influence; for example, Paine's starfish was strongly keystone on wave exposed shores, but not in sheltered but similar environments (Menge *et al.*, 1994). Other external factors may also play a role which may have important management considerations: Eddy *et al.* (2014) have shown through a marine reserve ecosystem model in New Zealand that the lobster is a keystone species negatively impacting the abundance of its prey species and indirectly positively influencing the abundance of the prey of the first prey. However, under current levels of fishing, lobster biomass has been decreased leading to significant impacts on the organisation and function of the ecosystem. Protection plans will lead the biomass to recover to historical levels where, it is believed, its keystone role will be restored.

Our knowledge on keystone species is still very limited, particularly how we identify them, even though the concept is well known and mature. With pressures on management bodies to protect marine ecosystems whilst allowing for sustainable use, important species such as keystones or potential keystone species, need to be systematically identified and monitored from at least a precautionary point of view.

A decade ago an attempt was made to catalogue European keystone species through the BIOMARE network (Féral *et al.*, 2003). This Biodiversity network tried to define and collate indicators of biodiversity including 9 species/groups of keystone habitat builders, 18 species groups of other keystone species and 11 species of invasive alien indicators. This was considered as a very first step, with species being identified through consensus hopefully inspiring further investigation. A major issue at that time was to differentiate between keystone species usable as indicators of biodiversity and so-called indicator species that were used more routinely and for comparison with previous data sets more for environmental purposes rather than biodiversity management (J-P Féral, pers. comm).

1.2. Objectives

The objectives of DEVOTES Workpackage 6.1, Task 6.1.3 were to list and review potential keystone species or processes that are important for biodiversity at the community or ecosystem level for the different habitats mainly in the European regional seas. This catalogue was to be based on literature reviews, modelling and expert knowledge. Keystone species were classified and the possibility of using them in an operational metric/indicator investigated. This document forms the major deliverable (D6.1) of the Workpackage.

The purpose of this document is:

- to present the catalogue survey design and the catalogue of keystone species in European regional seas at the major habitat level;

- to present the analysis of the catalogue;
- to review keystone species leading to the definition of when keystone species/processes are important for assessing biodiversity, and the possible production of an operational metric.

1.3. Defining Keystones in DEVOTES

With DEVOTES WP6.1.3 goal of listing keystones in European Seas the definition of Keystone species has been loosened so that more potential species may be included. Based on the MARBEF definition (Section 1.1) we decided to include: 1) keystone predator. Considering other species (or species groups) that may have impacts on biodiversity, we also included 2) habitat forming species (e.g. foundation species like seagrass), and 3) engineering species (e.g. large scale bioturbators that increase living space by increasing oxygen fluxes affecting the de/nitrification processes, etc.). Whilst the original Description of Work included keystone processes, we consider that most important processes (biogeochemical processes) will be strongly mediated by engineering species, so we have incorporated them in the latter group. In terms of processes, a separate substantial review (Strong *et al.,* 2014) has been undertaken within the DEVOTES 1.3.3 Task with the aim to investigate the Biodiversity Ecosystem Functioning (BEF) relationship across and between biodiversity components (e.g. microbes, macroalgae, etc.) as well as levels of biological organisation (cell, individual, population, community and ecosystem). In that review, comparisons are made against a standardised ecosystem function list which includes biomass production, organic matter transformation (e.g. organic matter decomposition), ecosystem metabolism (e.g. carbon mineralisation), elemental cycling, physical structuring (e.g. reef building, microbial film development), stability of ecosystem processes and the ecosystem properties of resistance and resilience. The use of conceptual models linking mechanisms of pressures (mediating state change to components and habitats) with risk assessment and management as well as of the potential of BEF relationships to underpin monitoring principles and policy on the marine system as a whole is further investigated in DEVOTES by Smith *et al.* (2014) and Strong *et al.* (2014).

2. Methods & Materials

The activities for the review entailed original presentation for the work plan by the Task leader at DEVOTES meetings, feedback from the Workpackage participants, creation of the blank catalogue with further feedback from the Workpackage participants, then distribution of the catalogue and the accompanying Guidance Document (Smith and Papadopoulou, 2014) to the participants for filling in.

The master catalogue was compiled from the participant contributions, returned complete to the participants for checking, with a final compilation by the task leader.

2.1. The DEVOTES Keystones Catalogue compilation

The DEVOTES Keystone Catalogue was compiled from participant entries. They were asked to provide entries based on their self-knowledge, colleagues and literature search. The catalogue was a simple Excel file with single row entries to be completed for individual keystone species and with a number of column categories of information to complete. Some categories were for free entries; others were restricted to a specific list (drop down menu). The catalogue had a 'Read me' datasheet (instructions and clarifications), a 'List' datasheet (for visualising the drop down list options) and the 'CATALOGUE' datasheet to be filled in (along with a few additional sheets showing the relevant DEVOTES and MSFD regions/subregions).

The entries were broken down into seven broad category groups and then individual categories in single columns as described below.

2.1.1. Data input identifier section

To identify data information source provider:

- Code: participant sequential number entry.
- Institution: the institution of the person providing the data.
- Name: name of the data provider.
- E-mail: contact e-mail address.

2.1.2. Keystone

- Common Name: if there is a common name for the keystone: e.g. Striped Dolphin, Dublin Bay Prawn/Scampi, Amberjack, Cod.
- Scientific name: e.g. *Stenella coeruleoalba*, *Nephrops norvegicus*, *Seriola dumerili*, *Gadus morhua*. Species names standardised according to the World Register of Marine Species (WORMS registry: www.marinespecies.org)
- Keystone Type: selection from: predator (feeding on the same or lower trophic level), habitat species, or engineer.
- Biological Component: selection from MSFD/DEVOTES list: microbes, phytoplankton, zooplankton, angiosperms, macroalgae, benthic invertebrates, fish, cephalopods, marine mammals, birds, reptiles.
- Biological Subcomponent: to provide extra detail e.g.:
    - phytoplankton: nano-, pico-, dino-, etc.;

- benthic invertebrate: meiofauna, macrofauna, megafauna.

2.1.3. Importance

- Primary Impact: impact on local biodiversity of the keystone species. Selection from reducer or promoter.
    - A reducer, for example, may be from competition/interference/reduction of living space;
    - A promoter from predation (e.g. Paine's starfish preventing mussels from becoming the dominant fauna) or a large bioturbator increasing living space.
- Brief Description of Importance: free text on importance and vulnerability;
- Size (cm): selection from (cm): <1, 1-5, 6-20, 21-100, >100;

  This was considered to be the average adult gross size categorisation and includes the major mass of the body. Plankton would mostly be <1, *Nephrops* 6-20, Cod 21-100, Striped Dolphin >100 cm;
- Abundance: selection from low, medium, high.

  This is for a gross abundance category related in most cases to the abundance of similar species categories around them. Plankton would mostly be high, Cod or *Nephrops* medium, Striped Dolphin low;
- Distribution: selection from scarce, patchy, widespread.

  This was for a gross distribution within the local habitat. A low abundance species was most likely scarce; many plankton species might be widespread. *Nephrops* perhaps patchy, Striped Dolphin perhaps scarce;
- Keystoneness: values that could be retrieved from the food web modelling approach Ecopath with Ecosim (EwE) using the index described from Libralato *et al.* (2006). Keystoneness is a term that has been used by EwE modellers to reflect species/group importance in relation to their biomass and impact on trophic webs.

2.1.4. Habitat

- Habitat types: selection from littoral, shallow sublittoral, shelf sublittoral, upper bathyal, lower bathyal, abyssal, reduced salinity water, variable salinity water, marine water, ice-associated habitats.
- MSFD Habitats: selection of the predominant habitat the keystone resides where it is impacting diversity from the list of MSFD defined habitats. This comprised of 24 defined habitats:
    - Benthic habitats: littoral (LT: approx 0–1 m – intertidal zone), shallow sublittoral (Sh Sub: approx 1–60 m), shelf sublittoral (Shelf Sub: approx 60–200 m), upper bathyal (UB: approx 200–1100 m), lower bathyal (LB: approx 1100–2700 m), abyssal (Abyss: approx >2700 m). With subdivisions of rock, biogenic, and sediment types. Depths were noted approximate and extracted from Cochrane *et al.* (2010), DIKE (2011) and Howell (2010);
    - Water column habitats: reduced salinity (RSW), variable salinity (VSW), marine waters (MWH) (coastal, shelf, oceanic);
    - Ice habitats: ice-associated habitats (IAH).

2.1.5. Region

- MSFD Region: geographical region, selection from drop down list (five options; Baltic Sea (BLT-Baltic), North-East Atlantic Ocean (NEA), Mediterranean Sea (MED), Black Sea (BCK-Black), Non-EU regional seas (Non-EU))
- MSFD Sub-region: geographical sub-region, selection from drop down list (only applicable to North East Atlantic and Mediterranean regions)
- Other subdivision: free text, to A) clarify a non-EU area e.g. Norwegian Sea, or FAO Area 27 and B) add a subdivision in any region, e.g. Gulf of Finland etc.).

2.1.6. More than one entry

- More than one entry: selection from list (more than one, or one entry) depending on how many lines have been added per species. Additional lines are added if the keystone species is found in more than one region or habitat, or was assigned more than one keystone role/primary impact.

2.1.7. Source

- Source: the information source concerning the keystone, selection from: Reference (a cited source), Expert Knowledge (DEVOTES participants selection), Model (if the keystone species was from model derived data)
- Reference: the cited reference, if there is one for the Keystone.

2.1.8. Notes

- Notes: Free text: any additional note/comment/habitat detail or additional information for that keystone species.

2.2. The DEVOTES Keystones Catalogue meta-analysis

On receipt of the individual returned catalogues, an accession number was given to every entry and another column for additional remarks was added (in order to elucidate specific aspects of the data entries, e.g. information on type of organisms included under a specific guild; or clarify issues and/or differences between partners, e.g. differences in habitat classification). Once the catalogue had been collated and checked, a meta-analysis of the data was undertaken to highlight the different data categories and ranges over, for example, coverage by regional sea, biological groups, importance, size range, etc. Results are given in the following section.

3. Results

3.1. Participants response

Catalogue responses were received from 10 Project participants each covering their own regional area with the exception of JRC, who provided a major part of the entries covering all the regional seas, and with the Norwegian Sea as an additional Regional Sea entry. Two of the participants, namely AKVAPLAN-NIVA and MARILIM, were not originally part of the Work Task, but kindly provided data. For many of the Participants there were multiple individual providers reported under the single institution. Data on the participant contributions are given in Table 1. Please note that Species/Groups in Table 1 and in the rest of the text refers to distinct species and groups of species either as a genera, higher groupings or functional groupings of species as proposed by the experts or given by models.

Table 1. DEVOTES participant contributions to the keystones catalogue.

Partner	Name	Individual Entries	Species/Groups	Geographical Area
5	UHULL	95	25	NE Atlantic
9 and 18	IO-BAS and MHI-NASU	38	30	Black Sea
10	JRC	401	95	All Regional Seas
11	HCMR	79	30	Mediterranean
12	KU-CORPI	7	5	Baltic Sea
13	AKVAPLAN-NIVA	27	9	Norwegian Sea
15	NIOZ	112	7	NE Atlantic
19	MARILIM	25	13	Baltic Sea
20	CNRS-IMBE	61	61	W Mediterranean

3.2. The DEVOTES Keystone Catalogue

The full catalogue is briefly described in Annex 1 and is given in Annex 2. In the following sections, data and metadata from the DEVOTES Keystone Catalogue is presented. Due to the large amount of data not all aspects can be presented or easily summarised in single tables or graphs, and the reader is asked to see the catalogue for specific queries.

3.2.1. Catalogue overview

Overall, the DEVOTES Keystone Catalogue has 844 entries which includes 210 distinct species and 19 groups. Benthic invertebrates account for 50% of the reported species/groups (110 species and 5 groups), while macroalgae contribute with 17% (39 species and 1 group) and fish with 12% (24 species and 4 groups) (Figure 1).

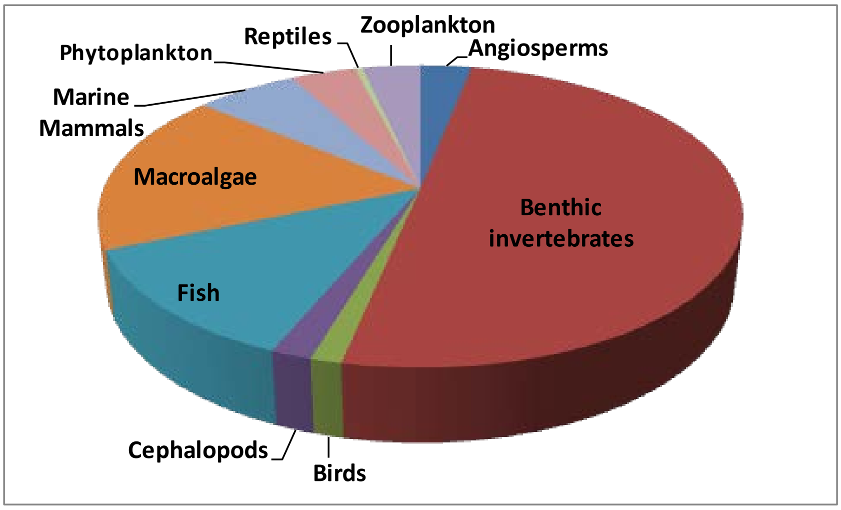

Figure 1. Major biological components contribution to the DEVOTES Catalogue of potential Keystone species.

Benthic invertebrates comprise most of the potential keystone species in all MSFD regions, except for the Non-EU regional seas where fish predominate (Figure 2).

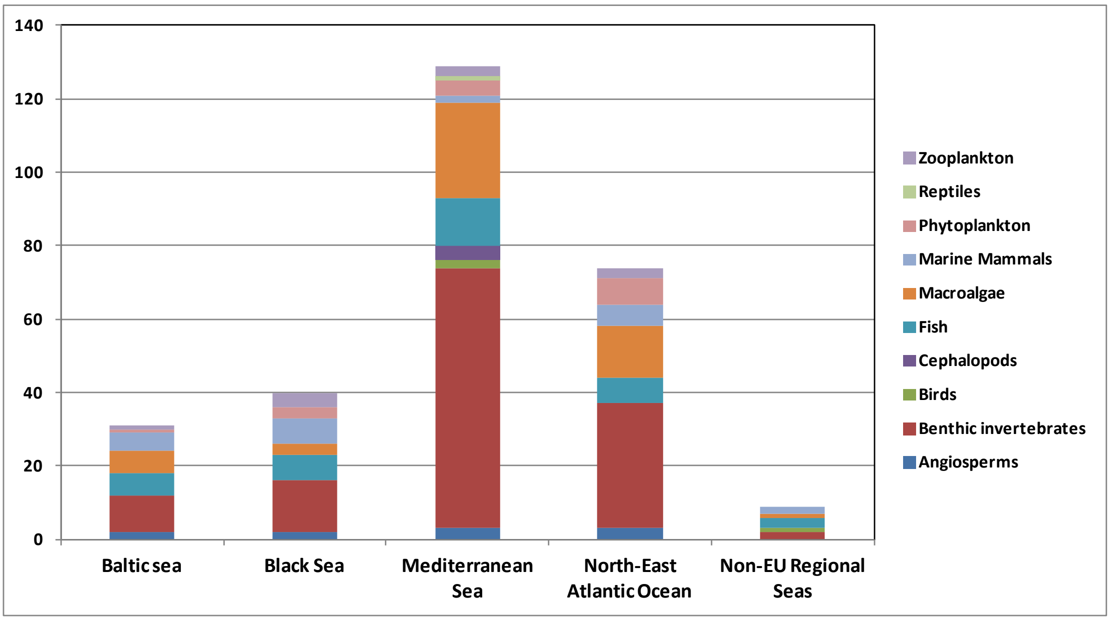

Figure 2. Number of species per major biological component and Marine Strategy Framework Directive region.

The detailed list of the proposed potential keystone species per major biological component and MSFD region is presented in Table 2 along with information on their abundance and distribution. The abundance and distribution type of the species have been considered in relation to the habitat or/and the sub-region they appear, and therefore some of the species belong to more than one abundance/distribution category. Angiosperm species are patchily distributed in all the habitats from where they were reported, and their abundances ranged from medium to high. Benthic invertebrates proposed as keystone species are either widespread or patchily distributed with mostly high abundances (76 species and 2 groups) while only a few of them are scarcely distributed (4 species) or with low abundances (7 species and 2 groups). Various cephalopod groups have been indicated as keystone species only for the Mediterranean as a result of the application of the Ecopath with Ecosim (EwE) model in different areas. Fish and marine mammal species exhibit the greatest variability with regard to their abundance and distribution type and span all the major MSFD regions. It is important to note that several species (e.g. *Thunnus albacares*, *Thunnus thynnus*, *Phocoena phocoena*) are considered to have low abundances and either scarcely or widely distributed. Macroalgae species are widely considered in the Mediterranean and they appear to have primarily high abundances and mainly patchy distribution. As for the plankton (phyto- and zooplankton), most species and groups are highly abundant, widely distributed in all seas and habitats.

Table 2. Potential keystone species per Marine Strategy Framework Directive (MSFD) region. Species are sorted in major biological components. Abbreviations are: BLT: Baltic Sea; BCK: Black Sea; MED: Mediterranean Sea; NEA: North-East Atlantic Ocean; Non-EU: Non EU Regional Seas; H: High abundance; M: Medium abundance; L: Low abundance. Font colour indicates the type of species distribution (Red: widespread; Purple: Patchy; Green: Scarce). Note: when both a species and subspecies are listed this is the result of choice by the experts/data providers and when this is shown for the same area it does not mean that there are two species/subspecies present.

MSFD Regions	BLT	BCK	MED	NEA	Non-EU
Angiosperms					
Cymodocea nodosa			M		
Halophila stipulacea			H		
Posidonia oceanica			H		
Ruppia sp.	H			H	
Zostera sp.		M			
Zostera marina	H/M			H	
Zostera noltei		H		H	
Benthic invertebrates					
Adeonella calveti			M		
Aglaophenia spp			H		
Amphibalanus improvisus	H	H		H	
Amphiura filiformis				H	
Anadara kagoshimensis			H		
Anadara transversa			H		
Anemonia viridis			H		
Aplysina cavernicola			H		
Arbacia lixula			M		
Arcuatula senhousia			H		
Arenicola marina	M			M	
Asterias rubens				L	
Austrominius (Elminius) modestus				H	
Axinella damicornis			H		
Axinella polypoides			H		
Axinella verrucosa			H		
Brachidontes pharaonis			H		
Callianassa sp.				H	
Centrostephanus longispinus			M		
Chaetaster longipes			M		
Chama pacifica			H		
Chamelea gallina		M			
Chondrosia reniformis			H		
Cidaris cidaris			M		
Clathrina clathrus			H		
Cliona celata			H		
Cliona viridis			H		
Corallium rubrum			H		
Cordylophora caspia	H				
Corynactis viridis			H		
Coscinasterias tenuispina			M		
Crambe crambe			H		
Crangon crangon				M	
Crassostrea gigas			H	H	

MSFD Regions	BLT	BCK	MED	NEA	Non-EU
Crepidula fornicata			H	H	
Dentiporella sardonica			H		
Donacilla cornea		M			
Donax trunculus		H			
Echinaster sepositus			M		
Echinus esculentus				H/M	
Echinus melo			L		
Ensis directus				H	
Epizoanthus arenaceus			M		
Eunicella cavolini			H		
Eunicella singularis			H		
Ficopomatus enigmaticus		H	H	H	
Hacelia attenuata			M		
Haploops sp.				M	
Hediste diversicolor				H	
Hydroides dianthus			H		
Hydroides elegans			H	H	
Hydroides ezoensis				H	
Lanice conchilega				H	
Lentidium mediterraneum		M			
Leptogorgia sarmentosa			H		
Leptopsammia pruvoti			M		
Limaria hians				H	
Lithophaga lithophaga			H		
Lophelia pertusa				H	L
Macoma balthica	H/M				
Madracis pharensis			L		
Marenzelleria neglecta	H			H	
Marenzelleria viridis	H			H	
Marthasterias glacialis			M		
Modiolula phaseolina		M			
Modiolus modiolus				H/H	
Monoporeia affinis	M				
Mya arenaria	H	H	H	H	
Myriapora truncata			H		
Mytilaster lineatus		H/M			
Mytilus sp.	H				
Mytilus edulis				H	
Mytilus edulis/trossulus	M				
Mytilus galloprovincialis		H/L			
Nephrops norvegicus			M		
Nucella lapillus				M	
Oculina patagonica			H		
Ophidiaster ophidianus			M		
Ophioderma longicauda			M		
Ophiothrix fragilis			M		
Oscarella lobularis			H		
Oscarella tuberculata			H		

MSFD Regions	BLT	BCK	MED	NEA	Non-EU
Ostrea edulis		L		H	
Paracentrotus lividus			H/M		
Paramuricea clavata			H		
Parazoanthus axinellae			H		
Patella vulgata				M	
Pentapora fascialis			H		
Petricolaria pholadiformis				H	
Petrosia ficiformis			H		
Pholas dactylus		L			
Phorbas tenacior			H		
Pinctada imbricata radiata			H		
Protula spp.			H		
Rapana venosa		H/M			
Sabellaria alveolata				H	
Sabellaria spinulosa				H	
Salmacina spp./*Filograna* spp.			H		
Serpula vermicularis				M	
Smittina cervicornis			H		
Sphaerechinus granularis			M		
Spirastrella cunctatrix			H		
Spondylus spinosus			H		
Spongia (Spongia) lamella			H		
Spongia officinalis			H		
Stylocidaris affinis			M		
Turbicellepora avicularis			H		
Upogebia pusilla		M			
Urothoe poseidonis				H	
Venerupis philippinarum			H	H	
Benthic invertebrates			H		
Burrowing megafauna					M
Macrofauna that feed on detritus				H	
Bivalves			L		
Gorgonians/Sponges in coralligenous habitats			L		
Birds					
Larus audouinii			H		
Phalacrocorax carbo					M
Seabirds			M/H		
Cephalopods					
Benthopelagic cephalopods			M		
Cephalopods			M		
Octopuses & cuttlefish			M		
Squids			M		
Fish					
Ammodytes tobianus				H	
Clupea harengus	M				M
Diplodus puntazzo			M		
Engraulis encrasicolus		H	H		
Epinephelus marginatus			H/ M / L		

MSFD Regions	BLT	BCK	MED	NEA	Non-EU
Gadus morhua	M			H	M
Lagocephalus sceleratus			M		
Merluccius merluccius			M		
Pomatomus saltatrix		M			
Salmo salar	M				
Salmo trutta	M				
Sander lucioperca	M				
Sarda sarda		M	M		
Sardina pilchardus			H		
Sardinella aurita			H		
Scomber scombrus		M			M
Scophthalmus maximus		H			
Siganus luridus			M/ M		
Siganus rivulatus			M/ M		
Sprattus sprattus	M	H			
Squalus acanthias		L			
Thunnus albacares				L	
Thunnus thynnus			L	L	
Ammodytidae				H	
Demersal (predatory) fish species				M	
Large Pelagic Fish			L/ M		
Predatory fish				L	
Sharks			M		
Macroalgae					
Acrothamnion preissii			H		
Alaria esculenta				H	
Asparagopsis armata			H	H	
Bonnemaisonia hamifera			H	H	
Caulerpa cylindracea			H		
Caulerpa taxifolia			H		
Cladophora spp.	H/M				
Codium bursa			M		
Codium coralloides			M		
Codium fragile subsp. *fragile*			H	H	
Cystoseira amentacea			H		
Cystoseira barbata		H			
Cystoseira crinita		H			
Cystoseira tamariscifolia			H		
Flabellia petiolata			H		
Fucus spp.	H				
Fucus vesiculosus	H/M				
Furcellaria lumbricalis	H/M				
Gracilaria vermiculophylla	H		H	H	
Grateloupia turuturu			H	H	
Halimeda tuna			H		
Laminaria digitata				H	
Laminaria hyperborea				H/ H	M
Laminaria ochroleuca				H	

MSFD Regions	BLT	BCK	MED	NEA	Non-EU
Lithophyllum cabiochiae			H		
Lithophyllum stictaeforme			H		
Lophocladia lallemandii			H		
Mesophyllum alternans			H		
Mesophyllum expansum			H		
Peyssonnelia spp.			H		
Phyllophora crispa		H/M/L			
Polysiphonia fucoides	M				
Polysiphonia morrowii			M		
Saccharina latissima				H	
Saccorhiza polyschides				H	
Sargassum muticum			H	H	
Stypopodium schimperi			H		
Undaria pinnatifida			M	H/M	
Womersleyella setacea			H		
Maerl beds (*Phymatolithon calcareum* + *Lithothamnion* spp.)			H	H	
Marine Mammals					
Balaenoptera acutorostrata				L	
Delphinus delphis		L			
Delphinus delphis ponticus		H			
Halichoerus grypus	L/ M			M	M
Lagenorhynchus albirostris	L			L	
Monachus monachus		M			
Pagophilus groenlandicus					M
Phoca vitulina	H/M			H/M	
Phocoena phocoena	L	L		L	
Phocoena phocoena relicta		H			
Pusa hispida	L/ M			M	
Tursiops truncatus		L	L		
Tursiops truncatus ponticus		H			
Dolphins			L		
Phytoplankton					
Alexandrium minutum			H	H	
Alexandrium monilatum		H			
Coscinodiscus wailesii				H	
Fibrocapsa japonica				H	
Gymnodinium catenatum			H	H	
Karenia mikimotoi			H	H	
Noctiluca scintillans		H			
Phaeocystis pouchetii		H	H	H	
Pseudochattonella verruculosa	H			H	
Reptiles					
Caretta caretta			L		
Zooplankton					
Aurelia aurita	H	H/M		H	
Beroe ovata		H/M			
Calanus finmarchicus				H	
Mnemiopsis leidyi		H/M		H	

MSFD Regions	BLT	BCK	MED	NEA	Non-EU
Rhizostoma pulmo		H			
Mesozooplankton			H		
Microzooplankton			H		
Zooplankton			H		

In Table 3, details about the species keystone type, primary impact and type of source of information are provided. A total of 79 species were considered to act as engineers, 66 as habitat forming species, 74 as predators, while a few (9 species) were thought of having multiple roles in their marine ecosystems (e.g. *Posidonia oceanica*, *Modiolus modiolus*, *Salmo salar*) (Figure 3). Most of the proposed species (126 species and 7 groups) are believed to have a promoting role in marine communities, 61 species and 8 groups act as reducers, 16 species could have both roles depending on region, habitat, or even abundance and distribution, while for 11 species the experts were unable to define their primary impact (Figure 4).

Most of the proposed species (52%) were suggested by the DEVOTES partners after consulting the literature (scientific papers, reports, books, thesis, guides and websites) and only a small number (10%) was identified as keystones, mainly major groups (e.g. zooplankton, demersal fish, macrofauna, etc.) after applying the EwE model (Christensen *et al.*, 2004, Libralato *et al.*, 2006) (Figure 5). This could be marginally higher, as few expert/literature based choices mention models.

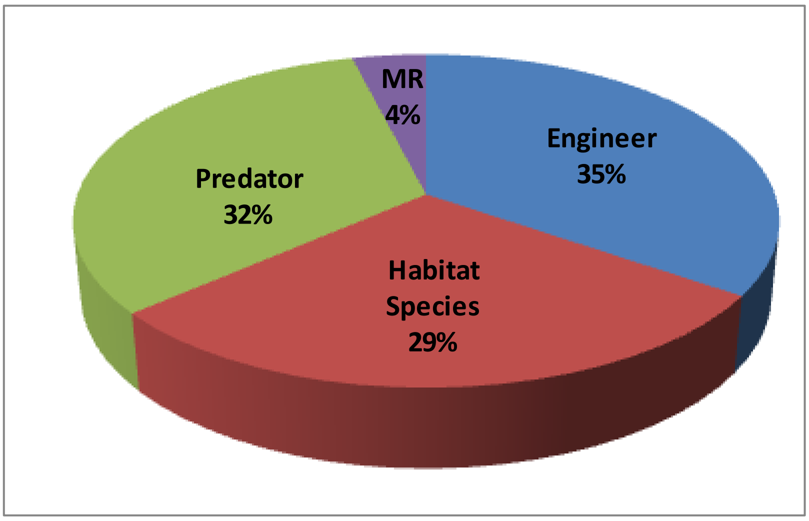

Figure 3. Percentage of Predators, Engineers and Habitat species appearing in the DEVOTES catalogue. MR: Multiple Role.

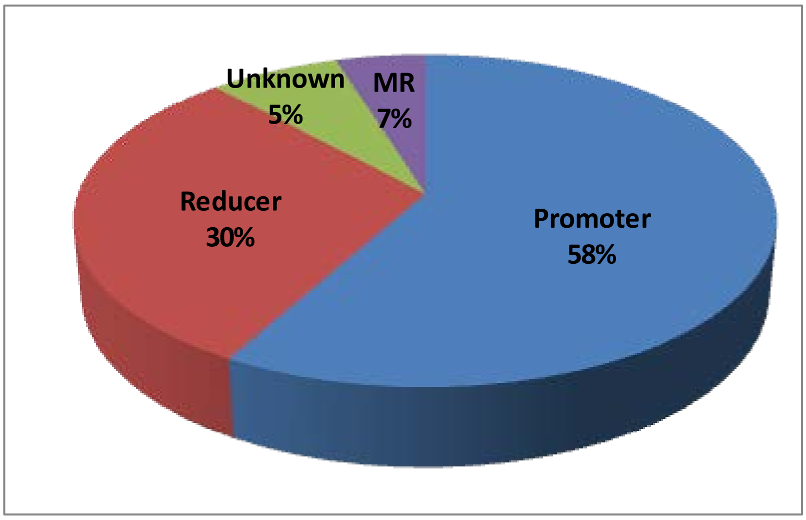

Figure 4. Percentage of Promoters and Reducers appearing in the DEVOTES catalogue. MR: Multiple Role; Unknown: Experts were unable to define the primary impact.

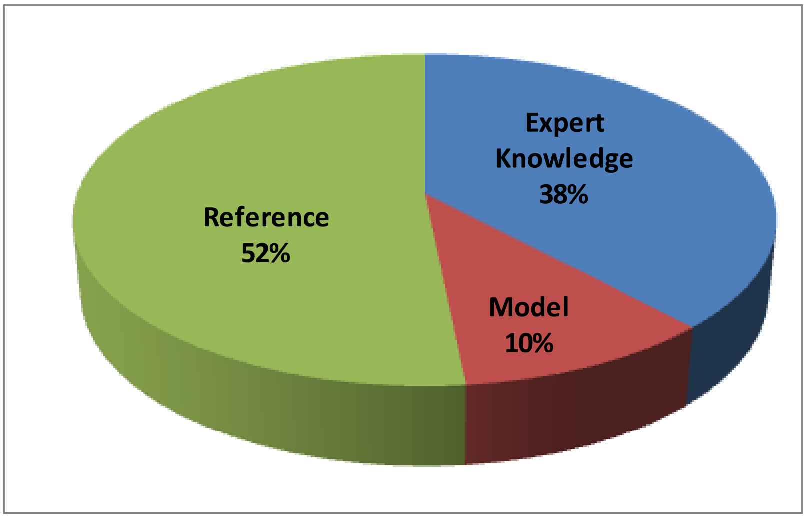

Figure 5. Percentage of potential keystone species per type of source information reviewed by the providers.

Table 3. Keystone type, Primary impact and Source of information for the proposed keystone species. Species are sorted in major biological components. Abbreviations are: Ha: Habitat species; Eng: Engineer; Pre: Predator; P: Promoter; R: Reducer; Ref: Reference; Exp; Expert Knowledge. Asterisk (*) denotes inability of the expert provider to decide on the Keystone Type/Primary Impact. Note: when both a species and subspecies are listed this is the result of choice by the experts/data providers and when this is shown for the same area it does not mean that there are two species/subspecies present.

	Keystone Type	Primary Impact	Source
Angiosperms			
Cymodocea nodosa	Ha	P	Ref
Halophila stipulacea	Eng	P	Ref
Posidonia oceanica	Ha/Eng	P	Exp/Ref
Ruppia sp.	Ha	P	Ref
Zostera sp.	Ha	P	Ref
Zostera marina	Ha/Eng	P	Exp/Ref
Zostera noltei	Ha/Eng	P	Exp/Ref
Benthic invertebrates			
Adeonella calveti	Eng	P	Exp
Aglaophenia spp	Ha	P	Exp
Amphibalanus improvisus	Eng	P	Ref
Amphiura filiformis	Eng	P	Exp
Anadara kagoshimensis	Eng	R	Ref
Anadara transversa	Eng	P	Ref
Anemonia viridis	Eng	R	Exp
Aplysina cavernicola	Ha	P	Exp
Arbacia lixula	Pre	*	Exp
Arcuatula senhousia	Eng	P	Ref
Arenicola marina	Eng	P/R	Exp/ Ref
Asterias rubens	Pre	R	Ref
Austrominius (Elminius) modestus	Eng	R	Ref
Axinella damicornis	Ha	P	Exp
Axinella polypoides	Ha	P	Exp
Axinella verrucosa	Ha	P	Exp
Brachidontes pharaonis	Eng	R	Ref
Callianassa sp.	Eng	P	Exp
Centrostephanus longispinus	Pre	*	Exp
Chaetaster longipes	Pre	R	Exp
Chama pacifica	Eng	P	Ref
Chamelea gallina	Ha	P	Ref
Chondrosia reniformis	Ha	P	Exp
Cidaris cidaris	Pre	*	Exp
Clathrina clathrus	Ha	P	Exp
Cliona celata	Eng	P	Exp
Cliona viridis	Eng	P	Exp
Corallium rubrum	Ha	P	Exp
Cordylophora caspia	Eng	R	Ref
Corynactis viridis	Eng	P	Exp
Coscinasterias tenuispina	Pre	*	Exp
Crambe crambe	Ha	P	Exp
Crangon crangon	Pre	P	Ref
Crassostrea gigas	Eng	P	Ref

	Keystone Type	Primary Impact	Source
Crepidula fornicata	Eng	R	Ref
Dentiporella sardonica	Eng	P	Exp
Donacilla cornea	Eng	P	Ref
Donax trunculus	Ha	P	Ref
Echinaster sepositus	Pre	R	Exp
Echinus esculentus	Pre	P/R	Ref
Echinus melo	Pre	*	Exp
Ensis directus	Eng	P	Ref
Epizoanthus arenaceus	Eng	P	Exp
Eunicella cavolini	Ha	P	Exp
Eunicella singularis	Ha	P	Exp
Ficopomatus enigmaticus	Eng	P	Ref
Hacelia attenuata	Pre	R	Exp
Haploops sp.	Eng	P	Ref
Hediste diversicolor	Eng	R	Exp
Hydroides dianthus	Eng	P	Ref
Hydroides elegans	Eng	P	Ref
Hydroides ezoensis	Eng	P	Ref
Lanice conchilega	Eng	P	Exp
Lentidium mediterraneum	Ha	P	Ref
Leptogorgia sarmentosa	Ha	P	Exp
Leptopsammia pruvoti	Ha	P	Exp
Limaria hians	Eng	P	Ref
Lithophaga lithophaga	Eng	P	Exp
Lophelia pertusa	Ha	P	Exp/Ref
Macoma balthica	Eng	P	Exp/Ref
Madracis pharensis	Ha	P	Exp
Marenzelleria neglecta	Eng	R	Ref
Marenzelleria viridis	Eng	R	Ref
Marthasterias glacialis	Pre	R	Exp
Modiolula phaseolina	Ha	P	Ref
Modiolus modiolus	Eng/Ha	P	Exp/Ref
Monoporeia affinis	Eng	P	Ref
Mya arenaria	Eng	R	Ref
Myriapora truncata	Eng	P	Exp
Mytilaster lineatus	Ha	P	Ref
Mytilus sp.	Eng/Ha	P/R	Ref
Mytilus edulis	Eng	P	Ref
Mytilus edulis/trossulus	Ha	P	Exp/Ref
Mytilus galloprovincialis	Ha	P	Ref
Nephrops norvegicus	Eng	P	Exp
Nucella lapillus	Pre	P	Exp
Oculina patagonica	Eng	R	Ref
Ophidiaster ophidianus	Pre	R	Exp
Ophioderma longicauda	Pre	*	Exp
Ophiothrix fragilis	Pre	*	Exp
Oscarella lobularis	Ha	P	Exp
Oscarella tuberculata	Ha	P	Exp

	Keystone Type	Primary Impact	Source
Ostrea edulis	Ha	P	Ref
Paracentrotus lividus	Pre	R	Exp
Paramuricea clavata	Ha	P	Exp
Parazoanthus axinellae	Eng	P	Exp
Patella vulgata	Pre	P/R	Ref
Pentapora fascialis	Eng	P	Exp
Petricolaria pholadiformis	Eng	P	Ref
Petrosia ficiformis	Ha	P	Exp
Pholas dactylus	Ha	P	Ref
Phorbas tenacior	Ha	P	Exp
Pinctada imbricata radiata	Eng	P	Ref
Protula spp.	Eng	P	Exp
Rapana venosa	Pre	R	Ref
Sabellaria alveolata	Ha	P	Exp
Sabellaria spinulosa	Ha	P	Ref
Salmacina spp./ *Filograna* spp.	Eng	P	Exp
Serpula vermicularis	Ha	P	Ref
Smittina cervicornis	Eng	P	Exp
Sphaerechinus granularis	Pre	R	Exp
Spirastrella cunctatrix	Ha	P	Exp
Spondylus spinosus	Eng	P	Ref
Spongia (Spongia) lamella	Ha	P	Exp
Spongia officinalis	Ha	P	Exp
Stylocidaris affinis	Pre	*	Exp
Turbicellepora avicularis	Eng	P	Exp
Upogebia pusilla	Eng/Ha	P	Ref
Urothoe poseidonis	Eng	P	Exp
Venerupis philippinarum	Eng	P	Ref
Benthic invertebrates	Ha	P	Model
Burrowing megafauna	Eng	P	Ref
Macrofauna that feed on detritus	*	P	Model
Bivalves	Eng	P	Model
Gorgonians/Sponges in coralligenous habitats	Ha	P	Exp
Birds			
Larus audouinii	Pre	R	Model
Phalacrocorax carbo	Pre	R	Model
Seabirds	Pre	R	Model
Cephalopods			
Benthopelagic cephalopods	Pre	R	Model
Cephalopods	Pre	R	Model
Octopuses & cuttlefish	Pre	R	Model
Squids	Pre	R	Model
Fish			
Ammodytes tobianus	Eng	P	Exp
Clupea harengus	Pre	R	Exp/Ref
Diplodus puntazzo	Pre	R	Model
Engraulis encrasicolus	Pre	P	Exp/Model/Ref
Epinephelus marginatus	Pre	P/R	Model/Ref

	Keystone Type	Primary Impact	Source
Gadus morhua	Pre	P/R	Exp/Model/Ref
Lagocephalus sceleratus	Pre	R	Exp
Merluccius merluccius	Pre	P	Model
Pomatomus saltatrix	Pre	P	Ref
Salmo salar	Eng/Pre	P/R	Ref
Salmo trutta	Pre	R	Ref
Sander lucioperca	Pre	R	Ref
Sarda sarda	Pre	P/R	Model/Ref
Sardina pilchardus	Pre	P	Exp
Sardinella aurita	Pre	P	Exp
Scomber scombrus	Pre	P/R	Exp/Ref
Scophthalmus maximus	Pre	P	Ref
Siganus luridus	Pre	R	Ref
Siganus rivulatus	Pre	R	Ref
Sprattus sprattus	Pre	P/R	Ref
Squalus acanthias	Pre	R	Ref
Thunnus albacares	Pre	R	Ref
Thunnus thynnus	Pre	R	Exp/Ref
Ammodytidae	Pre	P	Ref
Demersal (predatory) fish species	Pre	*	Model
Large Pelagic Fish	Pre	R	Exp/Model
Predatory fish	Pre	*	Model
Sharks	Pre	R	Model
Macroalgae			
Acrothamnion preissii	Eng	R	Ref
Alaria esculenta	Ha	P	Ref
Asparagopsis armata	Eng	R	Ref
Bonnemaisonia hamifera	Eng	R	Ref
Caulerpa cylindracea	Eng	R	Ref
Caulerpa taxifolia	Eng	R	Ref
Cladophora spp.	Ha	P	Exp
Codium bursa	Ha	P	Exp
Codium coralloides	Ha	P	Exp
Codium fragile subsp. *fragile*	Eng	R	Ref
Cystoseira amentacea	Ha	P	Exp
Cystoseira barbata	Ha	P	Ref
Cystoseira crinita	Ha	P	Ref
Cystoseira tamariscifolia	Ha	P	Exp
Flabellia petiolata	Ha	P	Exp
Fucus spp.	Ha	P	Ref
Fucus vesiculosus	Ha	P	Ref
Furcellaria lumbricalis	Ha	P	Exp/Ref
Gracilaria vermiculophylla	Eng	R	Ref
Grateloupia turuturu	Eng	R	Ref
Halimeda tuna	Ha	P	Exp
Laminaria digitata	Ha	P	Ref
Laminaria hyperborea	Ha	P	Ref
Laminaria ochroleuca	Ha	P	Ref

	Keystone Type	Primary Impact	Source
Lithophyllum cabiochiae	Ha	P	Exp
Lithophyllum stictaeforme	Ha	P	Exp
Lophocladia lallemandii	Eng	R	Ref
Mesophyllum alternans	Ha	P	Exp
Mesophyllum expansum	Ha	P	Exp
Peyssonnelia spp.	Ha	P	Exp
Phyllophora crispa	Ha	P	Ref
Polysiphonia fucoides	Ha	P	Exp
Polysiphonia morrowii	Eng	P	Ref
Saccharina latissima	Ha	P	Ref
Saccorhiza polyschides	Ha	P	Ref
Sargassum muticum	Eng	R	Ref
Stypopodium schimperi	Eng	R	Ref
Undaria pinnatifida	Eng/Ha	P	Ref
Womersleyella setacea	Eng	R	Ref
Maerl beds (*Phymatolithon calcareum* + *Lithothamnion* spp.)	Ha	P	Exp/Ref
Marine Mammals			
Balaenoptera acutorostrata	Pre	R	Ref
Delphinus delphis	Pre	R	Ref
Delphinus delphis ponticus	Pre	P	Ref
Halichoerus grypus	Pre	P/R	Exp/Ref
Lagenorhynchus albirostris	Pre	R	Ref
Monachus monachus	Pre	P	Ref
Pagophilus groenlandicus	Pre	P	Model
Phoca vitulina	Pre	P/R	Exp/Ref
Phocoena phocoena	Pre	R	Ref
Phocoena phocoena relicta	Pre	P	Ref
Pusa hispida	Pre	P/R	Ref
Tursiops truncatus	Pre	R	Model/Ref
Tursiops truncatus ponticus	Pre	P	Ref
Dolphins	Pre	P/R	Model
Phytoplankton			
Alexandrium minutum	Eng	R	Ref
Alexandrium monilatum	Eng	R	Ref
Coscinodiscus wailesii	Eng	R	Ref
Fibrocapsa japonica	Eng	R	Ref
Gymnodinium catenatum	Eng	R	Ref
Karenia mikimotoi	Eng	R	Ref
Noctiluca scintillans	Pre	R	Ref
Phaeocystis pouchetii	Eng	R	Ref
Pseudochattonella verruculosa	Eng	R	Ref
Reptiles			
Caretta caretta	Ha/Pre	P/R	Ref
Zooplankton			
Aurelia aurita	Pre	R	Ref
Beroe ovata	Pre	P	Ref
Calanus finmarchicus	Pre	*	Ref
Mnemiopsis leidyi	Pre	R	Ref

	Keystone Type	Primary Impact	Source
Rhizostoma pulmo	Pre	R	Ref
Mesozooplankton	Eng	P/R	Model
Microzooplankton	Eng	P	Model
Zooplankton	Eng	R	Model

Angiosperm is the single category indicated by all expert providers to promote biodiversity in marine ecosystems. Their role is mainly identified as habitat species, providing food, shelter, spawning and nursery areas to many organisms, while at the same time their structures increase habitat complexity and sediment stability, and therefore biodiversity. Angiosperms are also considered to be valuable engineering organisms as they oxygenate waters and sediments, are part of biochemical marine cycles, act as net carbon sinks, control the transparency of the water column by favouring retention of suspended particles, and protect shorelines by their networks of rhizomes that stabilize sediments.

The benthic invertebrates proposed as potential keystone species are mostly believed to promote marine biodiversity, acting either as engineer or habitat species, while some of them were indicated to have a predator role in the food web, in which case they were viewed as reducers (e.g. *Asterias rubens*, *Chaetaster longipes*, *Rapana venosa*). Nevertheless, there are certain species that are thought to exhibit either a promoting or reducing impact on the community depending on conditions, for example:

- The impact of *Arenicola marina* appears to relate to population density and area of consideration, as in the Baltic Sea where it is patchily distributed, it is considered a Promoter, while in the NE Atlantic, where it is widespread, it was assigned as a Reducer.
- The role of the edible sea urchin *Echinus esculentus* (or other urchins in the catalogue) appears to be density-dependent. When moderately abundant, its effect is believed to promote diversity, whereas when highly abundant the effect is important (defloration, urchin barrens) but whether the effect is disproportionate compared to the urchin abundance is unknown. Therefore uncertainty is associated to this species keystone role.
- *Mytilus* is a habitat-modifying genus that can influence biodiversity by facilitation and inhibition of species (Norling and Kautsky, 2008). Regional assessment by the expert providers of a few *Mytilus* species (*M. edulis*, *M. trossulus*, *M. galloprovincialis*) as keystone species leads to the conclusion that their role can be viewed both as habitat and engineer species. For example, *M. edulis* beds have a role in coastal sediment dynamics and provide an enhanced area of biodiversity in an otherwise sediment-dominated environment. The spaces between the mussels provide refuges for a diverse community of species increasing habitat complexity (role

as habitat species), while at the same time they can play a role in water purification, tackling pollution and in the cycle of trace- and other important elements (e.g. oxygen, nitrogen, hydrogen, carbon) (role as engineering species). The role of mussel beds can also be extended as they are also considered crucial food reserves to birds (role as resource species). *Mytilus* species are overall thought to promote biodiversity; however, they can also act as reducers when they compete for space with perennial macroalgae.

- *Patella vulgata*, the common limpet, grazes on fucoid algae, hence controlling their biomass and the system productivity and functioning (including nutrient sequestration and export of detrital material). This species is an example of a keystone species with a region-dependent effect on biodiversity. Their ability in controlling vegetation, hence, their impact, depends on algal recruitment, leading to latitudinal differences. While the species promotes small scale spatial variability in the algal coverage and improves algal biodiversity in northern areas (southern coast of UK, Isle of Man, Channel), thus acting as a promoter in these areas, in southern areas (coast of Portugal), the species prevents the establishment of heterogeneous assemblages, therefore its effect has been considered as a reducer (Coleman *et al.*, 2006).

All birds and cephalopods species/groups in the catalogue are predators indicated as keystone species through models, and are thought to act as reducers to the marine communities.

With the exception of *Ammodytes tobianus*, which was indicated as an engineering keystone species, all other fish species/groups were classified as predators. While most of the fish species were assigned to either one of the primary impact categories (promoter, reducer), there were a few species, which could have both effects on biodiversity, depending on how they were perceived to act. For example, *Salmo salar* is indicated as a potential keystone species in the Baltic Sea, which can however be considered to have a twofold effect on the ecosystem: as a predator but also as an engineer. In the first case, it reduces biomass by removing prey species from the food web, while when acting as a bioturbator (it scours the river bed while spawning) it cleans river beds from excess organic particles, therefore reducing over-sedimentation. However, it has to be pointed out that in most cases, when a dual primary impact was assigned to a species (e.g. *Sarda sarda*, *Gadus morhua*, *Scomber scombrus*), it was due to differences between the expert provider perspectives on what is the effect of the fish that act as food wed regulator in the marine ecosystem. This also holds for large predators such as marine mammals (dolphins, seals, porpoises) and reptiles (*Caretta caretta*).

All phytoplankton species included in the catalogue are believed to have a reducing effect on the ecosystem as engineers, except for *Noctiluca scintillans*, which is thought to have an effect on food webs as a consumer of lower food levels. It is of course accepted that phytoplankton as a group, will play a positive key role in ecosystems.

When considering zooplankton as a whole and major size classes (micro-, meso- zooplankton) it is considered to have an engineering role in marine ecosystems; yet individual species reported in this DEVOTES catalogue are considered predators mainly acting on phyto- and zooplankton stocks. Overall, zooplankton is considered to enhance biodiversity, although specific species, i.e. *Aurelia aurita*, *Mnemiopsis leidyi* and *Rhizostoma pulmo* act as reducers, primarily through strong grazing and depletion of zooplankton stocks leading to cascading effects in the food web.

3.2.2. Keystone Size

Table 4 shows the distribution of keystone component groups by relative size. Five of the biodiversity components (birds, cephalopods, marine mammals, phytoplankton and reptiles) appear under one size category only, two under three size categories (fish and zooplankton), two under four size categories (angiosperms, and macroalgae) and benthic invertebrates cover all size classes.

Table 4. Number of keystones by size category and biodiversity component (* number includes two subspecies).

Bio Component	<1 cm	1-5 cm	6-20 cm	21-100 cm	>100 cm
Angiosperms		1	2	4	1
Benthic Invertebrates	4	39	47	25	2
Birds				3	
Cephalopods				4	
Fish			7	17	5
Macroalgae		2	18	14	11
Marine Mammals					14*
Phytoplankton	9				
Reptiles				1	
Zooplankton	4		3	1	
Total Species	**17**	**42**	**77**	**68**	**34**

Size category <1 cm

Keystones in the size category <1 cm for biological component phytoplankton are represented by nine species. All nine species are stated to be of wide distribution and high abundance in the marine coastal water habitat. All nine species are reducers and eight out of nine are engineers (Keystone type, KT) and invasive alien species creating harmful algal blooms; the final one (*Noctiluca scintillans*), a predator, is a heterotrophic dinoflagellate noted as a dead-end of the food web. All regional seas are represented with 1, 3, 4 and 7 phytoplankton species for the Baltic, Black, Mediterranean Seas and NEA, respectively. Examples include *Alexandrium minutum* for the Mediterranean and NEA, *N. scintillans* for the Black, *Pseudochattonella verruculosa* for the Baltic and *Phaeocystis pouchetii* for Mediterranean-NEA. Keystones in the size category <1 cm for biological component zooplankton are represented by one calanoid copepod species (*Calanus finmarchicus*) and 3 groups micro-zooplankton, meso-zooplankton and zooplankton. All species/groups are stated to be of wide distribution and high abundance in the marine water coastal, shelf and oceanic habitats. *C. finmarchicus* is stated as a predator with a pivotal role in supporting food webs in the NEA but the expert was unable to decide on primary impact and to choose between key or keystone species. The zooplankton groups are all model chosen in the Mediterranean, their primary impact is as Engineers and their KT is stated as reducers and promoters (different experts, different opinion). Keystones in the size category <1 cm for biological component benthic invertebrates are represented by four species. All four of them are crustaceans (one shrimp, one barnacle and two amphipods) and their primary impact is as engineers. The barnacle is a reducer, while the amphipods and shrimp are promoters as food web regulator, and bioturbator, respectively. Baltic and NEA regional seas are represented with one (*Monoporeia affinis*, one of the two amphipods) and three species respectively.

Size category 1-5 cm

Three biological components provide 42 species/groups under this size category, namely angiosperms, macroalgae and benthic invertebrates. While benthic invertebrates of this size span all benthic habitat types except for the deep sea, and have a considerable number of species/groups (36 species and 3 groups), the other two biological components are represented by only a few species in the shallow sublittoral. Most species have high or medium abundances and their distributions are mainly patchy, some of them are widespread (e.g. *Corynactis viridis*, *Crangon crangon*, *Nucella lapillus*), while only the anthozoan *Madracis pharensis* is scarce. The only species of angiosperm in this size is *Halophila stipulacea*, reported as an invasive alien, engineer species in the Mediterranean Sea with a promoting impact on biodiversity. This is not only because of the previously described promoting role angiosperms have on ecosystems, but also because when growing on previously barren areas as a pioneer species, it provides new topography and shelter for the mobile fauna. The two species of macroalgae in this size category are *Acrothamnion preissii* and *Womersleyella setacea*, both described as invasive alien, engineer species in the Mediterranean Sea with a reducing effect on biodiversity. The first one impacts the Mediterranean ecosystems by reducing the diversity of seagrass and algal beds, by growing over calcareous red algae in maerl beds, by negatively affecting the available substrata for other epiphytic macro-organisms to settle on, and by reducing light for other species. *Womersleyella setacea* colonizes wide zones throughout the Mediterranean Sea, forming thick persistent carpets that completely cover deep sublittoral rocky substrata. It negatively affects the available substrata for other epiphytic macro-organisms to settle on and by reducing the light for other autotrophs, with substantial negative effects on native communities. It also modifies benthic assemblages, reduces diversity, affects food webs, and outcompetes key species.

The 39 benthic invertebrates of this size span all EU seas. In the Baltic they are in low number; the three species in this region are two bivalves, the *Mytilus* hybrid population *Mytilus edulis*/*trossulus* and *Macoma balthica*, and the barnacle *Amphibalanus improvisus*. The *Mytilus* population is considered promoter, habitat species that as a bioconstructor provides additional living space for macroalgae and invertebrates and also serves as a feeding ground for invertebrates, fish and birds. However, in some areas of the Baltic Sea *Mytilus* can act as a 'reducer' as it is a competitor for living space with perennial macroalgae and is, to a certain point, more favoured by nutrient and organic enrichment compared to perennial macroalgae. On the other hand, *Macoma balthica* is considered an engineer species promoting biodiversity by improvement of benthic-pelagic coupling of organic material and nutrients, oxygen fluxes in the sediment and benthic microflora and microfauna, while at the same time it is valuable food source for fish and birds. A similar role is described for *A. improvisus* (engineer and promoter species), which increases the 3-dimensional surface available for associated macro- and meiofauna in shallow-water hard bottoms and can enhance detritus-based food chains by supplying their habitat with particulate detritus. *A. improvisus* can promote the settlement success and further development of filamentous algae probably by increasing nutrient availability in benthic systems through biodeposition. On the other hand, it is a strong competitor for space.

In the Black Sea the 11 benthic invertebrate species reported are all thought to be promoters. With the exception of one polychaete and two crustacean species, the rest are bivalves all of which are considered habitat species except for *Donacilla cornea*; the latter along with the remaining three non-bivalve invertebrates act as engineers.

Among the 16 benthic invertebrates reported from the Mediterranean, only two are reducers, i.e. the bivalve *Brachidontes pharaonis* and the limpet *Crepidula fornicata*, both of which are invasive alien species in the Mediterranean acting as engineers. The establishment of massive beds of *B. pharaonis* has had significant effects on the biota of intertidal rocky areas, especially on the ecology of the vermetid platforms, a habitat that is unique to the Levantine basin, by excluding some species and facilitating others. It locally displaces the native mytilid, *Mytilaster minimus*. *C. fornicata* is a habitat engineer which causes substantial large scale changes in ecosystems such as trophic structure modification, changes in phytoplankton composition, enhanced siltation due to accumulation of faeces and pseudofaeces, and changes in benthic sediments and near-bottom currents. Such accumulating sediments on maerl beds cause their degradation. Dense populations spread and completely cover the ground, so that the sediment disappears under their stacks and water exchange is limited. The rest of the benthic invertebrates in this size category are mostly engineers (12/16) belonging to bivalves (e.g. *Anadara transversa*), polychaetes (e.g. *Ficopomatus enigmaticus*), and anthozoa (e.g. *Corynactis viridis*) promoting ecosystem's biodiversity through habitat modification, bioturbation and bioconstruction.

A total of 16 benthic invertebrate species including polychaetes, bivalves, gastropods and crustaceans were also reported in the NE Atlantic Ocean, with most of them (10) considered as engineering species. Among the 10 engineers only one, *C. fornicata* has a reducing effect, similar to the one described above for the Mediterranean. The polychaetes *Sabellaria alveolata* and *S. spinulosa* are habitat species. These worms form reefs (*Sabellaria* reef/crust) that provide structure for other organisms as crevices and shelter, thus supporting rich and diverse assemblages compared to similar habitats where the species are not present. Sites with *Sabellaria* reefs have been found to have more than twice as many species and almost three times as many individuals as sites with very few, or no *Sabellaria*; therefore, their primary impact is as promoters. Two gastropods (*Nucella lapillus* and *Patella vulgata*) and the decapod *Crangon crangon* are predators promoting biodiversity, except for the case of *P. vulgata* in southern latitudes, which, as described in an earlier section, has a reducing effect.

Size category 6-20 cm

Potential keystones in the size category 6-20 cm for Angiosperms include two species of littoral or shallow sublittoral habitats; the ditch grasses *Ruppia* sp. in the Baltic and the dwarf eelgrass *Zostera noltei* in the NEA and the Black Sea. Their primary impact is as promoters and their keystone role is as habitat or habitat and engineer species. Keystones for Benthic Invertebrates include a large variety of taxa (47) and taxa types; Polychaeta, Bivalvia, Crustacea, Anthozoa, Porifera, Echinodermata, Bryozoa, Hydrozoa, Gastropoda. All EU regional seas are represented in littoral, shallow and shelf sublittoral as well as upper bathyal habitats. As expected, with such variety of species they display different roles and impacts. Keystones for Fish include seven species of pelagic or benthopelagic fish. All EU and non-EU regional seas are represented in a large variety of water and sediment habitats including reduced salinity water (*Clupea harengus*). They display different roles (as predators and engineers) and impacts (promoters or reducers). Keystones for Macroalgae include 18 species/taxa in littoral and shallow or shelf sublittoral habitats of all four EU regional seas. They display different roles; nine species are engineers and invasive alien reducers (e.g. *Caulerpa cylindracea* and *Codium fragile* in the Mediterranean and NEA respectively) and nine are habitat species acting as promoters such as *Cladophora* sp. and *Phyllophora crispa* in the Baltic and Black sea respectively. Keystones for Zooplankton include three jellyfish species in marine waters of the Baltic, the Black Sea and the NEA. *Mnemiopsis leidyi* (NEA, Black Sea) is an invasive alien reducer and *Beroe ovata* (Black Sea) is an invasive alien promoter. *M. leidyi* is an invasive species also for the Baltic Sea. After the first detection in 2006 (Javidpour *et al.,* 2006) its abundance, distribution and spreading into the central Baltic Sea were studied (Jaspers *et al.,* 2011a,b; Schaber *et al.*, 2011). Similar negative effects on the Baltic Sea ecosystem as documented for the Black Sea, could not be verified and therefore this species is currently not regarded as a keystone species for the Baltic Sea. *Aurelia aurita* reported in all three areas is a reducer, but there is low confidence in its keystone role in the NEA.

Size category 21-100 cm

Potential keystones in the size category 21-100 cm for angiosperms include four species of littoral or shallow sublittoral habitats of all four EU regional seas; Neptune grass *Posidonia oceanica*, eelgrass *Zostera marina* and little Neptune grass *Cymodocea nodosa*. Their primary impact is as promoters and their KT is habitat and engineer species. Keystones for Benthic Invertebrates include a large variety of taxa (25) of a few taxa types; Bivalvia, Echinodermata, Bryozoa, but mostly corals and sponges in littoral, shallow and shelf sublittoral habitats, all of them present in the Mediterranean and one species *Crassostrea gigas*, is also found in the NEA. As expected with such variety of species they display different roles and impacts. Examples include *Eunicella cavolini* and *Chondrosia reniformis* as habitat species and promoters, and *Crassostrea gigas* as engineer and promoter. The only reducer of the group is the invasive alien coral *Oculina patagonica*. Seabirds appear in the keystone list of this size category with two species and as a group (model output for the Mediterranean). There are all predators and reducers. The cormorant *Phalacrocorax carbo* is representing the Norwegian Sea and the Audouin's gull *Larus audouinii* the Mediterranean. Cephalopods also appear in the keystone list of this size category with various groups (e.g. octopuses & cuttlefish) as model outputs for the Mediterranean. There are all predators and reducers. Keystones for fish include 17 species/taxa of demersal, pelagic or benthopelagic fish. All EU and non-EU regional seas are represented in a large variety of water and sediment habitats including reduced salinity water (*Sander lucioperca*). They are all predators (one is thought to be engineer too) and marginally more promoters than reducers with a few (4) cases stated as both by different or same expert. Keystones for macroalgae include 14 species/taxa in littoral and shallow or shelf sublittoral habitats of the MED, Baltic and Black seas. *Polysiphonia morrowii* is the only invasive alien engineer and promoter species, the rest are all promoter habitat species such as the Bladder wrack *Fucus vesiculosus* and *Phyllophora* sp. in the Baltic and Black Sea respectively. Zooplankton appears in this size category with the barrel or dustbin-lid jellyfish *Rhizostoma pulmo*, a Black Sea keystone species, a predator and a reducer, which can grow to very large size. Reptiles appear in the keystone list of this size category in the Mediterranean with the sea turtle *Caretta caretta*. It is thought to act as both a promoter and habitat species (the live carapace providing habitat to other species) as well as a reducer and a predator.

Size category >100 cm

Keystones in this size for angiosperms include the promoter species *Zostera marina* in the Baltic Sea. Benthic invertebrates include two species; the cold water coral *Lophelia pertusa* in the Norwegian Sea and Celtic Seas and the red gorgonian *Paramuricea clavata* in the Mediterranean, both as habitat species and promoters. Keystones for fish include five species/taxa of pelagic fish in the Mediterranean, NEA and Black Sea in coastal, shelf and oceanic water habitats. They are all predators and reducers. Examples include sharks and Bluefin tuna for both the NEA and Mediterranean. Keystones for macroalgae include 11 species/taxa in shallow habitats of all EU and non-EU regional seas. The invasive alien Japanese seaweed *Sargassum muticum* is the only reducer species, the rest (including the only other invasive alien species in this category the Japanese kelp Wakame *Undaria pinnatifida*) are all promoters. The two invasive alien species are engineers, the rest are habitat species. Marine mammals appear in this size category with 14 species and subspecies belonging to three groups: whales, seals, and dolphins in marine water habitats of all EU and non-EU regional seas. They are all predators. The whales are stated as reducers while the seals and dolphins can be promoters or reducers depending on species, area and expert.

3.2.3. Keystones By Regional Sea

More than half the potential keystone species are proposed from the Mediterranean (129 species/groups) while the NEA follows with 74 keystones (Table 5) (we do accept that this had the highest input of expertise and may reflect that effort). The poorest, by far, area is the Non-EU region, from where only 9 species have been listed in the catalogue. The Mediterranean is the only region where all biodiversity components (10 out of 10) are represented by at least one species/group, for the other three EU regional seas this number is seven and for the non-EU this is five. Benthic invertebrates, macroalgae, fish and marine mammals are represented in all regions with benthic invertebrates ranking first in all 4 EU-regional seas.

Table 5. Number of keystones by region and biodiversity component (Baltic: Baltic Sea; Black: Black Sea; MED: Mediterranean Sea; NEA: North-East Atlantic Ocean; Non-EU: Non EU Regional Seas; * includes three subspecies). Note: number in parenthesis denote actual number of species present, the bracketed number is the result of use of subspecies and experts not agree on this and roles.

Bio Component	Baltic	Black	MED	NEA	Non-EU
Angiosperms	2	2	3	3	
Benthic Invertebrates	10	14	71	34	2
Birds			2		1
Cephalopods			4		
Fish	6	7	13	7	3
Macroalgae	6	3	26	14	1
Marine Mammals	5	7*	2	6	2
Phytoplankton	1	3	4	7	
Reptiles			1		
Zooplankton	1	4 (4)	3	3	
Total Species/Taxa	31	41*	129	74	9

Table 6. Number of unique catalogue keystone species/taxa in the biological components per regional sea (Baltic: Baltic Sea; Black: Black Sea; MED: Mediterranean Sea; NEA: North-East Atlantic Ocean; Non-EU: Non EU Regional Seas). Note: unique in this case means that they have been proposed for one regional sea only, for example *Phyllophora* beds are only proposed for the Black Sea and Reptiles only for the Mediterranean (despite the fact that *Caretta caretta* is a widely distributed cosmopolitan species and in that sense not unique to any region).

Unique Species	Baltic	Black	MED	NEA	Non-EU
Angiosperms		1	3		
Benthic Invertebrates	5	10	65	22	1
Birds			2		1
Cephalopods			4		
Fish	3	3	10	5	
Macroalgae	5	3	18	5	
Marine Mammals		5	1	1	1
Phytoplankton		2		2	
Reptiles			1		
Zooplankton		2	3	1	
Total Species/Taxa	13	26	107	36	3
Grand Total Species/Taxa			**193**		

Table 7. Number of common catalogue keystone species in common to 4, 3, or 2 regional seas by biological components.

Bio Component	4 Regions	3 Regions	2 Regions
Angiosperms			3
Benthic Invertebrates	1	2	9
Birds			
Cephalopods			
Fish		1	6
Macroalgae		1	8
Marine Mammals		2	4
Phytoplankton		1	4
Reptiles			
Zooplankton		1	1
Total Species/Taxa	**1**	**8**	**35**

Table 8. Number of common catalogue keystone species between regional seas (Baltic: Baltic Sea; Black: Black Sea; MED: Mediterranean Sea; NEA: North-East Atlantic Ocean; Non-EU: Non EU Regional Seas).

Seas	Baltic	Black	MED	NEA	Non-EU
Baltic	-				
Black	5	-			
MED	2	6	-		
NEA	16	9	19	-	
Non-EU	3	1	0	4	-

Out of 229 species/taxa (Table 5) 185 (81%) are unique (i.e. uniquely proposed for one regional sea only) to one region only (Table 6). The number of unique species/taxa per region varies between 33% (non-EU) to 83% (Mediterranean). Examples of such unique potential keystone species include endemic, endangered, commercial, invasive alien and native species of all the biodiversity components, such as *Cordylophora caspia* and *Sander lucioperca* in the Baltic, *Beroe ovata* and *Monachus monachus* in the Black Sea (although the latter is in very low abundance), *Posidonia oceanica* and *Caretta caretta* in the Mediterranean, *Sabellaria spinulosa* and *Fibrocapsa japonica* in the NEA and *Pagophilus groenlandicus* in non-EU.

There is only one species that is keystone in all four EU regional seas (Table 7), the bivalve *Mya arenaria*. *M. arenaria* is stated to be an engineer and reducer species, showing invasive alien properties dominating in the soft substratum communities, causing regime shifts and replacing native species, causing structural changes in native communities. Its high abundance, high filtration capacity, ecosystem engineering characteristics and importance in food-web interactions, suggest that this species has dramatically impacted shallow coastal ecosystems (Katsanevakis *et al.*, in press).

Eight species are common to three regions and 35 species are common in two regions (Table 7). The common species between regions ranges from zero (between Mediterranean and non-EU) to 19 species (between Mediterranean and NEA)(Table 8). Cephalopods and reptiles are not relevant to the Baltic and Black Seas.

Baltic Sea

For angiosperms two keystone species are included, *Ruppia* sp. and the eelgrass *Zostera marina*, both promoters, habitat and engineer species. Eelgrass beds provide habitats for a wide range of species (shelter and food). The leaves and rhizomes provide substrata for the settlement of epibenthic species as well as nursery grounds for many commercially important species or endangered species (seahorses). Due to its low salinity limitation, *Zostera marina* is distributed from the Western Baltic Sea up to the Gulf of Finland. In lower salinities of the Bothnian Sea/Bay freshwater plants assume its role as habitat species. *Ruppia* sp. has a similar function to *Zostera marina*, but inhabits shallower areas and dominates within the large coastal lagoons and shallow bays along the southern coastline forming an important habitat for resting and migrating birds.

Benthic invertebrates, include, bivalves, polychaetes, and one amphipod, barnacle and hydroid. The blue mussel *Mytilus edulis/trossulus* is a habitat species. It is the only epibenthic invertebrate of the Baltic Sea that can grow in high densities, forming reef- or bank-like structures. Stable mussel banks provide habitats for a variety of epibenthic invertebrates (e.g. hydrozoans, bryozoans, sponges, barnacles) and filamentous algae. Between the mussel shells amphipods, isopods and predatory polychaetes are distributed. Additionally mussel beds form an important feeding ground for ducks. They also stabilise the sediment, act as sediment trap and influence the flux of organic particles so also acting as an engineer species. The other benthic invertebrates are all regarded as engineer species. In an organic rich environment, species reworking and oxygenating the sediment (e.g. *Arenicola marina* or *Monoporeia affinis*) are of special importance. The blue mussel and the Baltic clam or Baltic tellin *Macoma balthica* are high-medium abundance promoters. Five (out of 10) species are invasives of which only one is promoter, the bay or acorn barnacle *Amphibalanus improvisus*.

The six species of fish are primarily reducers (one both reducer and promoter). *Gadus morhua*, *Clupea harengus* and *Sprattus sprattus* have a wide distribution and are fundamental food-web species. Whereas *Gadus morhua* is regarded as a promoter (as predator for young herring and sprat) the others are regarded as reducers as high abundances of planktivorous fish negatively impact zooplankton abundance and diversity, leading to higher organic input (phytoplankton) to the benthic environment (Casini *et al.*, 2012). *Sander lucioperca* is distributed in low salinity areas only, where it acts as keystone predator. *Salmo salar* and *Salmo trutta* are the most important migrating species but due to their low number, their importance as predators is currently very low and the engineer role of *S. salar* is restricted to rivers and has therefore no effects for the Baltic Sea ecosystem.

Overall six macroalgae are included, although *Fucus vesiculosus* and *Fucus* spp. could be regarded as one entry. Due to the marine origin of the macroalgae, there are species-specific salinity based distribution boundaries. *F. vesiculosus* and *Furcellaria lumbricalis* have a wide range and are highly abundant, whereas *Fucus serratus* is only distributed in the Western Baltic Sea. *Cladophora* sp. and *Polysiphonia fucoides* also have a wide geographical range, but where they represent only two of many species in the Western Baltic Sea, they become important in the species-reduced Central and North-eastern Baltic Sea, where they form single species habitats and are a key food source for amphipods and isopods. With one exception, all macroalgae are regarded as promoters. Only the invasive species *Gracilaria vermiculophylla* is regarded as reducer. It is known to get entangled in eelgrass beds, macroalgae stands like *Fucus* and mussel beds but also occurs as drifting mats on soft bottoms (Weinberger *et al.,* 2008; Hammann *et al.*, 2013), blanketing and replacing species when in high abundance. Although documented for several years in the Baltic Sea, the overall occupied area (primarily harbours and close vicinities) is still small compared to native vegetation.

Five species of seals/whales are included under marine mammals. *Lagenorhynchus albirostris* is not a characteristic Baltic Sea mammal (not locally reproducing) and is better characterised as a vagrant. Harbour porpoises are the only native whales of the Baltic Sea. Their keystone role or effect as predators is currently very low due to their low population density. The effects of commercial fisheries are much higher and camouflage any top-down effects of predators on the food web. The same applies also to the three seal species, although their abundances might have been partly increased during the last few years (e.g. grey seal *Halichoerus gryphus*).

Only one Phytoplankton and one Zooplankton species are listed for the Baltic Sea. Both are regarded as reducers. The overall salinity gradient and high salinity variability of the Baltic Sea makes it difficult to choose a ‘key species’ for those biological components: several species may have a key role at certain localities. Although the Baltic Sea is important for resting and migrating birds, they do not have a major role in the Baltic Sea ecosystem.

Black Sea

Within the angiosperms the genus *Zostera* is regarded to have a keystone role in the littoral and shallow sublittoral habitats of the area, either through the dwarf eelgrass *Z. noltei* or *Z. marina*. Similar to the other angiosperm species, *Zostera* promotes the biodiversity of marine communities acting both as habitat species – providing food, shelter, spawning and nursery grounds – and engineer organisms as they oxygenate waters and sediments, recycle nutrients, contribute to cycling carbon, help control the transparency of the water column and stabilize sediments.

The benthic invertebrates considered as keystones in the Black Sea (14 species/groups) are primarily bivalves acting mostly as habitat species that promote biodiversity (*Mytilus galloprovincialis*, *Ostrea edulis*, *Modiolula phaseolina*, *Mytilaster lineatus*, *Donax trunculus*). Among the bivalves, *Mya arenaria* has also an invasive alien role, which has been described in a previous section.

Seven species of pelagic predator fish are indicated as potential keystone species. Only one of them is considered as a reducer, namely the dogfish *Squalus acanthias*, which feeds on several organisms, such as algae, molluscs, crustaceans and bony fish, while the rest are considered promoters. Among them are the large, migratory predators *Sarda sarda*, *Pomatomus saltatrix* and *Scomber scombrus*, the small pelagic planktivorous *Engraulis encrasicolus* and *Sprattus sprattus*, acting as prey for larger fish, and the demersal *Scophthalmus maximus*, which also sustains larger animals in the food web.

All three macroalgae species suggested as keystones are habitat species and promoters having a similar role to the angiosperms. The three phytoplankton species considered as keystones in the Black Sea are reducers, with two of them being engineer species (*Alexandrium monilatum*, *Phaeocystis pouchetii*) and one, the heterotrophic dinoflagellate *Noctiluca scintillans*, a predator. The latter is thought to have a reducing effect on the marine communities leading to a dead-end in the food-web, causing hypoxia/anoxia conditions at the bottom during bloom episodes. As for the four zooplankton species reported from the area, i.e. *Aurelia aurita*, *Beroe ovata*, *Mnemiopsis leidyi* and *Rhizostoma pulmo*, they are all considered predator species as they are consumers in the food web, but only *B. ovata* acts as promoter feeding on *M. leidyi*. As has already been stated in a previous section (*Overall* sub-section above), the rest of the zooplankton species have a reducing effect, primarily through strong grazing and depletion of zooplankton stocks leading to cascading effects in the food web.

Four marine mammals, the dolphins *Tursiops truncatus ponticus* and *Delphinus delphis ponticus*, the porpoise *Phocoena phocoena relicta* and the monk seal *Monachus monachus* are identified as keystones for the Black sea promoting biodiversity as top predators of the food web.

Mediterranean Sea

Three species of angiosperms are proposed as keystones for the Mediterranean Sea, i.e. *Halophila stipulacea*, *Cymodocea nodosa* and *Posidonia oceanica*. As has already been described elsewhere, the role of angiosperms in the marine environment is multiple and enhancing for marine communities.

The largest number of macroalgae keystones is reported from the Mediterranean Sea, 26 in total, including the association of *Phymatolithon calcareum* and *Lithothamnion coralloides*, which form widespread maerl beds. These formations are considered promoting habitat species, which by increasing habitat complexity increase marine biodiversity. Several invasive alien macroalgae are also reported in the catalogue (e.g. *Acrothamnion preissii*, *Asparagopsis armata*, *Bonnemaisonia hamifera*, *Caulerpa cylindracea*, *Caulerpa taxifolia*, *Lophocladia lallemandii*), all of which are considered reducer engineers that may outcompete native species for space and light and become dominant. In the western Mediterranean the nine macroalgae species proposed as keystones are viewed as habitat species with a promoting role. The same stands for the two *Cystoseira* species, *C. amentacea* and *C. tamariscifolia*, reported from the eastern Mediterranean.

No specific zooplankton species is proposed as a keystone, although as a group (including two size categories, micro- and meso- zooplankton) zooplankton is believed to have, being engineer organisms, either a reducing or promoting role in marine communities. The four species of phytoplankton listed in the catalogue (*Alexandrium minutum*, *Karenia mikimotoi*, *Gymnodinium catenatum*, *Phaeocystis pouchetii*) are all small-size, engineer species that create harmful algal blooms and act as reducers.

The high number of benthic invertebrate keystones from the Mediterranean (68 species and 3 groups) includes several components, such as bivalves, gastropods, polychaetes, corals, echinoderms, etc. Polychaete species (e.g. *Ficopomatus enigmaticus*, *Hydroides dianthus*) are engineer species that act as promoters. Bivalves have also been considered as engineers for the Mediterranean but their role can be either as promoters (e.g. *Chama pacifica*, *Crassostrea gigas*), or reducers (e.g. the invasive aliens *Brachidontes pharaonis* and *Mya arenaria*). Echinoderm species have been proposed as keystones from the western Mediterranean (e.g. *Ophiothrix fragilis*, *Echinaster sepositus*, *Hacelia attenuata*, *Marthasterias glacialis*) and in all cases they were regarded as predators with either a reducing or unknown effect on the communities. In contrast, the sponges species proposed from the W. Mediterranean (e.g. *Cliona celata*, *Crambe crambe*, *Spirastrella cunctatrix*) were in all cases considered to promote biodiversity either as habitat or engineer species.

Birds and cephalopods have been indicated as keystones at the group level through the application of the model EwE in different Mediterranean areas, the only exception being the bird *Larus audouinii*. In all cases, they were regarded as predator species with a reducing role.

A total of 13 fish species and groups spanning a wide range of habitats are predators that mostly have a reducing effect in Mediterranean ecosystems although a few, such as *Merluccius merluccius*, *Engraulis encrasicolus*, *Sardina pilchardus,* 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*. The *Siganus* species in particular, are thought as keystones because they greatly modify sublittoral ecosystems, creating and maintaining barrens, as they transform the ecosystem from one dominated by lush and diverse brown algal beds to another dominated by bare rock.

Dolphins are denoted by models as keystones in the Mediterranean, not only as a group but also through the bottlenose dolphin *Tursiops truncatus*. Dolphins are top predators and they are considered to be scarce and in low abundances in the Mediterranean. As a group they can have either a reducing or promoting effect, depending on which aspect of the community is considered; however, *T. truncatus* is believed to have a reducing effect in the central Mediterranean and the Ionian Sea. *Caretta caretta*, the only reptile species reported in the DEVOTES catalogue, appears also to be scarce and in low abundance in the eastern Mediterranean and can be viewed as both a habitat and predator species. In the first case, it promotes the ecosystem's biodiversity by hosting over 100 species from 13 phyla (such as barnacles, shrimp, algae and even small fish) on the carapace, making it somewhat of a mobile reef (Spotila, 2004). As a predator though, it may reduce biodiversity by feeding and therefore removing species from lower levels of the food web.

North-East Atlantic Ocean (NEA)

All seven species of phytoplankton listed from the Atlantic are invasive alien, engineer species that have a reducing impact on the ecosystem by creating harmful algal blooms. Among the three zooplankton species reported from the area, one is the calanoid copepod *Calanus finmarchicus*, a highly abundant, widespread species, exhibiting a pivotal role in supporting food webs through the transfer of energy between primary producers and a number of planktivorous fish and fish larvae (Aksnes and Blindhein, 1996). By its feeding activities contributes significantly to biogenic carbon export and nutrient recycling. Nevertheless, it is not clear what is the effect on the overall marine biodiversity; it might promote it, by favouring some species, but it might as well reduce it, by altering the abundance distribution across species, hence, the dominance relationships in the community. Apart from the calanoid copepod, the other two zooplankton species are the jellyfish *Aurelia aurita* and the ctenophore *Mnemiopsis leidyi*, both of which are characterized as predators with a reducing effect.

Seven out of 14 macroalgae species are invasive aliens in the NEA, all of which are engineer species and reducers. Their negative impact may be attributed to their competition with native species for space and light (e.g. *Asparagopsis armata*), to the altering of benthic communities and habitats and increasing sedimentation (e.g. *Codium fragile* subsp. *fragile*). The rest macroalgae species are kelps (e.g. *Alaria esculenta*, *Laminaria digitata*) and maerl (*Phymatolithon calcareum* and *Lithothamnion* spp.) that act as habitat species that promote biodiversity through the habitat complexity they provide. Two *Zostera* species (*Z. marina* and *Z. noltei*) and *Ruppia* are the angiosperms that have a promoting effect on NEA areas acting both as habitat and engineers.

A substantial number of keystone species from the NEA are benthic invertebrates, among which 13 invasive alien species are included. All the invasive alien species are engineers but surprisingly, not all of them are having a negative impact on the local ecosystems. For example, the serpulid polychaete *Ficopomatus enigmaticus* creates reef-like aggregates, in which tubes grow vertical to the substratum in clumps and attach to each other. *F. enigmaticus* aggregates provide substrata and shelter for many elisions and represents excellent food for many species including fishes and birds. The native species belong to all three keystone type categories (engineers, habitats, predators) and have mainly a promoting impact on the ecosystem (e.g. *Urothoe poseidonis*, *Amphiura filiformis*, *Lanice conchilega*).

The seven fish species/groups listed in the catalogue from this MSFD region expand to a wide variety of habitats and subareas. Among these are listed species that are predators and act as promoters (e.g. *Gadus morhua*) or reducers (e.g. *Thunnus albacares*) and engineer species with a promoting primary impact such as the sandeel (*Ammodytes tobianus*); for many sandeel-predators, inter-annual fluctuations in the availability of sandeel have direct effect on breeding success, growth and survival in general (van Deurs, 2010).

Six top predators marine mammals are in the list of NEA keystone species. Except for the porpoise *Phoca vitulina*, which is mostly believed to be a promoter, the rest of the marine mammal species (two seals, one dolphin, one porpoise and one whale) are thought to be reducers.

Non EU Regional Seas

Only nine species are suggested as keystones from this area (Norwegian Sea): three fish (*Gadus morhua*, *Scomber scombrus*, *Clupea harengus*), two seals (the ice-associated *Pagophilus groenlandicus*, and *Halichoerus grypus*), the cold coral *Lophelia pertusa* and the burrowing megafauna animals as a group from the benthic invertebrates, the kelp *Laminaria hyperborea*, and the seabird *Phalacrocorax carbo*. Among them, only the fish and the bird species, which are top predators, are thought to have a reducing impact on the ecosystem, while the rest enhance biodiversity either as habitat species (e.g. *Lophelia pertusa* is a reef building colony), engineers (the burrowing megafauna are bioturbators) or predators (the seals feed on cod and other large fish).

3.2.4. Keystones by habitat

Figure 6 illustrates how the number of potential keystone species is distributed among the habitat types considered in the study in the five regional seas. Overall, most species are reported from the sublittoral, both shallow and shelf habitats, while a considerable number is also reported from the marine water column and the littoral environment. The same trend is also observed in the Mediterranean Sea, as most species are found in the sublittoral (shallow sublittoral 42, shelf sublittoral 66 species/groups), while in the North-East Atlantic, the percentage of both marine water and littoral species/groups is increasing (40 shallow and 10 shelf sublittoral species/groups, 22 littoral and 20 marine water species/groups). In the Baltic Sea species/groups from the shallow sublittoral prevail (18), while in the Black Sea species from both the shallow sublittoral and the marine water column are suggested (17 and 21, respectively). It is worth noting that species from the two sublittoral habitats and the marine water environment are proposed as keystone species from all five areas.

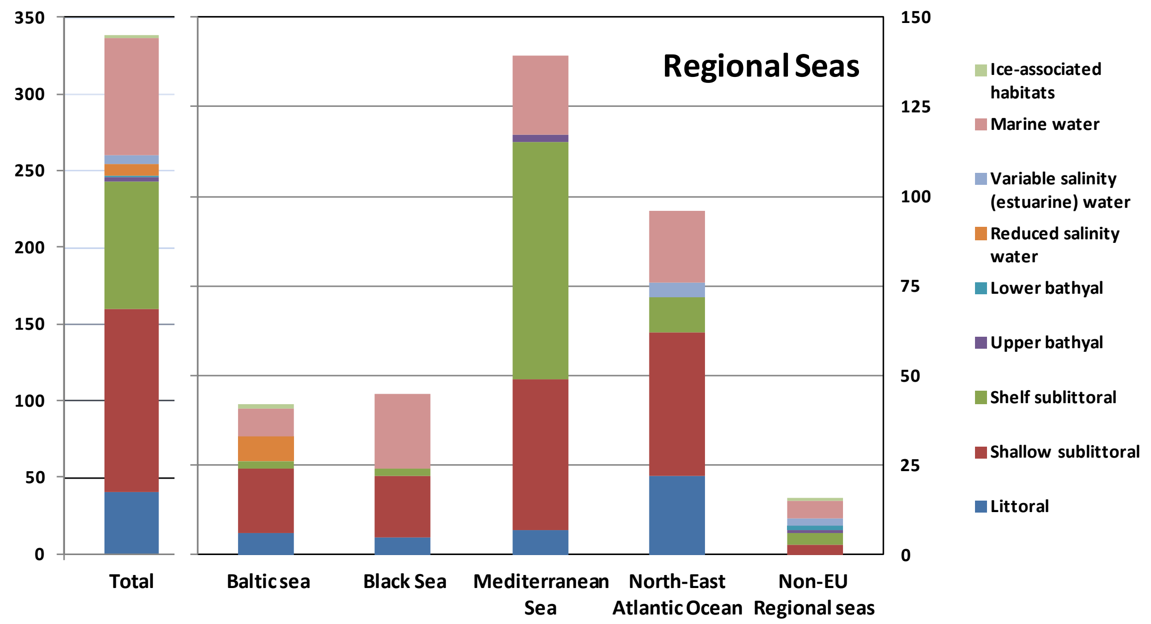

Figure 6. Overall number of species distributed in the different habitat types and for each regional sea. Note different scales between Total and regional seas.

Table 9 summarizes information on keystone component groups in relation to major habitat types. Certain biological components are by definition excluded from specific habitats, e.g. plankton species are only found in water column, benthic invertebrates are by definition reported in sea-bottom habitats, angiosperms are limited to the euphotic zone, therefore in shallow sublittoral habitats. On the other hand, fish species were reported as potential keystone species in almost all the habitats considered in the catalogue except for the lower bathyal, the abyssal and ice-associated habitats. As expected, the highest numbers of species were reported from the sublittoral, both shallow (88 species and 7 groups) and shelf habitats (76 species and five groups), where most benthic invertebrate species live (49 shallow and 68 shelf sublittoral species/groups). Besides benthic invertebrates, macroalgae species have also been considered as keystone species in the sublittoral, contributing to the keystone catalogue with 31 species in the shallow sublittoral and with 10 to the shelf sublittoral.

Table 9. Number of potential keystone species per Habitat type. Species are sorted in major biological components. Abbreviations are: LT: Littoral; ShSub: Shallow Sublittoral; ShelfSub: Shelf Sublittoral; UB: Upper Bathyal; LB: Lower Bathyal; Abyss: Abyssal; RSW: Reduced Salinity Water; VSW: Variable Salinity (estuarine) Water; MW: Marine Water; IAH: Ice-Associated habitats; * includes three subspecies.

	LT	Sh Sub	Shelf Sub	UB	LB	Abyss	RSW	VSW	MW	IAH
Angiosperms	2	7								
Benthic invertebrates	23	49	68	2	1			2		
Birds								1	3	
Cephalopods		1							3	
Fish	1	7	3	1			4	2	18	
Macroalgae	4	31	10							
Marine Mammals							2		14*	2
Phytoplankton									9	
Reptiles									1	
Zooplankton							1	1	8	
Total	**30**	**95**	**81**	**3**	**1**		**7**	**6**	**56***	**2**

A total of 56 species and groups were reported in the marine water habitat, 18 of which belong to fish, 14 to marine mammals, 17 to plankton (both phyto- and zoo-plankton), while the remaining seven are cephalopods groups, birds and one reptile species, the sea turtle *Caretta caretta*. A total of 30 species were reported as keystone species in the littoral environment, with benthic invertebrates again contributing the highest number (22 species and 1 group). Only three species were reported from the deep sea; the cold coral *Lophelia pertusa*, which is reported from both the upper and lower bathyal of the Norwegian Sea; the engineer species *Nephrops norvegicus*, reported from the upper bathyal of the Eastern Mediterranean Sea; and hake *Merluccius merluccius*, which was indicated by Ecopath with Ecosim model as a keystone species in the upper bathyal of the Catalan Sea (W. Mediterranean). The seven species listed as keystones under the reduced salinity water habitat are all reported from the Baltic Sea and include four fish species (*Clupea harengus*, *Gadus morhua*, *Sander lucioperca* and *Sprattus sprattus*), two seals (*Halichoerus grypus* and *Pusa hispida*) and the invasive alien zooplankton species *Aurelia aurita*. Although only a few species (6) are reported from the variable salinity (estuarine) water habitat, these span a broader range of biological components from zooplankton (the invasive *Aurelia aurita*) to benthic invertebrates (deposit feeders group, *Crangon crangon*), fish (*Gadus morhua*) and birds (*Phalacrocorax carbo*). Lastly, only two predator species were reported from ice-associated habitats, namely the seals Ha*lichoerus grypus* and *Pagophilus groenlandicus* from the Baltic and the Norwegian seas, respectively.

3.2.5. Invasive alien keystones

The potential keystone invasive alien species are shown in Table 10 by species component and regional sea. Overall, 52 invasive alien species were included in the catalogue. A total of 37 invasive alien species are reported from the Mediterranean Sea, where most are classified as macroalgae (14) and benthic invertebrates (15). The remaining 7 species are phytoplankton and fish species, while only one of them (*Halophila stipulacea*) is an angiosperm. Reports from the North-East Atlantic Ocean give a total number of 28 invasive alien species, of which, benthic invertebrates again dominate with 13 species. A few phytoplankton and macroalgae species (14 in number) are reported from the same region, while *Mnemiopsis leidyi* is the only zooplankton species found. Both the Baltic and the Black Sea are characterized by a small number of keystone invasive alien species (7 and 8 respectively), mostly benthic invertebrates, with the two important large zooplankton species in the Black Sea of *M. leidyi* and *Beroe ovata* (in terms of importance they might have a high level if their contribution is taken into account next to the reduced fauna of these seas). In the Norwegian Sea (Non-EU regional sea) no invasive alien keystone species have been recorded.

Table 10. Number of invasive alien species in the keystone catalogue by regional sea (Baltic: Baltic Sea; Black: Black Sea; MED: Mediterranean Sea; NEA: North-East Atlantic Ocean; Non-EU: Non EU Regional Seas).

	Baltic	Black	MED	NEA	Non-EU
Angiosperms			1		
Benthic invertebrates	5	4	15	13	
Birds					
Cephalopods					
Fish			3		
Macroalgae	1		14	7	
Marine Mammals					
Phytoplankton	1	2	4	7	
Reptiles					
Zooplankton		2		1	
Total	**7**	**8**	**37**	**28**	

The distribution of keystone invasive alien species within the component groups in different habitats is shown in Table 11. The invasive alien keystone species dominate Shallow Sublittoral habitats with a total number of 41 species being reported from them. Most of them are macroalgae and benthic invertebrates (37 species), while the remaining four consist of three fish and one angiosperm species (*Siganus luridus*, *S. rivulatus*, *Lagocephalus sceleratus* and *Halophila stipulacea* respectively). Marine Water habitats are invaded by eight phytoplankton (*Alexandrium minutum*, *A. monilatum*, *Karenia mikimotoi*, *Gymnodinium catenatum*, *Phaeocystis pouchetii*, *Coscinodiscus wailesii*, *Fibrocapsa japonica* and *Pseudochattonella verruculosa*) and two zooplankton keystone species (*Mnemiopsis leidyi* and *Beroe ovata*). The Littoral zone is characterized by species that belong to the biological component of benthic invertebrates (eight in number). There are no reports for the presence of invasive alien keystone species in the Shelf Sublittoral, Upper Bathyal, Lower Bathyal, Abyssal, Variable Salinity (estuarine) Water and Ice-Associated habitats.

Table 11. Number of potential keystone invasive alien species by habitat type. Species are sorted in major biological components.

	Littoral	Shallow Sublittoral	Marine Water
Angiosperms		1	
Benthic invertebrates	8	23	
Birds			
Cephalopods			
Fish		3	
Macroalgae		14	
Marine Mammals			
Phytoplankton			8
Reptiles			
Zooplankton			2
Total	**8**	**41**	**10**

4. Discussion

4.1. The DEVOTES Keystone Catalogue

The task for the participants to provide lists and information about regional sea keystone species has been extremely difficult. The major difficulty has been in answering the question: what is a keystone species, or rather, what makes a species keystone? In answer to the objectives of the task, a comprehensive list of potential keystone species has been provided. *Potential* should be emphasised because many of them may either not completely fulfil the original definitions that they have 'a disproportionate effect relative to their abundance', or because we do not know what the disproportionate effect would be, or because we have also included engineering species and habitat species. By 1996, more than 25 years after the concept was proposed, Power *et al.* (1996) were only able to review keystone studies on 14 species/groups. There is a dearth of literature on recorded marine keystone species (Würtz, 2010) and simple searches in scientific literature resources give very few positive finds. Consequently a large part of the catalogue entries are based on best expert knowledge and with an overall inclusion based on a precautionary principle rather than definite knowledge. As noted in the introduction, keystone identification is laborious without the use of removal/exclusion experiments, well-documented historical data on species removals/recoveries, predictions based on population, community, traits and patterns (Menge *et al.*, 2013), or from observation after trophic cascades (Würtz, 2010), which may still lead to difficulties in identifying the keystone.

Beyond difficulties in identifying the keystones, the data providers were also faced with difficulties to classify into fixed catalogue groupings. Amongst these, type of keystone (predator, habitat species engineer) and primary impact (promoter or reducer) are dealt with in following sections. Other aspects of their importance including size, abundance and distribution were aimed at exploring traits towards a metric or importance rating. The providers were asked to categorise the average adult gross size (major mass of the body) and in some cases this may differ between areas, especially when the size is close to the border of two categories, or possibly between providers, where the major mass of the body may be interpreted differently (e.g. sea urchin with or without long spines). Abundance and distribution is related to the specific area/habitat that is defined for that species, so care must be taken with comparisons between the catalogue species. We also understand that there may be some bias introduced by the number of experts, their choice and areas of expertise, which may, for example, partially explain the differences in numbers of keystones reported between the NEA and the Mediterranean Sea.

4.1.1. Highlight summary of the catalogue

- Overall, the DEVOTES Keystone Species Catalogue has 844 entries which includes 210 distinct species and 19 groups.
- Benthic invertebrates account for 50% of the reported keystone species/groups (110 species and 5 groups), while macroalgae contribute with 17% (39 species and 1 group) and fish with 12% (24 species and 4 groups).
- A total of 79 species were considered to act as engineers, 66 as habitat forming species, 74 as predators, while a few (9 species) were thought of having multiple roles in their marine ecosystems.
- Most of the proposed species (126 species and 7 groups) are believed to have a promoting role in marine communities, 61 species and 8 groups act as reducers, 16 species could have both roles depending on region, habitat, or even abundance and distribution, while for 11 species the experts were unable to define their primary impact.
- Expert knowledge accounted for 38% of the entries, models 10% with most entries (52%) from some form of literature reference.
- Angiosperms were consistently put forward as promoters, keystone habitat forming and engineering species in all areas.
- Benthic invertebrates were mostly classified as promoters, either engineer or habitat species with a few keystone predators.
- Most keystones were mid-range in size in the 6-20 and 21-100 cm size groups. The habitat and engineer species peak in these size ranges, whilst top predators keystones and habitat species dominated the largest size group (>100 cm).
- The Mediterranean Sea had the largest number of potential keystones (56% of the entries) with the least in the Norwegian Non-EU regional sea. The Mediterranean was also the only sea with proposed keystones (species or groups) from all 10 biodiversity components.
- Only one keystone, the bivalve *Mya arenaria*, was common to all four EU regional seas. Eight species were common to three regions and 35 common in two regions.
- There were very few keystones in deep waters, with most reported in sublittoral shallow and shelf seabeds or for pelagic species in marine waters with few in reduced/variable salinity and only two in ice habitats.

- A significant number of keystones were invasive alien species. The highest number (37) was noted in the Mediterranean closely followed by the North East Atlantic with fewer in the Black and Baltic Seas. These were predominantly on shallow seabeds or pelagic in marine waters.

Work on collating keystone species had previously been very limited; to our knowledge the first major review was undertaken by Power *et al.* (1996) on world occurrences which covered 14 marine species/groups (plus additional fresh water and terrestrial species) including benthic invertebrates, fish, seabirds and mammals. Just over a decade ago the first attempt was made within the BIOMARE network to catalogue European keystone species (Féral *et al.*, 2003). These authors defined and collated indicators of biodiversity including 9 species/groups of keystone habitat builders, 18 species groups of other keystone species and 11 species of invasive alien indicators. Their biological components included macroalgae, angiosperms, zooplankton (one alien invasive, *Mnemiopsis*), benthic invertebrates and fish. Under the current DEVOTES catalogue we have been able to considerably add to this coverage in terms of biological components (10), species, habitats and geographical coverage. It is emphasised that many are potential keystones and the collation is an open work.

4.1.2. Using the Catalogue

Whilst the catalogue is extensive with detailed information, with a large number of entries based on expert judgement, it should be noted that it is a list of potential keystone species following a more open keystone definition. The catalogue summarises a great deal of information that should be used in its context. It should be noted that:

- With multiple providers there may be judgmental differences that are reflected in the proposed keystones in the different regions.
- A species may be considered keystone in one habitat/area/region and not in another.
- Population characteristics (size, abundance distribution), are relevant to that unit area that has been defined.
- When a species entry has been defined as coming from ‘reference’, the reference given may not be a study that defines the species as keystone. The reference(s) may just be supporting the nomination of the species.
- Not every entry is given at the species level:
    - In several cases model entries with significant keystoneness values are at a functional or collective group level
    - In other cases there might be species groups made up of similar species or from a distinct habitat collection of species (e.g. maerl).

  - In a few cases entries have been given at the subspecies level for one region (e.g. *Phocoena phocoena relicta* for the Black sea but *Phocoena phocoena* for the North East Atlantic).
- At present there is no temporal aspect in the catalogue and it is possible for the keystone categorisation of a species to change over time as an ecosystem changes. Models have been used and can demonstrate changes over time in keystone importance.
- Within the Baltic Sea there has been some difference between the providers as to the pelagic habitat classification. Some providers classified species as occurring in marine habitats whilst others classified them as reduced salinity water. Despite some ambiguity in the MSFD guidance, the Baltic Sea is a sea with reduced salinity waters. Additionally the Baltic Sea is not divided further in MSFD subregions based on geography salinity regimes (e.g. between northern and Southern areas) or distance from shore (coastal/shelf habitats).

4.2. Gaps in coverage and expertise

4.2.1. Habitats and seas

In pelagic waters, coastal, shelf and oceanic marine habitats were all represented in the catalogue by keystone species in European seas. Reduced salinity waters entries were recorded from the Baltic Sea with variable/estuarine waters only considered in the North East Atlantic (NEA) and the Norwegian Sea, as the focus of the catalogue was primarily on marine waters. There are no gaps in the ice-associated habitats with a small number of entries coming from the Norwegian and Baltic Sea.

Littoral habitats have been identified as habitats for keystone species in the four EU regional seas but not in the Non-EU Norwegian Sea, though with relatively low number of entries. The question arises whether this habitat has been overlooked (a gap) or whether it was difficult to choose keystones in this very dynamic area. Certainly the Baltic, Black and Mediterranean Seas have very limited tides (if any) so the littoral zone is limited in extent compared to the NEA which had the highest proportion/number of littoral keystone species. It is an area where observations and manipulative experiments are easiest to undertake and was the starting point for the keystone concept with Paine’s keystone predator starfish (Paine, 1969); and it may be that there is more happening there than we currently realize.

All types of shallow sublittoral habitats (coarse, mixed, rock and biogenic, sand and mud) are well represented in the catalogue, with the only exception of shallow sublittoral muddy sediments in the Black Sea. Shelf sublittoral mud sediments also do not feature amongst the Black Sea entries. It could be that muddy sediments are overlooked, but it is more likely that its absence from the catalogue is the result of poor knowledge about the distribution of this habitat. Shelf sublittoral coarse sediments and shelf sublittoral rock and biogenic habitats only feature in the Mediterranean and NEA or the

Mediterranean and non-EU regional seas as keystone species providers. It may be that these habitats are not so relevant to general ecosystem functioning in the Baltic and Black Seas. It should however be noted that there are considerable errors in our existing seabed substrate maps for all areas. In order to understand the relationship between keystone species and physical habitats we would need to have an accurate and consistent description of the physical environment with appropriate coverage and resolution that would allow us to understand the spatial and temporal context of that habitat. DEVOTES is developing methods to create more biologically relevant and accurate habitat maps which will assist in such assessments in the future.

Deeper habitats are less well represented in the keystone catalogue. The bathyal region (upper and lower bathyal: 200-2700 m) was only represented by keystones in two seas, with the keystones *Nephrops norvegicus* and *Merluccius merluccius* proposed in the Mediterranean and *Lophelia pertusa* from rock and biogenic habitats in the Norwegian Sea. *Lophelia* is found in both the Mediterranean and the NEA at various locations and both the species and genus has been given keystone status across its worldwide area of distribution (King and Beazley, 2005; Flot *et al*., 2013). Is this a gap or a case of scale mismatch? It is true that *Lophelia* is present in Italy in Santa Maria di Leuca (an MPA and a fisheries protected zone) in the Northern Ionian Sea in the Central Mediterranean Sea. Does this make *Lophelia* a keystone species for the whole subregion? Our providers did not think so and would not consider this as a real gap. Likewise, in the OSPAR Maritime Area *Lophelia* is found from the Iberian Peninsula to Ireland, the Greater North Sea, the Celtic Seas, the Bay of Biscay/Golfe de Gascogne, around the Rockall Bank, the Faroe Islands, and along the Norwegian coast and is considered to be under threat and/or in decline in all the OSPAR Regions (OSPAR 2009). *Lophelia* is not listed as keystone species in the OSPAR region although it is recognised as important being included on the OSPAR List of Threatened and/or Declining Species and Habitats along with other habitats (such as coral gardens or carbonate mounds) where *Lophelia* coexists with other taxa and corals including gorgonians and seapens (OSPAR, 2008).

Only one seabed habitat type has not featured in the catalogue; the abyssal (>2700 m depth). Despite the extensive areas covering those depths in the NEA and the Mediterranean, the increasing scientific coverage and the existence of permanent deep sea observatories/regular monitoring of certain stations (for example, the Porcupine Abyssal Plain site (PAP) situated off the southwest coast of Ireland in the NEA), there seem to be no proposals for keystone species for our seas including the Norwegian Sea. In the Southern Ocean abyssal plain, Antarctic krill *Euphausia superba* is a keystone species and an important resource for whales, crabeater seals and birds (http://en.wikipedia.org/wiki/Antarctic_krill, Clarke and Tyler 2008). The krill utilize fallen algae in bottom sediments, the same way sea cucumbers exploit phytodetritus falls in the PAP (http://en.wikipedia.org/wiki/Porcupine_Abyssal_Plain). Sea cucumbers have a profound effect on the PAP abyssal ecosystem by reworking and completely turning over the surface layer of the seabed sediments (http://www.oceanlab.abdn.ac.uk/esonet/porcupine.php) while changes in particle flux can impact ecosystem functions, cause radical changes in the density and species diversity and even lead to population explosions such as that of *Amperima rosea*, as observed in 1997 and 2002 (Wigham *et al.*, 2003; Hartman *et al.*, 2012). *A. rosea* is considered a key species, but whether holothurians are considered a keystone group for the NEA abyssal habitats still remains an open question.

4.2.2. Biodiversity components

Most of the partners (66%) had covered more than half the designated biodiversity component types in their contributions. A third of the partners looked at 64% of the biodiversity component types (7-8 types) and 33% of partners looked at 2-3 biodiversity components only. It is worth noting that in the latter case, the remaining partners in the same regional sea always made up for this. It seems that all the regional seas were represented by both more generalists and narrower field experts. Gaps in expertise were therefore less relevant.

Among the 11 biological components considered in DEVOTES, the catalogue lacks microbial representatives, as shown also by DEVOTES Deliverable 3.1 on existing biodiversity indicators in Europe (Teixeira *et al.*, 2014). Microbes are essential to the oceans in terms of biomass, diversity and ecosystem functioning (Giovannoni and Stingl, 2005; Sevastou *et al.*, 2013; Falkowski *et al.*, 2008). Yet the study of their ecology, diversity and patterns in the marine realm has not been very extensive compared to other biological components, and therefore, we still lack the level of knowledge required to attribute keystone characteristics to them. Microbial ecologists are generally not in a position yet to identify and study the ecology of single species. The recent application of next generation sequencing technologies has unravelled the complexity of microbial communities showing that the diversity of free-living microbes is much higher than previously recognized (e.g. Zinger *et al.*, 2011). Zinger *et al.* (2011) showed the global distribution of the Gammaproteobacteria in coastal and deep sea sediments and Polymenakou (pers. comm.) analyzing bacterial and archaeal communities of the lower bathyal and abyssal sediments of the Eastern Mediterranean (1025 - 4393 m) reveal the key role of *Pseudomonas* and *Cenarchaeum* genera. Nevertheless, although specific microbial species cannot be identified as keystones, the keystone role of the group as whole should be appreciated.

Likewise, despite the extensive reporting of benthic invertebrates in the DEVOTES Keystone Catalogue, there are no records for meiofaunal invertebrates. Meiofauna are ecologically important because they occupy positions at the base of the marine food web, and hence ultimately sustain larger marine animals; they live within the sediments and move between the sediment grains, therefore acting as engineers; they also have stimulatory effects on microbial communities, thus indirectly controlling biogeochemical processes in benthic ecosystems (Gerlach, 1978; Rieper-Kirchner, 1989; Tietjen, 1980). However, assessment of the role of meiofauna in ecosystems, and in food webs in particular, is hampered by a lack of information on many meiobenthic groups. Therefore, the absence of meiobenthic species from the DEVOTES Keystone Catalogue should be viewed as a combination of the providers lack of relevant expertise and an incomplete understanding of meiofaunal dynamics.

Three biodiversity components in the catalogue were restricted to the Mediterranean only: reptiles, specifically the loggerhead sea turtle *Caretta caretta*, cephalopods and seabirds. The loggerhead sea turtle, an endangered and protected species under many Conventions, has a worldwide distribution inhabiting the Atlantic, Indian, and Pacific Oceans and the Mediterranean Sea. The Mediterranean is a nursery for juveniles, a host of scattered major nesting sites as well as a common place for the adult population, a part of which come from the Atlantic (Casale and Margaritoulis 2010). Sporadic minor nesting occurs in the Eastern Atlantic (e.g. coasts of Morocco) and the Black Sea (Márquez, 1990) and the species is absent from the Baltic Sea. While cephalopods are also absent from the Baltic and Black Sea, seabirds are present and even used as indicators, however there are no EwE models covered that include seabirds (see later) or marine ecologists voicing their opinion regarding them as keystone or key species for the Baltic. The same is true for the NEA where seabirds are often mentioned as environmental indicators or next to keystone fish species, which serve as prey for seabirds. However, not even ornithologists have put forward the case for seabird species to have a keystone role in the NEA region (A. Franco, pers. comm.).

Not all sub-biodiversity components are present in the catalogue. Echinoderm records do not include holothurians or crinoids, despite references, for example, for *Leptometra phalangium* in the Mediterranean being an important indicator species vulnerable to trawling (Smith *et al.*, 2000). Opisthobranchia are missing from the molluscs and from the fish there are no records (or published information) for skates as keystones. Sharks only appear in the catalogue as keystones in the Mediterranean with the exception of the Spiny dogfish (*Squalus acanthias*) in the Black Sea.

Phytoplankton: complexity within a component for keystone species role

Although marine phytoplankton have an essential ecological function for all aquatic life as organic matter producers and are an integral part of biogeochemical cycles, their keystone role at the level of individual species bear a number of constraints. On the one hand our knowledge of marine phytoplankton biodiversity is limited due to methodological restrictions of species identification techniques (Venter *et al.,* 2004), the effort and expense of gaining appropriate data (Irigoien *et al.*, 2004; Cermeño *et al.*, 2013) and mismatches between sampling and the scales of phytoplankton natural variability, for which species identity concepts within Biodiversity and Ecosystem Functioning are rather vague. On the other hand mechanisms regulating patterns of phytoplankton biodiversity still remain debated and largely unexplored (Garmendia *et al.*, 2012; Cermeño *et al*., 2013). Phytoplankton ecologists have expended great effort to explain the factors that determine distribution, community assemblies, blooms, and succession of species, applying macroecological and morphospecies approaches which have not been properly scaled to the ecophysiology and niche requirements of the phytoplankton phylogenetic groups and species present (Smayda, 2011). The insights into the speciation, genetic diversity, and ecophysiology being gained through molecular studies (Rynearson *et al.*, 2006; Härnström *et al.*, 2011) indicate the need to redefine the species behaviour of classic interest and apply a deeper conceptual and applied level of inquiry — a microecological approach.

Litchman *et al.* (2010) proposed a trait-based approach as an effective way to link species diversity and community structure in phytoplankton by providing mechanistic explanations of why certain species are found under given environmental conditions. However how traits evolve in response to different selective pressures (because traits may evolve rapidly owing to short generation times and large population numbers), making microevolutionary processes likely to affect community dynamics, is still poorly resolved (Hairston *et al.,* 2005; Litchman and Klausmeier, 2008). Harmful algal blooms (HAB) have a pronounced impact not only on water quality, but on species diversity, community structure and ecosystem functioning by their traits (best expressed in the toxic species) or by their abundance (hypoxia conditions and associated benthic species mass mortality), impairment of reproduction (chemical biomediation) and many ecosystem functions (GEOHAB, 2001, Paerl and Huisman, 2009). Ecophysiological flexibility in HAB species favours their success in different environments and may help maintain high fitness in a wide range of environmental conditions. For example, de Tezanos Pinto and Litchman (2010) showed that heterocystous nitrogen fixers grown in low nitrogen and high light gained dominance because of nitrogen fixation. However, when grown in low light, the traits providing higher fitness were related to light acquisition (low irradiance thresholds and high relative growth rates at low light) and behaviour (gas vesicles that enable positioning in better illuminated zones). Zimmer and

Ferrer (2007) linked chemical defences, chemical signals, and the keystone species hypothesis, providing examples where keystone species arise not from biological interactions, but as a consequence of chemistry and further develop the concept of ‘keystone molecules’ hypothesized by Baldwin *et al.* (2006) and Izaguirre *et al.* (2006) stating that the impacts of signal/defence compounds play keystone roles within natural community organization. The presence of saxitoxin (STX) in phytoplankton (genus *Alexandrium*) is known to determine the habitat and prey choices of higher order consumers, significantly impacting species compositions of coastal ocean communities (Kvitek and Bretz, 2004, 2005). Large, episodic die-offs of predatory fish and mammals also modify primary plant-herbivore relationships, and thus regulate trophic cascades in both benthic and pelagic environments (Myers and Worm, 2003; Bruno and O’Connor, 2005).

Genetic shifts in trait values of a given species can easily occur over relatively short timescales (within a single growing season), often because of clonal selection, as pointed out by Kardinaal *et al.* (2007). Predation, competition, or changing environmental conditions can exert sufficient selective pressures to cause such shifts. Kardinaal *et al.* (2007) observed a rapid decrease (within 30 days) in toxicity of the cyanobacterium *Microcystis* due to a competitive displacement of toxic strains by nontoxic strains with better competitive abilities for light. Most of the phytoplankton keystones species have episodic occurrences (Power *et al.*, 1996) with a probability and occurrence that is difficult to predict.

The complexity associated to a single phytoplankton species specific keystone role and the difficulty to classify it in a category *sensu* Menge *et al.* (2013), suggests the keystones in phytoplankton needs further development.

4.2.3. Gaps in knowledge and model outputs

Accessibility of information is always a problem in compiling synthesis catalogues where the grey literature can be very useful but usually is very hard to source. A good resource, project deliverable documents are quite often deposited online, but in restricted area websites, so require a direct access connection (a project partner) to access. Published work is also hard to access whether it is not open access or does not have the necessary detailed information that it is reporting on. An example of this is that not all the published papers with EwE models provide data on keystone species or give their keystoneness values, as they may have a different focus, for example, status change, or general food web relations (Tomczak *et al.*, 2013 for the Baltic; Akoglu *et al.,* 2014a for the Black Sea). Lassalle *et al.* (2011) propose phytoplankton and zooplankton as keystone groups for the NEA (Bay of Biscay) and in a subsequent study (Lassalle *et al.*, 2013) they compare ecosystem status and functioning in the NEA and the Baltic while providing for the Cantabrian Sea, the French Continental Shelf, the North Sea and the Central Baltic Sea the first four functional groups in decreasing order of keystoneness. For the Baltic Sea, keystones include cod, sprat and zooplankton, these among other species and groups also feature in our keystone catalogue (although the zooplankton species/groups are different). For the NEA the proposed top keystone groups include large piscivorous sharks, carnivorous zooplankton, sand eels, phytoplankton, small demersal fish, suprabenthic zooplankton (mostly euphausids), blue whiting, micro- and meso-zooplankton, large phytoplankton and suprabenthivorous demersal fish. From these groups, sharks are not listed in our catalogue for the NEA (as with some other information, this was obtained after the catalogue was finalized and could not be integrated due to time constraints of the project). For the Black Sea, Akoglu *et al.* (2014b) looked at differences in the keystones values of nine groups (dolphins, piscivorous fish, demersal fish, small pelagic fish, *Aurelia aurita*, *Mnemiopsis*, zooplankton, *Noctiluca* and phytoplankton) over four periods between 1960-2000. Despite the lack of Black sea models in our catalogue, all of these groups and species are present in our catalogue, based on expert judgment and published references (the DEVOTES Deliverable 4.1, on available models for biodiversity can be consulted also (Piroddi *et al.*, 2013)). On a more methodological note, the recommendations and choice of a cut-off point for the keystoneness index (only highest ranking species, first four, only around a specific value, etc.) is not as developed yet, making comparisons not very easy and increasing uncertainty for the value of some of the proposed keystone species that are not so close to the top/proper index value. The mathematics behind the index might be revisited as well in the near future (Piroddi pers comm).

4.3. Defining and categorising keystones

The original definition given by Paine (1969) narrowed the application of the keystone concept to predators controlling the densities of important competitor or predator species, hence having a top down bias toward community organisation (Paine, 1995). Although predation is an important regulating process, it has been widely recognised that consumer–resource interactions are only one of the types of interactions that operate within ecosystem networks (Olff *et al.*, 2009). Other interactions can be as important in structuring aquatic communities as food webs, for example, ecosystem engineers with modification of non-resource abiotic conditions that may introduce direct and indirect effects on other species. As a result, Paine's definition has been broadened to include non-trophic interactions in the community, with emphasis on species with a role disproportionately large compared to their abundance (Paine, 1995; Power *et al.*, 1996), leading to the identification of keystone prey, keystone modifiers, etc. (Mills *et al.*, 1993). However, a debate is open on such broadening of the keystone concept (Davic, 2003), and although attempts have been made at providing an operational definition for keystone species (e.g., Power *et al.*, 1996) a high level of ambiguity has been attributed to the keystone term (Mills *et al.*, 1993; Davic, 2003). As a consequence, the term has been often applied loosely (often using it as a synonym for key or even dominant species) and a degree of uncertainty has to be associated with their identification. The main sources of uncertainty in the keystone species definition and identification are discussed in the following paragraphs.

4.3.1. The issue of abundance – ecological dominants, habitat species, *et al.*

One of the key features of the keystone status of a species is associated with its disproportionate effect on the community/ecosystem compared to its abundance/biomass (Power *et al.*, 1996; the keyword being 'disproportionate'). In the absence of a quantitative evaluation of the strength of the effect and the relative abundance/biomass of the species (*cf.* food web models; Section 4.8), assessing the keystone role of a species may prove to be difficult, and a degree of subjectivity is introduced, even when it is based on sound evidence of a significant and important impact. Some authors have taken the keystone definition above as an indication that relative low abundance is a prerequisite of keystone species (Piraino *et al.*, 2002), also identifying them as subordinate species (Olff *et al.*, 2009), whereas species with high abundance are less likely to be considered keystones. Therefore, the abundance of a species may constitute an issue for its keystone definition.

Keystone species have been clearly contrasted with dominant species, the latter having similarly large effect on the system but only by virtue of their high abundance or biomass (Power *et al.*, 1996). Nevertheless, in some cases the keystone status has been attributed to species that have high abundance (often ecological dominants), and this has led to some criticism (Piraino *et al.*, 2002). The difficulty in deciding how disproportionately rare a species must be to be considered as a potential keystone has contributed to this ambiguity. A degree of uncertainty may be therefore associated with species that occur in high abundances. An example reported by Piraino *et al.* (2002) included the common jellyfish *Aurelia aurita*. This species has been included in the catalogue as a keystone predator in agreement with Olesen (1995) who reported a study in a shallow bay in Denmark, which showed the species ability to control zooplankton and consequently community trophic structure. Significant zooplankton depletion was reported to be most likely only with very high jellyfish abundance, where population clearance potential was considered as proportional to jellyfish density (Olesen, 1995). This proportionality between species effect and abundance seems to contrast with the requirement for keystone species definition therefore doubts have been arisen on whether the species has to be considered a key or keystone species (Piraino *et al.*, 2002). Similar considerations may apply also to other planktonic species, for example, *Calanus finmarchicus*, a dominant calanoid copepod in North Atlantic Ocean, reported as a keystone species in marine planktonic food webs due to its pivotal role in the transfer of energy between primary producers and planktivorous fish, fish larvae and higher trophic levels (Beaugrand *et al.*, 2003; Mayor *et al*., 2007).

The criticism on the attribution of keystone status to dominant species extends to habitat forming (or structural) species, which, by definition, are dominant in the habitat they create (although this is also a matter of scale, as explained in section 4.3.5), as well as to abundant habitat modifiers (Piraino *et al.*, 2002). An example is the gaping file shell (*Limaria hians*), a habitat modifier (engineer) species reported in the catalogue. Hall-Spencer and Moore (2000) identified *L. hians* as a keystone species, as through nest construction and reef forming the species modifies physical, chemical and biological processes at the sediment–water interface whilst the nests support a high diversity of associated organisms in coarse-grade sediments. The porous nature of the *L. hians* nests allows currents to circulate, preventing smothering of the underlying infauna, hence providing an additional biodiversity value to the system. Similar effects have been attributed to other structural species, whereby the promotion of biodiversity is through provision of additional substratum, and these include plants (e.g., eelgrass and *Posidonia*, having also an engineering role through promotion of sediment stabilisation; Boström *et al.*, 2006; Teixeira *et al.*, 2014), macroalgae (e.g., kelp; Birkett *et al.*, 1998; Teixeira *et al.*, 2014), corals (e.g., the cold water coral *Lophelia pertusa*; Rogers, 1999) and reef-building or bed-forming invertebrates (e.g., mussel beds, oyster beds, maerl beds, *Sabellaria* reefs; Holt *et al.*, 1998; Ragnarsson and Raffaelli, 1999; Dinesen and Bruntse, 2001; Saier, 2002; Smyth and Roberts, 2010; Crowe *et al.*, 2011; Ragnarsson and Burgos, 2012; Todorova, 2013; Teixeira *et al.*, 2014).

Although the occurrence of a species in high abundance may increase the difficulty in deciding how disproportionately large its effect is on the ecosystem, it should not necessarily be a reason to exclude *a priori* a species from keystone status. Other evidence may support the disproportionate effect of the species, hence a case-by-case assessment needs to be undertaken. An example is the tubeworm *Serpula vermicularis*, included in the catalogue as a keystone habitat species. This is a reef-forming species that has been reported to support a highly diverse community (e.g. in Scotland, a 0.1 m^2 reef area has been estimated to support 163 taxa and 12,756 individuals), compared to other biogenic polychaete habitats (Chapman *et al.*, 2012). The species may occur in high abundance as reefs, hence doubts might arise on its keystone role. However, Chapman *et al.* (2012) found that a hyperbolic relationship occurs between community diversity and the reef size. This would suggest that there is a disproportionate (positive) effect of the reef size on the biodiversity of the community, supporting the keystone status of the species. The question of locally dense populations of these habitat building species can also be linked to the broader question of the relationship between habitat complexity, scale (and resolution) of analysis and biodiversity. There is also the issue of whether the spatial configuration of a patchy distribution has significant ecological effects, a topic addressed in the terrestrial environment by the field of landscape ecology (but see below a corraligenous example).

Finally, it is noteworthy that some species may have a significant role in supporting and regulating the ecosystem they are part of, and, although their high abundance may lead to difficulties in deciding whether the formal definition of keystones applies in such cases or whether they are 'just' key species, their importance is not diminished and the removal of such species would still lead to drastic changes in the community. Therefore, these species were considered highly relevant to biodiversity assessment which is being addressed in the DEVOTES Project, hence their inclusion in the present catalogue.

4.3.2. Promoter or reducer

Through the assessment of the primary impact of keystone species on the community and ecosystem, keystones have been identified in this study as biodiversity promoters or reducers. General patterns could be observed, for example habitat species generally contribute to an increase in local biodiversity, with inevitably positive effects on the biodiversity at the wider (e.g. regional) scale (Jones *et al.*, 1997). A similar effect at the regional scale has been predicted for other physical engineering species (e.g., bioturbators), although these species may have variable (positive or negative) impacts at the local scale (Jones *et al.*, 1997), as evident from the catalogue. Such variability is clearly dependent on the species and how it modifies the environment, hence directly or indirectly controlling the availability of resources and non-resource environmental conditions important to other organisms (Jones *et al.*, 1997; Olff *et al.*, 2009).

The allocation of a keystone species as a promoter or reducer of biodiversity is not always straightforward, as the resulting effect is dependent also on the scale at which it is considered and the context provided by both biotic and abiotic conditions (see also section 4.3.4). As a result, some species can be considered as modulators (i.e., with both a promoter and reducer role), as for example the lugworm *Arenicola marina*. The effect this keystone ecosystem engineer has on the community is variable, as through bioturbation this species may inhibit or enhance meiofauna and micro-organisms, depending on the receptor species, with the potential for cascading indirect effects on the community (Lei *et al.*, 2007; Volkenborn, 2005; Volkenborn *et al.*, 2009; Engle *et al.*, 2012). As a reducer, it decreases surface sediment stability and may inhibit other macrofauna species, e.g. tube-building worms (Flach, 1992a). Strong negative, density-dependent effects (through interference competition) have been also reported on the density of *Corophium volutator* and the juveniles of many worm and bivalve species (Flach, 1992b; Tyler-Walters, 2008a). In turn, tube- and burrow building, surface feeding species (sediment stabilisers) may be facilitated in the absence of the lugworm, as confirmed by exclusion experiments, thus facilitating bivalve recruitment (Volkenborn *et al*., 2009). Negative interactions resulting in mutual exclusion have also been observed between *A. marina* and common cordgrass *Spartina anglica* (van Wesenbeeck *et al.*, 2007). As a promoter, through bioirrigation *A. marina* increases oxygen supply to subsurface sediments and facilitates small zoobenthos and meiofauna in the burrows, as well as free-burrowing subsurface feeding species. Its bioturbation has also been shown to enhance the diversity of benthic protistan communities (Engle *et al.*, 2012). The difficulty in predicting the net effect of *A. marina* on the sedimentary habitats at the wider scale is further increased by the spatial and temporal variability of such effects which often generate a dynamic mosaic of patches dominated by either sediment stabilizing or destabilizing species (Volkenborn *et al.*, 2009).

The type of primary impact a keystone species has on the biodiversity of the system (as a promoter or reducer) can be also density-dependent, as in the case for example of the edible sea urchin *Echinus esculentus*, identified as a keystone predator in the NE Atlantic Region (Birkett *et al.*, 1998; Curran *et al*., 2003; Tyler-Walters, 2008b). This is an important grazer of epiflora and epifauna in the subtidal, and it may have a keystone role in kelp communities, where its grazing may control the lower limit of *Laminaria hyperborea* beds and, when abundance is moderate, the formation of small clearings in the undergrowth helps increase understorey diversity and habitat diversity by making space for new larvae and spores to settle (Tyler-Walters, 2008b). Therefore, when moderately abundant the species can be considered as a promoter, but where abundance is high, heavy grazing can result in 'urchin barrens' with a significant reduction in the overall diversity (Birkett *et al.*, 1998; Norderhaug and Christie, 2009).

The occurrence of indirect and cascading effects may increase the difficulty in identifying the final impact of a keystone on the system, even when sound evidence is used to substantiate this role. For example, when results from removal experiments are used (this has been identified as the best way to assess keystones; Mills *et al.*, 1993; Power *et al.*, 1996), it should be noted that these studies often concentrate on the effect on a limited number of components/species considered relevant and cannot take into account all the indirect interactions regulating the whole community or ecosystem. The consequences of these indirect interactions on the system diversity can be highly variable and in some cases difficult to predict, as many factors (or conditional probabilities; Olff *et al.*, 2009) may contribute to the resulting organisation of ecological networks. Although emergent structural properties and behaviour at the system level can be identified (Olff *et al.*, 2009), a certain degree of expert judgement has to be applied to infer the effects of keystone species on the whole system biodiversity (as promoters or reducers) from results of experimental studies, and a certain degree of uncertainty is therefore associated with such assessment.

Although keystone predators have been often characterised as reducers of biodiversity based on evidence, modelling or expert knowledge (e.g., rapa whelk *Rapana venosa*, Katsanevakis *et al.*, in press; common starfish *Asterias rubens*, Saier, 2001; squids, Tsagarakis *et al.*, 2010; Atlantic cod *Gadus morhua*, Pedersen *et al.*, 2008; grey seal *Halichoerus grypus*, Teixeira *et al.*, 2014), their effect as promoters have been also reported, depending on the area and context of the assessment (e.g., dusky grouper *Epinephelus marginatus*, Guidetti, 2006; grey seal *Halichoerus grypus*, Österblom *et al.*, 2007; Harvey *et al.*, 2003; Casini *et al.*, 2012). Some results have been difficult to interpret, leading to uncertainty on the type of ecosystem impact. For example, the analysis of a food web model developed for the West coast of Scotland (Haggan and Pitcher, 2005; Sayer *et al.,* 2005) indicated demersal top predator fish species as a keystone group (Heymans *et al.*, 2011). A dominant top-down control on the food web was assessed for this functional group (Heymans *et al.*, 2011) under the assumption that it consumes benthic invertebrates, pelagic fish and prawns/shrimps (Haggan and Pitcher, 2005). Both positive and negative impacts on the different components of the food web were highlighted (Haggan and Pitcher, 2005), but whether this resulted in an increase, or decrease in the local biodiversity could not be clearly ascertained.

4.3.3. Predator or prey

Although the assessment as keystone predators was relatively straightforward for top carnivores (see examples above), in some cases species (or groups of species) were found to have a pivotal role in the food web, acting both as intermediate consumers while also being key prey for a wide variety of predators. Although these keystones were identified under the label 'predator' in the catalogue to account for the fact that they exert a control on the system via prey-predator interactions (as opposed to other types of interactions), a clear bottom-up contribution to the overall effect on the food web could be identified for some species/groups, with a key role as prey. Two examples are macrofaunal deposit feeders identified as a keystone group in food web models for the English Channel (Heymans *et al.*, 2011), and sandeels (Frederiksen *et al.*, 2006). In the former case, the keystone group included mostly small invertebrates (e.g. annelid worms, amphipods), which are the main prey for diverse species at higher trophic levels (e.g. whelk, small demersal species, mullet, sole, dab, seabream) and have an important role in linking the detritus-based and pelagic-based components of the food web (Stanford and Pitcher, 2004; Araujo *et al*., 2006). In the latter case, sandeels (Ammodytidae) feed on zooplankton (mainly copepods) and are a key prey of fish (cod, haddock, whiting, saithe and mackerel), marine mammals (e.g. harbour porpoises) and seabirds (Atlantic puffin, guillemot, razorbill, kittiwake and tern) (Frederiksen *et al.*, 2006). There is a strong density-dependent link with breeding success and survival of seabirds, and sandeel abundance may also influence mortalities in harbour porpoises, which rely heavily on sandeels for food. In both cases, the species groups have been indicated as promoter of biodiversity, by virtue of their importance in sustaining predator densities and the negative effects their removal from the system may have on such predators and consequently on the whole community structure. Control on predator density is a key property of a keystone prey as originally defined by Holt (1977). The strong dependency of certain predators on the identified keystone prey (e.g., with harbour porpoises starving to death in the absence of sandeels) would suggest this effect to be unlikely in the cases identified above, although this could be assessed based on the available information (e.g., presence and abundance of alternative prey in the system). In any case, Mills *et al.* (1993) has shown how the keystone prey concept has been modified since Holt's definition to account also for those cases where the coexistence between the keystone prey and alternative (sensitive) prey is possible and the keystone species removal leads to a decrease in species diversity, hence the validity of this term for the species groups identified in the catalogue.

4.3.4. Context dependency and generality of keystones identification

It is widely acknowledged that the keystone status of a species is dependent on the context (Paine, 1995; Power *et al.*, 1996; see also section 4.3.6), including the abiotic and biotic conditions the species lives in at the time of the assessment (hence the importance of both spatial and temporal scales). This is the most likely reason for the perceived lack in generalities in the current keystone species literature, which Olff *et al.* (2009) have identified as a long list of specific case studies. It is also most likely responsible for the variability of keystone assessments across regions and habitats observed in this study, although the use of different experts (with different backgrounds, expertise, etc.) assessing different regions may have contributed in part to such an effect.

The context a species lives in affects not only its potential for being a keystone, but also the type of impact the species may have as a keystone in the system. An example of this is given by the common limpet (*Patella vulgata*). The keystone role of this species for the North East Atlantic Region has been ascertained through exclusion experiments, and it is associated with the fact that it grazes on fucoid algae, thus controlling their biomass and system productivity and functioning (Hawkins, 1981; Johnson *et al.*, 1998; Coleman *et al.*, 2006). Coleman *et al.* (2006) reported that the effect of limpet grazing on rocky shore communities is not correlated with the species biomass, suggesting that a significant effect can be observed even with lower limpet abundance, in agreement with the keystone definition (Power *et al.*, 1996). However, the ability of the limpet in controlling vegetation (hence its impact) depends on algal recruitment, and latitudinal differences have been observed (Coleman *et al.*, 2006). In particular, at northern latitudes, limpets were found to promote small-scale spatial variability in the algal cover and their exclusion led to change of community into one dominated by *Fucus*. In turn, at southern latitudes (coast of Portugal), where fucoid algae were sparse/absent, limpet presence prevented the establishment of heterogeneous algal assemblages. As a result of this context dependency, a spatial variability was included in the assessment of the impact of this species within the wider regional area, with the role as a promoter or reducer of diversity having been ascribed to the common limpet at higher and lower latitudes, respectively.

The context dependency introduces a degree of uncertainty on the keystone species assessment and their generalisation at regional level, and it is a factor that needs attention when attempts are made at using keystone species as indicators.

4.3.5. Parallel functional roles and scales: a coralligenous example.

As explained in other sections, Paine's (1969) original concept was based on a strict/limited understanding, which has since expanded to cover different types of keystones. One of the ideas that it did not encompass was parallel keystone roles of different species over large geographical scales. An example of this is the case of coralline algae constituting maerl beds (notably genus *Phymatolithon* or *Lithothamnium*), in the Atlantic Ocean and the Mediterranean Sea and coralligenous habitats in the Mediterranean Sea (genus *Mesophyllum* or *Lithophyllum*). Other examples of this may be seen in the role of the coastal sedimentary habitat species *Zostera* spp. in northern waters and *Posidonia oceanica* in Mediterranean waters or, on hard bottoms, *Laminaria* spp. in northern waters and *Cystoseira* spp. in the Mediterranean playing similar roles. All these species create complex and sometimes quite extensive habitats sheltering a very high species richness that would simply disappear if the unique species disappeared in that geographical area. Numerous examples, probably at a smaller scale, are also significant such as engineer polychaetes (e.g. *Sabellaria* reefs, consolidated sediments by *Lanice*). Coralligenous and *Posidonia* meadows, by creating multiple habitats and sheltering species of commercial importance, they also play a significant socio-economic role (small scale fishing, angling, red coral harvesting, scuba diving) and provide other services (CO_2 sequestration, Martin, 2013; Noisette, 2013; sediment stabilisation, Pedel *et al.*, 2013).

The complexity generated by most habitat species requires that communities should be considered at different scales. Two types of 'theoretical' systems may be discriminated: i) large and homogeneous habitats with constant factors of influence, and common keystone species (this type of habitat have a lower species richness than complex habitats); and ii) patches of different communities distributed at very large scales but representing a very small surface in comparison to the surface ratio they occupy, for examples bio-construction by animals, algae or plants. This is the case of Mediterranean coralligenous communities (including those reported in the catalogue under specific species or gorgoanians or maerl): they are considered as an underwater landscape or ecological puzzle (UNEP–MAP–RAC/SPA, 2009), having a very complex structure, allowing the development of several community types (Laborel, 1961; Laubier, 1966; Hong 1980; Laborel, 1987; Ballesteros, 2006). These communities are patchworks. They are very attractive for numerous predators and often represent biodiversity hotspots in very small areas. They have an important role as nurseries and food provision areas for numbers of pelagic species, or can be reproductive focus areas. Coralligenous habitats concentrate more than 1600 species on dozens of micro-habitats (Ballesteros, 2006). These kinds of habitats are not continuous, and their distribution is very relative to surrounding micro-conditions (Virgilio *et al.*, 2006). These habitats can be considered as oases in the desert, concentrating communities but influencing surrounding environments. An example of this diversity can seen simply with communities with basal concretions made of coralline algae (*Lithophyllum* and *Mesophyllum*) from the infralittoral and circalittoral zones. Michez *et al.* (2011) has cited 10 remarkable facies, eight of which are illustrated in Figure 7, each facies characterised by one species.

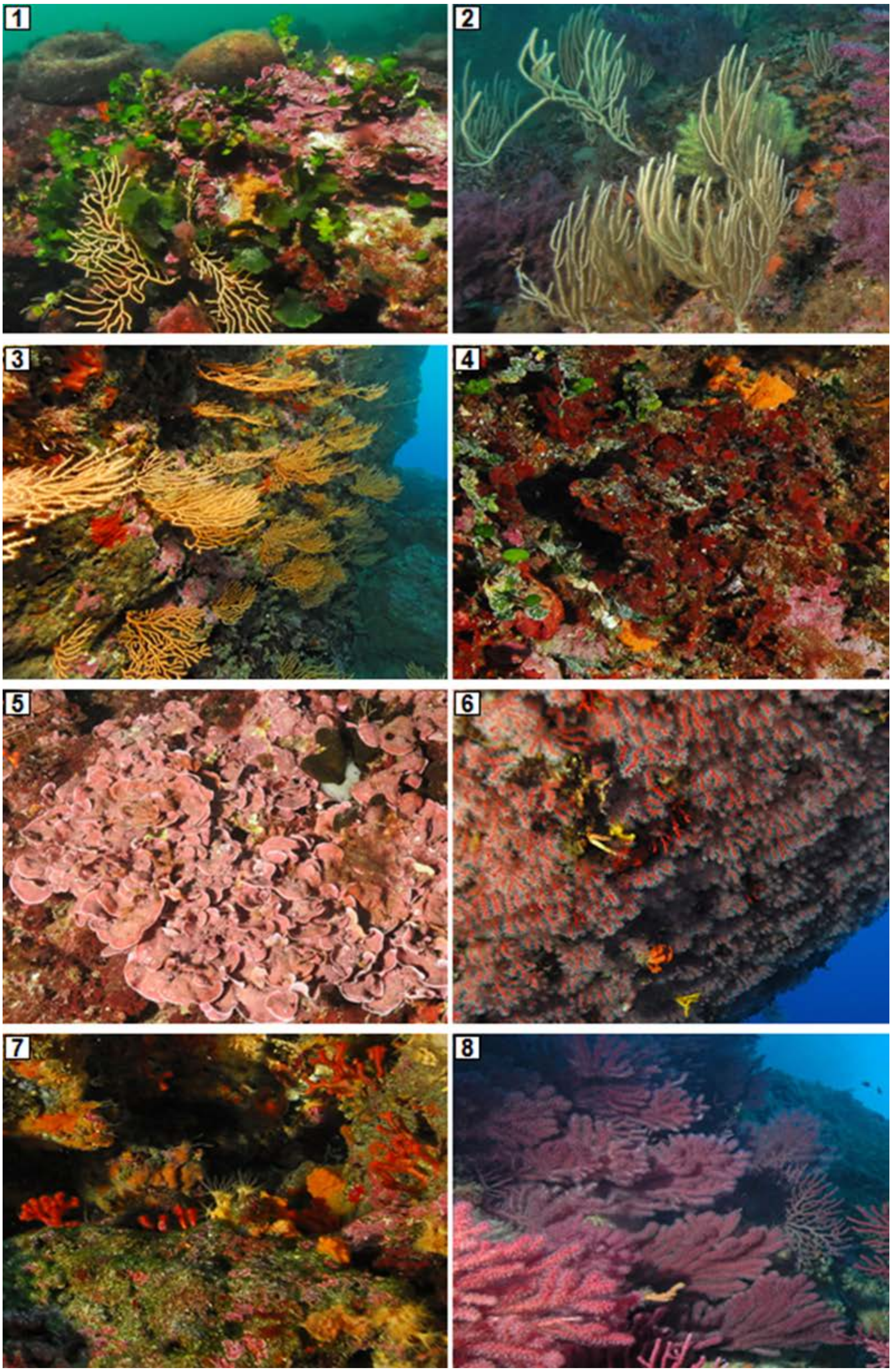

Figure 7. Examples of coralligenous facies of (1) *Udotea peteolata* and *Halimeda tuna*, (2) *Eunicella singularis*, (3) *Eunicella cavolinii*, (4) *Peyssonnelia squamaria*, (5) *Mesophyllum alternans*, (6) *Corallium rubrum*, (7) *Myriapora truncata* and (8) *Paramuricea clavata.* Photos courtesy of CNRS-IMBE.

A major issue is how to take in account all of the different keystones species of these diverse communities, representing small areas but certainly very high influences on ecosystem functioning on large scales considering that:

- these populations are connected,
- they have similar or comparable functioning on large scales,
- at regional and probably at subregional level, some keystone species with an identified role are often replaced by another close species (studies about this on coralligenous habitats are in progress in the CIGESMED project (Coralligenous based Indicators to evaluate and monitor the 'Good Environmental Status' of the Mediterranean coastal waters; http://www.cigesmed.eu)),
- many species are probably complex of species which can live in sympatric mode (Egea, 2011; Weber *et al.*, 2013).

A useful way to answer the question above could be to identify 'functional' keystone groups, by pooling together keystone species that belong to a coherent group of taxa within an identified functional group. This grouping allows the discrimination of a keystone species taking into account the probable area of influence of the keystone group, at a wider spatial scale than that defined by the considered habitat. This functional grouping also allows the accounting for the temporal aspects of the keystone species influence on communities, whether it is in months, years, centuries or more (Teixidó *et al.*, 2011). Other keystone qualities should be proposed with a standardised vocabulary. This then becomes a major challenge allowing for a proper assessment of human impacts on marine habitats (Claudet and Fraschetti, 2010). All these qualities would also form very useful criteria to improve quality of models and construct the necessary baselines to survey for Good Environmental Status.

4.3.6. Are some species keystone in some areas/habitats but not in others?

Functionality of keystone species

Central to the discussion on context dependency of keystones is that a species that serves a keystone role under a set of biotic and/or abiotic conditions may not be a keystone species under other conditions (Menge *et al.*, 2013). It is clear that for a species to have a keystone role, its removal from, or depletion within, the community would cause marked changes throughout the system. This in turn implies that the pivotal functions carried out by that particular species are not shared with any other species, at the same magnitude, or scale. Thus, assessment of functional redundancy can contribute to defining whether a species has a keystone role within a particular habitat/region or not (Nuñez and Dimarco, 2012 and references therein). Species richness is variably linked with productivity and functionality within marine ecosystems (see review in Gamfeldt *et al.*, 2014), and functional redundancy may contribute to population resilience, such as in fish stocks (Rice *et al.*, 2013). However, relationships between species richness, functional diversity and thus also functional redundancy are unlikely to be the same across all habitats within the four European seas. It is highly likely then, that some species which have a keystone role in one region, or habitat, will not be considered keystone in another.

The fact that a high number of taxa in the DEVOTES Keystone Catalogue (84%) are recorded as keystones only from one region ('uniques' in the catalogue), is in agreement with this idea, as we would not expect such a high number of taxa to have a very narrow, restricted distribution. It is rather the fact that under different environmental conditions the characterisation of a species may differ.

To assess the consistency of keystoneness across habitats and geographical areas, a number of questions and considerations can be posed to the marine environment keystone categories of Mills *et al.* (1993) (see Section 1.1):

1. *Keystone predators*: Is there another predator in the area/habitat, which has the capacity to prey upon the same ecologically significant species and could adopt the niche of the keystone species, were it to decline?
    - The niche potentially could be filled by another species switching to the prey of the initial keystone species, colonisation from other nearby habitats, or by rapid reproduction/establishment under conditions of reduced competition.
2. *Keystone prey*: Are there sufficient other prey species available to the predators, which would sustain those populations, even after the preferred prey is reduced?
    - The likelihood of other prey species being utilised is greater where the relevant predators are more generalist feeders, as opposed to being morphologically or behaviourally specialised to one or only few prey species. Thus the keystoneness of prey species is also influenced by the degree of flexibility of their predators.
3. *Keystone modifiers*: Would the effects of the habitat altering activities of species, such as bioturbation or substratum modification, persist after that organism is removed? Alternatively, would another organism occupy that niche to perform the same function (at the same scale)?

Region-specific keystone species and universal keystone roles

The zooplankton copepod *Calanus finmarchicus* is listed in the catalogue as being highly abundant in the NEA Regional Sea, where it extends northwards to the Arctic (Chust *et al.*, 2014). In the North Sea, the boreal *C. finmarchicus* overlaps in distribution with the more temperate *C. helgolandicus* (Jónasdóttir and Koski, 2010; Beaugrand *et al.*, 2014). Within its distribution range, *C. finmarchicus* has a keystone function both as a predator, preying on phytoplankton primarily diatoms, dinoflagellates and ciliates, and as a major prey item for fish, including commercial stocks of cod and herring. If *C. finmarchicus* was depleted, more phytoplankton would be available to other pelagic organisms, and a larger portion also may fall ungrazed to become available to the benthos. However, fish stocks would suffer a food shortage, unless another equivalent species were to fill the vacant niche. *C. helgolandicus*, may be prevented from moving north by the temperature barrier and although many other copepod species co-exist, they have a smaller individual biomass, such that larger numbers would be required to achieve the same energetic prey-value, assuming the predators could shift to smaller prey species. Although the other Regional Seas host various species of *Calanus* copepods, none are listed in the catalogue as being keystone. If it is assumed that the catalogue entries are representative of pan-European expert knowledge, then in other areas, no single copepod species dominates the pelagic food web to the same extent, as is the case in the NEA. If this were the case, then the presumably low functional redundancy of *Calanus finmarchicus* in the NEA may explain its keystone status as a single species, whereas in other areas, the keystone role is played by the group zooplankton (or conceivably copepods) as a whole.

The invasive jellyfish *Mnemiopsis leidyi* is also present in all regional seas considered in the report. Important effects on the ecosystem have been reported from the Black Sea and the NEA, whereas its influence in other European seas is currently too low to regard this species as keystone. This could be related to its lower abundance and narrower distribution in the other seas. As an invasive it may have non-optimal living conditions in those regional seas or too short time span between species introduction and impact and effects on the native ecosystem.

Another example of regional-specific keystones, but with universal keystone role, is within the angiosperms. The seagrasses *Cymodocea nodosa*, *Halophila stipulacea* and *Posidonia oceanica* are listed as keystone species in the Mediterranean, but not elsewhere, simply due to their distribution. Likewise *Zostera* species are listed with an equivalent keystone role in the Baltic, Black Sea and the North-east Atlantic. *Zostera noltei* is distributed in all regional seas, but is only regarded as keystone species for the NEA and the Black Sea. In the Baltic Sea it is distributed in the West only at salinities above 15 psu and it occurs locally with low abundances. Other species, such as those of the genus *Ruppia*, have wider distribution and are more abundant in the same (littoral) habitat. *Zostera*'s role as habitat species is taken over by *Ruppia*, which is more adapted to the specific environmental conditions of the Baltic Sea. In the Mediterranean Sea, *Z. noltei* is important in estuaries and lagoons, where it may form dense stands, but *Posidonia oceanica* (followed by *C. nodosa*) is the primary seagrass species forming extensive coastal underwater meadows hosting a diverse community of other species (MESMA, 2010; Salomidi *et al.*, 2012). Thus, seagrasses as a group can be considered to have a keystone role across all the Regional Seas, but the characteristic species are geographically determined.

For the same reason, burrowing megafauna was listed in the catalogue as having a keystone role as an engineer species and enhancer of biodiversity (Norwegian Sea). Large populations of various decapods (e.g. *Nephrops norvegicus*, *Pandalus borealis*, *Munida* species) have a strong bioturbatory function in North and Norwegian seas shelf sediments (OSPAR 2010a). Exactly which species dominates in a particular area is dependent on physical and geographic factors, but their role in sediment irrigation is similar. *N. norvegicus* was only listed as a keystone species in the Mediterranean Sea (perhaps demonstrating the difficulty in including 'disproportionate effect' against abundance as a criterion for assessment). As was the case for *Calanus*, defining whether an individual species or functional group should be considered the keystone is a matter for discussion, and will depend on the scientific questions asked. This issue is likely most problematic for species-rich groups such as invertebrates, where hundreds of species co-exist within the same area, relative to, for example, marine mammals, where the species pool is smaller.

Habitat-specific keystone species and keystone functional groups

Many keystone species or keystone functional groups, such as the above-mentioned burrowing megafauna, occur in association with specific habitats, including those provided by other organisms. One of the habitats listed by OSPAR (2010b) as being of environmental concern, or potentially 'rare or declining', is deep-sea sponge assemblages, primarily characterised by the large *Geodia*, within which several species co-exist (*Geodia* will be included in the next catalogue version). Squat lobsters in burrows can be seen under almost every *Geodia* sponge, such that not only do the sponges have a keystone role in benthic remineralisation through their pumping activities, but they provide habitat for bioturbating organisms, thus also contributing to sediment irrigation. Sponge aggregations are sensitive to demersal trawling, and thus sponge grounds in fishery areas are vulnerable to deterioration by physical destruction/removal. This, in turn, removes the shelter for other organisms, which likely would cause cascade changes throughout the benthic system. Hence, the squat lobsters might be considered as key species because of their bioturbating activities, but they in turn are benefitted by the properties of the sponge aggregations. Environmental regulation, in this case regarding restriction of bottom trawling in sponge-dominated areas, has to take into consideration not only individual keystone species, but keystone functional groups and associations.

4.4. Do keystones belong to specific habitats, areas, or biological components?

With the looser keystone definition used in this review, 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, habitats and areas. Undoubtedly, that was a result to expect 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; Begon *et al.*, 1996). Nevertheless, there is an apparent emphasis in the DEVOTES list of keystones towards more benthic invertebrate species (50%), more Mediterranean species (56%) and more species from the sublittoral habitat (71%), with 30% of the listed species falling within all three categories (Mediterranean benthic invertebrates from sublittoral habitats). 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 is not without a reason. However, we cannot exclude the possibility of a bias towards the indication of benthic invertebrates as potential keystone species, which could relate to the higher number of ecological studies focusing on benthos, resulting in increased knowledge on their community strength and interactions; as well as to a higher expertise in this field of the scientists involved in the specific task. It could be also argued that size (and a few other attributes) does matter; the Mediterranean is a very large and a very deep sea encompassing different environments and habitats, and the largest and deepest enclosed sea on Earth (Coll *et al.,* 2010). Moreover, the increasing threats to Mediterranean marine ecosystems, such as habitat loss and degradation, fishing impacts, pollution, climate change, eutrophication, alien species, may cause significant biodiversity loss, which may, in turn, affect keystone status and increase the number of species that could have keystone role (Power *et al.*, 1996).

The increased percentage of keystone species listed under the sublittoral habitats reflects the extensive investigation of this zone, but it can further be viewed as a result of the high environmental complexity, the high biodiversity, and the wide variety of marine communities present in this zone, which result in many different species being candidates in many different habitats for largely affecting community structure, characteristics and status. It is also a zone of multiple drivers acting together and of numerous uses and threats leading to cumulative impacts in many regional seas (Halpern *et al.,* 2008; Micheli *et al.,* 2013; Coll *et al.*, 2012; Korpinen *et al.,* 2013).

4.5. Do keystone species have the same impact/importance and types of effect?

The keystone species concept rests on the idea that not all species have equal significance in community dynamics. Following the discussion on uncertainties in defining and categorising keystone species, where context-dependent issues were raised, could we broaden our scientific questioning and possibly extend the idea of unequal species within keystones?

Menge *et al.* (2013) note that keystone species are distinguished by both the strength of their interactions with other species and the large indirect consequences of these effects through the food web. It is safe though to assume that among the many and diverse species and groups listed in our catalogue, there must be wide variability in the strength, mechanism and effects of their interactions. In previous sections we emphasise the problems we face with assessing the role and impact the same keystone species have on communities, which may differ depending on abundance, area, scale and overall conditions. Having this in mind, is it safe to reckon that there exists an extra point of consideration, which is the relative importance between keystone species? It is not a question we can necessarily answer here but the following examples from DEVOTES Keystone Catalogue will help to illustrate this issue.

Alexandrium minutum and *Nephrops norvegicus*: two contrasting engineers

Despite these two potential keystone species are listed in our catalogue as having an engineering role, their impact and the way through which they affect their communities differ. This is certainly something to be expected not only because they belong to different biological components but also due to the different environments they occur. *A. minutum* is a dinoflagellate member of the phytoplankton, which is viewed as having a reducing effect on water-column communities by creating harmful algal blooms, which subsequently reduce light penetration, thus affecting primary production. On the other hand, the megabenthic decapod *N. norvegicus* is a biological bulldozer that can dig and live 20-30 cm deep in the sediment. Its bioturbating life mode has a promoting effect on benthic diversity by increasing habitat complexity as well as by reworking/resuspending the sediment and associated food particles.

Mytilus spp. and *Posidonia oceanica*: the engineer, habitat forming role from a different perspective

Species of the bivalve genus *Mytilus* and the seagrass *Posidonia* are included in the catalogue as both engineer and habitat species. In the case of *Mytilus*, which is overall believed to have a positive effect on its ecosystem, there is a diversity of ways by which it can affect the benthic communities: the spaces between the mussels provide refuges for a diverse community of species increasing habitat complexity (Donadi *et al.*, 2013); they participate in water purification, thus tackling pollution, and in the cycle of trace- and other important elements (e.g. oxygen, nitrogen, hydrogen, carbon); they are also crucial food resources to birds. *Posidonia* also has a promoting impact on the ecosystems in which it occurs, through different paths. It is the species itself that increase habitat complexity through the complexity of its structure (rhizomes and leaves at small scale, matte and extensive meadows at larger scale), providing food, shelter and spawning fields to many organisms, but also by enhancing sediment stability. Further to this, *Posidonia* meadows oxygenate water and sediment, are part of biochemical marine cycles, control the transparency of the water column as they favour retention of suspended particles, and protect shorelines by stabilizing sediments through the networks they form with their rhizomes.

Cystoseira spp. and *Serpula vermicularis*: habitat species forming different substrata

Several species of the macroalgae genus *Cystoseira* have been included in the catalogue from the Mediterranean and the Black Sea, their promoting keystone role stemming from the fact that by forming extensive meadows on wave exposed sites they provide habitat and shelter to many epiphytes, invertebrates and fish, therefore increasing biodiversity. *Cystoseira* forests are part of the brown algae fucoid beds that include the *Sargassum* and *Fucus* genera present in the NEA and the Baltic Sea respectively. Sabellid and serpulid polychaetes are inhabiting and are parts of several habitats, including those of red algae concretions, coralligenous communities, gorgonian gardens, caves caverns and vertical walls as well as deep circalittoral waters. They are considered bioconstructors and form reefs throughout European waters although more frequently in the NEA (OCEANA, 2006). As noted in a previous section, the intertwining of the tubes of *Serpula vermicularis* produces extensive reefs that support highly diverse communities (Chapman *et al*., 2012).

Tursiops truncatus ponticus and *Mnemiopsis leidyi*: predators of contrasting size and impact

This pair of species was selected to provide an example of keystone predators from the same region but with a different primary impact. In the Black Sea, the jellyfish *M. leidyi* is a major carnivorous predator of edible zooplankton, pelagic fish eggs and larvae and it is associated with fishery crashes. Its presence in the food web causes cascading effects, as the strong grazing on zooplankton reduces food resources for planktivorous and predatory fish, while favouring phytoplankton growth. In contrast, the Black Sea bottle-nose dolphin, which is by far larger but has lower abundance compared to the reducer jellyfish, will have cascading effects if removed from the food web. It is primarily a piscivorous feeder on both benthic and pelagic fishes, and represents the functional group of top predators in the Black Sea, fishing down the food web and therefore controlling the populations of other predators. Therefore, its impact is believed to enhance biodiversity as the removal of this top predator is expected to have cascading effects on the whole pelagic food web down to phytoplankton, and nutrient and regime shifts.

From the above examples it is obvious that species that have been assigned under the same keystone type may have a different primary impact on their communities, or even the same impact but through different and often diverse mechanisms. The magnitude of keystone species significance could be roughly assessed by the multitude and type of mechanisms through which they participate and affect the ecosystem. For the *Mytilus*/*Posidonia* case, both species participate in coastal ecosystems through various processes and we would expect that their removal will cause the disappearance of all the associated organisms and will disturb the ecosystem. However, we could speculate that the multiplicity and magnitude of mechanisms provided by *Posidonia* would outweigh those of *Mytilus*, leading to more dramatic effects on coastal ecosystems. Nevertheless both species and their ecosystems are completely different reflecting different environmental conditions and unless systematic observation and monitoring is involved and experiments are carried out, we cannot conclude on their relative importance.

4.6. Keystones and alien species

Biological invasions are considered to be one of the most important direct drivers of biodiversity loss and a major pressure on several types of ecosystems, with both ecological and economic impacts (MEA, 2005). In marine ecosystems, alien marine species may become invasive and displace native species, cause the loss of native genotypes, modify habitats, change community structure, affect food-web properties and ecosystem processes, impede the provision of ecosystem services, impact human health, and cause substantial economic losses (Katsanevakis *et al*., in press).

Most alien species that were herein included as keystones were due to their role as ecosystem engineers, and their capacity to “directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain, and/or create habitat” (Jones *et al.*, 1994). These novel habitats differ in composition and structure from past and present native habitats, and result in different species interactions and functions. In general, ecosystem engineers benefit the populations of some species, while they cause the local decline of others (Katsanevakis *et al.*, in press). Berke (2010) classified ecosystem engineers into four broad process-based categories that are not mutually exclusive: structural engineers, bioturbators, chemical engineers, and light engineers.

Alien structural engineers generally enhance diversity and richness, although not in every context. This category consists of organisms that create or modify structural elements of the habitat, such as reef-builders (e.g. *Ficopomatus enigmaticus*, *Hydroides* spp., *Crassostrea gigas*, *Spondylus spinosus*), tube-builders (e.g. *Petricolaria pholadiformis*, *Mya arenaria*), macroalgae (*Acrothamnion preissii*, *Asparagopsis armata*, *Bonnemaisonia hamifera*, *Caulerpa cylindracea*, *Caulerpa taxifolia*, *Codium fragile* subsp. *fragile*, *Gracilaria vermiculophylla*, *Grateloupia turuturu*, *Lophocladia lallemandii*, *Polysiphonia morrowii*, *Sargassum muticum*, *Stypopodium schimperi*, *Undaria pinnatifida*, *Womersleyella setacea*), and seagrasses (*Halophila stipulacea*). With the exception of most alien macroalgae and the coral *Oculina patagonica* that might diminish structural complexity and species richness by outcompeting native assemblages, these species generally increase the spatial complexity of benthic habitats, offer novel microhabitats, and provide nursery grounds, shelter for macro- and microfauna, and strongholds for a diverse community of algae and invertebrates (Katsanevakis *et al.*, in press).

Burrowing infauna has important roles in the geophysical environment and in community dynamics, being agents of sediment transport and porewater flux (Aller *et al.,* 2001). The following alien species fall into this category of ecosystem engineers: *Marenzelleria* spp., *Eriocheir sinensis*, *Anadara kagoshimensis*, *Anadara transversa*, *Ensis directus*, *Mya arenaria*, and *Venerupis philippinarum*. Due to their burrowing activity, these species can increase sediment water and oxygen content and enhance solute exchange with the overlying water column, thereby affecting nutrient cycling (e.g. Vaughn and Hakenkamp, 2001; Queirós *et al*., 2011; Norkko *et al.*, 2012). They also increase sediment erosion and re-suspension rates (Sgro *et al.*, 2005), substantially modifying both benthic and pelagic habitats.

Chemical engineers alter the chemical matrix of their environment through physical or physiological activities; many of them are also structural engineers or bioturbators (Berke, 2010). All the burrowing species mentioned above are also included in this category as their activity extends the oxygenated layer deeper into the sediment, thereby increasing local redox potential and contributing to sediment-water solute exchange (Aller *et al.*, 2001). Other alien chemical engineers are: the bivalve *Arcuatula senhousia*, as it deposits large amounts of organic matter, leading to the shallowing of the redox potential discontinuity layer (Mistri *et al.*, 2004); *Caulerpa cylindracea*, as it can form compact multilayered mats up to 15 cm thick that trap sediment, beneath which an anoxic layer may develop (Klein and Verlaque, 2008); *Crepidula fornicata*, as it precipitates the transformation of sandy sediment into a muddy one with a high organic content that becomes rapidly anoxic and unsuitable for other species; the phytoplanktonic species *Karenia mikimotoi* and *Phaeocystis pouchetii*, whose dying, sinking blooms cause anoxia; the diatom *Coscinodiscus wailesii*, whose copious mucilage can aggregate, sink and cover the seabed, likely causing anoxic conditions; *Mnemiopsis leidyi*, which can cause anoxia in near-bottom waters due to massive deposition of dead individuals (Streftaris and Zenetos, 2006).

Light penetration is an important physical property of euphotic habitats, as it defines the depth at which photosynthesis can occur. Bloom-forming phytoplanktonic species, such as *Alexandrium minutum*, *Alexandrium monilatum*, *Karenia mikimotoi*, *Phaeocystis pouchetii*, *Coscinodiscus wailesii*, *Fibrocapsa japonica*, and *Pseudochatonella verruculosa*, reduce light penetration. *Mnemiopsis leidyi* causes the collapse of zooplankton, an increase in phytoplankton (which is free from grazing pressure), and thus a reduction in light penetration. All alien filter feeders, such as the bivalves *Anadara kagoshimensis*, *A. transversa*, *Arcuatula senhousia*, *Brachidontes pharaonis*, *Chama pacifica*, *Crassostrea gigas*, *Ensis directus*, and *Pinctada imbricata radiata*, the gastropod *Crepidula fornicata*, the barnacle *Amphibalanus improvisus*, and the reef-forming polychaete *Ficopomatus enigmaticus* reduce turbidity and may substantially increase light penetration, leading to increased depths at which macrophytes grow and thus supporting greater biomasses per unit area by providing more three-dimensional habitat (Katsanevakis *et al.*, in press). On the other hand, many of the alien macroalgae either build up thick mats or are so large that they reduce the amount of light reaching other primary producers.

Apart from alien ecosystem engineers, the alien herbivores *Siganus luridus* and *Siganus rivulatus* were considered as keystone species due to their massive impact on sublittoral shallow algal communities. *Siganus* spp., through overgrazing, radically alter the community structure and the native food web of the rocky infralittoral zone, depriving the ecosystem of the valuable functions of algal forests (Sala *et al.*, 2011). These species contribute to the transformation of the ecosystem from one dominated by lush and diverse brown algal forests to another dominated by bare rock. Some of these algal forests, such as *Cystoseira* spp. forests (also keystone species), are ecologically very important as nurseries for a number of littoral fish species.

4.7. Ecosystem models and keystones assessment

As shown from the catalogue analysis, ecosystem models (i.e., models describing trophic interactions within the ecosystem) are among the methods used to identify species or functional groups with a keystone role in marine communities. Graph theoretical methods have been applied to the analysis of food web topology (or structure) to allow *a priori* identification of keystone species through the evaluation of the impact of species removal on the web fragility and persistence (e.g., through measures of network fragmentation and secondary extinctions) (Jordan *et al.,* 1999; Solé and Montoya, 2001; Ortiz *et al.*, 2013). Such studies have highlighted the high strength of interaction links in model food webs (e.g., highly connected species, omnivory) as possible characteristics for *a priori* identification of keystone species.

The species interactions in an ecosystem have been investigated also through qualitative loop models (based on Loop Analysis), whereby relationships between species and/or functional groups are assessed qualitatively based on the type of reciprocal (positive, negative or zero) influence between the elements (Ortiz *et al.*, 2013). A qualitative keystone species index was obtained by determining the effect of a change in these qualitative relationships on the stability of benthic ecosystems (Ortiz *et al*., 2013).

Mass balance models (Ecopath with Ecosim, EwE; Christensen *et al.*, 2004) have been widely used in recent years to assess the role of marine food web components, with different approaches being applied. For instance, Okey *et al.* (2004) assessed the keystone potential of food web components by evaluating the effects that functional groups removal has on the biomass of marine food webs through dynamic simulations. Mixed trophic impact (MTI) analysis has also been recently applied to mass balance models in EwE to estimate to what degree (also called ‘keystoneness’) functional groups have a keystone role in marine ecosystems (Libralato *et al.*, 2006). This approach assesses the strength of the impact a component (species or functional group) has on the different elements of the ecosystem, as resulting from small change in biomass of such component in the dynamic simulations and the MTI analysis respectively. More recently Lai *et al.* (2012) have used the EwE software to assess and quantify species importance through their centrality and uniqueness in the food web, as a central node may affect others in the network and a unique position cannot be easily compensated.

Despite the existence of different modelling techniques to assess keystone species, our catalogue has evidenced the strong role of the mass balanced modelling approach for evaluating keystone species within marine ecosystems. Ecopath with Ecosim was indeed the only model able to provide keystone entries for the different European regional seas. In particular, the Keystone catalogue was built on the work conducted by DEVOTES WP4 Deliverable 4.1, which aimed at reviewing the current capability of the modelling community to inform on indicators outlined in the MSFD (Piroddi et al., 2013). This study focused mainly on biodiversity related descriptors: biological diversity (D1), non-indigenous species (D2), food webs (D4), and seafloor integrity (D6) (Piroddi *et al.*, 2013; submitted a). As the WP4 catalogue was comprehensive, few models with keystone information were missed and a few models not included in WP4 were added (see gaps section above). This is a common limitation that occurs because of the strong presence of certain models/areas targeted in our survey that influence and reduce the inclusion of other models/model applications available.

In accordance with the criteria for the operational definition for keystone species given in Power *et al*. (1996), a keystone/keystoneness index has been defined for the web elements as a function of both their interaction strength and their contribution to the total biomass of the food web (Okey *et al*., 2004; Libralato *et al.*, 2006), with the level of keystoneness being defined as a continuum across elements of the system (Libralato *et al.*, 2006). In particular, EwE assigns a keystoneness index to each component/functional group of the food web with low values being the least important and high values the most significant ones. As such, high values of the index denote higher keystone potential and they have been attributed to components with both high overall effects and low biomass proportion (hence their disproportionate effect; Power *et al.*, 1996), as opposed to structural and dominant functional groups whose high impact on the ecosystem (hence their key role) is associated with their high biomass (Piraino *et al.*, 2002; Libralato *et al.*, 2006; Heymans *et al.*, 2011). However, there is a limitation associated with the selection of keystone species following this approach, as identified during the catalogue compilation, regarding in particular the cut off point for a species to be defined keystone. Although some authors have identified keystoneness index values higher or around zero as indicative of a keystone role (Libralato *et al.*, 2006; Heymans *et al.*, 2011), several species or functional groups in the food web may fulfil this criterion. As a result of this ambiguity, some partners have included in the catalogue several keystone species/groups present at the top of the ranking, some others instead have included only the first keystone species with the highest score.

Modelling studies have shown a marked variability in the results upon the keystone role of the food web components and a great variability in the trophic role of the different keystone species (from top predators to organisms at the bottom of the food web) was also seen from the catalogue analysis. For example, a great variability is evident in the catalogue entries for the Mediterranean Sea region, where there is the majority of data entries (73%) and where marine mammals, seabirds and large predatory fishes appear to be important keystone species together with cephalopods, benthic invertebrates and zooplankton groups. The reason for this variety partly depends on the modelled habitat, in agreement with the context dependency of the keystone status of a species (Power *et al.*, 1996). Top predators are important keystone species in several food webs representing open sea/ shelf areas of the Mediterranean Sea region (e.g., Adriatic Sea: Coll *et al.*, 2007; Catalan Sea: Coll *et al.*, 2008; Aegean Sea: Tsagarakis *et al*., 2010; Ionian Sea: Piroddi *et al.*, 2010 and the whole Mediterranean Sea: Piroddi *et al.,* submitted b). The strong keystone role attributed to functional groups at high trophic level has been mostly associated with their effect on the other components of the ecosystem mainly via top-down impacts (Okey *et al.*, 2004; Libralato *et al.,* 2006; Heymans *et al.*, 2011). Power *et al.* (1996) also reported a higher probability of keystone species to be found near the top of the food chain, and with the importance of predator regulation (top-down control) on community dynamics (Davic, 2003). However, several authors have reported that the keystone role is not restricted to high trophic levels (Bond, 1993; Davic, 2000; Libralato *et al.*, 2006; Heymans *et al.*, 2011), as observed also in the example of the catalogue entries for the Mediterranean Sea region. Here, benthic invertebrates and zooplankton groups constantly appear as important key species, probably because of the general oligotrophic condition of the Mediterranean Sea, characterized by low levels of phytoplankton and zooplankton biomass, which seems to constrain the trophic activity of the food web and drive the ecosystem with bottom up processes when changes in their biomass (Piroddi *et al.*, submitted b). In the general literature on modelling of marine ecosystems, Heymans *et al.* (2011) also found that the lower components of the trophic web (e.g., phytoplankton, large zooplankton, macrobenthic deposit feeders) can have high keystoneness, particularly in shallow coastal ecosystems (Libralato *et al.*, 2006). Davic (2003) suggested that it is the topology of the food web (e.g., the degree of interactions) rather than the trophic position of the species that determines which species are keystones. Variability in the trophic level of species with keystone properties has been observed also by Ortiz *et al.* (2013) when using a different modelling approach (qualitative loop analysis) applied to different benthic ecosystems.

Time plays also an important role. Changes in keystone species have indeed been observed for example in the Catalan Sea, where the Atlantic bonito *Sarda sarda* appeared at the end of 1970s as the most important keystone replaced in more recent years (2000s) by the Audouin's gull *Larus audouinii* (Coll and Libralato, 2006).

In all these models/areas, the resolution of the biodiversity components differs greatly: from the inclusion of single species e.g., *Tursiops truncatus* to large functional groups e.g., marine mammals. The reason for this heterogeneity is given by the final targets/goals of the models, which influence the different outputs produced (Piroddi *et al*., submitted a).

The use of food web models has the advantage of providing an objectively and quantitative means for assessing keystones. Such an approach has been considered as a means to overcome some of the weaknesses associated with the identification of keystone species through field-based experimental quantification (Libralato *et al.*, 2006; Ortiz *et al.*, 2013). Field-based experiments (e.g. species removal or introduction) by necessity focus on few species and their interactions, mostly assessing those ecosystem components that are easier to manipulate and control (e.g., macrobenthic or microbic species), and as such they ignore indirect interactions that might have important effects on the ecosystem (e.g., through cascading effects; Pace *et al.*, 1999). In turn, through trophic models, the keystoneness of a species or functional group is assessed by considering its overall effect on the food web, as an integration of its direct and indirect impacts on the other elements of the food web (Libralato *et al.*, 2006). Such an approach is likely to provide a more integrative assessment of the keystone role of species in the ecosystem, while also allowing the evaluation of components like nektonic predators (e.g. fish or mammals) for which field-based experimental manipulation would be more difficult. However, there are also limitations associated with food web models and the fact that they focus only on interactions mediated by trophic links. Although this allows keystone species to be assessed in the strict (food-web focused) sense, as per Paine's (1969) original definition, other types of interactions between species are not taken into account, hence limiting the ability of such models to identify other keystone roles (e.g. competitors, habitat modifiers, engineers). Moreover, the trophic level of an organism can change over different development stages so that different demographic classes reflecting different functional classes (e.g. juvenile planktotrophic or invertivorous; adult apex predator) have to be taken into account for many species. It should be noted also that, as mentioned above, food web models often give a simplified representation of the reality of the trophic interactions in an ecosystem. For example, such simplification is often achieved by grouping species into functional groups (i.e. groups of species with similar sizes and feeding habits). Considering the importance of identifying and protecting keystone species due to their role in maintaining the stability of an ecosystem (Solé and Montoya, 2001), the assessment at the functional group level might lead to difficulties in the implementation of conservation efforts in the framework of the existing relevant legislation (e.g., Habitats Directive) which usually operate through management of species identities.

4.8. Are there common keystone species in all European seas?

Despite the high number of entries included in the DEVOTES catalogue of potential keystone species, there is only one species common to all European regional seas, the alien invasive bivalve *Mya arenaria*. The soft-shell clam is an ecosystem engineer that has invaded European estuarine, coastal and marine habitats from the Western Atlantic Ocean. In the DEVOTES Catalogue of potential keystone species, it is reported to have invaded the littoral and shallow sublittoral sand sediments of the Black Sea, Baltic Sea, Celtic Sea, North Sea, Bay of Biscay, Iberian Coast, Western Mediterranean and the Adriatic Sea. It is considered a structural and chemical engineer, and a bioturbator (Katsanevakis *et al.*, in press), with an overall reducing effect, as it dominates the communities it invades causing regime shifts and displacement of native species. These result in structural changes of native communities, changes in sediment and water column characteristics (e.g. changes in sediment chemistry, grain size, and organic matter content via bioturbation, increased light penetration in the water column due to filter feeding, changes in near bed flows and shear stress due to the presence of shells, provision of colonisable substrata and refuges by shells) and an overall modification of the invaded habitat. Due to its inherent characteristics (high filtration capacity, engineering properties), high abundance and food web interactions, this species appears to have dramatic effects on invaded ecosystems. For example, in the Black sea, *M. arenaria* is the key species of a biocoenosis covering about 1,000 km^2 of the north-western shelf. Nevertheless, there are two sides to the impact *M. arenaria* has had on the Black Sea ecosystem. On the one hand, it has had a negative effect since it forced out the indigenous bivalve *Lentidium*, which had been an important food source for the fry of many fish species. On the other hand, *M. arenaria* itself became a food source for fish. Moreover, it became an additional biofilter in the coastal zone, which is quite important ecologically (Zaitsev and Mamaev, 1997).

The case of *M. arenaria* is an example of how naturally occurring experiments can provide support to ecological theory. Menge *et al.* (2013) in their seminal article on keystone species suggest that in the lack of experimentation and other rigorous approaches to identify keystones, the study of natural or accidental invasions can be an alternative approach for studying and revealing the dynamics of communities and ecosystems.

The fact that only one species has been reported as potential keystone species for all European seas does not necessarily mean that there is only a single species with consistent keystone features across European marine ecosystems, notwithstanding the spatial variability highlighted in previous sections (and associated context dependency). It is rather an indication that there are differences among the expert providers on the choice of keystone species from a suite of species inhabiting an area; this is supported by the fact that *M. arenaria* has been suggested as a keystone species for all European seas by the same expert. It is also worth noting, that in nature the communities may differ between geographically spaced areas in respect to their species identities, nevertheless, they may be structured by species, which are ecologically equivalent and possibly belonging to the same taxon or functional guild. In this respect, there are several such instances in our catalogue: the angiosperm species *Posidonia oceanica* in the Mediterranean Sea and species of the genus *Zostera* in the rest European seas, acting both as habitat and engineer species; several bivalve species primarily with an engineer role (e.g. *Macoma balthica*, *Arcuatula senhousia*, *Crassostrea gigas*, *Venerupis philippinarum*, *Mytilus galloprovincialis*); the protist phytoplankton species of the genus *Alexandrium* and *Pseudochattonella*; dolphins, such as *Delphinus delphis*, *Lagenorhynchus albirostris* and *Tursiops truncatus*.

4.9. Currently protected keystones

A small proportion of the proposed keystone species are protected by Regional sea conventions with a few species also being protected under International, EU and/or National legislation. This proportion in the catalogue ranges between 10% and 20%, the exact numbers for regions varying depending on the inclusion of groups and species within these. It is expected that not all the keystone species would require or even be desirable to protect. Out of the 10 biodiversity component types in the DEVOTES catalogue, phytoplankton, zooplankton and cephalopods have no protected keystone species. Most of the species in these components are reducers although for zooplankton mixed, uncertain roles and different roles were allocated (e.g. *Beroe* is a promoter while *Aurelia* is a reducer).

Whilst the Mediterranean has protected representatives in all the remaining groups, in all four regional seas the most common groups of protected species include fishes (e.g. *Gadus morhua* in the Baltic and the NEA) and mammals in all regions, followed by macroalgae (e.g. maerl) in the NEA and Mediterranean and angiosperms (e.g. *Posidonia*) in the Mediterranean.

The protected fishes in the NEA, Baltic and Black Sea include eight species (e.g. *G. morhua* in the NEA and Baltic, and *Sarda sarda* in the Black Sea) mostly predators, either promoters, reducers or both. The protected fish in the Mediterranean include only one group, i.e. the predators and reducers keystone group sharks as indicated by EwE models. Annex II (strictly protected species) of the Barcelona Convention includes 14 species of sharks and two sawfish and Annex III (regulated species) includes seven more shark species. Of these, seven species are critically endangered (CR), two are endangered (EN) and several are assessed as vulnerable (VU). Some of these have been historically the subjects of targeted fisheries while current threats include bycatch, habitat loss and other human disturbances (Cavanagh and Gibson, 2007). Similarly for the NEA the OSPAR list of threatened species (OSPAR, 2008), includes two species that might have been keystone species in the past and are currently on the critically endangered sharks list in the Mediterranean. *Lamna nasus*, the Porbeagle shark is an apex predator, occupying a position near the top of the marine food web, which may have a role in ecosystem function and regulation although not in its currently greatly reduced abundance in the OSPAR Area. *Squatina squatina* the angel shark may formerly have been sufficiently common and as an important demersal predator might have had a controlling influence upon its community, but is now probably ecologically extinct throughout the OSPAR Area (OSPAR, 2008).

The protected marine keystone mammals include nine species/groups; *Phocoena phocoena*, *Phoca vitulina* and *Pusa hispida* in the Baltic Sea (CR, VU and VU IUCN status respectively), *Delphinus delphis*, *P. phocoena* and *Tursiops truncatus* in the Black Sea (all EN IUCN status), *Balenoptera acutorostrata*, *Halichoerus grypus*, *Lagenorhynchus albirostris* and *P. phocoena* in the NEA, and *T. truncatus* (EN status) and dolphins as a group for the Mediterranean Sea. Annex II of the Barcelona Convention lists four dolphin species (one EN and one VU status) in addition to *T. truncatus* (VU status) and *P. phocoena* that (although present in the region and in the catalogue) was not considered keystone for the Mediterranean. The protected and critically endangered monk seal *Monachus monachus* was not considered a keystone species in the Mediterranean, but in the Black Sea where its population was depleted due to overfishing and habitat loss and it is now considered extinct (e.g. Bulgaria) or possibly extinct (e.g. Romania, http://www.iucnredlist.org/details/13653/0). As with sharks, these protected dolphins and seals have been the subject of past severe direct threats now removed or considerably reduced (such as fishing or deliberate killing) but still are the subject of ongoing threats from incidental mortality, habitat degradations and prey depletion (Reeves and Notarbartolo di Sciara, 2006).

All the proposed protected macroalgae species (maerl, *Cystoseira* and *Phyllophora* in the Black Sea) are also habitat builders and promoters. Maerl beds (EUNIS habitat A5.51) are protected by the Barcelona Convention and the Mediterranean Regulation (Council Regulation (EC) No. 1967/2006), the Habitats Directive in the Mediterranean and NEA and are the subject of a Habitat Action Plan under the UK Biodiversity Action Plan (Salomidi *et al*., 2012). They have been heavily and unsustainably exploited for many years and have suffered from physical disturbance and water quality deterioration (Airoldi and Beck, 2007). As habitat species they provide three dimensional structure and functional complexity thus supporting rich and diverse associated communities and hosting numerous other species. *Phyllophora* beds have suffered from exploitation and eutrophication and could qualify to be protected under the habitat Reefs of the Habitats Directive (for Bulgaria and Romania), while they are currently protected by a very large (402,500 ha) offshore Marine Protected Area (MPA) in Ukraine as 'Zernov's Phyllophora field' (Salomidi *et al*., 2012).

AS regards the angiosperms, while *Posidonia* and *Cymodocea nodosa* are keystone in the Mediterranean region, *Zostera* spp. are proposed as keystones in the other three EU regions; all have the same role as habitat/engineer species and as promoters. European seagrasses have suffered considerable historical losses and declines from direct exploitation (e.g. *Zostera* was harvested for various uses from packing, upholstery to insulation and as a resource for salt, and *Posidonia* for packing, bedding for animals, felted shoes and fertilisers), physical disturbances (e.g. trawling in *Posidonia* grounds), pollution, eutrophication, water front coastal developments and more recently from alien invasions (e.g. *Caulerpa* species competing for space with *C. nodosa* and *Posidonia*) (Airoldi and Beck, 2007; Boudouresque *et al*., 2012). *Posidonia*, *Cymodocea* and *Zostera* spp. are protected species in the Mediterranean. *Zostera* spp. are currently directly and indirectly legally protected under the BERN convention, the EU Habitats Directive, and various national legislation/measures, depending on their habitat area and type (e.g. as features of habitats protected under the Habitats Directive, including lagoons, code 1150; shallow sandbanks slightly covered by seawater all of the time, code 1100; shallow inlets and bays, code 1160). They feature in both the OSPAR and HELCOM Red lists (OSPAR, 2008[1]; HELCOM Red List Biotope Expert Group, 2013[2]). *Posidonia* is also protected through its designation as a priority habitat under the Habitats Directive. It is estimated that only 10% of *Posidonia* is protected under existing MPAs in the Mediterranean (Papadopoulou *et al*., 2013), when the target for priority habitats is set to 60%. It is also protected through the Mediterranean Regulation that prohibits fishing by towed gears (including trawling) in the meadows and by spatial regulations that regulate trawling based on depth and distance from shore as well as gear closures and Fisheries Restricted Areas. These joint measures bring protection levels (at least 'on paper') much closer to the 60% target (Papadopoulou *et al*., 2013), although spatial measures are not stopping degradation caused by nutrient built-up, agricultural run-off, smothering from construction work or even invasion of MPAs by alien species that can threaten the integrity of seagrass beds (Katsanevakis *et al*., 2010).

As with *Posidonia*, a number of fish and benthic invertebrate keystone species are (partially) protected via fishing regulations. *Thunnus thynnus* is for example protected by being regulated under Annex III of the Barcelona Convention and by quotas and live closures by ICCAT. The red coral *Corallium rubrum* is protected by having its exploitation regulated and by banning very damaging gear and practices. The deep cold water coral *Lophelia*, a keystone species in the Norwegian Sea and NEA (Celtic Seas), is also protected by various spatial measures/MPAs in the NEA and in the Mediterranean. Five benthic invertebrate keystone species are listed in the Annex II of the Barcelona Convention, including sponges, echinoderms, and the bivalve date mussel *Lithophaga lithophaga*, an engineer promoter species protected also by the Habitats Directive and the BERN and the CITES Conventions. Protection can be sub-optimal if not accompanied by enforcement, as surveys of illegally traded species show these to be frequently served in seafood restaurants (Katsanevakis *et al*., 2011).

[1] http://qsr2010.ospar.org/media/assessments/Species/P00426_Zostera_beds.pdf

[2] http://www.helcom.fi/Red%20List%20of%20biotopes%20habitats%20and%20biotope%20complexe/HELCOM%20Red%20List%20AA.H1B7,%20AA.I1B7,%20AA.J1B7,%20AA.M1B7.pdf

Protected keystone birds and reptiles include predators such as *Larus audouinii* and predators/habitats species such as *Caretta caretta*. Both have seen declines and have been/continue to be under various threats. *Caretta caretta*, for example, is no longer traded or directly targeted but is competing for space for its nesting sites with beach bars. It is also suffering from incidental by-catch, entanglement or hooking in derelict fishing gears, boat strikes and its inability to distinguish its preferred jelly fish prey from floating plastic bags.

From a conservation point of view it would seem that top predators, habitat and engineer species are protected when there is already some damage done and usually considerably more as seen in the case of the so-called critically endangered or emblematic species. The very recent inclusion of 11 deep sea coral species (including *Lophelia*) in the Annex II of Barcelona Convention, or uplisting from Annex III to II, and the decision to implement the Action Plan on Dark Habitats can be seen as acting upon scientific advice and NGO pressure to protect before it is too late.

4.10. Future keystone operational metrics

The way species are used in ecological indicators depends mostly on the purpose for applying the indicator (Niemi and McDonald, 2004). In this sense, one might target a wide range of different kinds of species, e.g.:

- tolerant species to pollution or disturbance;
- opportunistic species that take advantage of abrupt environmental changes;
- sentinel species that may act as an early warning for the ecosystem health, either because they are sensitive species to changing environmental conditions or species that bio-accumulate chemical substances (e.g. Mussel Watch Program in the USA);
- declining and threatened species under special conservation or protection status (e.g. IUCN list);
- flagship species to represent and raise awareness and action towards a certain environmental cause (polar bear for global warming) or conservation efforts (blue whale for ocean conservation) (WWF);
- invasive alien species that may alter significantly the host ecosystem;
- toxic species that may cause a direct or indirect problem for human health;
- commercial interest species and other footprint-impacted species (*sensu* WWF) that inform on human activities pressures in the ecosystem.

All these indicator and umbrella species share the fact that they provide or hold valuable information that goes beyond their taxonomic identity and therefore, they are often used as indicators by informing on the environmental conditions or on the effect of pressures impacting the state of the ecosystem.

Keystone species by definition are those species that have a crucial role in the ecosystem. Through strong/critical interaction linkages within the community, and notwithstanding their relatively low abundance, keystone species have a major effect on maintaining ecosystem integrity, both structurally and functionally. The protection of such species is therefore of major importance to ensure system stability and functioning (Solé and Montoya, 2001; Piraino *et al.*, 2002; Mouillot *et al.*, 2013). In this sense, taking these species into account in monitoring programmes would also provide relevant information for future consequences of environmental changes in the entire ecosystem. Keystoneness is thus an appealing concept to support the selection of essential ecosystem components towards which monitoring could be more effectively directed. Ecologists have devoted a great deal of attention to identifying keystone species in different ecosystems, as it was suggested that the future of conservation management might lie in maintaining keystone species rather than attempting to protect and manage all species (Power *et al.*, 1996; Cury *et al.*, 2003).

Ings *et al.* (2009) have pointed out that conservation efforts have, possibly from expert knowledge of systems, often targeted 'keystone' species, whose loss can cause cascading effects (e.g. Pimm, 1980; Solé and Montoya, 2001; Dunne *et al.*, 2002; Srinivasan *et al*., 2007). The Catalogue of Indicators compiled within the scope of DEVOTES project Deliverable 3.1 (Teixeira *et al.*, 2014) revealed exactly that; many species included in indicators or used as indicators are potentially keystone species and, therefore, have also been added to the catalogue of Keystone species presented in this report (Annex 2). Also within the BIOMARE project (Féral *et al.*, 2003) the question of keystone species was central at the time of choosing biodiversity indicators. They have compiled a list of indicator species, some of which could be potential keystone species with different roles in the ecosystem. Both projects found evidence that, specifically for keystone habitat species, many operational indicators already exist and have long been applied in the context of environmental assessment and conservation initiatives. But these indicators are mostly status indicators that inform poorly on the interaction or the role of the species in the ecosystem.

An index developed to integrate information on such keystone species role for the entire ecosystem would of course be of utmost relevance for conservation actions and to direct restoration efforts. However, this implies a great knowledge of the species dynamics and its ecology to be able to use it in indicator development. There are several types of keystone species as already described in this report, and evidence coming from experimental studies and observations (e.g. Menge *et al.*, 1994; Estes and Duggins, 1995), and more recently the development of network analysis, have helped demonstrate their keystone role. Food web models have used such an index to identify species with critical roles in the maintenance of the food web structure and functioning (Okey *et al.*, 2004; Libralato *et al.*, 2006). Analysis of ecosystems from a network perspective may thus provide useful information to managers on the potential effects (via links in the network) of interventions (Parrot, 2010). Current network analysis research is moving beyond food webs to study more general ecological interaction webs, in which all types of ecological interactions (exploitation, mutualism, facilitation, neutralism, etc.) are included (Ings *et al.*, 2009), allowing that potential keystone species with relevant roles other than predator/prey are better scrutinized.

When talking of a keystone operational metric it is important therefore to distinguish whether such a metric would: a) help identifying potential keystone species, or b) provide information on the status of species whose keystone role in the ecosystem is already acknowledged and understood. As referred previously, both approaches are not new and metrics have been used in both ways, although with limited scope and not always assuming keystone motivation directly. Modelling approaches seem the natural place to identify and understand keystones role, as they integrate information on the interactions of the species within its ecosystem and also allow understanding the effects of external pressures on the species dynamics, and hence, its consequences for the entire network (Piroddi *et al.*, submitted a). On the other hand, other type of indicators, not necessarily model-derived and therefore less data demanding (Teixeira *et al.*, 2014), may be more efficient to follow such a species once its keystone role has been identified. These two steps are complementary and, whether keystoneness is context dependent (Power *et al.*, 1996) or an intrinsic property of the species that arises as a consequence of species' evolutionary histories, as has been recently suggested by Stouffer *et al.* (2012), identification of keystones has to become part of the routine. Only then it is possible to develop or select the most adequate tools to monitor the status and evolution of targeted species. It is very unlikely that a unique tool is sufficient to provide all information needed, moreover since, as literature shows and our review also supports, keystones identification and their specific roles are still poorly understood in most cases. The context is defined not only by the environmental background where the species occurs (e.g. habitat), affecting the resources availability, but also by the community where the species occurs and the interactions that the species creates with the community components. Such conditions may vary both in space and time, and this might create difficulties in the identification of an operational metric based on keystones that has general validity (at least at the regional spatial scale).

An additional element that needs to be taken into account when talking of a keystone operational metric is that the keystone status of a species in a community is likely to contribute to the vulnerability of the system, considering that a minor effect on the keystone species (e.g. due to disturbance, anthropogenic impact) would result in drastic changes to the system phenology, with possible consequences for the ecosystem functioning. The keystone role of a species in a community has been associated with the concept of functional redundancy, i.e. where different species sustain similar functions. Keystone species have been defined, for example, as functional groups with no redundant representatives (Shulze and Mooney, 1993), and the low levels of functional redundancy in the food web have been associated with the pivotal role of keystones in the ecosystem (Power *et al.*, 1996). Functional redundancy is particularly important where a system is subject to changing conditions (e.g., disturbance or climate change), as the potential for functional compensation in a community is seen as an insurance mechanism against the loss of ecosystem functioning following biodiversity erosion, hence supporting the system stability (Walker, 1992; Power *et al.*, 1996; Fonseca and Ganade, 2001; Scherer-Lorenzen, 2005). Therefore, although keystone species can be seen as indicators of the current stability of the system, their presence can also be a sign of potential (future) instability associated with a higher vulnerability and lower resistance of the system and its functioning to changing conditions. This aspect needs to be taken into account when considering the potential suitability of keystone species as indicators (metrics) of biodiversity, particularly if the functioning of the system is to be assessed, as required by the MSFD.

For the present, different modelling approaches together with other standard types of indicators seem to comprise the essential toolkit to support keystone species conservation, thus help promoting the integrity of the entire ecosystem. For the MSFD this most closely relates to Descriptors 1 – biodiversity, 2 – aliens 4 – food webs and 6 – seafloor integrity.

4.11. In Conclusion

The challenge to assemble a list of potential keystones species for different habitats in the European regional seas has been accomplished with the DEVOTES Keystone Catalogue. The catalogue has 844 individual entries, which includes 210 distinct species and 19 groups classified by major habitat in the Baltic Sea, North East Atlantic, Mediterranean, Black Sea (EU Regional Seas) and Norwegian Sea (Non-EU Sea). We have covered all the Marine Strategy Frameworks Directive designated habitats and have catalogued species from a wide range of groups and trophic levels.

The catalogue is seen as good start to producing a list of up-to date European potential keystone species. We would certainly like the catalogue to be refined further, clarified/confirmed for the species that have been listed to date, added to with new information, and new expertise, in consideration of the uncertainties, limitation and gaps discussed above. For the latter points, the gap analysis has pointed out several areas for future attention. For specific habitats, the littoral habitat has a limited number of identified keystones. The shallow and shelf sublittoral habitats have numerous keystones and because of the high level of anthropogenic activities and associated pressures on biodiversity, it is an area with management priority. From another point of view, deeper waters were seen to have an even more limited set of identified keystones, but these are extensive in area, much less well known and becoming frequently touched by anthropogenic pressures through expanding resource extraction, telecommunications and accumulation of pollution (chemicals and litter/dumping residues). For specific biological components, there is certainly a level of importance in smaller fractions (e.g. microbes and sedimentary meiofauna) in trophic linkages but currently unknown for any species or subgroup level for keystone importance.

Writing and reviewing this document by various authors and contributors within the DEVOTES Keystone Task 613 and the wider partnership of the WP6 has already sparked renewed interest for the subject including the modelling teams of WP4. As our collective understanding is being enriched by some of the highlighted examples in this report we target our efforts towards gaps and differences of opinions on keystones (or even outputs by models). Our experts are already addressing some of the specific gaps mentioned earlier. This includes, for example, new proposals from Norway for bivalve and gastropod keystones for the littoral habitats and a sponge and an echinoderm for sublittoral habitats. Similarly, for the Baltic Sea the addition on an invasive goby species might be worthwhile as there is growing awareness and some evidence of its impact on local populations of other keystone species such as the mussel beds (Zaiko, pers comm.). Another point that is being addressed is that of temporal changes/succession/substitution of keystones (e.g. in the Black Sea) and especially so for the case of the invasive species. It is recognized that due to the changes in alien species communities (arrival of new species, spread of existing species, shifts in their status from benign to invasive), this part of the catalogue should be regularly revised and updated.

Looking beyond the species names in the catalogue and the examples presented in this document, this Deliverable report offers a comprehensive list of European keystone species/groups building on the following inclusion criteria (i.e. when is a species a keystone at a particular area or habitat):

- Species distributions: whether other species could move in to replace a depleted keystone species, or whether physiological or biogeographic barriers exist (population connectivity).
- Functional redundancy: whether the functions of the keystone species are unique within the system or whether other species or species groups which have parallel or similar ecological roles exist within the same community. Grouping coherent groups of taxa within an identified functional group as a "functional" keystone group might be possible.
- Predator/prey equivalence: whether keystone predators could switch to other available prey (with equivalent energetic rewards) or whether such prey are available within the system.
- Habitat engineering: whether the engineering effects of the keystone species are dependent on its existence or whether another species could perform the same function (see functional redundancy). Alternatively, whether the engineered habitat is independent of the continued life of the constructing organisms.
- Scale: temporal and spatial scale issues apply for both native and invasive species and for habitat patches (e.g. bioconstructors) within otherwise homogenous habitats.

Finally, although we employed a range of expertise with contributors from different seas with different areas of expertise, we still feel that we do not know enough. We may have a strong feeling to nominate certain species, but if we were very strict in adhering to Paine's original definition we might only have 10 or so species in our catalogue. We do not have the concerted funding efforts, resources, or facilities to undertake the extensive experimentation required to tease out the effects of a wide range of individual species in less accessible habitats, nor do we yet have the developed level of fully parameterised ecosystem models to allow us to simulate ecosystems in a way that would give us definitive answers. We do feel confident with presenting the large number of potential species that we have, purely from a precautionary view and as a basis for future work. This includes work on refining metrics and modeling approaches, operationalising indicators and the use of keystones in management and risk assessment and in GEnS assessments for descriptors 1, 2, 4, and 6 for the MSFD.

4.12. Keystone species: the final word

There is one species not included in the catalogue that could be said to meet the full definition of a keystone species. It is a species that has a disproportionate effect on its environment relative to its abundance, and its activities can cause trophic cascades. It is not an aquatic species, but its activities cross all marine habitats and regions. It is us, *Homo sapiens*. It has many keystone effects through its activities mainly mediated through different pressures (see DEVOTES Deliverable 1.1 on conceptual models for the effects of marine pressures on biodiversity: Mazik *et al.*, 2013; Smith *et al.*, 2014). It is a predator having a negative effect by directly removing marine species (fishing, harvesting, collecting) at many different trophic levels (from seaweeds to top predators) and indirectly affecting many more. It is also an engineer species with activities that affect sedimentary processes (e.g. sediment abrasion/ploughing from anchoring, dredging or fishing activities). Finally, it is also a habitat creating species with both negative and positive effects, covering natural marine habitats but also providing new ones, mostly coastal, with concrete/stone/metal structures for developmental purposes (coastal infrastructure, renewable and non-renewable energy) that will bring other associated pressures. These structures may then form substrata for colonisation by different communities. *H. sapiens* also deliberately introduces structures in the form of artificial reefs into the marine environment in order to increase local biodiversity and production, although this is primarily restricted to shallow shelf sedimentary environments.

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7. Annex 1

7.1. Introduction

The purpose of Annex 1 is to physically describe Annex 2, which is the Keystones Catalogue database.

The data catalogue is a simple Excel file entitled **DEVOTES_613 Keystone Catalogue_v8.xls**

The file consists of 8 separate pages

- Sheet 1: Citation Page for the Catalogue and Deliverable
- Sheet 2: Readme: instructions for the data providers of the catalogue
- Sheet 3: Lists: lists and data entry options for preselected categories for various data entry points for each of the keystone entries.
- Sheet 4: Definitions: further definitions for each of the entry columns in the catalogue
- Sheet 5: CATALOGUE: the Keystones Catalogues entries and associated data
- Sheet 6-8: Regional and sub-regional maps for defining geographical entries.

7.2. Catalogue

The CATALOGUE page of the Keystones Catalogue contains the individual keystone entries with single row entries for individual keystone species/groups, with a number of categories of associated information to complete.

7.2.1. Category groups and categories

The entries are broken down into seven broad category groups and then individual categories in single columns. Some categories were for free entries; others were restricted to a specific list (drop down menu).

- Data Input identifier section: to identify who is putting in the data information including institution name and contact
- Keystone: identifying the Keystone by common name, scientific name, keystone type (predator, habitat species, or engineer), biological component group and sub-component group.

- Importance: primary impact (biodiversity reducer or promoter), brief description of importance, size category, abundance category, distribution category, keystoneness value (if available from Ecopath with Ecosim model).
- Habitat: habitat type, MSFD habitats
- Regions: MSFD Region and sub-region, other subdivision
- More than one entry: indicating if the species/group has more than one entry in the catalogue
- Sources: source of Keystone information (reference, expert knowledge or model) and any bibliographical refrence.
- Notes and additional remarks: any particular notes concerning the entry.

7.2.2. Catalogue entries

There are a total of 844 entries in the catalogue with data given for almost every category for each entry. The entries concern a total of 210 distinct species and 19 groups. The catalogue is also citing 164 references