



WP 3

Deliverable 3.1

D 3.1: State of knowledge on key eco-evolutionary processes and factors driving the resilience of the shallow hard bottoms and mesophotic habitats

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INTRODUCTION

The main goal of Deliverable 3.1. is to synthesize the information available on key eco-evolutionary processes and factors to guide the development of novel and efficient restoration actions to be planned, developed and performed within WP3. We focused on macroalgae and mesophotic coralligenous habitats since i) there are increasing evidences of relevant changes and lost of these two habitats across the whole Europe and ii) they are featured by the presence of species that are considered critical for the functioning of the coastal marine systems. In addition, these habitats display contrasted characteristics in terms of dominant groups (macroalgal species vs. macroinvertebrate), driving processes (trophic interactions-physical factors vs. competition), dynamics (fast vs. low turnover) and environmental conditions (shallow-light vs. deep-dim light habitats).

Macroalgal forests such as kelps and fucoids are dominant habitat-forming species in rocky intertidal and subtidal habitats around all the Mediterranean and Atlantic/Norway coasts. Macroalgal forests are recognized hot spot of diversity and provide food and habitat to diversified assemblages of understory species and enhance coastal primary productivity. Macroalgal forests can potentially thrive from the intertidal to the circalitoral, then depth can be considered a driver for algal development. Macroalgal forests are featured by different dominant species dwelling at each depth and generally, community structure (i.e. diversity and species richness) increases in complexity, and population and community dynamics (i.e. productivity, turnover and growth rates) slows with depth (e.g. Ballesteros, 1989; 1990; Ballesteros et al., 1998; 2009; Garrabou et al., 2009; Capdevila et al., 2016). As a response to multiple stressors, including urbanization, eutrophication and increasing sediment loads in coastal areas, these habitats (shallow and deep) are being lost at alarming rates and descriptive and manipulative experiments have demonstrated that these systems may switch towards the dominance of barrens or algal turfs if the canopy is removed or damaged (references in Ling et al., 2015).

Coralligenous outcrops are hard bottoms of biogenic origin that are mainly produced by the accumulation of calcareous encrusting algae growing at low irradiance levels. Coralligenous outcrops harbour approximately 10% of marine Mediterranean species, most of them are long-lived algae and sessile invertebrates, which exhibit low dynamics and belong to various taxonomic groups such as sponges, corals, bryozoans and tunicates (Ballesteros, 2006, Teixidó et al., 2011). This habitat is extended around all the Mediterranean coasts with a bathymetrical distribution ranging from 20 to 120 m depth depending on the local environmental variables, mainly light conditions (Ballesteros 2006; Martin et al., 2014). Coralligenous assemblages are affected by several pressures such as nutrient enrichment, invasive species, increase of sedimentation, mechanical impacts, mainly from fishing activities, as well as climate change (Ballesteros 2006; Balata et al., 2007; Garrabou et al., 2009; Piazzzi et al., 2012).

For the review we selected 7 main topics relevant for restoration activities: i) Reproduction – Recruitment - Population dynamics, ii) Impacts and Mortality, iii)

Functional role - Biodiversity, iv) Trophic interactions, v) Population genetics and vi) Previous restoration activities and a final summary on main vii) insights for restoration protocols. Since we worked in two different habitats (macroalgal and mesophotic coralligenous) we decided to work in parallel in the literature search and compilation as well as its synthesis. This was also a convenient approach to share effort among participants.

During our regular meetings previous to the WP3 workshop in Barcelona (19-20 January 2017) we agreed on the main topics for the literature research and we defined the core list of targeted species for restoration activities in WP3. During the workshop, the species list was reviewed and minor changes were adopted. Likewise, two writing teams (one for each habitat) were identified: Macroalgal (Simonetta Fraschetti and Giuseppe Guarnieri CoNISMa, Emma Cebrian and Jana Verdura UdG-CSIC, Bernat Hereu UB, and Jean Baptiste Ledoux CSIC, Camila With Fagerli NIVA) and Coralligenous (Joaquim Garrabou and Jean Baptiste Ledoux CSIC, Cristina Linares UB and Carlo Cerrano UNIVPM). The writing teams were supported by the other participants in WP3.

The first step to produce the Deliverable 3.1. was to gather the most relevant literature to address the review. To this end prior to the WP3 Workshop, all participants provided the PDF files of papers potentially relevant for the 6 defined topics. The participants in the WP3 compiled the references based in their domain of expertise in the different topics as well as using selective literature searches with different criteria and databases (mainly ISI Web of Knowledge, Google Scholar). We created two dropbox folders (one for each habitat, folder 1: D3.1-Macroalgal-literature, folder 2: D3.1-Coralligenous-literature) where the participants could directly drop off the PDF files. A total of 343 (151 macroalgal plus 192 coralligenous habitats) files were collected. Prior to the workshop the writing teams reviewed the reference list and ensure that all references were relevant for the Deliverable 3.1. To help to sort out the information contained in the papers two Google Spreadsheets (one for each habitat) were created and presented during the Workshop. With the final list of references, during the WP3 workshop we worked in small groups (2-3 persons) to review all 343 papers extracting relevant features of the studies and indicate the main topics. To ensure the coherence of the database obtained, most of the fields had a set of pre-selected options. During the process some of the options were updated online and thus made available to all instantaneously to all teams to fit all potential features. These files were the basis for the writing teams to produce the Deliverable 3.1.

Besides this introduction section, the document is organized in two main parts, one for each habitat, and within each habitat we followed the same text structure in coherence with the working plan.

1. PART I MACROALGAL HABITATS

In the macroalgal habitats, the restoration actions will be focused on erect macroalgae belonging to the genus *Cystoseira* spp. In particular, transplanting experiments on adults and juveniles will be carried out on the species *Cystoseira balearica*, *C. amentacea*, *C. barbata*, *C. crinita*, *C. zosteroides*. Cage experiments will be run on *Laminaria hyperborea*, *Saccharina latissima*, the sea urchin *Strongylocentrotus droebachiensis* and the crab *Cancer pagurus* for the restoration of kelp forest in overgrazed areas in Norway. Cage experiments will be also used with the fish *Siganus luridus*. In addition,

the sponge *Chondrilla nucula* will be included in facilitation process to test the potential for this species to facilitate the recovery of shallow rocky habitats. The removal of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* will be also used in some sites to further facilitate the recovery of disturbed assemblages.

Cystoseira zosteroides C. Agardh: it is the dominant alga in deep-water *Cystoseira* forests. These assemblages occur on rocky bottoms exposed to strong unidirectional currents and with light levels ranging between 1% and 0.3% of surface irradiance (Ballesteros et al., 2009). Although these assemblages seem to be widespread throughout the Mediterranean, quantitative available data are extremely scarce (Ballesteros, 1990), but the high diversity of these assemblages and the low growth and low mortality rates of *C. zosteroides* (Ballesteros et al., 2009) indicate high vulnerability to natural and anthropogenic disturbances, and call for effective measures to ensure their conservation.

Cystoseira crinita Duby: it is a Mediterranean endemic species that forms dense stands in shallow, rather sheltered, well illuminated areas (Sales & Ballesteros, 2009, 2011). Assemblages dominated by *C. crinita* are characteristic of shallow rocky habitats for the entire Mediterranean and are considered to be the most complex photophilic Mediterranean seaweed assemblage that develops in shallow rocky areas (Molinier, 1960; Blanfuné et al., 2016).

Cystoseira balearica J. Agardh: it is an endemic Mediterranean species widely distributed in the western Mediterranean. It is a photophilic species that forms dense populations on hard substrata of the upper infralittoral zone, being an important element of infralittoral benthic vegetation, always in sheltered and unpolluted waters (Ballesteros, 1990).

C. amentacea var. *stricta*: it forms complex communities providing habitats for numerous epiphytic species and shelter for many organisms. Due to its structuring role on superficial Mediterranean communities and to its endemic status in the Mediterranean Sea, *C. amentacea* var. *stricta* has been exposed to a strong anthropogenic pressure and many studies have reported severe degradations or even disappearance of *Cystoseira amentacea* populations across the whole basin.

Laminaria hyperborea (Gunnerus) Foslie, 1884: this dark brown algae is widely distributed along the coasts of northeast Atlantic Ocean (from Scandinavia south to Spain and the Canary Islands, the Baltic Sea and the North Sea) where it forms extensive communities from 0 up to 24 m depth. It commonly occurs in the intertidal in wave-exposed areas, and in the subtidal in clear waters on rocky bottoms, where it is able to provide habitats for several organisms (Christie et al., 2003; Norderhaug et al., 2002). Commonly used for alginate production through the collection of stipes cast up on the beaches (e.g. France, Ireland, Scotland), but also harvested by trawling (in Norway). However the latter activity has ceased in recent years.

Saccharina latissima (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006: this yellow brown algae (also known as *Laminaria saccharina*) can be found in northeast Atlantic Ocean and the Barents Sea south to Galicia in Spain, very common around the coasts of British Isles. This kelp species typically dominates intertidal pools in sheltered areas, but occasionally it can be found in the shallow subtidal. Recognized

as an ecologically important system, since besides its role of primary producer (i.e. delivering plant material to the coastal food web) its three-dimensional structure also provides suitable habitat for many organisms, resulting in a high biodiversity (Christie et al., 2009). The increase in ocean temperature and eutrophication are suggested as the most threatening drivers of species degradation along the coasts.

Strongylocentrotus droebachiensis (O.F. Müller, 1776): it is commonly known as the green sea urchin due to its characteristic color. It commonly occurs in northern waters on rocky bottoms from the intertidal up to 1000 m depth. The size of adults range between a diameter of 50 mm and 87 mm. The grazing behaviour of this invertebrate can strongly affect the development of *L. hyperborea*. If sea urchin densities increase, whole areas normally dominated by kelp may become urchin barrens, thus supporting a much less biodiverse community based on encrusting coralline algae (Norderhaug & Christie, 2009).

Cancer pagurus (Linnaeus, 1758): commonly known as the edible crab or brown crab, it can be found principally in the North Sea and North Atlantic Ocean on mixed coarse grounds, mud and sand from the shallow sublittoral up to approximately 100 m depths. It is frequently found inhabiting cracks and holes in rocks but occasionally also in open areas. Smaller specimens may be found under boulders in the littoral zone. There is evidence suggesting that *C. pagurus* may also occasionally occurs in the Mediterranean Sea and Black Sea. It is subjected to overfishing in Western Europe, mainly on the coasts of the British Isles, with more than 60,000 tonnes caught annually. Anyway, their collection is regulated by a number of legal restrictions.

Chondrilla nucula (Schmidt, 1862): also known as the "Caribbean Chicken-liver sponge," is an amorphous shaped sponge that grows in flat, sometimes bulbous sheets in benthic communities on rocky shores. Very common in the Mediterranean Sea where it can be found in the shallow subtidal (from 1 to 6 m depth). The color is due to the presence of photosymbionts. However, it can be sometimes found in marginal, stressful systems such as caves where it is white because of the lack of photosymbionts. It is highly toxic for a great part of marine organisms excepting for the hawksbill turtle, *Eretmochelys imbricata*.

Paracentrotus lividus (Lamarck, 1816): commonly known as the purple sea urchin, it is very common in the Mediterranean Sea but also in the eastern Atlantic Ocean (from western Scotland and Ireland to the Azores, Canary Islands and Morocco). It usually occurs from the first meters below the low water mark up to 50 m depth. It is found on rocks and boulders, and in seagrass meadows of *Zostera marina* and *Posidonia oceanica*, occasionally also in *Cymodocea nodosa* meadows. The grazing behaviour of these invertebrates strongly affects subtidal rocky assemblages. In the Mediterranean Sea, the disproportionate proliferation of this herbivore is widely recognized one of the main drivers of shift from complex macroalgal beds to barren grounds, dominated by encrusting Corallinaceae species, and characterised by a low biomass of erect macroalgae with a small number of associated species (Guidetti et al., 2003; Sala et al., 2012). Non-selective grazing of this invertebrate, coupled with another common sea urchin (i.e. *Arbacia lixula*), on macroalgae impairs the recovery of benthic populations and contributes to the maintenance of the barren status in the long term (Fraschetti et al., 2001; Bevilacqua et al., 2006). *P. lividus* is unable to tolerate low salinity, moreover gametogenesis of this invertebrate is negatively affected by high temperature, suggesting

that climate warming may results in unfavourable environment conditions for its survival (Shpigel et al., 2004). Sea urchin are subjected to fishery because of its edible gonads, but this activity is regulated by legal restrictions.

Arbacia lixula (Linnaeus, 1758): commonly known as black sea urchin, it is very common on the coast of the Mediterranean Sea and Macaronesian Islands (Azores, Madeira, Canary Islands), Balck Sea and less commonly, on the Atlantic coast of Western Africa and the Brazilian coast. It can be found typically at shallow waters, from 0 up to 50 m depth, in rocky shores. It is characterized by a high resistance to hydrodynamism due to a good attachment strength to rocks. This invertebrate feeds mainly on crustose red algae and small filamentous algae. It is thought that higher sea water temperatures favour this species. As well as for *P. lividus*, the grazing behaviour of these invertebrates strongly affects subtidal rocky assemblages driving switches between one complex state, dominated by a stratified assemblage of several erect algae (including the *Cystoseira* genus), to a simpler one, dominated by few encrusting algae, the so-called barren grounds (Hereu et al., 2008; 2012 Sala et al., 2012).

1.1. Reproduction - Recruitment - Population dynamics

Despite of the key role of macroalgae in coastal ecosystems, it is surprising how scarce our knowledge about most species and their population dynamics still are. Separate research traditions between ecologists and phycologists may have prevented our understanding of macroalgae dynamics (Schiel & Foster, 2006). Ecological studies have been focused on trophic and community dynamics, but they have to a large extent not taken into account macroalgal life histories and their environmental interactions, studied traditionally by phycologists. Nevertheless, understanding algal population dynamics is pivotal for conservation and restoration, as well as to predict their responses to environmental change (Schiel and Foster, 2006; Smallegange & Coulson, 2013).

1.1.1 Life cycle and reproduction

Kelp life cycle involves a diploid sporophyte phase that produces spores which, after a planktonic phase, settle and develop into a haploid male or female gametophytes. Spores are liberated from the sporophyte in large numbers, they are relatively small (in comparison with fucoids), resulting in a very variable dispersal capability, between 3 m (*Postelsia palmaeformis*, Dayton, 1973) to 400 m (*Pterigophora californica*, Reed et al. 1988). The spores germinate into microscopic, unisexual gametophytes. Eggs are extruded in female gametophytes but remain inside the oogonium while males liberate sperm from antheridial cells and fertilize the egg cells. This results in diploid zygotes which develop into mature sporophytes that encompass a huge range of sizes, from spores measuring 10^{-5} m to adult sporophytes larger than 10 m.

Kelps can be annual (e.g. *Postelsia palmaeformis*, Dayton, 1973), but most of the species are perennial, such as *Saccharina latissima* which may live 3-5 years (Borum et al., 2002) while others, e.g. *Laminaria hyperborea* reach ages above 15 years such as *Laminaria hyperborea* (Kain, 1975). The reproductive maturity is also reached relatively early in life in *S. latissima* (8-15 months, Kain, 1975), while it takes longer for *L. hyperborea* (3-5 years, Lüning 1990 and references therein).

Most kelp species have fast growth rates, with some species such as *S. latissima* which growth from 1.1 cm/day to 4.87 cm/day (Sjötun, 1993) or *L. hyperborea*, which growths 0.94 cm/day (MarLIN, 2006). Indeed, kelps have some of the fastest growth rates of any primary producer on the planet, (Schiel & Foster, 2006) with values close to 15 g fixed carbon m⁻² day⁻¹ (*Macrocystis pyrifera*, Graham, 2007).

Although the furoid life cycle is very similar to kelp, there are distinct differences that should be considered in a conservation context. In contrast to kelp, fucales only produce one type of thallus, corresponding to a sporophyte diploid phase, while the reproductive, haploid gametes are generated within specialized compartments (receptacles) on the algal thallus. During the reproductive season specialized regions, develop into cavities named receptacles, where gametangia are produced (e.g. *Cystoseira* sp.). These specialized compartments (conceptacles or receptacles) are usually located at the top of the deciduous part of individuals, e.g. in *C. mediterranea*, *C. barbata* and *C. crinita*, while in *C. zosteroides* they are developed at the base of the deciduous branches. Fertilization is usually external, and adults can be either monoecious or dioecious, depending on species. Zygotes, which are the dispersal phase, are larger than kelp spores, making its dispersal capability shorter, from 0.20 cm (*Cystoseira compressa*, Mangialajo et al., 2012) to 30 meters (*Sargassum muticum*, Deyser and Norton, 1982). Nevertheless, floating portions of fertile algae have also been strongly implicated in the process of long distance dispersal (Dayton, 1973; Deysher & Norton, 1982).

Almost all furoid species are perennial. Some species develop deciduous fronds seasonally on perennial thallus (e.g. *Cystoseira* spp.), and others have an annual thallus which is lost at the end of summer and only the holdfasts overwinter and regrow in the next year (e.g. *Sargassum* spp.). Longevity in furoid is generally longer than for kelps. Many species live up to 5–10 years (Chapman, 1995), and some can live longer than 50 years (e.g. *Ascophyllum nodosum*, Svensson et al., 2009; *C. zosteroides*, Ballesteros et al., 2009; Capdevila et al., 2016). However, as in the case of kelps, longevity is unknown for most of the furoid species.

Reproductive maturation is as long as 3 years in the case of *C. zosteroides* (Capdevila, unpublished data). Growth is also generally slower in furoids than for kelps. In the case of *Cystoseira* species, although the vegetative part is developed annually, the perennial part usually has a slow growth rate, from 0.5 cm/year (*C. zosteroides*, Ballesteros et al., 2009) to 2 cm in 9 months (*C. crinita*, Sales et al., 2011). The development of the vegetative part in deep-water species (*C. zosteroides*) begins earlier (February; Ballesteros 1990) than for shallow-water species (spring; *C. crinita*, *Cystoseira* sp., *C. barbata*, *C. mediterranea*; Barceló, 2001).

The reproductive season can significantly variate between species and regions (Schiel & Foster, 2006). *L. hyperborea* reproduces from September to April, while *S. latissima* may remain reproductive during the entire year (MarLIN, 2006). For those regions where there is a marked seasonality, like in the Mediterranean, reproduction begins at the productive season, usually spring, when nutrients are more abundant and there is a high light availability. Shallow species usually remain fertile until late summer (*Cystoseira* sp., *C. barbata* and *C. mediterranea*), while *C. zosteroides* is only reproductive from March to early June (Capdevila et al., 2016) and *C. crinita* is fertile from autumn to early spring in the Balearic Islands (Barceló, 2001).

In both cases (kelp and furoids), by far the most mortality takes place during the first stages of their life cycle. There are many natural factors that can influence the survival of early stages, such as light and temperature (Irving et al., 2009) or sediment load (Airoldi, 2003), as well as human-derived impacts (Ferrario et al. 2016). In the case of some long-lived species, as *C. zosteroides*, recruitment can be very scarce over long-time periods (Ballesteros et al., 2009).

It is worth to mention that intraspecific competition can substantially modulate the survival of early life stages. However, there are no clear patterns among the different

studied species, with studies showing positive (Brawley & Johnson, 1991), negative (Capdevila et al., 2015) or no effect (Piazzi et al., 2017) of conspecifics on the survival of early stages. For instance, it has been suggested that the effects of the adult canopy on recruitment may change across physical stress gradients, being positive at low depth and negative to deeper waters (Bennett et al., 2015). This information is relevant in the context of restoration, given that by providing adequate conditions, recruitment can be enhanced (Mangialajo et al., 2012; Piazzi et al., 2017).

1.1.2 Population dynamics and macroalgae strategies

As mentioned before there is a scarcity of information about the population dynamics of macroalgae species. Most studies have used a functional approach, based on morphological characteristics of species (Steneck & Dethier, 1994), rather than taking into account their life history and population dynamics. To our knowledge, only one study has compared the population dynamics of different macroalgae species (Capdevila et al., 2016). This study showed that shallow-water species and most kelp species have population dynamics that highly depend on reproductive processes and growth rates. This is not surprising given that kelp abundance is strongly variable; a kelp forest can be eliminated within a year, but are also able to recover quickly (Dayton & Tegner, 1984). In contrast, the viability of long-lived species as *C. zosterooides* or *A. nodosum* depends mostly on the survival of large individuals, hence their recovery may take decades (Capdevila et al., 2016).

Despite they may have a similar ecological role, species with distinct life cycles and dynamics doesn't have the same response to disturbances. Understanding these differences is fundamental to design effective management and restoration tools. For example, for kelp species which have high growth rates and great dispersal abilities, a good understanding of local hydrodynamics, together with the protection of potential "source" populations may be enough to ensure their recovery. In contrast, the recovery of fucoid populations can take decades, probably due to their poor dispersal ability and the slow population dynamics (slow growth and reproduction maturation), suggesting that fucoid populations may require further protection and their recovery may need restoration actions. Given their paucity and the contribution of adults to the population maintenance, adult transplantation should be balanced against other techniques that require less impact to the adult population, such as culturing recruits or artificial seedling.

1.2. Impacts and Mortality

Macroalgae in shallow and sheltered parts of coastal areas are subject to great pressure from various human activities as well as being at risk due to climate change (Wernberg et al., 2011). The decline or disappearance of habitat building species forests from many coastal areas is leading to severe habitat transformations, with the loss of tri-dimensional structures (Airoldi et al., 2014; Benedetti-Cecchi et al., 2001; Thibaut et al., 2005; Benedetti-Cecchi et al., 2012; Tamburello et al., 2013). Loss of perennal macroalgae, either by natural or anthropogenic disturbances, generally results in barrens with an overall loss of biodiversity or an increase of filamentous turf algae.

The loss of large areas of sugar kelp (*Saccharina latissima*) beds observed in southern Norway (Moy & Christie, 2012) has been linked to increased nutrient levels and warmer water causing increased fouling of plants, and the observed decline of kelp and fucoids in southern Europe has been explained by high temperature causing high adult mortality (Fernandez, 2011). Fouling of macrophytes, such as growth of filamentous

algae and sessile animals (e.g. bryozoans or tunicates) on kelp laminas, causes decreased photosynthesis and reduced biological quality of the plants (Andersen et al., 2013).

In the Mediterranean sea, *Cystoseira* forests has undergone heavy decline.

Reasons for *Cystoseira* populations regression are multiple. Some studies have detected the modification, regression, and even disappearance of *Cystoseira* populations related to increased pollution levels (Bellan- Santini, 1966, 1968; Belsher, 1977; Munda, 1974; 1982; Hoffman et al., 1988; Soltan et al., 2001). Although, some *Cystoseira* species seems to resist a certain degree of nutrient enrichment, eutrophication in high concentrations can replace *Cystoseira* forests for other habitats dominated by stress tolerant species (e.g. Arevalo et al., 2007).

Unfortunately, nutrients are not the only compounds that are likely to produce shifts in macroalgal communities. Chemical pollution, from metals to several persistent organic pollutants (POP), which are emitted by industries or used in agriculture, are increasing in concentration in several coastal areas and effect *Cystoseira* populations negatively. Sales et al. (2011) demonstrated that heavy metals may have lethal effects on *Cystoseira* species at relatively low concentrations. *Cystoseira specimens* that were transplanted to polluted areas absorbed heavy metals and showed lower growth and survival rates. The increase of water turbidity during the last thirty-five years (Guille, 1970; Gros, 1978), due to an increase in suspended material, particulate organic matter (POM) and sedimentation is believed to have caused decline of *Cystoseira* populations in the Adriatic Sea (Cormaci & Furnari, 1999).

However, among all anthropogenic pressures, habitat loss, due to coastal development and urbanization (e.g. Ferrario et al., 2016; Frascchetti et al., 2012; Perkol-Finkel & Airolidi, 2010, 2012; Tamburello et al., 2013), frequentation (Milazzo et al., 2002), or even natural storms (Navarro et al., 2011) are among the perturbations frequently associated with fragmentation and loss of *Cystoseira* populations.

Other studies have related the disappearance of *Cystoseira* species and other canopy forming algae to outbreaks of grazer populations (Gros, 1978; Vukovic, 1982; Verlaque, 1987; Arrighi, 1995; Sala et al., 1998; Hereu, 2004; Gianni et al., 2013). Along the northern coast of Norway an extensive overgrazing of kelp forest (dominantly *Laminaria hyperborea* and *Saccharina lasissima*) occurred during the early 1970s. The grazing event was caused by a sudden increase in the green sea urchin (*Strongylocentrotus droebachiensis*) population density and the resulting barren ground area covered approximately 2000 km² (Norderhaug & Christie, 2009). In the Mediterranean Sea, sea-urchins are considered the most important herbivores, being able to graze the macroalgal communities and to create barren grounds (i.e. rocky reef, bare or covered by encrusting coralline algae) (Gianguzza et al., 2011; Guidetti, 2006). High densities of sea urchins are usually associated with over-fishing of their predators (sea-brems of the genus *Diplodus*) (Guidetti, 2006; Sala et al., 1998; Guidetti & Sala, 2007). Another important herbivore in Mediterranean rocky bottoms is salema (*Sarpa salpa*), known to selectively graze on some *Cystoseira* species (Vergés et al., 2009). Its contribution to the general loss of *Cystoseira* in the Mediterranean Sea cannot be quantified with the present knowledge, but we cannot exclude an increase of salema abundances due to the over-fishing of their predators (Sala, 2004; Ferretti et al., 2008; Guidetti & Micheli, 2011).

In recent decades, two exotic herbivorous rabbitfishes, *Siganus rivulatus* and *Siganus luridus* have become abundant along the eastern part of the Mediterranean (Sala et al.,

2011). Experimental evidence show that these rabbitfishes have profoundly transformed shallow rocky reefs, removing all canopy-forming macroalgae and preventing the establishment of new algae, shifting the system towards deforested areas covered by a thin layer of epilithic algae and detritus (Sala et al., 2011). This shift from productive algal forests to largely denuded areas has occurred across of hundreds kilometres, and has led to a 60% reduction in overall benthic biomass and 40% decrease in species richness (Vergés et al., 2009; 2016). Although the geographical distribution of areas deforested by rabbitfish is restricted to the southeastern Mediterranean Sea (Vergés et al., 2015) the fast warming rate of the Mediterranean basin (Nykjaer, 2009) may lead to an expansion of rabbitfish through Mediterranean Sea potentially threatening overall shallow water *Cystoseira* forest.

Besides rabbitfish other invasive species, such are invasive macroalgae, may pose important threat for *Cystoseira* forest by competing interactions. Some studies have already stressed the decline of kelp populations due to invasive algae competition (e.g. Scheibling & Gagnon, 2006). Although, some authors point out that structured, dense and healthy *Cystoseira* forest may prevent the spread of some invasive algae (Ceccherelli et al., 2002); others have already documented that depending on the *Cystoseira* species identity, invasive algae may spread and colonize dense macroalgae forest dominated by *Cystoseira* (Bulleri et al., 2016). Once established in dense meadows, invasive algae may prevent re-colonization by *Cystoseira* and persists prolonged periods. In this line, Ballesteros et al. (2009) observed a decrease on of *C. zosteroides* recruits agreeing with the introduction and invasion of *W. setacea* in Scandola RP.

Climate change also influence marine macroalgae and their associated ecosystems. Seaweed survival, growth, and reproduction are known to vary with numerous climatically sensitive environmental variables including temperature (Serisawa et al., 2004). Predicting true individual-level responses to climate change in seaweeds is challenging owing to the numerous life history stages and transitions upon which environmental change can act (Schiel & Foster, 2006). Increased temperature is generally thought to have negative effects on spore production (Buschmann et al., 2004), germination (Buschmann et al., 2004), recruitment (Deysher & Dean, 1986, Buschmann et al., 2004), and sporophyte growth (Rothäusler et al., 2009; 2011) for other kelp species as *Macrocystis*. Changes in the environment will result in changes in seaweed distributions. Drastic population declines and even local extinctions have been documented at the warm (lower latitude) end of species' biogeographic ranges during periods of warming (e.g., Serisawa et al., 2004). Range retraction at low latitudes can be offset by expansion into higher latitudes, as in western Europe where warm-water species have expanded northward (Lima et al., 2007). Experimental studies on the consequences of climate change on Mediterranean macroalgal forest are lacking, but we do not expect they will extremely differ on the general trends globally described.

Besides global stressors, multiple other local stressors such as abandoned fishing gears (nets, trammel nets, threads) (Capdevila et al., 2016) or trampling may threat local and restricted *Cystoseira* populations on a local scale.

Unfortunately, all of the anthropogenically forced changes in the physical and chemical environment are occurring simultaneously, and in many cases, the impact of any particular stressor on the physiology and performance of marine macrophytes will

depend upon the presence and magnitude of additional limiting or disruptive stressors. For example, in the Adriatic, the sudden decline of the *Cystoseira* forests, with 70% of the canopies lost during 2002–2005, appeared to be related to combined acute disturbance from beach nourishments (in the form of gravel and cobbles) and severe storms which were frequent during this period. However, available historical data suggest that the loss was probably facilitated by long-term natural and human-induced changes in the biotic and abiotic conditions in the system (Perkol-Finkel & Airoidi, 2012). Contrarily, well conservation status of macroalgae forest in Port Cros NP is the result of the absence of habitat destruction, high seawater quality and the regulation of human activities (fishing, tourism, diving).

1.3. Functional role-Biodiversity

In the last years, the role of biodiversity on the functioning of marine ecosystems has received increasing attention. This requires knowing the role of species, alone or in different combinations, in the marine environment. This information is not always available. Quantitative information at species level on life history traits, and on ecological traits in general, contributing to specific functions are still scattered (Piraino et al., 2002). The same consideration applies to the ecological attributes of species that allow the recovery of these systems.



Figure 1. Schematic representation of a *Cystoseira crinita* forest structure and biodiversity (from Sales et al., 2011)

Macroalgal canopies such as kelps and fucoids, dominant habitat-forming species in rocky intertidal and subtidal habitats along the European temperate coasts (Bulleri et al., 2012; Crowe et al., 2013), are paradigmatic under this respect. They provide biogenic structure, food and shelter to diversified assemblages of understory species and enhance coastal primary productivity (Fraschetti et al., 2012; Bianchelli et al., 2016) (Fig. 1). In the Mediterranean coastal areas, the fucoid algae *Cystoseira* spp. form dense canopies

able to maintain species rich understory assemblages of sessile and vagile invertebrates and smaller-sized algae by providing shade and reducing physical stress due to aerial exposure (Fraschetti et al., 2002; Thiriet et al., 2016; Pitacco et al., 2014). The disappearance of *Cystoseira* always causes a consistent decrease in invertebrates' abundance (Benedetti-Cecchi et al., 2001). *Cystoseira crinita* and *C. balearica* forests have a high nursery value and the consequences of the alteration of this habitat on the recruitment of rocky reef fish assemblages are great. In fact, densities of several reef fish juveniles—particularly *Symphodus* spp.—have been found 9 to 12 folds greater in *Cystoseira* forests than in other erect, turf, barren habitats (Cheminée et al., 2013). The nursery value and the functional importance of *Cystoseira* forests suggest that their loss strongly affects the recruitment of littoral fishes in the Mediterranean Sea with serious consequences on the goods and services they provide. Clearly, the effects of canopies on other biodiversity compartments can be different across species: *Cystoseira compressa* has short fronds, so the understory environment can be limited compared to that provided by other congeneric species with larger fronds (Benedetti-Cecchi et al., 2001; Bulleri et al., 2002).

The decline or disappearance of *Cystoseira* forests from many Mediterranean areas is leading to severe habitat transformations, with the loss of tri-dimensional structures (Airolidi et al., 2014; Benedetti-Cecchi et al., 2001; 2012; Tamburello et al., 2013). Loss of *Cystoseira*, either by natural or anthropogenic disturbances, generally results in the increase of turfs or barrens with an overall loss of biodiversity. A simple model suggested the existence of a critical threshold in the *Cystoseira*–turf system, with a tipping point at about 75% of canopy loss (Benedetti-Cecchi et al., 2015). The functional consequences of canopy loss are still unclear: direct measures showed idiosyncratic changes in ecosystem functioning (e.g. community respiration, gross primary productivity, net primary productivity) in space and time (Crowe et al., 2013).

Despite being among the most important habitat-forming organisms in temperate seas, almost nothing is known about the life history traits of these species contributing to specific functions resulting in differences in resistance/resilience to disturbance. This limits our ability to understand the susceptibility of macroalgal canopies to global and local stressors, and to predict future trends under ongoing environmental change, which, in turn, hinders conservation actions.

Recruitment seems to play a key role in recovery processes. Recent studies on the population dynamics of *C. zosteroides* showed that this species, after mortality pulses, increases the number of recruits (and probably recruit survival) due to the new space liberated and, therefore, lower intraspecific competition. Nevertheless, it was observed that when storm disturbances were more frequent than once every 50 years, *Cystoseira* populations collapsed, and this effect worsened when several stressors acted simultaneously (Capdevila et al., 2016). *C. zosteroides* forests display slow population dynamics, similar to terrestrial perennials and trees and conclusions about the effects of global and local stressors and their interaction can be potentially extended to all underwater macroalgal forests.

Healthy canopies exert a strong control on the physical and biological environment, for example by sweeping away detrimental sediments or inhibiting potential competitors such as algal turfs (Kiirikki, 1996; Airolidi, 2003; Irving & Connell, 2006), thus triggering positive feedbacks that facilitate self-recruitment and maintenance (Connell, 2005). Recent experimental work in other canopy systems (Schmidt & Scheibling,

2007) also reports that canopies formed by different species may differently affect both the physical and biological environments, which could be related to variations in morphology and habitat architecture of the species. Bulleri et al. (2016) demonstrated that the effects of macroalgal canopies on *Caulerpa* differed markedly according to the species by which they were formed. The presence of *C. compressa* decreased invasion, that of *C. crinita* enhanced invasion and that of *C. barbata* had no effect. The experiment shows that the effects of disturbance on invasion depend upon its intensity, the main mechanism through which biodiversity generates invasion resistance and the life-traits selected within the native species pool. Disturbance can sustain invasion resistance when promoting the dominance of competitively subordinate species possessing traits that allow outperforming invaders.

Recovery is always the result of interactions between species (dominance, inhibition or facilitation) and extrinsic factors (e.g. colonist supply and environmental setting), and there are circumstances where such interactions can feedback negatively limiting recovery for decades.

1.4. Trophic interaction

On shallow rocky reefs in temperate areas, the loss of macroalgal habitats and their replacement by persistent coralline barren grounds are of increasing concern (Fraschetti et al., 2001; Guidetti et al., 2003; Sala et al., 2012). Direct and indirect trophic interactions can be considered responsible for this increasingly observed regime shifts. The Mediterranean has only two major native herbivorous fishes, *Sarpa salpa* and *Sparisoma cretense* (Azzurro et al., 2007). Although at large abundances *Sarpa salpa* should be able to reduce the biomass of some benthic algae (Verges et al., 2009; Tomas et al., 2011), only introduced herbivorous fishes (*Siganus* spp.) have been shown to cause strong algal declines (to the extent of creating barrens) in the Eastern Mediterranean (Sala et al., 2011). The spreading throughout the Mediterranean of these species by the effect of climate change, may determine the structure and functioning of benthic communities. Thus, to manage Mediterranean algal forests, we will have to take into account the functional traits of range-shifting species to determine potential mechanisms of impact on ecological communities (Verges et al., 2014).

Sea urchins are the main predators of canopy-forming algae (Hereu et al., 2008), which, in high densities can transform algal forests into barren communities, with a consequent loss of biodiversity and ecosystem functions (Bevilacqua et al., 2006). Predatory fish have a major role in determining the sea urchin densities and, by trophic cascades, algal communities (Sala et al., 1998). At high fish abundance, predation tends to maintain low sea urchin abundances (Guidetti & Sala, 2007), while at low predatory fish abundance, often driven by overfishing, sea urchin abundance is regulated by many other factors and thus their abundance becomes less predictable (Hereu et al., 2012).

Although trophic cascades have been described in several areas, this deterministic predator-sea urchin-algal relationship has been demonstrated not to be linear (Moksnes et al., 2008). In an extensive survey, Sala et al. (2012) observed a non-clear pattern of the structure of benthic communities associated with a gradient in fish biomass. These results indicate that factors other than fishing are largely responsible for the structure of Mediterranean benthic communities.

This trophic cascade was recently revised under the perspective discontinuous regime-shift dynamics, in which the transition from algal forests into urchin dominated barrens is produced by a nonlinear shift, whereby a critical threshold in sea urchin abundance triggers overgrazing of algal beds. Moreover, the threshold of urchin abundance triggering destructive overgrazing of algal forests (forward shift) is markedly greater

than the threshold in urchin abundance at which algal beds can begin to recover (reverse shift), implying discontinuous regime-shift dynamics with hysteresis (Ling et al., 2009). This dynamic implies also the existence of feedback mechanisms increasing the resilience which maintains stable both algal forests and urchin dominated barrens (Ling et al., 2015). On algal forests, these mechanisms are identified as the presence of fish predators (Guidetti & Sala, 2007) and the abundance of invertebrates which feed on post-settled and juvenile sea urchins (micropredators) (Bonaviri et al., 2012), the escaping behavior of sea urchins in the presence of predators (trait-mediated interactions) which inhibit the urchin grazing (Hereu et al., 2006), or the propagule supply of algae which facilitate the algal recuperation after grazing episodes.

When urchin barren communities are formed, they are also stable maintained by feedback processes enhancing their resilience. Sea urchins have a high trophic and morphologic plasticity, and at high densities can switch their diet from large macroalgae to encrusting/ filamentous forms, and increase their spines length (Hernandez & Russell, 2010), increasing thus their survival and reducing their mortality by predation. Moreover, the presence of adults can facilitate the survival of juveniles by reducing micro-predator abundance by eliminating macroalgae (Bonaviri et al., 2012) and also offering refugia under adult urchin spine canopy (Hereu et al., 2012). Increasing the barren size reduce the macroalgal propagule supply, impeding thus its recovery. Moreover, the growth of ephemeral algae and the formation of turf communities restricts *Cystoseria* forests re-growth (Perkol-Finkel & Airolidi, 2010).

Consequently, the restoration of algal forests not only requires the restoration of sea urchin predators, but also to take in account this hysteresis effect. Implementing such management can be achieved not only on building resilience of the desirable macroalgal bed state by increasing predators and algal recovery, but also eroding resilience of the urchin barrens state once it has formed by eliminating those feedback mechanisms.

1.5. Population genetics

In this section, we considered the data available for species potentially targeted by removal actions in macroalgae habitats. Population genetics studies were conducted in *Arbacia lixula* and *Paracentrotus lividus* in the Mediterranean Sea. Focusing on *Arbacia lixula*, the global phylogeographic study of Wangensteen et al. (2012) included samples from 17 populations inhabiting three Mediterranean subregions: the Alboran sea and the western and eastern Mediterranean basins. No significant genetic differentiation was observed at the different spatial scales considered. Based on the Analysis of Molecular Variance (AMOVA) the three different subregions were not differentiated, and none of the 136 pairwise comparisons among populations based on F_{ST} were significant. These results support a genetic homogeneity of *Arbacia lixula* over the Mediterranean Sea. This homogeneity may be explain by two alternative hypothesis which remain to be tested: a high levels of gene flow or a recent colonization of the Mediterranean by *Arbacia lixula* inducing that the populations in the different basins have not yet diverged from each other. The spatial genetic structure of *Paracentrotus lividus* was described over the Mediterranean Sea including the eastern and western basins and the Adriatic Sea. While the lack of genetic structure over the western Mediterranean reported by Duran et al. (2004) and Calderon et al. (2008) supported high levels of gene flow, Penant et al. (2013) demonstrated significant genetic structure between populations separated by 40 to 60 km. This last study thus suggests that gene flow in *P. lividus* may be more restricted than previously thought. Interestingly, patterns of temporal genetic structure (i.e. between cohorts from the same site) were also described furthering our knowledge regarding the reproduction in this

species. The levels of genetic diversity within cohorts were high without reduction from recruit to adult cohorts and no or very low genetic differentiations were observed between cohorts (Calderon et al., 2009). This suggests that mortality due to stochastic or selection processes act only marginally on the studied cohorts. Moreover, estimations of effective population size (N_e) suggest that N_e is large in the study sites and that reproductive success of adults is high. However, the generalization of these results remains to be formally tested and Calderon et al. (2012) demonstrated some yearly variations in the pattern of recruitments and temporal genetic structure.

The patterns of spatial genetic structure were characterized with different types of markers in *Strongylocentrotus droebachiensis*. In their pioneering study, Addison & Hart (2004) used four microsatellites to demonstrate a lack of genetic structure in the North-West Atlantic and a low but significant genetic structure between samples from three different regions (North Pacific, the North-West Atlantic and North East Atlantic) separated by more than 6000 kms. While these results suggest a high gene flow between populations from the same region, some populations separated by only 50 kms were significantly differentiated suggesting that the spatial patterns of genetic structure in this species may be described as “a chaotic genetic patchiness” with populations homogeneous over large geographic scales but including some significant genetic heterogeneity at lower scale. In their recent study using a new set of microsatellites, Norderhaug et al. (2016) described a peculiar pattern of genetic structure in the North East Atlantic including isolation by distance and chaotic genetic patchiness. Indeed, the genetic differentiation between populations was generally low and increased with the geographic distances. As previously, some populations showed higher levels of divergences. While the pattern of isolation by distance is consistent with long distance larval dispersal following the main currents in the studied region, the occurrence of strong genetic differentiation in some populations may result from two hypotheses: larval retention due to local hydrographical features or introgression by another species. While these hypotheses remain to be tested, these two studies demonstrated that overall gene flow is high in *Strongylocentrotus droebachiensis*.

These studies suggest that the three sea-urchin species demonstrate high gene flow which suggesting high colonization capacities. Accordingly, removal actions over very local spatial scales (few square meters) may not be efficient. Alternative solutions should be designed such as large-scale removal actions focused for instance on reproductive individuals to decrease the reproductive outputs of a particular population.

In a second step, we considered the habitat forming species that will be targeted by transplantation actions in macroalgae habitats. This survey included: brown macroalgae belonging to the genus *Cystoseira*, *Laminaria* and *Saccharina*.

Population genetics data regarding *Cystoseira* species are scarce and nothing is known for the model species of the WP3. We thus expand our bibliographic survey to close species belonging to the same genus. Accordingly the direct application of the following results should be done with caution. Using microsatellite markers, significant genetic structure was reported in *Cystoseira amentacea* var. *stricta* between nearby populations suggesting a low dispersal capacity of the species (Susini et al., 2007; Robvieux et al., unpublished). Microsatellites were developed in *Cystoseira tamariscifolia* (Engelen et al., 2017), nevertheless to our knowledge population genetics data are not yet available. In the most comprehensive study to date, Thibault et al. (2016) demonstrated that populations of *Cystoseira amentacea* separated by 2.6 km in the bay of Marseilles (France) were significantly differentiated. These preliminary data suggest that restoration actions in these species should be considered over local scale (meters). The

optimal size of transplants patches and distances between patches remains to be estimated but will likely be spatially restricted. Moreover, complementary data are thus urgently needed to complement our knowledge regarding the ecology of *Cystoseira* spp. A comparative study (Robuchon et al., 2014) was conducted between *Laminaria hyperborea* and *Laminaria digitata* in the North East Atlantic along the coast of Brittany. This study demonstrated different levels of genetic diversity and connectivity in the two species. In *Laminaria digitata*, significant genetic differentiation was observed at low geographic scale including between sites separated by less than 1km, while the minimum geographic distance to observed significant genetic structure was between 10 and 15 kms. The two species showed hierarchical genetic structure with significant differentiation among regions and among populations within region. In addition, isolation by distance was observed in the two species but it was stronger in *L. digitata* than in *L. hyperborea*. While the two species showed low levels of gene flow, the populations of *L. digitata* are less connected than those of *L. hyperborea*.

Interestingly, similar patterns of spatial genetic structure were observed *Saccharina latissima* along the Danish coast and using 12 microsatellites. The regional genetic structure was complemented by a significant isolation by distance between populations, with the F_{ST} being significant for populations separated by 80 km (Nielsen et al., 2016). Levels of genetic diversity were in the same order as those reported from *L. digitata*.

From the bibliographic survey, we can conclude that the species targeted in the WP3 macroalgal habitats show two main and contrasted spatial patterns of genetic structure. The level of structure is low inducing high gene flow and strong recolonization capacities in the species targeted by removal actions. On the contrary, the habitat forming species targeted by restoration actions are characterized by significant population genetic structure from local to regional scale involving restricted gene flow and low recolonization capacities. This suggests that restoration and removal actions should be conducted on contrasted spatial scales.

1.6. Previous restoration actions

Ecological restoration is an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability (SER, 2004) which became a prominent tool when natural recovery of degraded, damaged or destroyed ecosystems is hardly expected or require long periods of time.

For terrestrial, transitional and freshwater ecosystems, restoration ecology has been widely used and studied (Bradshaw & Chadwick, 1980; Vallauri et al., 2002; Blignaut et al., 2013), while their application in marine ecosystems is fairly recent (Elliot et al., 2007) and mainly related with coral reefs and seagrasses (Fonseca et al., 1996; Van Katwijk et al., 2009; Jaap, 2000).

Concretely, in northwestern Washington, USA, Carney et al. (2005) examined and compared two different restoration techniques to establish *Nereocystis luetkeana*, one by out-planting recently settled zoospores and microscopic sporophytes cultured in the laboratory, and the other one by transplanting juvenile saprophytes from natural populations. Moreover they did a cost benefit analysis, which in most cases is uncertain but is a very important aspect to consider (Bayraktarov et al., 2016). For the cultured out-plants the cost per installed plant was approximately 13 USD, due to no recruitment was obtained with this method, the authors concluded that the costs far exceeded the benefits. In the case of juvenile transplants, the calculated cost per transplant was approximately 12 USD. With this method they obtained a 28% survival rate of sexually mature *Nereocystis luetkeana*, which contributed propagules to the surrounding area.

The method mainly failed due to the fixation system used to subject transplants in the substrate.

Two different techniques for restoration of damaged *Macrocystis integrifolia* beds, in the Atacama region of Chile were developed by Westermeier et al. (2014). They explanted laboratory-grown juvenile sporophytes fastened to different substrata with fast-drying glue, moreover they tested a spore-based technique employing direct inoculation of spores onto rocky substrata placing mature sporophylls on the sea bottom. Respect to the first restoration method, juvenile sporophyte explants, no statistical differences in growth rates or reproductive phenology were found between the different tested substrates and they obtained a 40% of survival in 9 months. Whereas in the case of sporophyte seedling, the first recruits were detected 3 months later on beach and sea bottom boulders with 60 and 20 % effectiveness (% of boulders with recruits), which was 50 and 10 after one year, and with final densities of 1 and less than one recruits per boulder.

Similarly, we can find more restoration examples on the literature about different macroalgal forests around the world (e.g. Hernandez-Carmona, 2000; Terawaki et al., 2001, 2003; Campbell et al., 2014) and most of them were restricted to localized (small scale) actions and involved adults transplants with moderate economic cost.

Concretely, ecological restoration studies of *Cystoseira* species in the Mediterranean Sea has been less well studied in comparison with Kelps and other Fucoids around the world (Gianni et al., 2013) and economic cost and long term viability of the restoration actions have not been assessed yet. Thus, the knowledge about different restoration techniques and their potential for different species of *Cystoseira* is limited.

Different transplantation techniques for the shallow species *Cystoseira barbata* and *Cystoseira compressa* var. *compressa* were carried out in the North-center Adriatic Sea. Two different adult transplantation techniques were investigated to improve habitat enhancement procedures and to test their feasibility as a restoration tool (Falace et al., 2006). The success of the different technique was related with the structural differences between the replanted population and the natural ones. With this study, got a suitable adult transplantation procedure for *C. barbata*, whereas the transplantation procedure employed for *C. compressa* was not successful. Furthermore, Perkol-Finkel et al. (2012) collected small fragments of broken boulders holding juveniles of *C. barbata* (2-3 months old) and transplanted them onto the new substrate using epoxy putty, to test whether the survival and growth of transplants differed between different habitat type and which factors could influence its establishment. They assessed the transplantation success for the first 9 months (Jul 2008- Feb 2009), recording the survival rates and comparing the transplanted juveniles growth rates with the unmanipulated ones, which was more or less satisfactory. All transplanted juveniles were larger than naturally non manipulated juveniles, although survival hardly reached the 33 % . Additionally, even the authors did not establish the restored populations as a substantial self-sustaining, few transplanted thalli reached the adult size and held reproductive structures with some recruits proximal to these transplants. Additionally, the ability of *C. barbata* to proliferate and recruit onto different structural complexity artificial substrata was analysed, placing plates of different complexity and materials close to the natural substratum and adult fronds. The density of recruits among plates was highly variable. Additionally, in the western Mediterranean Basin, France, Susini et al. (2007), developed a cheap and easy transplantation technique for *Cystoseira amentacea* var. *stricta* and *Cystoseira compressa*. The technique consisted in fix *Cystoseira* thalli, collected from nearby natural population, with epoxy glue in holes made by a drill. The success indicator of the technique was the number of remaining transplanted thalli after

different periods of time (3 weeks, 3 and 6 mo) after transplantation, and the fitness of transplanted thalli in comparison to the natural population individuals. After 6 month 75% of both species were still in place, accordingly the success of the technique was high during the first 6 months for both species, although *C. amentacea* individuals seemed to be better adapted than *C. compressa* ones, which seems to be in agreement with the results of Falace et al. (2006).

However, Robvieux et al. (2013) using a similar technique transplanted more than 200 adult individuals from natural populations of *C. barbata*, *C. crinita* and *C. foeniculacea f. tenuiramosa* fixed onto boulders with epoxy putty to the new area. The results were not satisfactory, since almost no individuals survived after 9 months.

Till now, available examples are mainly based on adult or juvenile transplanting from a donor healthy population to a new area to restore. Although there are examples of less destructive restoration techniques for other brown seaweeds (Vasquez & Tala, 1995; Carney et al., 2005; Yu et al., 2012), studies on *Cystoseira* spp. recruitment enhancement, which are specially desirable, considering their critical conservation status, are less explored. Most available information of *Cystoseira* recruits cultures comes from short-term ex-situ cultures with different purposes than restoration (e.g. effects of environmental changes) for different *Cystoseira* species (Motta et al., 1988; Baghdadli et al., 1990; Pellegrini & Lahaye, 1990; Susini et al., 2006; Irving et al., 2009), as for other large brown seaweeds (Vasquez & Tala, 1995; Hwang et al., 2006; Pang et al., 2009; Yatsuya, 2010; Yu et al., 2012).

Nevertheless, Perkol-Finkel et al. (2012) run out a first approach to obtain *in situ* recruits (during three months) which could then be used to restore new areas, although restoration success was not tested. Similarly, Falace et al. (2006) tested sporeling cultures to provide nurseries for transplantation, after 4 months young plants size was enough to face transplantation, but it failed because all recruits fastly detached from the substratum.

Verdura et al. (in prep.) is the first one that developed a new methods to restore new populations from new recruits obtained without removing adult individuals of healthy populations. By means of two different techniques (in situ and ex situ seeding), Verdura et al., restored two different extinct populations of *Cystoseira barbata* in 2011. After 5 years, although survivorship of the new recruits hardly reached the 10%, the final density of the new populations was similar to the control ones. In only one year some of the transplanted individuals reached a fertile conditions, self-providing new recruits to the new populations, leading to a comparable size-structure with the control ones.

In any way, the viability of any population, either natural or restored, will depend on settlement, post-settlement and recruitment effectiveness, then, pressures (biotics or abiotics) occurring during and soon after propagule settlement (competence, temperature, herbivorism), are key for the conservation of the population (Benedetti-Cecchi & Cinelli, 1992). For that reason, studies to improve ecological understanding for early life-history stages of species to restore are not less important.

We can found, some studies focused on understanding the influence of temperature, light intensity, sedimentation on the survival or growth of recent settled germlings of *C. barbata* (Motta et al., 1988; Baghdadli et al., 1990; Pellegrini & Lahaye, 1990; Susini et al., 2006; Irving et al., 2009). Furthermore, restoration techniques, which allow to reduce or remove the impacts of herbivorism either in the first life stages or in juvenile individuals are essentials.

1.7. Insights for restoration actions for macroalgal/kelp forests

No evidence of natural recovery has been reported in macroalgae forest impacted by other human-induced impacts, even when environmental conditions switch back to the reference status (Scheffer et al., 2001; Duarte et al., 2009; Perkol-Finkel & Airoidi, 2010). Thus, once macroalgae forests shift to other impoverished habitats, these can be highly persistent features of rocky bottoms, lasting many decades (Connell, 2007; Dexter & Scheibling, 2014), highlighting the need to mitigate/remove the threat of persistently degraded habitats after amelioration of environmental conditions.

For example, a study on macroalgal assemblages carried out in 1982 and 1999 along the coast of Catalonia (Northwestern Mediterranean, Spain) revealed significant differences in species composition and abundance between the two study periods. The number of stations with indicators of eutrophication decreased from 1982 to 1999 resulting from the implementation of sewage treatment management. However, this decrease was not balanced by an increase in species typical of pristine environments (e.g. *Cystoseira mediterranea*), but rather by an increase of stress-resistant species such as *Corallina elongata* (Pinedo et al., 2013). Probably, the low resilience of *Cystoseira* could prevent it from returning even after one and a half decades of low disturbance. The low dispersion of *Cystoseira* zygotes (Chapman, 1995) that limits new individuals to the proximity of parents (Soltan et al., 2001) could also contribute to limit the recovery of *Cystoseira* populations. The wastewater treatment alone is insufficient to allow *C. mediterranea* to recover. Thus, caution is necessary in using the natural recovery of *Cystoseira* populations to monitor the improvement in water quality, as other factors can hinder their recovery (Sales et al., 2011).

Viability of any population, either natural or restored, will strongly depend on settlement, post-settlement and recruitment effectiveness, then, pressures (biotics or abiotics) occurring during and soon after propagule settlement (competence, temperature, herbivorism), are key for the conservation of the population (Benedetti-Cecchi & Cinelli, 1992). For that reason, studies to improve ecological understanding for early life-history stages of species to restore are especially welcome.

Actually, some studies deal with the influence of temperature, light intensity, sedimentation on the survival and growth of recent settled germlings of *C. barbata* (Motta et al., 1988; Baghdadli et al., 1990; Pellegrini & Lahaye, 1990; Susini et al., 2006; Irving et al., 2009).

In parallel, natural recovery of algae forests involving forests impacted by overgrazing (Filbee-Dexter & Scheibling, 2014) are limited by a hysteresis effect of approximately one order of magnitude in grazer biomass between critical thresholds of overgrazing and recovery (Ling et al., 2015). Therefore, many restoration actions of overgrazed populations will need of a continuous control of the grazing activity, besides increasing recruitment enhancement or adults density from donor populations. In this framework, there are available examples of restoration methods that include the exclusion or limitation of herbivores, as well as cages (McCook, 1996), nets (Sjötun et al., 2007) or manual removal (Falace & Bressan, 2002; Watanuki et al., 2010; Perkol-Finkel et al., 2012; Guarnieri et al., 2016), as well as restoration methods that include the *ex-situ* culture of recruits in the laboratory and consequently avoiding all these first life stage impacts (Verdura et al., in prep.).

It's widely accepted that to carry out a restoration action is necessary to reverse or mitigate the impact. However, it has to be taken into account that species of *Cystoseira* grow in many different type of habitats, with different ecological requirements: to

properly select the transplantation habitats, the appropriate donor population, and the optimal transplantation technique will ultimately determine the restoration success.

According to the available literature, the critical state of conservation and the low recruitment of many *Cystoseira* populations (Thibaut et al., 2014; Ballesteros et al., 2009) the advice for restoration methods is to enhance recruitment without manipulating juveniles or adults from existing populations, which are in many cases already under multiple pressures. On the other hand, many *Cystoseira* populations have specific ecological requirements, so that successful restoration actions have to be planned in areas where the existence of *Cystoseira* was already recorded and thus ecological conditions will completely fit with *Cystoseira* needs, once potential disturbances will be completely removed (e.g. Sales et al., 2011). Finally, the restoration actions should take into account the specific population dynamics for each species, which in some cases can be relatively slow (e.g. *C. zosteroides* Ballesteros et al., 2009; Capdevila et al., 2015), leading to long time for a complete recovery.

However, when a restoration action is tackled, the final and the most important question is *When* we can consider an ecosystem restored? Generally, it is considered that an ecosystem is restored when it contains sufficient resources (biotic and abiotic) to continue its development without further assistance, it will sustain the ecosystem structure and services, and it will be resilient to normal ranges of environmental stress and disturbance (SER, 2004).

We have to select different response variables and measure them both in reference areas and in areas where *Cystoseira* populations were restored. First, we can select and monitor a suite of response variables to follow restored populations (e.g. survival rate and growth of restored populations vs. reference ones). However, in the case of macroalgal forests, the restoration success evaluation will also require long term monitoring (specially for long-live species) to evaluate some attributes than can be complex and involve long-term processes. It is the case of some functional traits, such as the first age/size of sexual maturity of the restored population individuals to ensure the self-maintaining population (which for some species can be after 3 or 4 years, Capdevila et al., 2015). However, whether or not restored population provides all services to the habitat, and therefore habitat restoration has been successfully reached, is difficult to assess. Some ecological indicators such as population size-structure or habitat biodiversity are the most reliable candidate to assess the restoration success.

2. PART II MESOPHOTIC CORALLIGENOUS HABITATS

In coralligenous habitats, the restoration actions are focused on different habitat forming species including three main taxonomic groups Antozoans/Gorgonians (*Paramuricea clavata*, *Corallium rubrum* and *Eunicella spp.*), Sponges/*Demospongiae* (*Aplysina spp.* and *Spongia spp.*) and bryozoans (*Pentapora fascialis*; *Myriapora truncata*) (Fig. 2).

Sponges/Demospongiae

Spongia officinalis Linnaeus, 1759 is the typical bath sponge, collected for commercial purposes. It has a soft skeleton made by primary and secondary spongine fibers with very small amounts of embedded sediments. It lives in areas with continuous water movement, both in light, dim-light and dark habitats. The colour can change according with the light gradient, from dark-grey to white. Its depth range is mainly limited at 40 m depth, with the highest densities usually between 5 and 20 m depth. Depending on the water movement, specimens can develop different shapes from flat and large specimens rich in oscula to massive ones with diameters of 40-50 cm.

Spongia lamella (Schulze, 1879) is able to bear high levels of sedimentation and seems to prefer sites characterized by unidirectional currents, as found at some stations of the Portofino Promontory cliffs. The typical orientation of elephant-ear specimens allows the collection of suspended sediments from the horizontal water flow by the incurrent surface. The vase-shaped specimens living on deep detritic bottoms show that their external and internal surfaces are differently involved in water pumping: the external surface is incurrent, while the opposite, internal surface presents oscula only. This orientation is in agreement with different excurrent and incurrent surfaces reported for other horny sponges, in the foreign materials incorporation both in the primary fibers and choanosome, and in the build up of the skeleton (Teragawa, 1986a; Teragawa, 1986b).

Aplysina cavernicola (Vacelet, 1959) has been studied especially from a chemical point of view owing to the production of chemical compounds of pharmacological interest. It lives on steep cliffs, in semi-dark or dark caves. After the thermal anomaly recorded in the Western Mediterranean during summer 1999, its upper limit is shifted from 25 m to about 30/35 m depth. Its soft tissue may create some problem during the handling in case of transplantation.

Petrosia ficiformis (Poiret, 1789) is distributed across the Mediterranean and in the Eastern Atlantic (Guo et al., 1998). It is considered a good model for several studies: (i) the chemistry of the sponge and its associated microorganisms (Seidel et al., 1986; Pagliara & Caroppo 2011), (ii) the production of primmorphs (Valisano et al., 2006; Pozzolini et al., 2014), (iii) the symbiosis with cyanobacteria (Usher et al., 2004; Burgsdorf et al., 2014). *P. ficiformis* is known with two different morphs (Sarà et al., 1998): (i) a massive, pink pigmented form, living in illuminated habitats harbouring a dense population of intracellular cyanobacteria in the sponge cortex (the superficial layer of the sponge); and (ii) a slender pinkish or white morph, commonly found in shaded habitats (pink) and particularly in dark caves (white), where the sponges are devoid of phototrophic symbionts. It can show striking changes in its morphology according to the presence or absence of cyanobacterial symbionts. These changes have been considered adaptive and related to the size (light-exposed specimens are bigger than their dark cave counterparts), shape, surface skeleton, density of pores, and the metabolism (Vacelet & Donadey, 1977; Sarà et al., 1998). In the large and tabular

specimens living on light-exposed cliffs, inhalant pores are very rare. Light-sheltered specimens have a lower symbiont concentration and the sponge becomes cylindrical in shape (Sarà et al., 1998).

Axinella polypoides Schmidt, 1862 is an erect ramose sponge. Yellow in colour, it has dichotomous and occasionally anastomosing branches circular or oval in section. The ectosome skeleton is absent and the choanosome contains a central hard stalk. This species shows some interesting, biochemical peculiarities due to very high values of cyclasic activity (Zocchi et al., 2001).

A. cannabina (Esper, 1794) is an erect, ramose sponge. Orange in colour, it has dichotomous and flattened branches generally without anastomosis. The surface is irregular.

Anthozoa/Gorgonians

Eunicella singularis (Esper, 1794) (Orden: Alcyonacea, Family: Gorgoniidae) is the only symbiotic gorgonian in the Mediterranean Sea. The autotrophic contribution to the diet, supplies more energy than the heterotrophic feeding (zooplankton) (Coma et al., 2015; Ferrier-Pagès et al., 2015). *E. singularis* tolerates a wide range of environmental conditions (Linares et al., 2008a). In the WM the gorgonian assemblages are generally monospecific, even if *E. singularis* can be observed together with *P. clavata* and *L. sarmentosa* in deep and shallow waters, respectively (Gori et al., 2011).

Eunicella cavolini (Koch, 1887), together with *P. clavata*, is the most common gorgonian of the coralligenous assemblages, even if *E. cavolini* shows a wider bathymetric range (4-220 m). Regarding the morphology of the colonies and the pattern of distribution of the populations, Sini et al. (2015) highlighted divergences between populations of *E. cavolini* habiting different areas in the Mediterranean Sea: the NW Mediterranean is dominated by dense assemblages mainly composed of small colonies (<20 cm), with a ≤ 15 m upper limit of distribution; while in the North Aegean Sea, prevailed assemblages characterized by lower densities but larger colonies - suggesting lower recruitment rates - and a deeper, upper limit of distribution (over 30 m), probably due to higher food availability (Sini et al. 2015). Moreover, light penetrates deeper in oligotrophic seas, and semi-sciaphilous species shift their bathymetric range (Kefalas et al., 2003).

E. verrucosa (Pallas, 1766) is a temperate and cold-water species that lives between 2 and 60 metres in the Atlantic Ocean (Sartoretto & Francour 2012; Pikesley et al., 2016), while in the WM it is reported from about 20 to 200 m (Carpine & Grasshoff, 1975; Sartoretto & Francour, 2011); in exposed areas, with high turbidity, it can live also in shallower waters.

Paramuricea clavata (Risso, 1826) (Orden: Alcyonacea, Family: Plexauridae) is one of the most typical species of coralligenous assemblages and can be found to 200m depth. It normally inhabits vertical rocky bottoms dominated by strong currents (True, 1970; Weinberg, 1976; Ponti et al., 2014). It is heterotrophic and its diet is constituted by zooplankton and POM (Coma et al., 1994; Ribes, 1999). Its reproduction occurs in spring.

Corallium rubrum (Linnaeus, 1758) normally lives in dense patches in crevices, overhangs or cave entrances (Riedl, 1984), between 7 and 800 m depth; its bathymetrical range varies considerably in different areas (Carpine & Grasshoff, 1975; Riedl, 1984; Rossi et al., 2008; Costantini et al., 2010). It is a heterotrophic species mostly feeding on detrital POM, followed by live POM and zooplankton (Tsounis et al., 2006a; Picciano & Ferrier-Pagès, 2007).

Bryozoa

Myriapora truncata and *Pentapora fascialis* are two erect bryozoans, very sensitive to mechanical stress. Especially *P. fascialis* can built important facies and, creating many microhabitats, is able to support the recruitment of several species.

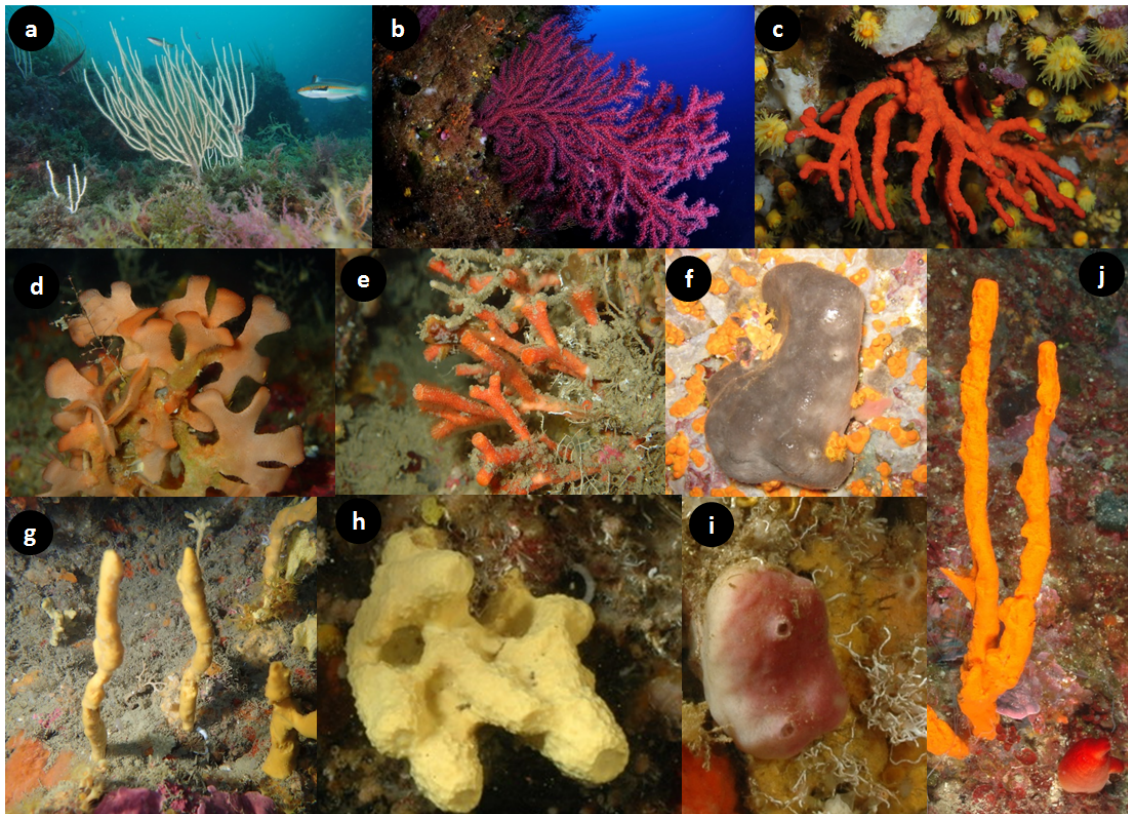


Figure 2. Main targeted species for the restoration activities for mesophotic coralligenous habitats: Gorgonians a) *Eunicella singularis*; b) *Paramuricea clavata*; c) *Corallium rubrum*; Bryozoans d) *Pentapora fascialis*; e) *Myriapora truncata*; Demospongiae f) *Spongia officinalis*; g) *Axinella polypoides*; h) *Aplysina cavernicola*; i) *Petrosia ficiformis* and j) *Axinella cannabina*.

2.1. Reproduction-Recruitment-Population dynamics

2.1.1 Life cycle and reproduction

All gorgonian species are gonochoric (colonies are either female or male) and iteroparous species displaying different reproductive modes. The red gorgonian *Paramuricea clavata* is a surface brooder, a mode of development in which released eggs are retained on the surface of the female colonies. This species synchronically spawn every year in June (Coma et al., 1995a; Gori et al., 2007; Linares et al., 2008a). In contrast, the red coral *Corallium rubrum*, *Eunicella singularis*, *E. cavolini* and *E.*

verrucosa are internal brooders. These species brood the larvae internally and the mature larvae are released from late June and throughout July (Santangelo et al., 2003; Tsounis et al., 2006b; Ribes et al., 2007; Gori et al., 2007; Torrents & Garrabou, 2011). Regardless of the mode of reproduction, gametogenesis in all gorgonian species is characterized by a long period of oogenesis (lasting 13–18 months), which is much longer than the spermatogenesis period (lasting 6–7 months) (Ribes et al., 2007 for a review). Depth-related differences in the reproductive cycle of the gorgonian *E. singularis* were observed in the gonadal output (with the shallow population producing more and larger sexual products), but not in the reproductive timing (Gori et al., 2012). Sexual maturity of gorgonians such as *P. clavata* and *E. singularis* is attained at a size of about 10–20 cm (from 8.5 to 30 cm) and the minimum age at first reproduction is estimated around 5–15 yr (up to 20 yr, Coma et al., 1995b; Cupido et al., 2012). In *Corallium rubrum*, sexual maturity is achieved at relatively small sizes (about 2 mm in diameter and 30 mm in height) which corresponds to ages between 7 and 10 years old (Torrents et al., 2005; Gallmetzer et al., 2010). However, the colony size has a significant effect on the reproduction output of colonies. Large colonies have most of the polyps gravid and the total number of polyps per colony increase exponentially with size (Coma et al., 1995; Santangelo et al., 2003; Torrents et al., 2005; Tsounis et al., 2006b).

While the reproductive biology of some gorgonian species such as *P. clavata*, *E. singularis* and *C. rubrum* have been deeply studied, there is lack of information on the reproductive biology of *E. cavolini* and *E. verrucosa* in the Mediterranean, including the size at first reproduction.

There is also a lack of studies on the reproduction of Mediterranean bryozoans such as *Pentapora fascialis* and *Myriapora truncata*. However, the reproduction should be similar that the observed in other bryozoans. Most bryozoans are hermaphroditic, with individuals containing both ovaries and testes and the fertilization is in general internal (brooding their eggs) but some species shed both eggs and sperm directly into the water where they fuse.

Regarding to sponges, little is known about their reproductive biology among the target species for restoration actions. Only the reproductive cycle of the few Mediterranean species has been investigated to date, there is only information for *Spongia officinalis*. This sponge is gonochoric (with very few cases of hermaphroditism) and viviparous. Young oocytes occur almost all year round, whereas large mature eggs show a peak in October–November. The size had not effect on the reproduction output. Larvae are released from June to July, asynchronously, either at the individual or population level (Baldacconi et al., 2007).

2.1.2 Recruitment rates

As a long-lived and slow-growing species, gorgonians display low recruitment rates as shown the values obtained for *Corallium rubrum* and *Paramuricea clavata* in several studies. The recruitment of *C. rubrum* is very limited in most studied populations. Long-term studies have shown (<0.25 recruits / dm^2) (Garrabou & Harmelin, 2002; Teixidó et al., 2011; Linares et al., 2012a;b; Montero-Serra et al., 2015). However, the maximum recruitment rates measured were $6,24 \pm 4,26$ recruits/ dm^2 have been observed in Italian localities using experimental plates (Bramanti et al., 2005; Santangelo et al., 2012) while one of the highest recruitment rate measured in the field were 2 recruits / dm^2 (Linares et al., 2012a). In both cases the populations displayed also high adult density (Bramanti et al., 2005; Santangelo et al., 2012; Linares et al., 2012a). This fact

seems to indicate a positive relation between density and recruitment (Santangelo et al., 2007; Linares et al., 2012a).

The recruitment rate of the red gorgonian *Paramuricea clavata* is also low ranging between 1.3 and 2.6 recruits /m², being the lowest values estimated in Medes Islands and Cap de Creus (Coma et al. 2001, Linares et al. 2007) and the largest values estimated in La Spezia and Portofino (Cerrano et al., 2005; Cupido et al., 2009). However, in some areas affected by mortality events linked to positive thermal anomalies such as La Spezia and Portofino, the population recruitment rate was 2-fold and 8-fold higher greater than the pre-mortality values (Cerrano et al., 2005; Cupido et al., 2009; Cupido et al., 2012). This increase in recruitment rates after mass mortality events did not always counterbalance the mortality rates due to the high mortality rate (about 50%) of these new recruits as observed in the Port Cros National Park (Linares et al., 2005).

In contrast to the low recruitment rates observed in *C. rubrum* and *P. clavata*, *Eunicella singularis* and *E. cavolini* display a size distribution that is dominated by early life history stages, suggesting that the species is not limited by recruitment (Linares et al., 2008b, Gori et al., 2011a;b). However, the presence of turf algae can sharply reduce the recruitment of *E. singularis* about 5 fold the observed in the absence of algal turfs (Linares et al., 2012b)

Similarly to reproduction, there is an important lack of information on recruitment rates for the target sponges and bryozoans for restoration actions. Only one published study provided information about this variable showing no recruitment of *Pentapora fascialis* during one year in Tino Island in the Ligurian Sea (Cocito et al., 1998).

2.1.3 Growth rates

In general, the targeted species in natural conditions display slow growth rates, i.e. small changes in body sizes are reported in annual basis. Bryozoans have the highest growth rates while gorgonians and sponges showed the lowest rates. Methods used for growth measurements were based on repeated measurements on specimens dimensions either using visual/manual census or obtained from photographic surveys. Besides for the red coral *Corallium rubrum* and the bryozoan *Pentapora fascialis* the analysis of the skeleton features using different sclerochronology method which allows the observation and quantification of annual growth bands.

Regarding the quantification of changes in body dimensions, different methods have been used depending on species growth form, arborescent or massive, and specimens fragility (e.g. calcareous skeletons and soft tissues). In general, in arborescent species linear growth rates (i.e. changes in size of branches) were quantified while in massive species weight and/or volume changes were reported.

In the literature we found studies for growth rates for all targeted species except for three sponges *Spongia lamella*, *Axinella cannabina* and *A. polypoides* and one bryozoan *Myriapora truncata*.

However studies based on sclerochronology and long-term photographic series integrated growth rates over several years or even decades (Marschal et al., 2004; Lombardi et al., 2006; Linares et al., 2010; 2012; Garrabou & Harmelin, 2002; Teixido et al., 2011).

Anthozans/Gorgonians

The growth rates for the 3 *Eunicella* species and *Paramuricea clavata* were obtained from repeated measures on tagged colonies (visual and photographic surveys). The results showed values varying between 0.6 up to 4.5 cm year⁻¹ in height but most mean values for reproductive colonies were around 1 cm year⁻¹ in height (Coma et al., 1998; Mistri & Ceccherelli, 1994; Weingberg & Weingberg, 1979; Weinbauer & Velimirov, 1995a). While the red coral *Corallium rubrum* grow between 0.8 and 1.2 mm year⁻¹ in height resulting in the slowest growth rates of all gorgonian species. (Garrahou & Harmelin, 2002; Linares et al. 2010; 2012; Priori et al., 2013; Garrahou et al., unpublished data) On the other hand, the analysis of growth rings indicated that red coral colonies grow 0.25 mm year⁻¹ in diameter providing similar slow growth rates than in height.

In general, for all targeted species growth rates are up to two times faster in non-reproductive (smaller in size) compared to mature (larger in size about > 15 cm in height for soft gorgonians and around 3 cm in height for red coral) colonies (Coma et al., 1998; Marschal et al., 2004; Bramanti et al., 2005).

Measures on growth rates

Eunicella singularis 2.2 - 4.52 cm year⁻¹ (Weinberg & Weinberg, 1979; Munari et al., 2013)

Eunicella cavolini 0.85 –1.14 cm year⁻¹ (Velimirov, 1975; Weinbauer & Velimirov, 1995b)

Eunicella verrucosa 0.62–3.3 cm year⁻¹ (Sartoretto & Francour, 2012)

Paramuricea clavata 0.8-3.0 cm year⁻¹ (Mistri & Cecherelli, 1994; Coma et al., 1998)

Corallium rubrum 0.13 – 0.26 mm year⁻¹ in diameter and 0.78 -1.19 mm year⁻¹ in height (Garrahou & Harmelin, 2002; Linares et al., 2010; 2012; Priori et al., 2013)

There are few studies investigating seasonal patterns in growth rates in gorgonians. The studies available indicate that growth rates are larger during spring and autumn (Coma et al., 1998; Marschal et al., 2004).

Finally is noteworthy that in the red coral growth rates of transplanted colonies were similar to rates quantified in natural conditions (Montero-Serra et al., 2017).

Sponges/Demospongiae

There are few studies dealing with growth rates of the targeted (or other sponge species dwelling coralligenous). We analyzed two kind of studies providing growth rates from i) quantifying size changes of explants (transplants) under different conditions which fit well for the planned restoration actions and ii) monitoring specimens dwelling in natural community. As a general pattern growth rates obtained studying explants when positive are faster than those obtained monitoring specimens within the community. The main shortcoming of this studies are the limited number of specimens included (rarely exceeding 30 specimens), the limited temporal span of studies (generally less than 5 years) and finally the high inter-specimen variability in growth rates.

Spongia officinalis information on growth rate for this massive specie was obtained from the monitoring of explants in different conditions. The main aim of the studies reviewed was to analyze the viability of sponge farming in *Spongia* spp. as well as in other bath sponges (e.g. *Hippospongia communis*) from the Mediterranean and from

other seas (Pronzato et al., 1999; Corriero et al., 2004). This species can increase by 100% its weight per year despite the initial size of the cutting (explants) (Corriero et al., 2004). For instance, explants of about 55 g after 3 years of growth can reach 200 g wet weight. The mortality of explants is high during the first year up to 20% but after this period the survivals remains stable (Corriero et al., 2004).

Studies dealing with similar species from other temperate areas displayed more contrasted results. In some experiments growth rates resulted in increases in specimens' weight up to 100% in about one year (e.g. *L. wellingtonensis* and *P. croceus*; Duckworth et al., 2004), however in other setups showed no growth or even negative the growth rates (*Spongia manipulates*; Kelly, 2004). The main factors explaining these differences in growth rates were the season when the explants were setup and environmental conditions associated to the selected experimental sites (Duckworth et al., 2004; Kelly, 2004).

Petrosia ficiformis growth rates were obtained both from long-term surveys of natural communities and from explants experiments. Both cases showed extreme slow growth rates in this species. In natural conditions the surveys carried out on 12 specimens during 5 to 15 years indicated decrease in surface areas of these specimens (Teixido et al., 2011) while small change in size were detected during 1 year on the monitoring of 4 specimens (Ferretti et al., 2009). Regarding the transplants on plastic plates showed negative or small positive changes (+2%) in volume on one year (Wilkinson & Vacelet, 1979).

Aplysina cavernicola growth rates were obtained both from long-term surveys of natural communities and from explants experiments. Both cases showed extreme slow growth rates in this species. In natural conditions the surveys carried out on 26 specimens during 5 to 25 years indicated decrease in surface areas of these specimens (Teixido et al., 2011). Regarding the transplants on plastic plates showed a wide array of outcome from negative to doubling the volume in one year (Wilkinson & Vacelet, 1979). However, in general the transplants of *A. cavernicola* displayed small changes in volume between 5 to 10% (Wilkinson & Vacelet, 1979).

Other sponge species dwelling in the coralligenous with massive growth forms such as *Chondrosia reniformis*, *Scalarispongia scalaris*, *Haliclona fulva* displayed, in general, slow growth rates as those described for the target species included in the WP3 restoration actions (Wilkinson & Vacelet, 1979; Garrabou & Zabala, 2001; Teixido et al., 2011). Specimens of *C. reniformis* and *H. fulva* showed almost no changes or decrease in surface during 2 to 15 year monitoring (Garrabou & Zabala, 2001, Teixido et al., 2011) while *S. scalaris* displayed the highest growth rates with significant increase of surface (in average from 0,5 to 20 cm²) over colonization plates monitored during 25 years (Teixido et al., 2011).

Bryozoans

For the two bryozoan species, *Pentapora fascialis* and *Myriapora truncata*, targeted for restoration actions we have only found information on growth rates for *P. fascialis*. Studies on growth rates were based on i) the repeated measures on identified specimens and ii) analysis of growth bands using radiographic methods.

P. fascialis grow between 2,9 and 3.6 cm year⁻¹ (Cocito & Federgheni, 2001; Lombardi et al., 2006). While in a study quantifying the changes in surface of colonies of *P.*

fascialis, the net growth rate resulted on about 65% change over 11 months (Cocito et al., 1998). Finally studies on growth rates on *P. fascialis* using radiographic methods determined the existence of two growth periods within a year; “winter” and “summer” growth bands corresponding to the cold and warm periods. In general, the bands can be clearly distinguished in the skeletons and the colonies grow faster during the warm (2.3 cm) than during the cold one (0.6 cm) (Lomabardi et al., 2006).

For *M. truncata* as we mentioned there is no information available on growth rates but it is likely that their branches should grow at similar rates as those found for *P. fascialis* and other similar erect branching bryozoan species.

A review in growth rates of bryozoan species indicated that bryozoan erect calcified species generally grow vertically 0,2-1,5 cm year⁻¹, though articulated species such as *Cellaria* may reach rates of 4,0 cm year⁻¹ (Smith, 2014). Thus *P. fascialis* should be considered among the most dynamic species within the erect calcified species.

2.1.4 Life span

The slow growth rates characterizing the targeted species indicate that the potential life span of this species can easily reach many decades. The lifespan estimates were not available for all the targeted species for restoration actions in WP3. We provided the information on potential lifespan available as well as an indication on potential lifespan when the information was not found in the literature.

Anthozoan/Gorgonians:

Eunicella singularis can reach between 25-30 years (Weingberg & Weingberg, 1979)

Eunicella cavolini can reach between 54-73 years (Weinbauer & Velimirov, 1995b)

Eunicella verrucosa can reach 30 years (Sartoretto & Francour, 2012)

Paramuricea clavata can reach between 50 and 100 years old (Weingberg & Weingberg, 1979; Coma et al., 1998; Linares et al., 2007)

Corallium rubrum can reach up to 200 years or more (Garrabou & Harmelin, 2002; Teixidó et al., 2011; Priori et al., 2013; Bramanti et al., 2014)

Sponges/Demospongiae:

Spongia officinalis information not available probably several decades.

Spongia lamella information not available probably several decades.

Petrosia ficiformis between 35-45 years old (Teixido et al., 2011)

Axinella polypoides information not available probably several decades.

Axinella cannabina information not available probably several decades.

Aplysina cavernicola between 15-45 years old (Teixido et al., 2011)

Bryozoans:

Pentapora fascialis 11 years (Cocito et al., 1998)

Myriapora truncata information not available probably a decade

2.1.5 Abundance, colony sizes and population size structure

Information on abundance of targeted species for restoration is unbalanced. Most information found in the literature concern gorgonian species. For the sponges and the other bryozoan species the information is scarcer. Despite this, all selected species can be considered common in the coralligenous habitats (Ballesteros, 2006; Kipson et al., 2011; Gatti et al., 2015; Casas-Guell et al., 2016).

In general density of colonies of gorgonian species vary between 1-5 up to 50-60 per m² (e.g. Linares et al., 2008; Sini et al., 2015). However in the case of red coral *Corallium rubrum* densities up to 1300 colonies per m² have been reported from some Italian locations (Garrahou et al., 2017). The differences in the density between the soft gorgonians and the red coral may be explained partially by the colony sizes found in the populations mean 15-20 cm and maximum up to 60-70 cm for *Eunicella* spp. and 30-40 cm and maximum size up to 150 cm for *P. clavata* while red coral *Corallium rubrum* colonies found in the present populations on average have around 3-5 cm in height (e.g. Weinbauer & Velimirov, 1995; Linares et al., 2007; 2008a; Sini et al., 2015; Garrahou et al., 2017).

Size distribution information for Mediterranean populations is available for all gorgonian species except for *E. verrucosa*. In general, populations show unimodal size frequency distribution and more or less bell-shaped. However, *E. singularis* and *E. cavolini* display a larger proportion of smaller, non-reproductive colonies (<15 cm) compared to *P. clavata* which is dominated by intermediate size 20-30 cm. This implies differential recruitment success across the species (Cerrano et al., 2005; Cupido et al., 2009; Coma et al., 2006; Linares et al., 2008a; Kipson et al., 2015; Sini et al., 2015). Regarding the red coral populations from harvested locations are also dominated by small sized colonies while in marine protected areas the proportion of large colonies increase and the size frequency distribution encompassed a larger range of size and sometimes is dominated by large colonies (Garrahou et al., 2017).

There are almost no studies on population structure of targeted sponges. The information available indicates that the sponges are common in the coralligenous but display moderate to low densities (Pansini et al., 2000; Voultsiadou, 2005; Pronzato & Manconi, 2008; Voultsiadou et al., 2008; Parravicini et al., 2013; Teixido et al., 2013; Di Camillo & Cerrano, 2015). For instance *Axinella cannabina* showed densities ranging from 1 to 10 specimens m⁻² (Voultsiadou et al., 2008), *Petrosia ficiformis* 0.1 - 5 specimens m⁻² (Cerrano et al., 2001; Voultsiadou et al., 2008; Ferreti et al., 2009) and *Spongia officinalis* 1-2 specimens m⁻² (Pronzato & Manconi, 2008; Voultsiadou et al., 2008). In general, specimens show medium-large sizes 5-20 cm in diameter and up to 40 cm in height (*A. polypoides*, *A. cannabina*). However specimens in some species can reach extra-large sizes up to 70 cm for *P. ficiformis* (Cerrano et al., 2011). Information on size distribution is very scarce. A comprehensive study in the Aegean Sea indicates that *S. officinalis* and *Hipospongia communis* display size distribution more less bell shaped with the dominance of small size specimens (between 3-6 cm in diameter) (Voultsiadou et al., 2011).

The two bryozoan *Pentapora fascialis* and *Myriapora truncata* can be abundant in the coralligenous. Density of colonies of *P. fascialis* can range from 2 to 12 m⁻² (Cocito et al., 1998; Cocito & Fedreghini, 2001; Garrahou et al., 1998; Cocito et al., 2014) and colonies of this species can reach large sizes up to 40-70 cm in diameter covering a large proportion (>40%) of the basal substrate (Cocito et al., 1998; Cocito & Fedreghini, 2001; Cocito & Sgorbini, 2014; Garrahou et al., 1998). Regarding *Myriapora truncata* there is less information but when present this specie is quite abundant displaying densities up to 30 colonies m⁻² (De La Nuez-Hernandez et al., 2004). However colony sizes are smaller than *P. fascialis* rarely reaching more than 10 cm in diameter (De La Nuez-Hernandez et al., 2004, personal observation). This species

has usually a single point of attachment to the substrate which might hinder the colonies to reach large sizes.

Information on size distribution was only found for *P. fascialis* (Garrahou et al., 1998; Cocito et al., 2014). In general, populations show unimodal size frequency distribution and more or less bell-shaped. Small colonies (<10 cm in diameter) dominate the populations indicating a recruitment success in the populations. However in some populations large colonies (> 40 cm) in diameter can represent more than 30% of colonies. Thus, in absence of major disturbances *P. fascialis* has the potential to reach large sizes. Probably, due its fragility to physical impacts, the recurrent breakage and regrowth as well as recruitment might explain the observed patterns.

2.2. Impacts - Mortality

Several ongoing disturbances affect the Mediterranean gorgonian populations, including *Corallium rubrum*, *Paramuricea clavata*, *Eunicella singularis* and *Eunicella cavolini* populations. Destructive fishing practices, anchoring, uncontrolled and over-frequent diving, mucilaginous algal aggregates and algal invasions present more localized threats whereas mass mortalities caused by positive seawater temperature anomalies can present a regional threat.

Anchor lines, ropes connecting lobster pots, gill nets placed across gorgonian populations and lost monofilament lines may cause tissue abrasion or detachment of the whole colonies (Bavestrello et al., 1997; Tsounis et al., 2012; Sini et al., 2015). Mechanical injuries may reduce colony's reproductive output (Tsounis et al., 2012) and can also lead to destabilization of the associated microbial community (Vezzulli et al., 2013).

Intense diving activity may result in an increase of gorgonian total mortality rates - due to the detachment of entire colonies, while the colonies' extent of injury was not shown to be significantly affected by visitation level (Coma et al., 2004; Linares & Doak, 2010; Linares et al., 2012a). This threat is only likely to affect shallower populations where the recreational diving activity is more intense (Linares et al., 2012a). Furthermore, in this surface-brooding gorgonian, bubbles from divers passing below colonies may remove the eggs prior to fertilization (during spawning period in June-July) and thus affect its reproductive success (Tsounis et al., 2012).

Dense and thick formations of mucilaginous aggregates, caused by seasonal proliferation of several phytoplankton species (e.g. *Acinetospora crinita*, *Chrysonephros lewisii*) may be trapped by gorgonian branches, preventing polyps' food supply and inducing colonies' partial mortality (Mistri & Ceccherelli, 1996; Giuliani et al., 2005; Kersting & Linares, 2006; Sini et al., 2015). In addition, these aggregates may facilitate the spread of microbial pathogens (Danovaro et al., 2009).

Invasive algae *Caulerpa cylindracea* and *Womersleyella setacea* may negatively affect the viability of gorgonian juvenile colonies, causing their lower survivorship, higher necrosis rates and decreased biomass (Cebrian et al., 2012). These invasive algae can also pose a threat for the recruitment of the *Eunicella singularis*, given that they form thick and persistent turfs that completely cover the substrata (Linares et al., 2012b).

Mass mortality events (MME) in the Mediterranean Sea have been recorded from 1980s onwards with increasing frequency (Coma et al., 2009). During the two largest MMEs to date (in 1999 and 2003), linked to positive temperature anomalies of 3-4°C above the average that were detected up to 25 (in 2003) and 40 m depth (in 1999), the gorgonians *Corallium rubrum*, *Paramuricea clavata*, *Eunicella singularis* and *Eunicella cavolini* were affected over ~1000 km of the North Western Mediterranean coastline (Cerrano et al., 2000; Pérez et al., 2000; Coma et al., 2006; Garrahou et al., 2009; Benssousan et al.,

2010; Crisci et al., 2011). These events have shown different impacts depending on the region affected, but the mortality rates can reach to values of 50-80% of the mortality of gorgonians (Linares et al., 2005; Coma et al., 2006; Garrabou et al., 2009; Cupido et al., 2009). Among the most important effects are the loss of density and biomass loss and the shift of dominant size classes towards smaller colonies (Cerrano et al., 2005; Linares et al., 2005; 2008a; Cupido et al., 2008; 2009; Huete-Stauffer et al., 2011), as well as a sublethal impact on its reproductive output (Linares et al., 2008c, Cupido et al., 2012). Besides positive temperature anomalies, additional factors such as physiological status of organisms and activity of pathogens are suspected to modulate the final extent of impact (Bally & Garrabou, 2007; Coma et al., 2009; Vezzulli et al., 2010; Crisci et al., 2011; Ezzat et al., 2013). In addition, mortality events were recently observed also in deep gorgonian populations (below 60 m depth) where neither anomalous temperature increases nor recognized microbial pathogens could be assigned as likely triggers of these events (Vezzulli et al., 2013).

Regarding only to the red coral *Corallium rubrum*, intensive harvesting (legal and illegal) is the oldest and most significant disturbance for red coral populations, driving significant shifts in the size structure of shallow red coral populations in the Mediterranean Sea (Tsounis et al., 2007; Linares et al., 2010; Tsounis et al., 2010; Montero-Serra et al., 2015). Recent experimental aquarium studies have shown the negative effects of acidification on this species. Calcification, growth rates and polyps' (feeding) activity of *C. rubrum* are significantly reduced at pCO₂ scenarios predicted for the end of this century. This threat will potentially contribute to the population fragmentation and increase the risk of potential extinction of red coral populations in a near future (Bramanti et al., 2013; Cerrano et al., 2013).

Fishing, warming and acidification seem to be the most important threats for sponges in the Mediterranean Sea. Some Mediterranean sponge species belonging to the genera *Spongia* and *Hippospongia*, have been harvested for commercial purposes since ancient time. In addition, diseases have affected several of these species during different events (Pronzato, 1999; Voultsiadou et al., 2011). A combination of overfishing and disease has resulted in a large population of *Spongia officinalis* coming to the brink of extinction (Pronzato et al., 1996). In addition, among the target species, *Spongia officinalis* have been also affected by the mass mortality events linked to warming waters in the Mediterranean Sea (Perez et al., 2000; Cerrano et al., 2000; Garrabou et al., 2009).

Focusing on bryozoans species, several studies have reported diving impacts on bryozoans, including the target species *Pentapora fascialis* and *Myriapora truncata* (Garrabou et al., 1998; De la Nuez-Hernández et al., 2014; Casoli et al., 2016). Regarding to global stressors, these species have also been affected by mass mortality events (Perez et al., 2000), however, no quantitative data about the impact on these species are available to date. In addition, experimental studies have shown the impact of acidification on *M. truncata* (Lombardi et al., 2011; Cocito & Lombardi, 2012).

2.3. Functional role-Biodiversity

The coralligenous bioconstruction is formed by the superposition of living calcareous organisms on dead skeletons of previous generations, creating a secondary hard substrate. Considering the scheme proposed by Riedl (1996) it is possible to recognize four main layers: i) cryptic/boring, ii) encrusting, iii) massive, and iv) arborescent organisms (Fig. 3).

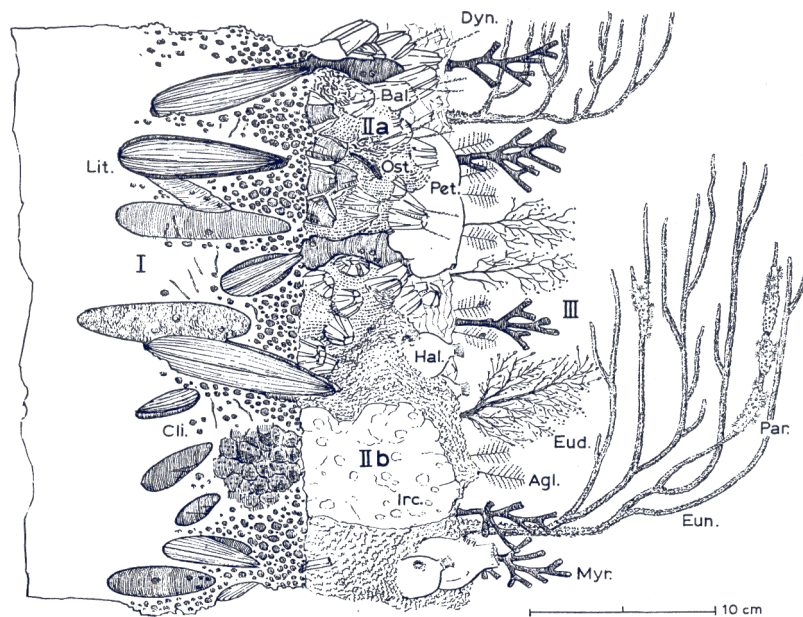


Abb. 182: Der Schichtenbau der Höhlenbestände, am Beispiel zentraler Wandgebiete. Halbschematische Darstellung eines geöffneten Bestandes von 25 bis 30 cm Länge (etwa Hauptproben-Größe). I Endolithion mit vorwiegend *Lithodermis* und *Cliona*-Arten. II Krusten-Bestände: IIa Kalkschaler-Element (mit toten Oberflächen) vorw. *Balanus* und *Ostrea*, IIb Massenformen-Element (mit belebten Oberflächen) vorw. *Halocynthia*, *Petrosia* und *Ircinia*-Arten. III Aufwuchs-Schichte mit vorw. *Dynamena*, *Eudendrium*, *Aglaophenia*, *Myriapora*, *Eunicella* und *Parerythropodium* (Details in Abb. 183–185).

Fig.3. Schematic representation of a coralligenous assemblage (from Riedl, 1996)

Perforating and insinuating species may affect the interface water/substrate owing to their filtering activity; encrusting and massive specimens help to trap and stabilize sediments; erect organisms, if present with high densities, reduce light penetration and water movement (Scinto et al., 2009). For this reason, erect organisms can be actually considered as ecosystem engineers. The integrity of these layers guarantees a higher stability of environmental variables at small scale and can affect the local diversity, influencing both the sediment characteristics with the related meiofauna (Cerrano et al., 2010) and the associated vagile fauna (Ponti et al., 2016; Valisano et al., 2016). The abrasive effects that human activities play on sea floor (fishing, anchorage, diving), on the coralligenous communities act primarily on the most exposed layers (Bavestrello et al., 1997). Once these layers are damaged, lower layers are involved in further erosion, down to the coralligenous bioconstruction. These processes are not homogeneously distributed and can lead to the fragmentation of the populations involved in the structuring of coralligenous assemblages.

These effects can be faced only with a quick interruption of the activities playing the impact. If it does not happen, the community begins to offer space to new pioneer and/or opportunistic species (Cebrian et al., 2012) triggering new successional stages and a shift in the community structure.

Despite strong, growing interest in the functional role of ecosystem engineering over the recent years, compared to food web analyses, the conceptual understanding of engineering-mediated species interactions is still in its infancy (Bouma et al., 2009).

Foundation species are declining throughout the world, as result of number of natural and anthropogenic drivers that modify the engineering community by removing

autogenic ecosystem engineers, introducing invasive engineers, whose impact is often hard to predict (Bouma et al., 2009).

Ecosystems dynamics, controlled by one or a few foundation species, appear to be dominated by a small number of strong interactions and may be highly susceptible to shift stable states and even small perturbations (Ellison et al., 2005). Hence, identifying and managing probable engineering species and responsive ecosystems should be a key priority for conservation (Bouma et al., 2009), and a promising opportunity for restoration ecology (Crain & Bertness, 2006).

Sponges play a key ecological role, which is both functional and structural (Cerrano et al., 2006; Wulff, 2006; Bell & Carballo, 2008). Owing to their efficient filter feeding activity they couple water column productivity with the secondary productivity of benthic communities (Gili & Coma, 1998) besides their filtering activity can limit algal blooms and they are one of the most important living habitat for microorganisms; thanks to their complex net of cavities and canals i) they offer unique refuge numerous small species or juvenile stages, ii) they behave like a “depot” for the biodiversity. Functional roles of sponges include: substrates stabilization by binding and reworking of solid carbonate through bioerosion. Finally, sponges can control the coralligenous dynamics affecting the community structure in terms of sessile and vagile fauna and they can be an important food source for highly specialized predators. In conclusion sponges may have a large effect on community structure modifying environmental condition, through their actions (filtering activity) and not only their presence (Fig. 3).

Regarding gorgonians, i) they built a greater variety of habitats and refuges for several invertebrates compared to sites with low densities of colonies, ii) decrease current but increase turbulent flow, which enhances the contact rate of planktonic prey with benthic suspension-feeding organisms (Shashar et al., 1996), iii) increase the delivery of pelagic larvae to benthic surfaces (Walters et al., 1997), iv) increase the flux rate of metabolically important substances as result of a thinner diffusive boundary-layer (Hearn et al., 2001), v) they create a sort of “buffered zone” where modifications may occur slower respect to the surrounding ambient, vi) they can control temporal shifts in the ecosystem, being a long living species, vii) they control the coralligenous dynamics affecting the community structure in terms of sessile and vagile fauna, viii) they create the optimal conditions for the development of coralline algae, the main builders of these bioconstructions.

Gorgonians seem to have a large effect on community structure modifying environmental conditions, through their physical presence and not their biological actions (Fig. 4).

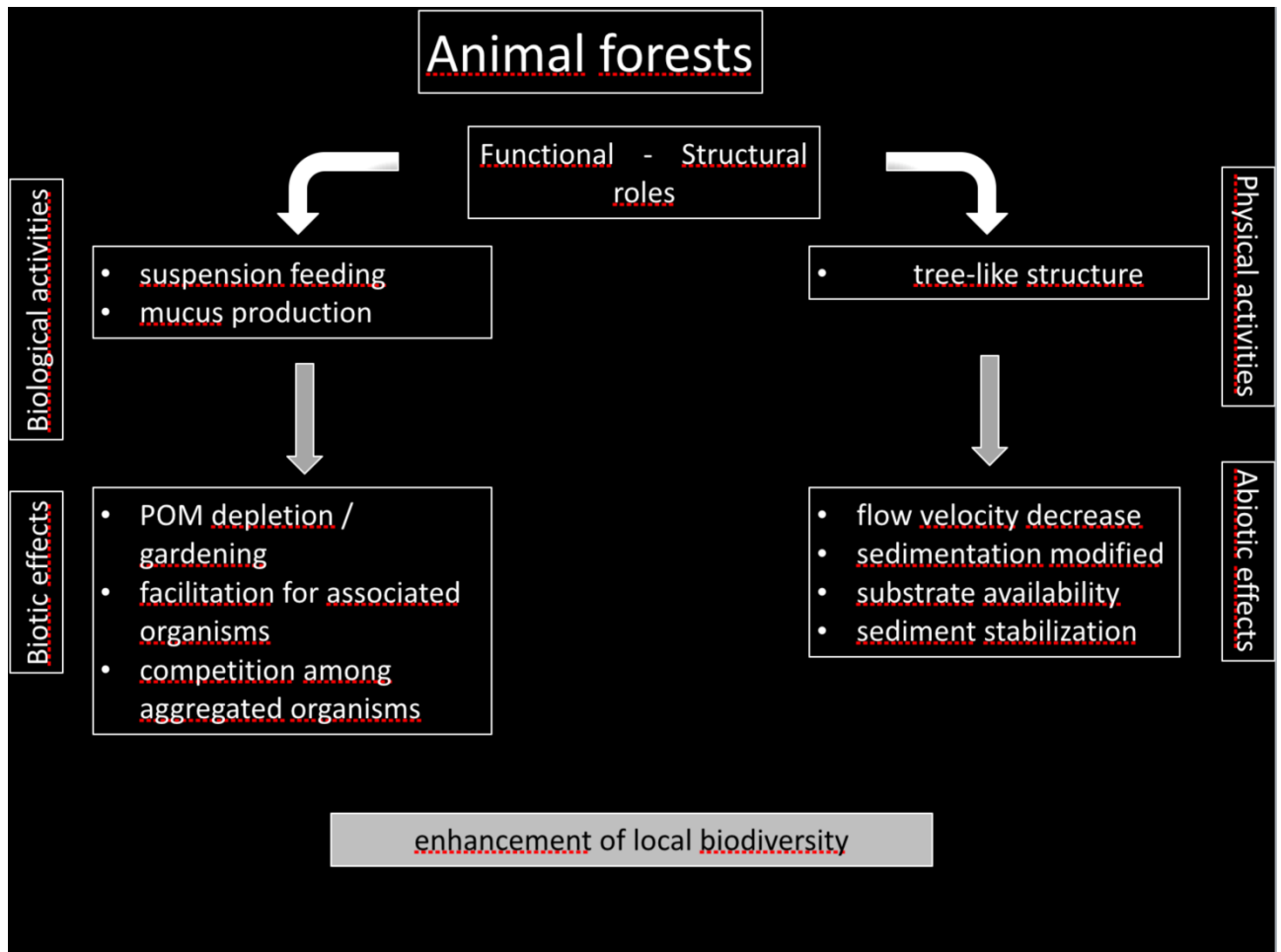


Fig. 4. Schematic representation of functional and structural effects of animal forests

2.4. Trophic interaction

Sponge pumping rates are variable within and between species (with regular temporary cessation due to their relative physiological rhythm) and affected by environmental features as water movement or disturbances (Reiswig, 1971; Reiswig, 1974; McMurray et al., 2014). Generally, sponges with high microbial abundances (HMA) have lower pumping rates than low microbial abundance (LMA) species (Weisz et al., 2008). Some species are contractile and can actively open and close their ostia and oscula (Reiswig, 1974; Ilan & Abelson, 1995; Elliott & Leys, 2007); expand and contract both ectosome and choanosome (Nickel, 2004; Nickel et al., 2011); and even coordinate behavioural patterns (Ludeman et al., 2014). Despite the potential pivotal role of the filtration activity of sponges in benthic assemblages, this process has been poorly investigated but it is generally assumed that sponges can filter up to 900 times their body volume of water per hour, recycling nutrients and coupling a benthic-pelagic food web, in fact they can act as both a sink and/or a source of DOM and nutrients, preventing energy and nutrient losses in the open ocean (Maldonado et al., 2012). Sponges can pump over a half liter of water $\text{s}^{-1} \text{kg}^{-1}$ sponge dry mass (Weisz et al., 2008) removing suspended cells ($< 10 \mu\text{m}$) from the column water with a retention efficiency up to the 99% (Pile et al. 1996; Coma et al. 2001; Yahel et al. 2007).

More recently it has been proposed that sponges may play a fundamental role in organic matter cycling similar to that of the microbial loop; by removing dissolved organic matter from the water column and making it available in form of detritus to higher trophic levels (De Goeij et al., 2013) and simultaneously feed on bacteria. The actual

ecological implications of the so called “sponge loop” are still under debate (De Goeij et al., 2013; Khan et al., 2016) but it is evident that where a reduction of sponge diversity is documented, the effect on the community will be likely very negative even if unpredictable and restoration procedures should be activated.

Gorgonians are passive filter feeders and represent one of the main links joining pelagic and benthic food webs on rocky cliffs (Gili & Coma, 1998). They grow perpendicularly to the direction of dominant water movement (Riedl, 1971) and change colony morphology to optimise filtering rate under different conditions of water movement intensity (Weinbauer & Velimirov, 1995). Moreover, the flexibility of their axial skeleton allows continuous colony form adjustment to cope with the variation of water movement intensity (Leversee, 1976; Velimirov, 1976). Recent massive mortalities affect colonies at different intensities, causing either total or partial mortality. In this latter case, regeneration processes can shape irregular colonies without the typical planar pattern of growth (Cerrano & Bavestrello, 2008). In any case, gorgonians are strongly suited to extract food from column water, but knowledge about quality and quantity of the collected food is fragmentary.

Studies on the feeding activity of gorgonians are usually evaluated studying i) coelenteron contents, ii) expansion/contraction rhythms of polyps, iii) natural diets directly *in situ* or iv) simplified diets in laboratory.

The study of coelenteron content is not easy, owing to the difficulty to find identifiable preys inside the gastrovascular cavity (Lasker, 1981; Coma et al., 1994). On this base, many authors assume that dissolved organic matter or amorphous detrital matter are among the main food sources of gorgonaceans in natural environments (Murdock, 1978; Lasker, 1981; Coffroth, 1984).

The analysis of expansion/contraction rhythms indicates that the contraction of anthozoan polyps is associated with a decrease of metabolic rates (Robbins & Shick, 1980; Lasker, 1981), leading to preservation of energy reserves (Campbell, 1974; Sebens & DeRiemer, 1977). It was estimated that contracted colonies consume practically half the energy of expanded ones (Sebens, 1987). This condition ensures colony survival even during periods with low food availability. Rhythmic activities are widespread in filter feeding organisms and are usually affected by environmental conditions: when food availability or water movement are low, filter feeders decrease their metabolic rate (Lasker, 1981; Dai & Lin, 1993). For this reason, the increase in the number of colonies of *Paramuricea clavata* with contracted polyps, generally recorded during summer, has been correlated with a low concentration of zooplankton organisms in this season (Coma et al., 1994), confirming the importance of food as a regulating factor in polyp activity. From these observations, it is possible to assume that, when environmental conditions are not optimal for a species, polyps maintain a contracted condition (Coma et al., 2000). On the contrary, expanded polyps suggest that the colony is in a suitable environment, at least for food availability. For this reason, polyp activity rates can be used to evaluate the health status of the colonies also during experiments (e.g. Torrents et al., 2008).

In tropical habitats, Fabricius et al. (1995) found that also phytoplankton can be an important feeding source for soft corals. Herbivory was confirmed also in the feeding of tropical gorgonians by Ribes et al. (1998), using continuous flow incubation chambers.

Experimental studies on feeding have considered gorgonians as consumers of zooplanktonic prey items, and *Artemia salina* cysts or nauplii have been the most utilised food under laboratory conditions (Roushdy & Hansen, 1961; Leversee, 1976; Lasker, 1981; Sponaugle & LaBarbera, 1991; Dai & Lin, 1993). The extent of herbivory

among cnidarians has been underestimated and should be properly evaluated, especially in case of restoration projects, when multispecific transplant are scheduled.

2.5. Population genetics

Population genetic studies were conducted from local (meters) to global (1000 of kms) in *Corallium rubrum* (Costantini et al., 2007a;b; Ledoux et al., 2010a;b) and *Paramuricea clavata* (Mokhtar-Jamaï et al., 2011; 2013; Arizmendi-Meija et al., 2015). At global scale including various regions of the Mediterranean and more than 30 populations in each species, *C. rubrum* and *P. clavata* displayed the same pattern of spatial structure combining IBD and regional clusters. This suggests that the two species are characterized by restricted gene flow. At local scale, sibship analyses conducted between colonies belonging to the same site and separated by cm to m, revealed the occurrence of dense networks of relationships due to a family structure in the two species. This underlines the importance of local processes (e.g. local recruitment) in the population functioning of *C. rubrum* and *P. clavata*, a rare pattern for marine species. Nevertheless, the results of the IBD analyses are contrasted between the two species. Regarding *C. rubrum*, we demonstrated a significant IBD between colonies. We were thus able to quantify the small effective dispersal ability of the species (between 22 and 32 cm) (Ledoux et al., 2010a). Accordingly, breeding units in the red coral seem to be highly restricted in space. On the contrary, IBD was not revealed in *P. clavata* suggesting that breeding unit may be bigger than the sampling area (2 m²) (Mokhtar-Jamaï et al., 2013).

This trend of restricted gene flow was also reported in the other octocorals targeted by the WP3. *Eunicella singularis* and *Eunicella cavolini* showed significant genetic structure between populations separated by > 10kms. Nevertheless, while populations from different depths at the same site were not differentiated in *E. cavolini*, Costantini et al. (2016) reported significant structure in *E. singularis* supporting the occurrence of a break in gene flow between shallow and deep (>30 m) populations. Regarding *Eunicella singularis*, Pey et al. (2013) and Costantini et al. (2016) suggested that while being restricted, the dispersal capacities may be higher than in *C. rubrum* and *P. clavata* particularly between depths within the same site. This pattern was also recently confirmed in *Eunicella cavolini* (Masmoudi et al. 2016). Population genetics studies at low geographic scale remain to be conducted in order to better characterize the reproductive biology of these *Eunicella* spp.. Nevertheless, these results suggest that restoration actions should be conducted at local scale and that policies defined for *C. rubrum* and *P. clavata* should be efficient also in the species.

From a conservation perspective, these studies at local scale suggest that the populations of the two species are mainly closed and that recovery from larvae coming from external sources may be limited. In this context, restoration actions may be an important conservation tool. Based on our data, these actions should restore dense and small-size patches of colonies in order to re-establish functional breeding units. Overall, these studies suggest a low recolonization capacity in Mediterranean gorgonian species and restoration should be designed at very local scale.

Our knowledge regarding the patterns of spatial genetic structure of sponges studied in the WP3 is limited with one study in *Spongia officinalis* and one in *Spongia lamella*. In the two species significant genetic differentiation was observed at the lower spatial scale under survey (around 20kms) suggesting restricted gene flow and low recolonization

capacities. In both cases, regional genetic structure was reported. Isolation by distance was observed in *Spongia lamella* but not in *S. officinalis*.

2.6. Previous restorations actions

There are very few studies dealing with the active restoration of coralligenous species to date. Specifically, for the target coralligenous species within WP3, we found only two studies focused on the restoration of gorgonians and other two focused on sponges. No information was found in relation to restoration actions for bryozoans.

The first study about gorgonian restoration examined the usefulness of this technique in the management of red gorgonian *Paramuricea clavata* populations damaged by diving activity in intensively visited marine protected areas (MPAs), such as Medes Islands, Catalan sea (Linares et al., 2008c). Field experiments as well as simulations from size-structured matrices were used to assess the utility of transplantation of living fragments from damaged colonies to increase the viability of threatened populations. Well-attached transplants achieved survival rates (80%) similar to those of natural colonies. The simulations showed the annual population growth rate improved substantially only under a high frequency of transplantation (Linares et al., 2008c). In other study, explants of the most common Mediterranean gorgonians (*P. clavata*, *Eunicella cavolinii*, *E. singularis*, and *E. verrucosa*) were transplanted in Portofino, Ligurian sea. Colonies of each species overcame transplantation stress and during the first three months they showed a mean survival rate of 98% and an average positive growth rate of 7.65%. Unfortunately, in the summer season 2003, during the heatwave that affected the Mediterranean basin, the transplants were affected, showing a mean negative growth rate and a reduction of survival (Fava et al., 2010).

A transplantation experiment for the extremely slow-growing and threatened octocoral *Corallium rubrum* in the Medes Islands MPA was highly successful over a relatively short term due to high survival and reproductive potential of the transplanted colonies. However, demographic projections predict that from 30 to 40 years may be required for fully functional *C. rubrum* populations to develop (Montero-Serra et al., 2017).

Regarding to the previous published studies about restoration of sponges, we found one study focused on *Spongia officinalis*. Transplants of *S. officinalis*, collected from a wild population along the Apulian coasts (Ionian Sea, Italy), were moved into an area where the species was present in the past. All transplanted sponges showed complete cicatrization of the cut surfaces within a month of the initial manipulation and had a survival rate of 100% over one year (Baldaccioni et al., 2010).

2.7. Insights for restoration actions for mesophotic coralligenous habitats

The information available on gorgonians and sponges included to conduct restoration actions in the mesophotic coralligenous habitats indicate that they share similar life-history traits: slow growth, low recruitment and mortality rates, long lifespans (decades to hundred of year). For bryozoans the information is scarcer but the selected species are characterized by faster population dynamics and lower lifespans (10-20 years). Except for the bryozoans species for which no information on dispersal capacity is available, we can conclude that the targeted gorgonian and sponges species are characterized by significant population genetic structure from local to regional scale involving restricted gene flow and low recolonization capacities. All species are considered habitat-forming species since they are commonly found in the coralligenous and in the case of gorgonians can exhibit high abundances (densities $> 100 \text{ m}^{-2}$). Besides playing a major

structural role, the presence of the targeted species support important functions at community level (e.g. matter transfer, nutrient recycling).

The transplants can be obtained from colonies/specimens found in the habitats without causing severe damage to the donors due the clonal nature of all species. There are few studies dealing with the potential effect of the size of fragments, for gorgonians apical branches between 5 to 10 cm (representing a small part of mature gorgonian colonies) have been currently used in previous experiences with a quite high success. In sponges the studies available did not find an effect of the size of the explants used in the experiments (270 to 2500 cm³ or “cubes” from 3 to 5 cm). It is noteworthy that in sponges the growth rate of explants are significantly higher than those measured in natural assemblages when the explants are set in environmental conditions similar to the origin. For bryozoans, we did not find any previous restoration actions but due to the fragility of their skeletons fragments not larger than 5-10 cm should be used. Regarding the timing avoiding summer periods when this species may suffer mass mortalities due exceptional warming. Likewise, for demonstration restoration actions, working in Marine Protected Areas where mainly fishing are limited or absent can enhance the success of transplants.

From the collected information, restoration protocols on the targeted species for the mesophotic coralligenous habitats should be mainly based on transplants of small medium individuals collected from donor specimens. The spatial arrangements of transplants may include relatively small patches (0.2-1 m in diameter) separated by distances similar to the sizes of the transplant patches. The density within the transplant patches may be moderate-high densities (up to 50 transplants or more per m²). This will fit with the natural densities while may enhance the reproductive success and potentially increase the recruitment in the space inter-transplant-patches. Overall this kind of arrangement should enhance the resilience of restored populations firstly by the grow of the transplants and secondly by enhancing the reproduction success of the populations. Finally, bearing in mind the tradeoff between initial transplantation efforts and the speed of recovery. Transplantation of slow-growing species, such as those targeted in WP3, will tend to require lower initial effort due to higher survival after transplanting, but the period required to fully recover habitat complexity will tend to be far longer, i.e. decades (Montero-Serra et al., 2017). Survival and growth of transplants and recruitment would be the most suitable indicators of the success of the restoration actions.

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