Rendiconti Lincei. Scienze Fisiche e Naturali
https://doi.org/10.1007/s12210-018-0725-4

CHANGES AND CRISIS IN THE MEDITERRANEAN

Climate change impacts on the biota and on vulnerable habitats of the deep Mediterranean Sea

Roberto Danovaro[1,2]

Received: 31 January 2018 / Accepted: 8 June 2018

Abstract

Deep sea is the largest and likely the most biologically diverse ecosystem of the world, but it is also the most unknown. The Mediterranean Sea (< 1% of the ocean surface and contains only the 0.3% of its volume) is a hot spot of marine biodiversity containing ca 7.5% of the world marine biodiversity, associated with a multitude of habitats spreading from the coast to its dark portion (e.g., coral banks, seamounts, canyons, and hydrothermal vents). Its deep-sea ecosystems are increasingly subjected to direct anthropogenic impacts (including overfishing, chemical pollution, dumping, litter, and plastics), which are often over-imposed to the increasing effects of global change. Here, are illustrated the expected impacts of shifts in the main variables such as temperature, food supply, pH, and oxygen on the deep Mediterranean Sea ecosystems. One of the most consequences is related to shifts in the quality and quantity of the inputs of organic matter to the deep seafloor. The deep Mediterranean Sea is far more oligotrophic than other oceans at equal depths, and although deep-sea biota reacts to food shortage by increasing their efficiency in its use, a decrease in food availability can have dramatic effects on its food webs. The deep Mediterranean Sea is showing a clear rise of deep-water temperatures. In the last decades, deep-water warming is accelerating at unprecedented rates, causing a significant shift in biodiversity even for variations in the order of 0.1 °C. Higher temperatures increase deep-sea metabolism, thus exacerbating the effects of food limitation. Moreover, ocean acidification reduces the calcification capacity of corals and alters their metabolism. Although it can be expected that increasing temperatures might increase the potential spread of oxygen minimum zone, so far, only ipoxic events were reported in Mediterranean Sea. The analysis of potential ecosystem vulnerability indicates that the ecosystems that are most sensitive to global change are deep-water coral systems and deep-sea plains. In addition, deep-sea canyons are also likely increasingly subjected to physical disturbance as a result of the increase in the frequency and intensity of climate-driven episodic events. Available information also suggests that biodiversity and ecosystem functioning of the deep Mediterranean Sea is undergoing dramatic changes, which result in accelerated organic matter biogeochemical cycling, miniaturization of the organisms' size, increased metabolism, dominance of the microbial components, and mortality rates of deep-sea biota. Given the high sensitivity of the Mediterranean Sea to global change in comparison with other oceanic regions, and the vulnerability of its deep-sea habitats/ecosystems, specific policy measures are needed to protect its biodiversity, restore damaged habitats, and increase deep-sea ecosystems resistance and resilience to the ongoing impacts of global change.

Keywords Global change · Deep Mediterranean Sea · Deep-sea biology · Ecosystem vulnerability

This contribution is the written, peer-reviewed version of an invited talk presented at the Conference "Changes and Crises in the Mediterranean Sea" held at Accademia Nazionale dei Lincei in Rome on October 17, 2017.

✉ Roberto Danovaro
r.danovaro@univpm.it

[1] Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Via Brecce Bianche, Ancona, Italy

[2] Stazione Zoologica Anton Dohrn, Villa Comunale, Naples, Italy

1 Global Change in the global oceans and trends in the deep Mediterranean Sea

Anthropogenic activities are progressively increasing the atmospheric concentrations of CO_2, and the fluxes of greenhouse gases (CH_4 and N_2O), which are triggering global climate change and the consequent warming, oxygen depletion, and acidification of the oceans, altered precipitation regimes as well as increased ice melting. Changes in the physico-chemical conditions are also inducing shifts (generally, a decrease) in global primary production and carbon export to the ocean interior. All these changes have been reported to influence the biodiversity and functioning of marine ecosystems (Le Treut et al. 2007; Tittensor et al. 2010). Marine organisms are key actors in the cycling of all key elements and drive ecosystem processes (Snelgrove et al. 2017). These organisms are profoundly influenced by ongoing changes, but to a different extent at different latitudes and biogeographic regions, with stronger impact on marine ecosystems at high latitudes (Brierley and Kingsford 2009). Primary production is expected to decrease at tropical and mid-latitudes (Sheridan and Bickford 2011; Kroeker et al. 2010), altering the quantity and quality of food supply to the seafloor (Danovaro et al. 2014), with downstream consequences on organic matter cycling and supply of ammonia needed for sustaining the metabolism of all organisms.

Deep-sea ecosystem (i.e., > 200-m depth) represents the largest biome of our planet, covering more than 65% of the Earth's surface and hosting 95% of the global biosphere; nevertheless, it is one of the least investigated (Gambi et al. 2017 and references therein). Global change is progressively expanding into the deep sea. Many observational studies are showing that present-day climate change is already determining an increase of the deep-sea temperature (Purkey and Johnson 2010), deoxygenation (Stramma et al. 2008, 2010, 2012; Keeling et al. 2010), lowered pH of intermediate deep waters (Byrne et al. 2010), and altered POC (i.e., particulate organic matter) flux to the seafloor (Ruhl and Smith 2004; Smith et al. 2013). Despite emerging evidence that climate-driven changes in deep-sea environmental conditions may perturb the functioning of deep-sea ecosystems (Danovaro et al. 2001; Smith et al. 2008; Dunlop et al. 2016; Yasuhara and Danovaro 2016), our understanding of the extent to which projected physical and chemical changes will lead to deleterious ecological consequences is still very poor (Philippart et al. 2011). Given that, deep-sea ecosystems are vitally important for the Earth system (Danovaro et al. 2014) and are at considerable risk from ongoing climate change (Mora et al. 2013; Jones et al. 2014; Levin and Le Bris 2015), an increasing number of studies indicate that physico-chemical conditions in the deep ocean are changing rapidly (Yasuhara and Danovaro 2016 and references therein). According to Sweetman et al. (2017), negative effects of global change in terms of all of these variables have been already reported in the deep oceans.

Actual predictions indicate that temperatures at abyssal depths (3000–6000 m) could increase by 1 °C over the next 84 years (Sweetman et al. 2017). While, abyssal seafloor habitats under areas of deep-water formation may experience reductions in term of oxygen concentration in the water column, by as much as 0.03 mL L^{-1} by 2100 (Sweetman et al. 2017). Furthermore, bathyal depths (200–3000 m) will show the most significant reduction in pH values in all oceans by the year 2100 (from 0.29 to 0.37 pH units) accompanied by a decline of 3.7% in the North-East Pacific and Southern Oceans. Yet, the most noticeable predicted change regards the reduction of organic matter flow especially in the Indian Ocean (with decrease value of 40–55% by the end of the century) (Sweetman et al. 2017).

The Mediterranean Sea, with an average depth of ca 1450 m (vs 3750 m of the global oceans), is expected to react faster to global changes than it does in the real oceans (Bianchi 2007; Boero et al. 2008; Lejeusne et al. 2010). This is due also to its peculiar environmental settings. The main hydrological features of the deep Mediterranean Sea are: (a) highly constant temperatures from roughly 300–500 m to the bottom, and bottom temperatures of about 12.8–13.5 °C in the western basin and 13.5–15.5 °C in the eastern basin (i.e., there are no thermal boundaries, whereas in the Atlantic Ocean the temperature decreases with depth) (Emig and Geistdoerfer 2004); (b) high salinity, from about 38–39.5 ppm with the stratification of the water column; (c) limited freshwater inputs (the freshwater deficit is equivalent to about 0.5–0.9 m^3 year^{-1}, compensated by the Atlantic inflow of surface water), which influence also the deeper salinity values; (d) high oxygen concentrations; and (e) food limited conditions, with strong energetic gradients and low nutrient concentrations in the eastern basin (Danovaro et al. 2010). Moreover, seasonally, during late spring and summer, the whole Western Mediterranean Sea is strongly stratified with a thermocline at 20–50 m deep. In winter, the water column is more homogeneous, especially in the open sea.

The Mediterranean basin is characterized by the presence of small gyres (eddies) that have implications for the upwelling of deeper waters and the influence on primary productivity. This consequently affects the flux of organic matter settling to the deep seafloor. The trajectories of deep and bottom currents are largely unknown, but strong currents of speed up to 1 m s^{-1} have been documented in submarine canyons, in relation with climate-driven episodic events (Canals et al. 2006), rapid vertical transport of surface waters to great depth occur as a result of dense water convection when surface waters become denser owing to evaporation and cooling. These phenomena known as cascading occur periodically over short terms (weeks). Given the limited average depth of the Mediterranean basin, the deep-water turnover is relatively rapid (from 50 to 80 years; Lacombe and Tchernia 1972; Danovaro et al. 2010) when compared with the wider oceanic regions, but this is largely compromised by its vulnerability to climate change and the much higher rates of deep-water warming, which have shown an acceleration in the last decades (Fig. 1).

For these reasons, the Mediterranean Sea has been proposed as a "miniature ocean" that can be used as a model to anticipate the response of the global oceans to various kinds of human pressures. The Mediterranean Sea is

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

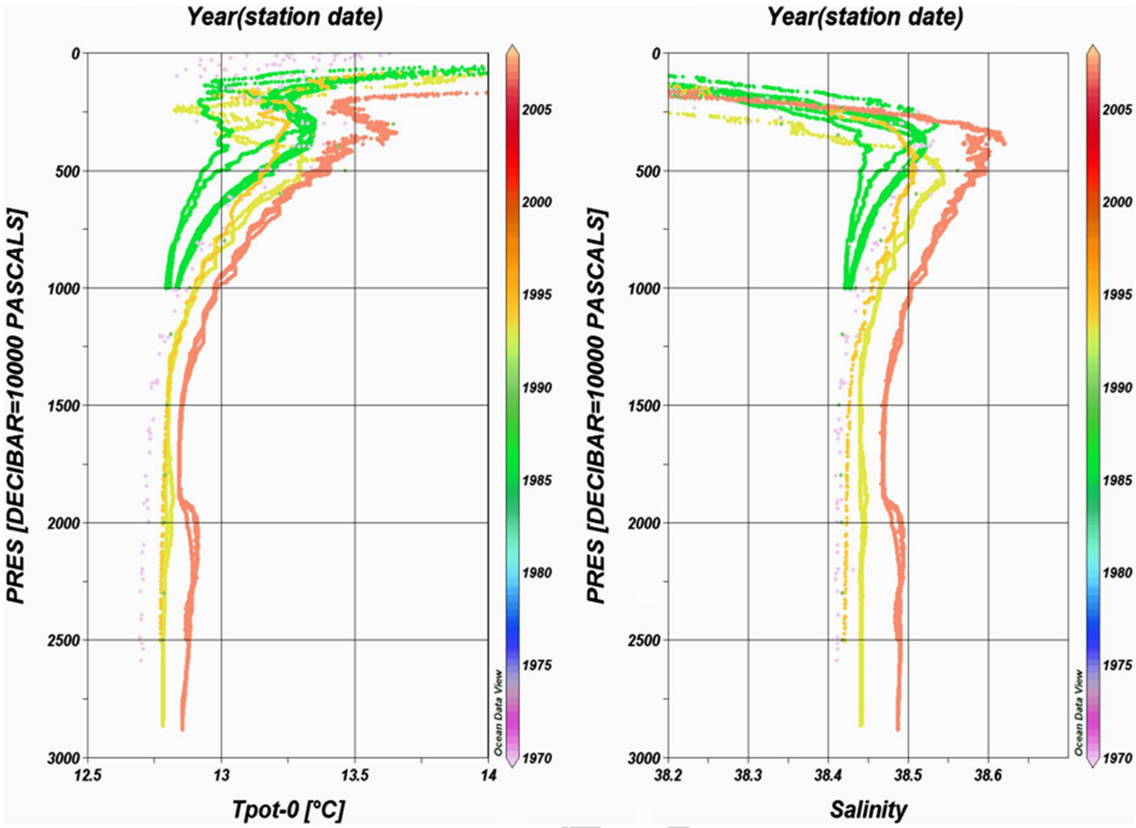

Fig. 1 Changes in temperature and salinity in the Western Mediterranean deep waters in the last decades (depth expressed in meters, T-pot is potential temperature, colors reflect the different sampling times; courtesy A. Russo)

also one of the areas in which different aspects of climate change have been better documented. Among these, three processes have been described in detail: (1) the increase in surface temperature at basin scale, starting from 1980 (Nykjaer 2009); (2) the increase in temperature and salinity of the deep waters of the western Mediterranean Sea, starting from 1950 (e.g., Rixen et al. 2005); (3) increasing salinity and cooling of Levantine Intermediate Waters (LIW) (Brankart and Pinardi 2001; Painter and Tsimplis 2003); and (4) the increase in the frequency of episodes of stratification of the summer thermocline with consequent massive mortality of benthic organism since the 90s (Rivetti et al. 2014). It is a combination of these types of important processes that are leading to profound changes in the biodiversity of the entire basin. These changes represent a possible model for understanding the ecosystem processes that, driven by climate change, will act at global scale. In addition, the Mediterranean Sea is experiencing various typologies of climate-induced changes, which can be summarized as follows: (a) episodic, short-term events of surface water warming; (b) transient phenomena occurring in relatively short terms but with long lasting effects; and (c) chronic changes in water column conditions.

2 Biodiversity and ecosystems of the deep Mediterranean Sea

The overall surface of the Mediterranean basin is approximately 0.82% of the world ocean surface. It has an average depth of 1500 m and the deepest point at 5267 m depth in the Ionian Sea. Its total volume is approximately 0.3% of the oceans' volume. Thus, the Mediterranean Sea represents a negligible portion of the global oceans. Yet, despite its limited dimensions, the Mediterranean Sea hosts approximately 7.5% of the marine species (Coll et al. 2010). Although it is difficult to estimate accurately the number of deep-sea species, a recent estimate (excluding prokaryotes) indicates that the deep Mediterranean Sea can host ca 3000 species vs ca 17000 of the entire basin (Danovaro et al. 2010). Most of these species (prokaryotes excluded), on average 66% (range 50–90%) are still unknown to science (Danovaro et al. 2010). Among these, most of the unknown species are within the phylum Nematoda, followed by Foraminifera, but an important fraction of macrofaunal and megafaunal species also remains unknown. These unique biological features are related to

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

the highly complex characteristics of the Mediterranean basin, which is divided into western and central-eastern basins, separated by the Strait of Sicily. The western basin (Mean depth, about 1600 m) consists of two deep basins: the Algero Provençal basin and the Tyrrhenian Sea. The central-eastern Mediterranean Sea consists of three main deep basins: the Ionian, Aegean, and Levantine (Sardà et al. 2004; Danovaro et al. 2010).

The Mediterranean deep seafloor includes a number of diverse habitats related to specific and complex topographic features, such as: (a) continental shelves and slopes; (b) submarine canyons and landslides; (c) base-of-slope deposits; (d) seamounts; (e) cold seepage, "mud volcanism", and pockmarks; (f) deep-water biogenic reefs; and (g) bathyal or abyssal plains with abundant deposits of mud; h) deep-hypersaline anoxic basins, which increase considerably the topographic complexity of the seafloor; and (i) volcanism and its influence on various typologies of topographic features. A schematic representation of the various habitat types considered in the present and of the topographic complexity of the deep seafloor is illustrated in Fig. 2.

Deep-water corals can form locally elevated secondary hard substrates associated with strong bottom currents that enhance food supply. These corals play also an important role as refuge or nursery habitats for a rich-associated fauna, some of commercial interest. Deep-water corals are preferentially distributed on topographic irregularities, such as escarpments, prominent steps on canyons and seamounts, where currents are strong (Bo et al. 2014 and references therein). However, they can be present also in continental shelves and open slope. They are mostly composed of azooxanthellate scleractinians; moreover, they are often associated with other sessile invertebrates such as hydrozoans (Stylasteridae), sponges and giant oysters (Neopycnodonte),

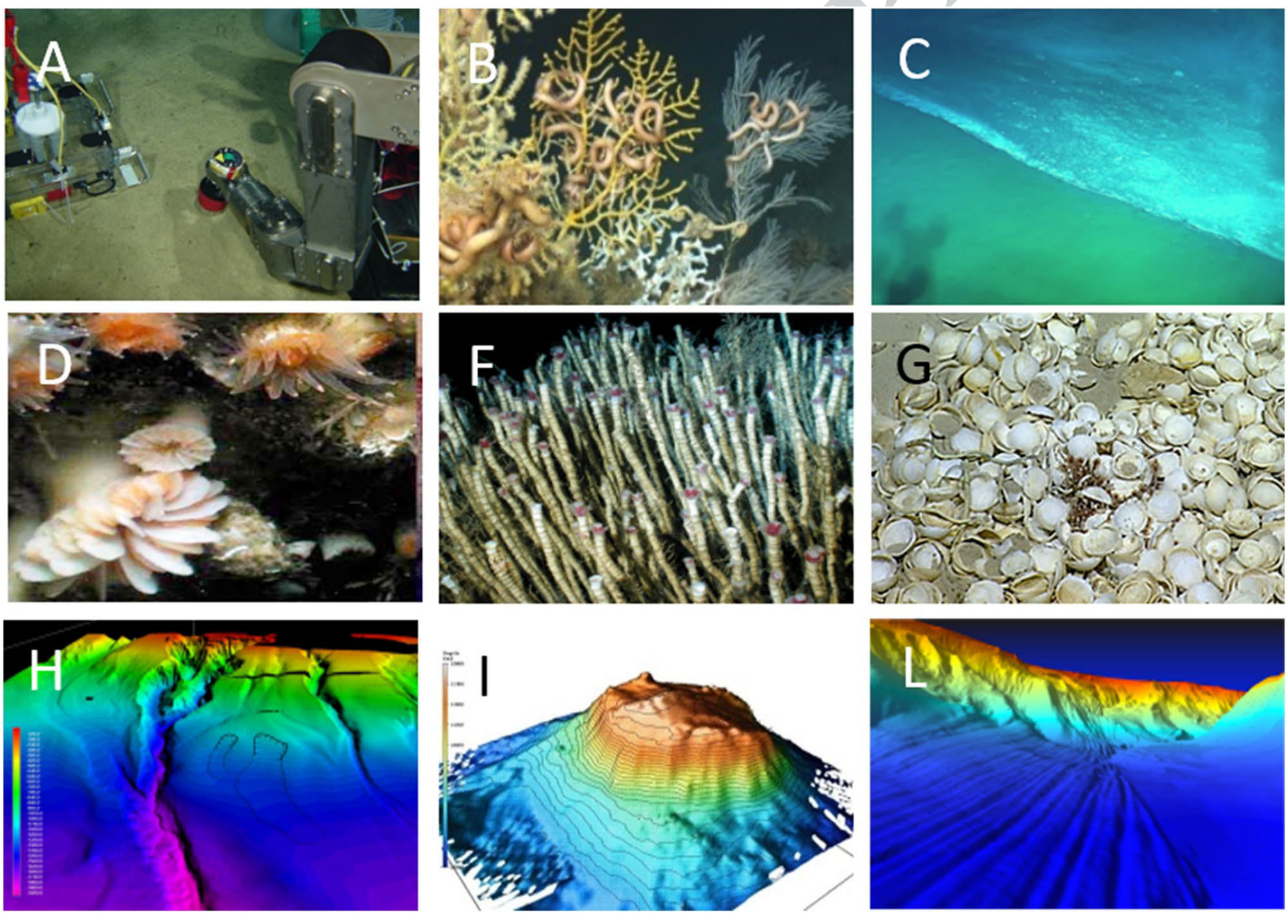

Fig. 2 Overview of some of the main habitat-forming species and ecosystems considered the present study. Reported are **a** most widespread and relevant deep-sea habitat, the soft bottoms at bathyal–abyssal depths in the western Mediterranean, **b** deep-water coral forest, with gorgonians and cold-water corals in the Tyrrhenian Sea, **c** a cold seep of a mud volcano in the eastern Mediterranean Sea; **d** hard-bottom fauna of seamounts of the central Mediterranean Sea; **e** syboglinidae worms from a cold seepage of the eastern Mediterranean Sea; **f** lucinid clams from a deep-sea cold seepage (modified from Taviani, 2014); and an example of some of the most interesting topographic features such as: **g** canyon of the Catalan margin (courtesy M. Canals); **h** seamount, **i** furrows over a continental slope (courtesy M. Canals)

Journal : Large 12210 | Article No : 725 | Pages : 17 | MS Code : LYNC-D-18-00035 | Dispatch : 13-6-2018

and octocorals (Alcyonaria, Gorgonacea, and Pennatulacea); furthermore, some hexacorals (Antipatharia) are present in a range from 40 m to > 2000 m making deep-water coral banks important habitats as biodiversity hotspots (Fanelli et al. 2017). Deep-water corals may be locally very abundant and represent key habitat-forming species of the Mediterranean deep seafloor (Bo et al. 2014). These habitats depend on the hydrodynamic regime, which supplies the needed food and the availability of suitable substrates. The most important deep-water coral systems of the Mediterranean basin are located along the Calabrian margin and in the Tyrrhenian Sea, Ionian Sea, and Ligurian Seas, and large colonies have been reported along the Catalan margin (Sánchez et al. 2008, Bo et al. 2012; Maynou and Cartes 2012; Fanelli et al. 2017). These systems support a high biodiversity, associated both to the living corals and to coral rubbles (Bongiorni et al. 2010). In January 2006, the General Fisheries Commission for the Mediterranean Sea prohibited the use of dredges and trawl nets in the deep-water coral banks of Santa Maria di Leuca (Italy), thus creating the new legal category of ''Deep-sea fisheries restricted area". Yet, it only includes the coral bank, while as explained above, it would be necessary to include also the coral rubble habitat (Bongiorni et al. 2010).

Seamounts Seafloor elevations rising at least 100 m from the surrounding deep seafloor are defined seamount or seamount-like structures (Würtz and Rovere 2015). In the Mediterranean Sea, over 242 seamounts, banks rises, highs, hills, spurs, and other kind of sea floor elevations have been identified and described (Würtz and Rovere 2015). These likely represent about 1% of the seamounts present in the world (Kitchingman et al. 2007). In the Western Mediterranean Sea, the Tyrrhenian bathyal plain is characterized by the highest concentration of seamounts of the entire basin. They have been well studied from geological point of view; however, scare information is available about their ecological aspects (Galil and Zibrowius 1998; Acosta et al. 2004; Cocchi et al. 2017). Volcanic bodies are either associated with north–south oriented crustal faults (Magnaghi, Vavilov, and Marsili seamounts) or with crescent-shape bathymetric ridges (e.g., Vercelli and Cassinis). The eastern Mediterranean basin, on the other hand, is characterized by a higher topographic heterogeneity than the western sector and a large number of seamounts, including the Eratosthenes Seamount, an impressive structure situated in the Levantine Sea. Available knowledge about biodiversity on seamounts has been mainly focused on benthic habitat and less on the pelagic life. Suspension feeders, particularly deep-sea corals and sponges, usually dominate the hard-bottom habitats of seamounts. Here, the most important habitat-forming cnidarian taxa are alcyonaceans (as sea fans and soft corals and, at least for soft bottoms, sea pens), antipatharians (also called black corals forming large forests up to 500 m depth), and scleractinians (such as *Dendrophyllia cornigera, Desmophyllum dianthus,* and the white reef-forming corals *Madrepora oculata* and *Lophelia pertusa*) (Robinson et al. 2014). Besides, encrusting foraminiferans, poriferans, bryozoans, annelids, abundant scyphozoans, small actiniarians, along with different species of bivalves, sipunculids, asteroids, and fishes are also found on these environments. The influence of seamounts is also observed on the community assemblages in the sediments close to these systems with remarkable differences from the adjacent sediments typically from the adjacent bathyal plain (Danovaro et al. 2009; Pusceddu et al. 2009).

Canyons Most of the Mediterranean coasts are incised by a large number of canyons, which rapidly reach the deep-water bottoms. Mediterranean canyons are indeed different from the canyons of other regions, as they are more closely spaced (14.9 km), more dendritic (12.9 limbs per 100,000 km^2), shorter (mean length of 26.5 km), and steeper (means slope of 6.51; Harris and Whiteway 2011). Trawling activity and marine litter are relevant in most Mediterranean canyons as documented in detail for the Gulf of Lion, and the Ligurian Sea (Fabri et al. 2014; Fanelli et al. 2017). Mediterranean canyons are typically colonized by *Madrepora oculata*, *Isidella elongata,* and *Funiculina quadrangularis*. Yet, significant differences are present between the canyons located in the west and east coast of the Gulf of Lyons (Fabri et al. 2014). The Levante Canyon is the most prominent morphological feature of the Ligurian's Apennine margin (North-west Italy; Fanelli et al. 2017) and incise the outer continental shelf around 6 km from the Punta Mesco, running in parallel with respect to the coast merging with the Bisagno Canyon south of the city of Genoa. The Levante canyon is mainly colonized by *Madrepora oculata* and *Desmophyllum dianthus*, but its muddy seabed hosts a rich fauna, including the tube-dwelling anemone Cerianthus sp., the euphausiid *Meganyctiphanes norvegica*, the decapods *Plesionika martia* and *Nephrops norvegicus*, the mysid *Boreomysis sp.*, brittle stars, *polychaetes*, and fishes including *Nezumia sp*. (Fanelli et al. 2017). Most Mediterranean canyons are still largely unknown in terms of benthic fauna, yet it is well known that some of them, such as the Polcevera canyon plays an important role in forming a suitable habitat for cetaceans (Tepsich et al. 2014).

Cold seeps Cold-seep habitats (i.e., hydrogen sulfide, methane, and other hydrocarbon-rich fluid seepage) are marine seafloor ecosystems that form around hydrocarbon emission pathways. Seep-related structures include also pockmarks and mud volcanoes. Mud volcanoes (MVs) "conic edifices constructed by surface extrusion of cold fluids, like mud, saline water, and gases expelled from a pressurized deep source layer up through structurally controlled conduits" (Kopf 2002). A mud volcano is a sort of "seep", generally occurring in hydrocarbon basins often (but not always) linked to natural gas or oil reservoirs. Supply of

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

hydrocarbons sustain chemosynthetic communities, which are fuelled by chemical energy originated from microbial utilization of methane and other hydrocarbons (Levin and Sibuet, 2012; Pop Ristova et al. 2015). Cold seeps in the deep Mediterranean Sea have been described from the top of the Napoli mud volcano in Crete, at 1900 m depth (Corselli and Basso 1996). Cold-seep habitats are also present along the Catalan margin, the Pomo/Jabuka Pit (Adriatic Sea) and the Gela Basin (Strait of Sicily, Central Mediterranean Sea). In the south-eastern Mediterranean Sea, polychaetes and bivalves associated with cold seeps have also being found in front of Egypt at depths of 500–1000 m depth (Coleman and Ballard 2001), characterized by the presence of large fields of bivalves, siboglinid tube worms, large sponges, and endemic fauna. They also appear to host-rich megafauna, including giant sponges (*Rhizaxinella pyrifera*) and crabs (*Chaceon mediterraneus*) as well as some endemic chemosynthetic species and large size bivalves (genera *Calyptogena* or *Bathymodiolus*).

Hydrothermal vents Hydrothermal vents in the Mediterranean Sea are generated from the collision of the African and European plates, and most of them are at less than 200 m depth (Dando et al. 1999). Although Mediterranean hydrothermal vents are not characterized by a specific fauna, a lower diversity sediment fauna and higher diversity epifauna were reported. Moreover, a large number of novel prokaryotes, especially hyperthermophilic crenarchaeota, have been isolated from Mediterranean hydrothermal vents (Dando et al. 1999). However, a study performed on macrofaunal of shallow hydrothermal vent of Aegean Sea found a higher biodiversity (Morri et al. 1999). Moreover, a study performed by Yakimov et al. (2007) investigated a deep Mediterranean hydrothermal mud vent, and its results indicated the presences of a metabolically active prokaryotic community in hydrothermal mud, which showed a great genetic diversity. Most of the bacteria were phylotypes affiliated with the epsilon-Proteobacteria subdivision recognized as an ecologically significant group of bacteria inhabiting deep-sea hydrothermal environments. Moreover, a significant percentage of delta-Proteobacteria was present, which indicate that sulfate reduction was one of the most important metabolic processes in warm mud fluids.

2.1 Bathyal and abyssal plain

In the Western basin, close to the 3000 m isobaths have been used as the upper limit of the abyssal plain. This plain covers a large portion of the deep Western Mediterranean Basin with an overall area of about 240,000 km^2. With water temperatures at 3000/4000 m of about 13–14 °C (rather than 4 °C or colder as other deep oceanic basins), the entire benthic environment displays unique features. The Mediterranean Sea also differs here from other deep-sea ecosystems in its species composition, notably the absence of the deep-water grenadier fish *Coryphaenoides armatus* and the amphipod *Eurythenes gryllus* (replaced by *Acanthephyra eximia*, a scavenging crustacean). Typical deep-water fauna groups, such as echinoderms, glass sponges, and macroscopic foraminifera (Xenophyophora), are also scarce or absent, while other groups (i.e., fishes, decapod crustaceans, mysids, and gastropods) appear much less abundant in the deep Mediterranean Sea than in the north-eastern Atlantic plains. Here, bacteria, archaea, and the small eukaryotes play the main role in C production, nutrient cycling as well as energy transfer to higher trophic levels (Danovaro et al. 2016b).

3 Change and shifts in the deep Mediterranean Sea and their effects on the biota

Since environmental conditions in most deep-sea ecosystems are remarkably constant over time (i.e., typically change only over geological time scales), the impact of these changes on deep-sea organisms and ecosystems could be particularly important (Danovaro et al. 2017b). Possibly, the best known features of all deep-sea ecosystems is their constant temperatures over time. Temperatures sharply decline with increasing water depth, and at bathyal and abyssal depths, they reach values from 10 to 4 °C. However, the Mediterranean Sea has a warm deep-sea basin and its temperature at the seafloor range from > 14 to 12.8 °C, and these values are ca 10 °C higher than those of other oceans at equal depths. This makes deep-sea fauna different from that of other oceans. Deep-sea biota are characterized by slow growth rates and late maturation; thus, they are particularly vulnerable to all impacts and could show a limited resilience (Danovaro et al. 2017a).

Climate-induced changes in deep seas can occur primarily in two ways: (1) by deep-water warming, linked to surface temperature increases and to intermediate layer warming and (2) by the formation of new deep waters, which occurs when surface waters, preconditioned by high salinity, become sufficiently dense by cooling to cause them to sink. Both kinds of climate-induced change have been recorded in the Mediterranean Sea. In the deep Mediterranean Sea, both phenomena are observed. The formation of new deep waters in the Mediterranean Sea can occur primarily in two ways: (a) the dense shelf water cascading (DSWC) and the so-called “transient event”.

Dense shelf water cascading is a specific type of buoyancy-driven current, which occurs when dense water forms over the continental shelf by cooling and/or by an increase in salt content of the coastal waters due to atmospheric forcing. When the dense waters overflow the shelf edge, they descend

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

down the continental slope, until they reach the corresponding matching density. Suspended sediment concentration in the dense water plume also contributes to the excess density, and affects the dynamics of the plume by enhancing its equilibrium depth (Fohrmann et al. 1998). Major DSWC possibly contributes to the ventilation of deep waters, and leads to large suspended particle and organic matter fluxes (Heussner et al. 2006; Sanchez-Vidal et al. 2009).

The "transient event" refers to large changes in the physico-chemical characteristics of the eastern Mediterranean Sea deep water 'Transient event'. Changes in the deep waters in this area occurred in two phases: the first, between 1987 and 1992, was characterized by a massive formation of dense, relatively warm water in the south Aegean (the Cretan Deep Water), mainly as a result of increased salinity; the second phase, from 1992 to 1994, was characterized by a drop in deep-water temperature of ~ 0.4 °C, which resulted in even denser deep water being formed (Danovaro et al. 2001 and citation therein). Consequently, the old eastern Mediterranean Sea Deep and Bottom Waters were uplifted by several hundred meters and formed a distinct nutrient-rich intermediate-water layer (the Transitional Mediterranean Water), which, under the influence of cyclonic circulation, reached shallower depths (100–150 m; i.e., close to the euphotic zone).

Life in the deep sea depends on the constant rain of settling particles produced in the photic zone and/or exported from the continental shelf. One of the main characteristics of the deep Mediterranean is food limitation displaying strong energetic gradients and low nutrient concentrations in the central-eastern basin (Danovaro et al. 2009). Indeed, the Levantine region of the central-eastern basin is one of the most food limited deep-sea areas of the world (Psarra et al. 2000; Tselepides et al. 2000). Inputs of organic carbon are 15–80 times lower than in the western basin and there are extremely low concentrations of chlorophyll-*a* in surface offshore waters (about 0.05 $\mu g\ L^{-1}$) (Yacobi et al. 1995; Krom et al. 1991). The concentrations of food sources decline sharply with increasing distance from the coast and depth.

Oxygen is naturally low or absent, where biological oxygen consumption through respiration exceeds the rate of oxygen supplied by physical and biological processes. This is the case of the oxygen minimum zones (OMZs) of the open ocean, the coastal upwelling zones, deep basins of semi-enclosed seas, and deep fjords. Low oxygen levels and anoxia leave a strong impact on biogeochemical and ecological processes (Diaz and Rosenberg 2008). Biodiversity and eukaryotic biomass decrease, and microbes increase their relevance. Another important factor is the increased evidence of the progressive acidification of the oceans (Stramma et al. 2010; Koslow et al. 2011), but the available information for the deep Mediterranean Sea is almost non existent.

The CO_2 sequestration by the oceans leads to a pH decrease in seawater (ocean acidification) and a variety of chemical changes known collectively as "the other CO_2 problem" phenomenon. The impact of OA (i.e., ocean acidification) on marine biogeochemical cycles and biota has been well documented by laboratory studies and already documented in some ocean areas (Orr et al. 2005). The Mediterranean Sea could represent one of the world's most sensitive ocean regions to ocean acidification (Bramanti et al. 2013). Recent investigations suggested that the Mediterranean Sea has shown a decrease of pH values ranging from − 0.005 to − 0.156 units (according to the method of calculation) with respect to the preindustrial levels, (Hassoun et al. 2015; Palmiéri et al. 2015). A 3 year investigation conducted in the Mediterranean Sea at the Strait of Gibraltar documented a remarkable decreasing annual trend of − 0.0044 ± 0.00006 in the pH, present in both the Levantine Intermediate Water (LIW) and the Western Mediterranean Deep Water, particularly in the deep waters due to their different biogeochemical nature (Flecha et al. 2015).

3.1 Temperature shifts

A general warming trend has been observed in the deep waters of the western Mediterranean Sea, where water temperatures have increased by ~ 0.12 °C in the past 30 years as a possible result of greenhouse gas-induced global warming (Bethoux et al. 1990). However, subsequent investigations have revealed a significant increase of the rate of warming in deep-water masses (Fig. 1). Changes in temperature are particularly relevant from an ecological point of view, since they can influence deep-sea biodiversity and its attributes over wide spatial scales. The life history, longevity, and metabolic rates of deep-sea organisms are influenced by temperature (and body size, according to the metabolic theory of ecology; which explains how metabolic rate varies with body size and temperature see Brown et al. 2004). Deep-sea ecosystems see a progressive (both chemical and thermal) energy limitation with increasing water depth. However, since the Mediterranean Sea is characterized by high temperature at depths, these effects are expected to be much less relevant in the Mediterranean Sea, rather the problem for deep Mediterranean species can be related to the limit of thermal tolerance, especially for species with affinity for cold waters (Naumann et al. 2014). The effects of temperature shifts on Mediterranean deep sea are poorly investigated and the experience made with coastal ecosystems cannot be easily applied to the deep. In the Mediterranean Sea, most planktonic and benthic species show clear temporal trends (Coma et al. 2000), and species with higher affinity to warm temperatures expand their reproductive and growth periods, while those with affinity for lower temperature see a

Journal : Large 12210 | Article No : 725 | Pages : 17 | MS Code : LYNC-D-18-00035 | Dispatch : 13-6-2018

reduction of the periods suitable for their reproductive cycles (Boero et al. 2008).

Changes in deep-water temperatures and particularly the increase of sea-surface temperatures can alter the vertical distribution of coastal species pushing them towards deeper depths, and possibly determining an extinction of vulnerable species at shallow depths (Boero et al. 2013; Yasuhara and Danovaro 2016). Changes in temperature might also lead to altered life cycles, inducing dormancy and production of resting stage of phyto- and zooplankton species, which sink and accumulate in deep-sea sediments (Della Tommasa et al. 2004). Although, intensive and prolonged warming periods can lead to the presence of episodic mass mortality events (Cerrano et al. 2000), most of these species respond to changes in temperature by adapting to warmer conditions and/or modifying their phenology. However, conversely to coastal marine areas, the deep sea is characterized by stable temperatures and does not tolerate temperature shifts. Using a decadal data set (from 1989 to 1998), Danovaro et al. (2014) provided evidence that deep-sea nematode diversity can be strongly and rapidly affected by temperature shifts. The abrupt decrease in temperature (of about 0.4 °C) and modified physico-chemical conditions that occurred between 1992 and 1994 caused a significant decrease in nematode abundance and a significant increase in diversity. Such changes promoted a strong turnover diversity with the replacement of ca 50% of the species present at 1000 m depth. Temperature shift also resulted in decreased functional diversity and species evenness and in an increase in the similarity to colder deep-Atlantic fauna. When the temperature recovered (after 1994–1995), the biodiversity only partially returned to the previous values, also indicating that also climate-driven episodic events are not reversible, at least in the scale of decades. This study also showed that deep-sea biodiversity is highly vulnerable to environmental alteration and that deep-sea biodiversity is also significantly affected by very small temperature changes (even in the order of 0.1 °C).

3.2 Food limitation

The inputs of organic material produced by photosynthesis at the ocean surface decrease exponentially with increasing water depth, thus limiting benthic production and controlling the biodiversity of some large species (i.e., Ophiuroidea; McClain et al. 2012; Smith et al. 2009; Woolley et al. 2016). An increasing number of studies predict that global change, enhancing water column stratification through increased sea-surface temperature, might reduce the input of food resources in the Mediterranean Sea (Coma et al. 2009; Smith et al. 2008; Sweetman et al. 2017). Such progressive food limitation in the deep sea can have different effects on different benthic components. Recently, McClain et al. (2012) highlighted that the relative influence of chemical (i.e., food) and thermal energy (bottom water temperature) on deep-sea organisms varies considerably across levels of biological organization and that chemical energy has a major effect on larger organisms (at higher levels of biological organization).

Although the response of the deep-sea assemblages to the constant food depletion is largely unknown, it is known that a reduction of food availability can significantly affect the growth rates, survival, and recruitments of benthic organisms, with severe consequences on the deep-sea community (Gambi et al. 2017; Roberts and Cairns 2014). Finally, the effects of global change on food supply to the deep sea might change significantly among different regions and habitats (e.g., northern vs southern Mediterranean Sea, or active canyons vs passive open slopes; Cartes et al. 2015; Pusceddu et al. 2013, 2016; Sweetman et al. 2017).

The potential of deep-sea assemblages to adapt to progressive food depletion is completely unknown. Gambi et al. (2017) used the Mediterranean Sea as a model for evaluating the possible effects of changes in food supply [i.e., organic carbon (OC) fluxes] and bioavailability (as quantity of food sources) on the abundance and biomass of different deep-sea benthic components. The results of this study show that microbes, meiofauna, macrofauna, and megafauna will display a different response in terms of abundance and biomass to increasing food limitation. The effects of food depletion are particularly evident for macrofauna and megafauna and to a lesser extent for meiofauna (Gambi et al. 2010; Rex et al. 2006; Rogers 2015; van der Grient and Rogers, 2015; Wei et al. 2010). while microscopic components (e.g., bacteria, archaea and protozoa) remained invariant along bathymetric patterns (Danovaro et al. 2002; Deming and Carpenter 2008; Rex et al. 2006; Wei et al. 2010). The decrease of benthic faunal abundance and biomass with increasing water depth is explained by the exponential decrease in organic matter supply (Smith et al. 2009; McClain et al. 2012; Jones et al. 2014). A reduced food availability can significantly affect the growth rates, survival, and recruitments of benthic organisms, with severe consequences on the potential of deep-sea assemblages to sustain their abundance, growth rate, reproduction, and recovery of degraded habitats (Smith et al. 2008; Barbier et al. 2014; Van Dover et al. 2014).

3.3 Oxygen decline

Changes in the deeper ocean oxygen may have their origin in basin-scale multi-decadal variability, oceanic overturning slow-down and a potential increase in biological consumption (Breitburg et al. 2018). Although periodic hypoxic events have been observed in the Adriatic Sea, in the deep Mediterranean Sea, there is no evidence of hypoxic conditions this fact is likely due to very low inputs of organic

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

material to the deep seafloor. Although it can be expected that increasing temperatures might increase the potential spread of OMZs, the decreased primary productivity might balance such a risk. However, other authors sustain that global warming can increase the primary production (see Hare et al. 2007). Direct effects from depletion of O_2 levels and rising water temperatures may impact embryonic survival rates of vulnerable deep-sea oviparous (egg-laying) elasmobranchs (Henry et al. 2016), including the deep-sea shark *Centroscymnus coelolepis*, a key stone species in the deep Mediterranean (Catarino et al. 2015). The deep-hypersaline anoxic basins present in the eastern Mediterranean Sea are extreme ecosystems for their high salt concentrations and anoxic conditions, but they can represent a model of the potential consequences over the deep-sea biota (Danovaro et al. 2005, 2008a, 2016a).

3.4 Acidification

Ocean acidification represents an additional major threat for the calcifying species (e.g., cold-water corals) given its potential effects on growth rates, reproduction and resistance to environmental changes. With increasing pCO_2 (i.e., –log of the CO_2 concentration), reduced calcification rates have been observed for a variety of calcareous organisms even when aragonite or calcite saturation exceeds 1.0. However, the sensitivity of marine organisms to acidification varies among different taxa and some species may increase calcification rates with increasing CO_2 levels. A recent analysis of the trend in pH in the Mediterranean waters revealed a significant decreasing trend with a Δ pH of − 0.0044 units per year in the Mediterranean Outflow Waters, which is largely influences by deep Mediterranean waters. This rate of pH decline is two- or threefold higher than acidification rates reported in several oceanic sea-surface time series. The range of pH change in Mediterranean deep waters has been estimated recently through a modelling approach (− 0.005 to − 0.06 pH units Palmiéri et al. 2015). Such changes can affect significantly also economically important species, such as the cold-water coral *Corallium rubrum*, which is distributed in a range between 3 and > 1000 m. The decrease of pH value causes a reduction of its biocalcification process. Since *C. rubrum* is a long-living species (200 years), this suggests that ocean acidification predicted for this century will significantly increases its extinction risk; thus preserving its associated biodiversity is important to contrast its decline (Cerrano et al. 2013).

4 Vulnerability of Mediterranean deep-sea ecosystems to global change

Available information suggests that more diverse deep-sea systems are characterized by higher rates of ecosystem functioning than less diverse systems, as well as by an increased efficiency how the different processes (e.g., biomass production) are performed (Danovaro et al. 2008b). However, in the case of the vulnerable deep-sea habitats of the Mediterranean Sea, the overall impact of global changes is expected to be related to a combination of factors. In the following sections, the vulnerability of different deep-sea habitats and ecosystems is analyzed, based on the experimental of field evidence of their sensitivity to changes in the environmental conditions present in different deep-sea- habitats and ecosystems based on the assessment of two main variables: (a) the sensitivity/tolerance of deep-sea Mediterranean species/assemblages to shift in climate-sensitive variables and (b) the degree by which every system is expected to be exposed to a higher intensity of the climate change-induced shifts (Table 1).

4.1 Impact on deep-water corals systems

Cold-water coral habitats are expected to be severely threatened by global change either in terms of tolerance to increasing water temperature and acidification. Locally, the adaptive capacity of communities and habitats still needs to be assessed and supported by reducing other stressors, arising

Table 1 Sensitivity of various habitat types to the variables affected by global change in the deep Mediterranean Sea

Deep-sea habitat type	Temperature	Food limitation	Acidification	Oxygen depletion	Cumulative potential Impact	References
Deep-water forests and corals	Very high	High	High	Moderate	Very high	Brooke et al. (2013) Hennige et al. (2014)
Bathyal–Abyssal Plains	Very high	Very high	Low	Moderate	High/Very high	Pusceddu et al. (2013)
Canyon systems	High	Moderate	High	High	High	Brooke et al. (2013) Hennige et al. (2014)
Seamounts	High	High	Moderate	Low	Moderate	Brooke et al. (2013) Hennige et al. (2014)
Cold seeps	Low	Low	Very low	Low	Low	Brazelton (2017)
Vent systems	Very low	Very low	Very low	Very low	Very low	Brazelton (2017)

from direct impacts. Another main threat is certainly represented by the increase of deep-water temperatures, which might surpass the upper limits of tolerance of these species that show a high affinity for cold waters. Indeed, the study conducted by Brooke et al. (2013) through a laboratory experiment, where living colonies of the deep coral *L. pertusa* were kept at 5, 8, 15, 20 and 25 °C, of which the latter three encompassed the known range derived from field observations (~4–14 °C), while the first two temperature were used as controls. The results showed that after 24 h, all of the fragments in the 5, 8, and 15 °C treatments were alive and healthy; however, at 20 °C, survival was reduced to a mean of 68.3%, while a 100% mortality was observed at the highest temperature. In addition, the decrease in primary production and changes in water circulation can cause severe food shortage with consequent effects on the survival of these organisms. Finally, their zonation in proximity of the margins and prevalently on the upper slope, often at close distance from the shore, makes these systems potentially susceptible to oxygen limitation.

4.2 Impact on seamounts

Seamounts in the Mediterranean Sea can reach shallow depths, which make these systems susceptible to water warming. At the same time, the increased water column stratification can alter significantly both the production/inputs of organic matter and the hydro-dynamism (possibly including Taylor column dynamics that creates circulation cells above the seamount summit and enhanced vertical mixing leading to increased primary production). Changes in water temperature and food supply can cause significant alterations (Carney 2005). The impact of acidification can be relevant for deep-water corals colonizing the seamount, but possibly less impacting for other benthos and nektonic species as reported by Hennige et al. (2014) who treated living colonies of *L. pertusa* with high CO_2 concentrations (up to 750 ppm). The results showed that corals exposed to high CO_2 conditions reduced significantly respiration rates (11.4 ± 1.39 SE, μmol O2 g^{-1} tissue dry weight h^{-1}) than corals in control conditions (28.6 ± 7.30 SE μmol O2 g^{-1} tissue dry weight h^{-1}).

4.3 Impact on canyon systems

Continental margins represent approximately 20% of the world ocean's surface and the relevance of the canyons in continental margins of the Mediterranean Sea is even higher. The topographic and hydrodynamic features of some submarine canyons make these sites of intense exchange between the continental shelf and the deep margin and basin (Flexas et al. 2002, 2008; Palanques et al. 2006; Heussner et al. 2006). Canyons contain a large number of endemic and vulnerable species and habitats and play an important role in the biogeochemical cycles at the global scale. Canyons can favor or even amplify the effects of dense shelf water cascading events (DSWC; Allen and Durrieu de Madron 2009). Therefore, it has been hypothesized that DSWC could have a great influence on the biodiversity and functioning of canyon ecosystems and the deep margins and basins (Durrieu de Madron et al. 2000; Duineveld et al. 2001; Martin et al. 2006; Skliris and Djenidi 2006; Bianchelli et al. 2008; Company et al. 2008). Canyons are subjected to episodic temperature shifts; thus, local assemblages can be adapted to such variability, but are at the same time vulnerable, as such shifts are associated with strong currents that cause an intense physical disturbance over large portions of the canyon (Font et al. 2007). At the same time, canyons are typically rich in organic matter (largely derived from shelf export) and could suffer less from changes in primary production (Vetter and Dayton 1998). On the contrary, their sensitivity to acidification can be high due to the presence of habitat-forming species/bio-constructors (Sánchez et al. 2014). Finally, their proximity to the coast makes these systems highly vulnerable to deoxygenation.

4.4 Impact on seepage systems

These systems release a cold-water flow containing methane or other hydrocarbon sources, which cause an environmental gradient and represent a suitable habitat for species using this energy sources for their bacterial and/or archaeal symbionts. Sometimes, the seepage, which is highly variable in time and space, is associated with moderate warming (up to ca 40 °C), so that the impacts of minor temperature shift are expected to be negligible. Active cold seeps are also systems, where chemoautotrophic primary production prevails, and make the assemblages and related food webs largely independent from the organic carbon inputs from the photic zone. These systems might also show an important variability in terms of pH and oxygen concentration, so that their associated fauna is likely to tolerate shifts in these variables related to global change.

4.5 Impact on vent systems

Vents release a very hot water flow, which causes an environmental gradient that provides a suitable habitat for warm-affinity species. This water flow contains abundant concentration of hydrogen sulfide, gas, and other reduced chemical compounds that represent an energy reserve for bacteria and archaea (Bell et al. 2017). The most frequent vent-associated animals are annelids, polychaetes, mussels, clams, and shrimp (Brazelton 2017), which live in symbiosis with chemoautotrophic bacteria (De Leo et al. 2010; Bo et al. 2014; Davies et al. 2015). These organisms are thus

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

largely (or completely) independent from the food supply from the water column. Since these systems are subjected to high (and highly variable) temperatures, oxygen, and pH, the deep-water warming is expected to have very limited (if any) impact on these assemblages, although it could alter the dynamics of the surrounding assemblages (Brazelton 2017).

4.6 Impact on bathyal and abyssal plain

In the last decades, the impacts of global change on the deep sea have been modelled (Mora et al. 2013; Sweetman et al. 2017), but field data on the impact on deep-sea bathyal and abyssal plains remain extremely scant. The Mediterranean deep-sea plains have been characterized by two main processes: the transient events in the eastern Mediterranean Sea and the cascading events in the Central and Western basin (along the Catalan margin and in the southern Adriatic-Ionian sea). The two phenomena originate in surface waters, but the density effects spread into the deeper waters reaching the basins down to ca 2000 m depth. These phenomena are associated with temperature shifts (abrupt decrease determining the formation on dense waters) or change in salinity (rapid increase of salinity causing increase water density). In the case of the cascading, the process is coupled with a massive transfer of sediment and organic loads. These processes cause, from one side, the disturbance due to bottom currents and sediment resuspension, but at the same time supply the deep sea with important food sources (Pusceddu et al. 2013). Pusceddu et al. (2013) investigated the effects of cascading process on the meiofaunal assemblages of a submarine canyon and a deep margin. During the cascading period, only nematodes were found in the canyon and three taxa (i.e., nematodes, copepods, and polychaetes). After the cessation of cascading, a fast recovery of deep-sea meiofaunal assemblages has been observed. Six months after the event, meiofaunal abundance, biodiversity, and community composition recovered to values typically observed in all other sampling periods, when a total of 5–11 taxa are recorded within the canyon sediments and in the deep margin. The apparent quick recovery of the deep-sea assemblages after cascading can be explained by the high turnover (up to > 10 generations year^{-1}) and opportunistic life strategies of meiofauna. In addition, the increased food availability observed in the deep margin and the ecological space released by the meiofauna killed or brought away by cascading could have favored the fast recovery of meiofaunal assemblages. These results generally have a limited temporal effect, observed for the recruitment and catch of the deep-sea shrimp *Aristeus antennatus*, which were abated by the cascading and showed a strong recovery after the cessation of the episodic event (Company et al. 2008).

The transient event and the consequent uplift of nutrient-rich deep waters in the eastern Mediterranean Sea resulted in increased biological production. From the early 1980s to the 1994–1995 season (i.e., after cooling), primary productivity over the continental shelf and upper slope increased threefold, reaching values comparable with those in mesotrophic environments (i.e., 60–80 g C m^{-2} year^{-1}). Such changes in primary productivity were also coupled with changes in phytoplankton assemblage composition (measured as the diatom:dinoflagellate ratio), species dominance and average phytoplankton cell size (which increased by between two and five times). Increased primary production and phytoplankton cell size are known to enhance vertical fluxes of phytodetritus and organic C to deep-sea sediments. This was observed in the eastern Mediterranean Sea, where phytodetritus input to the deep-sea floor increased by up to two orders of magnitude. This flux determined an accumulation of organic C and N on the sea floor and enhanced the quality of sedimentary organic matter, evident in terms of protein accumulation, increased the total protein: carbohydrate content ratio and decreased the C:N ratio (carbon: nitrogen) ratio. Such phenomena are the opposite to those described during El Niño events, in which a reduced export production from the euphotic zone has been reported. This phenomenon caused a significant decrease in nematode abundance and a significant increase in diversity. This temperature decrease also resulted in decreased functional diversity and species evenness and in an increase in the similarity to colder deep-Atlantic fauna. When the temperature recovered, the biodiversity only partially returned to the previous values (Danovaro et al. 2004).

It is concluded that deep-sea fauna is highly vulnerable to environmental alterations and that deep-sea biodiversity is also significantly affected by very small temperature changes (even in the order of 0.1 °C) and to changes in food availability as these systems are drastically dependent on the organic carbon supply from the water column. Oxygen decline could have major impacts on these systems, but the spreading of OMZ at bathyal and abyssal depths is expected to be relative modest. Moreover, the effects of acidification are expected to be important on species inhabiting the deep-sea plains, but the low rate of expansion of the acidification at such depths makes this risk relatively modest.

5 Global change impacts on ecosystem services and societal values of the deep Mediterranean Sea

Ecosystem good and service benefits that human population derive, directly or indirectly, from ecosystem functions (e.g., food and other natural resources or waste abatement) play a crucial role in sustaining people's well-being (Costanza et al. 1997), but global change poses serious risks for their sustainability. Valuing both the benefits and the costs of ecosystem

Journal : Large 12210 | Article No : 725 | Pages : 17 | MS Code : LYNC-D-18-00035 | Dispatch : 13-6-2018

degradation can represent a way to contribute to decision-making processes (UNEP-WCMC 2011; MEA 2005). The high biodiversity allows maintaining the deep-sea ecosystem functions, providing a wide variety of ecosystem services some of which are unique, irreplaceable, and play a key role in sustaining human well-being (Armstrong et al. 2012, Thurber et al. 2013; Balvanera et al. 2014). Among the supporting and regulating services, it is important to mention the role of deep-sea ecosystems in the C storage (Liquete et al. 2013). Deep sea has already absorbed a quarter of the carbon released from human activities (Sweetman et al. 2017). The storage of CO_2 influences also climate and many other deep-sea functions and services. Climate mitigation by the deep ocean may ultimately compromise many of the ecosystem services we value. At the same time, sequestration of methane, another powerful greenhouse gas into carbonates, is largely driven by seafloor microbial communities interacting with specialized fauna. The deep sea also represents an area, where waste products are stored and detoxified through biotic and abiotic processes. For example, persistent organic pollutants, macro- and micro-plastics, sewage, and oil can be removed through bioremediation, facilitated by bioturbation (a process that regulates the decomposition and/or sequestration of waste by biogenic mixing of sediments performed by organisms; Snelgrove et al. 2017). Non-market supporting services are provided by deep-sea ecosystems in the form of habitat provision, nursery grounds, trophic support, refuges, and biodiversity functions provided by assemblages on seamounts, coral and sponge reefs, banks, canyons, slopes, and other settings (Armstrong et al. 2012; Mengerink et al. 2014; Thurber et al. 2013; Levin and Le Bris 2015). The extensive species, genetic, enzymatic, and biogeochemical diversity hosted by the deep ocean also holds the potential for new pharmaceutical and industrial applications, as well as keys to adaptation to environmental change. Among the provisioning services, fish stocks are one of the most tangible ecosystem services provided by the deep sea (Norse et al. 2012). However, the mean depth of fishing is increasing at a rate of ca 62.5 m per decade, from below 200 to 1000 m. Currently, fishing beneath 1000 m depth is banned in the Mediterranean Sea, but there are clear evidences that the ban is often not respected (De Juan and Lleonart 2010). Other crucial provisioning services for human activities are represented by oil and gas reserves stored in the deep seabed. During recent years, we are witnessing the development of new technologies for offshore drilling and large reserves of hydrocarbons have been found. Consequently, the oil and gas industry has moved from the land to the deep waters; however, there is a risk that increasing deep-water temperatures can cause the release of the gas hydrates from the deep seafloor. Behind oil and gas, deep-sea beds are characterized also by reserves of metals, which are also rare earth elements. Mining is not limited to resources such as metals, but also supplies "ornamental" services, as the exploitation of some species for jewelry (e.g., red coral and other precious corals). Finally, deep-sea ecosystems offer also a variety of social (i.e., aesthetic and inspirational) services, including literature, entertainment (many movies have focused on the Abyss and its creatures), ethical considerations, tourism, and spiritual wealth and well-being. Some of the main cultural services provided by the deep sea are important for education and science. Deep-sea ecosystems thus play an important role, since they provide a number of services required to support the current way of life for humans and human well-being. At the same time, the importance of intangible values of deep-sea ecosystems makes it difficult to fully assess their global value (Van den Hove and Moreau 2007). Valuation results are often difficult and complex environmental goods depend on the level of the previous knowledge of the participant stakeholders and the information provided to them. A recent study conducted by Zanoli et al. (2015) applied the Q methodology to explore subjective perspectives on Mediterranean deep sea. In this experiment, Ph.D. students, half of which with a Marine Life Sciences degree and half with a degree in a different topic, were asked to perform a Q-sorting experiment, and rank a sample of 36 deep-sea pictures of the bathyal–abyssal wildlife, landscapes/habitats, and ecosystems in the Mediterranean deep sea. All pictures were sorted by topic according to a subjective priority relative to (a) a personal overall view; (b) their perception of the potential interest for fishermen; and (c) as if they were fishermen. The results of this test demonstrated that the education is a key step in the appreciation and consciousness of the importance of deep sea in our societies.

The societal impacts of global climate change in the deep sea will be undoubtedly widespread and complex. It is already evident in the migration and change in the distribution of deep-sea populations of commercially interest. This impact will result from warming-induced changes in metabolism (Deutsch et al. 2015) and body size (Cheung et al. 2013) linked to latitudinal or depth shifts in species distributions, in addition to vertical habitat compression from OMZ expansions (Prince and Goodyear 2006; Stramma et al. 2010, 2012; Yasuhara and Danovaro 2016). Less clear are the impacts of acidification stress on precious species, such as the red coral (Bramanti et al. 2013; Cerrano et al. 2013). Other effects could be the altered fisheries production, which in the Mediterranean Sea is expected to be very strong due to reduced food availability.

6 Conclusions

In conclusion, although the actual knowledge is still scant, it is clear that global change poses serious threats on the biodiversity and functioning deep-sea ecosystems in the

Journal : Large 12210 | Article No : 725 | Pages : 17 | MS Code : LYNC-D-18-00035 | Dispatch : 13-6-2018

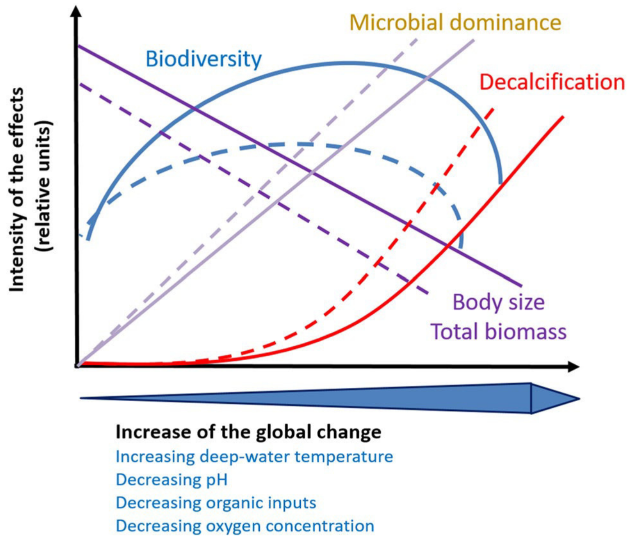

Fig. 3 Conceptual illustration of the expected impact of global change in the Mediterranean (dotted lines) as compared to the effect on global oceans (continuous lines). The rates of increase of microbial dominance and decalcification are higher than those expected for the other oceans, while the loss of total biomass and the body size decrease more rapidly than elsewhere. A hump shaped curve is expected for biodiversity, with values initially increasing with increasing temperatures and then collapsing. However, such trend in the Mediterranean, as for other tropical systems is subjected to an anticipated negative impact and more rapid collapse

Mediterranean Sea, which on the bases of the higher food limitation and higher deep-sea temperatures appears far more vulnerable to climate change effects than other oceanic regions. A conceptual representation of the possible differences in terms of vulnerability of the deep Mediterranean Sea ecosystems and their counterpart in oceanic waters is illustrated in Fig. 3.

Furthermore, the impacts of global change are expected to be stronger if we considered synergistic effects (Mora et al. 2011) with other human impacts such as marine litter widespread, overfishing, chemical pollution, and eutrophication. As a result, the global ability of providing ecosystem goods and services (e.g., food resources CO_2 sequestration) can be seriously compromised (Barkmann et al. 2008). The knowledge on the impact of global change on deep-sea biota of the Mediterranean Sea is still extremely scarce and requires immediate actions. Therefore, it is clear the need to increase the research on the deep sea. In this perspective, the EU' Marine Strategy Framework Directive (MSFD) can play a crucial role. The MSFD require that the member states achieve the good environmental status not only in coastal areas, but also in the offshore area up to 200 nautical miles from the coast line. In this perspective, planning and implementing ecological investigation and monitoring of deep-sea ecosystems is of vital importance (Danovaro et al. 2017a). Some deep-sea ecosystems are severely impacted or damaged and require restoration actions (Barbier et al. 2014) and scarce methodological information exist to date, and future research projects should take this topic into account. Finally, improving environmental conditions and increasing environmental cultural awareness (especially on the deep sea) is of particular importance to empower stakeholders involved in marine resource exploitation (Van Dover et al. 2014). The deep Mediterranean Sea provides an important part of the ecological and ecosystem services needed for our society, which are likely to expand and be more appreciated in the coming decades. At the same time, a number of co-occurring anthropogenic stressors coupled with global climate change are likely impacting these systems. As society makes critical decisions about the use of the Mediterranean Sea and its conservation, it is important that we recognize the vulnerability of life and habitats of these systems and take actions in this perspective (Davies et al. 2007; Ramirez-Llodra et al. 2011).

Acknowledgements This study was conducted within the frame of the projects MERCES (Marine Ecosystem Restoration in Changing European Seas), funded by the European Union's Horizon 2020 research and innovation program (Grant agreement no. 689518), and IDEM (Implementation of the MSFD to the Deep Mediterranean Sea) (DG ENV Grant agreement no. 11.0661/2017/750680/SUB/EN VC2).

References

Acosta J, Ancochea E, Canals M, Huertas MJ, Uchupi E (2004) Early Pleistocene volcanism in the Emile Baudot seamount, Balearic promontory (western Mediterranean Sea). Mar Geol 207:247–257

Allen SE, Durrieu de Madron X (2009) A review of the role of submarine canyons in deep-ocean exchange with the shelf. Ocean Sci 5:607–620. https://doi.org/10.5194/os-5-607-2009

Armstrong CW, Foley N, Tinch R, van den Hove S (2012) Services from the deep: steps towards valuation of deep sea goods and services. Ecosyst Serv 2:2–13

Balvanera P, Siddique I, Dee l, Paquette A, Isbell F, Gonzalez A, Byrnes I, O'Connor MI, Hungate BA, Griffin JM (2014) Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. Bioscience 64:49–57. https://doi.org/10.1093/biosci/bit003

Barbier EB, Moreno Mateos D, Rogers AD et al (2014) Protect the deep sea. Nature 505:475–477

Barkmann J, Glenk K, Keil A, Leemhuis C, Dietrich N, Gerold G, Marggraf R (2008) Confronting unfamiliarity with ecosystem functions: the case for an ecosystem service approach to environmental valuation with stated preference methods. Ecol Econ 65:48–62

Bell JB, Woulds C, Van Oevelen D (2017) Hydrothermal activity, functional diversity and chemoautotrophy are major drivers of seafloor carbon cycling. Sci Rep 7:12025

Bethoux JP, Gentili B, Raunet J, Tailliez D (1990) Warming trend in the western Mediterranean deep water. Nature 347:660–662

Bianchelli S, Gambi C, Pusceddu A, Danovaro R (2008) Trophic conditions and meiofaunal assemblages in the Bari Canyon and the adjacent open slope (Adriatic Sea). Chem Ecol 24:101–109

Bianchi CN (2007) Biodiversity issues for the forthcoming Mediterranean Sea. Hydrobiologia 580:7–21

Bo M, Canese S, Spaggiari C, Pusceddu A, Bertolino M, Angiolillo M, Giusti M, Loreto MF, Salvati E, Greco S, Bavestrello G (2012) Deep Coral Oases in the South Tyrrhenian Sea. PLoS One 7:e49870

Bo M, Cerrano C, Canese S, Salvati E, Angiolillo M, Santangelo G, Bavestrello G (2014) The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). Mar Ecol 35:332–342

Boero F, Féral JP, Azzurro E, Cardin V, Riedel B, Despalatovi M, Munda I, Moschella P, Zaouali J, Fonda Umani S, Theocharis A, Wiltshire K, Briand F (2008) Climate warming and related changes in Mediterranean marine biota. In: Briand F editor. Climate Warming and Related Changes in Mediterranean Marine Biota: CIESM Workshop Monographs No. 35. Monaco. pp 5–21

Boero F, Carlton J, Briand F et al (2013) Marine extinctions. Patterns and processes. CIESM Workshop Monogr 45:5–19

Bongiorni L, Mea M, Gambi C, Pusceddu A, Taviani M, Danovaro R (2010) Deep-water scleractinian corals promote higher biodiversity in deep-sea meiofaunal assemblages along continental margins. Biol Cons 143:1687–1700

Bramanti L et al (2013) Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). Glob Change Biol 19:1897–1908

Brankart JM, Pinardi N (2001) Abrupt cooling of the Mediterranean Levantine Intemediate water at the Beginning of the 1980s: observational evidence and model simulation. J Phys Oceanogr 31:89–114

Brazelton W (2017) Hydrothermal vents. Curr Biol 27:R450–R452

Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J (2018) Declining oxygen in the global ocean and coastal waters. Science 359(6371)

Brierley AS, Kingsford MJ (2009) Impacts of climate change on marine organisms and ecosystems. Curr Biol 19(14):R602–R614

Brooke S, Ross SW, Bane JM, Seim HE, Young CM (2013) Temperature tolerance of the deep-sea coral Lophelia pertusa from the southeastern United States. Deep Sea Res Part II 92:240–248

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7):1771–1789

Byrne RH, Mecking S, Feely RA, Liu X (2010) Direct observations of basin-wide acidification of the North Pacific Ocean. Geophys Res Lett 37:L02601. https://doi.org/10.1029/2009gl040999

Carney RS (2005) Zonation of deep biota on continental margins. Oceanogr Mar Biol Annu Rev 43:211–278

Cartes JE, Maynou F, Fanelli E, López-Pérez C, Papiol V (2015) Changes in deep-sea fish and crustacean communities at 1000–2200 m in the Western Mediterranean after 25 years: relation to hydro-climatic conditions. J Mar Syst 143:138–153

Catarino D, Knutsen H, Veríssimo A, Olsen EM, Jorde PE, Menezes G et al (2015) The Pillars of Hercules as a bathymetric barrier to gene flow promoting isolation in a global deep-sea shark (*Centroscymnus coelolepis*). Mol Ecol 24(24):6061–6079

Cerrano C, Bavestrello G, Bianchi CN, Cattaneo-Vietti R, Bava S, Morganti C, Morri C, Picco P, Sara G, Schiaparelli S, Siccardi A, Sponga F (2000) A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean), summer 1999. Ecol Lett 3:284–293

Cerrano C, Cardini U, Bianchelli S, Corinaldesi C, Pusceddu A, Danovaro R (2013) Red coral extinction risk enhanced by ocean acidification. Sci Rep 3:1457

Cheung WWL, Sarmiento JL, Dunne J, Frölicher TL, Lam VWY, Palomares MLD, Watson R, Pauly D (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nat Clim Change 3:254–258

Cocchi L, Passaro S, Caratori Tontini F, Ventura G (2017) Volcanism in slab tear faults is larger than in island arcs and back-arcs. Nat Commun. https://doi.org/10.1038/s41467-017-01626-w

Coleman D, Ballard R (2001) A highly concentrated region of cold hydrocarbon seeps in the southeastern Mediterranean Sea. Geo Mar Lett 21:162–167

Coll M, Piroddi C, Steenbeek J, Kaschner K, Ben Rais Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T et al (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS ONE 5(8):e11842

Coma R, Ribes M, Gili JA, Zabala M (2000) Seasonality in coastal benthic ecosystems. Trends Ecol Evol 15(11):448–453

Coma R, Ribes M, Serrano E, Jiménez E, Salat J, Pascual J (2009) Global warming-enhanced stratification and mass mortality events in the Mediterranean. Proc Natl Acad Sci USA 106(15):6176–6181

Company JB, Puig P, Sardà F, Palanques A, Latasa M, Scharek R (2008) Climate influence on deep sea populations. PLoS ONE 3:e1431. https://doi.org/10.1371/journal.pone.0001431

Corselli C, Basso D (1996) First evidence of benthic communities based on chemosynthesis on the Napoli mud volcano (Eastern Mediterranean). Mar Geol 132:227–239

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'NeillR V, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Dando PR, Stüben D, Varnavas SP (1999) Hydrothermalism in the Mediterranean sea. Prog Oceanogr 44:333–367

Danovaro R, Dell'Anno A, Fabiano M, Pusceddu A, Tselepides A (2001) Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. Trends Ecol Evol 16:505–510

Danovaro R, Manini E, Dell'Anno A (2002) Higher abundance of bacteria than of viruses in deep Mediterranean sediments. Appl Envir Microbiol 68:1468–1472

Danovaro R, Dell'Anno A, Pusceddu A (2004) Biodiversity response to climate change in a warm deep sea. Ecol Lett 7:821–828

Danovaro R, Corinaldesi C, Dell'Anno A, Fabiano M, Corselli C (2005) Viruses, prokaryotes and DNA in the sediments of a deep-hypersaline anoxic basin (DHAB) of the Mediterranean Sea. Environ Microbiol 7(4):586–592

Danovaro R, Dell'Anno A, Pusceddu A, Gambi C, Heiner I, Kristensen RM (2008a) The first metazoa living in permanently anoxic conditions. BMC Biol 8(1):30

Danovaro R, Gambi C, Dell'Anno A, Corinaldesi C, Fraschetti S, Vanreusel A, Vincx M, Gooday AJ (2008b) Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr Biol 18:1–8

Danovaro R, Canals M, Gambi C, Heussner S, Lampadariou N, Vanreusel A (2009) Exploring Benthic biodiversity patterns and hotspots on European margin slopes. Oceanography 22:16–25

Danovaro R, Company JB, Corinaldesi C et al (2010) Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. PLoS One 5(8):e11832

Danovaro R, Snelgrove PVR, Tyler P (2014) Challenging the paradigms of deep-sea ecology. Trends Ecol Evol 29:465–475

Danovaro R, Carugati L, Marco B, Cahill AE, Spinola SDC, Chenuil A et al (2016a) Implementing and innovating marine monitoring approaches for assessing marine environmental status. Front Mar Sci 3:213

Danovaro R, Gambi C, Dell'Anno A, Corinaldesi C, Pusceddu A, Neves RC, Reinhardt Møbjerg Kristensen RM (2016b) The challenge of proving the existence of metazoan life in permanently anoxic deep-sea sediments. BMC Biol 14(1):43

Journal : Large 12210 | Article No : 725 | Pages : 17 | MS Code : LYNC-D-18-00035 | Dispatch : 13-6-2018

Danovaro R, Molari M, Corinaldesi C, Dell'Anno A (2016c) Macroecological drivers of archaea and bacteria in benthic deep-sea ecosystems. Sci Adv 2:e1500961

Danovaro R, Aguzzi J, Fanelli E, Billett D, Gjerde K, Jamieson A et al (2017a) An ecosystem-based deep-ocean strategy. Science 355:452–454

Danovaro R, Corinaldesi C, Dell'Anno A, Snelgrove PV (2017b) The deep-sea under global change. Curr Biol 27:R461–R465

Davies AJ, Roberts JM, Hall-Spencer J (2007) Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. Biol Cons 138:299–312

Davies JS, Stewart HA, Narayanaswamy BE, Jacobs C, Spicer J, Golding N et al (2015) Benthic assemblages of the Anton Dohrn Seamount (NE Atlantic): defining deep-sea biotopes to support habitat mapping and management efforts with a focus on vulnerable marine ecosystems. PLoS One 10:e0124815

De Juan S, Lleonart J (2010) A conceptual framework for the protection of vulnerable habitats impacted by fishing activities in the Mediterranean high seas. Ocean Coast Manag 53:717–723

De Leo F, Smith C, Rowden A, Bowden D, Clark M (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proc R Soc B Biol Sci 2783–2792

Della Tommasa L, Danovaro R, Belmonte G, Boero F (2004) Resting stage in the biogenic fraction of surface sediments from the deep Mediterranean Sea. Sci Mari 68(S1):103–111

Deming JW, Carpenter SD (2008) Factors influencing benthic bacterial abundance, biomass, and activity on the northern continental margin and deep basin of the Gulf of Mexico. Deep Sea Res Part II 55(24–26):2597–2606

Deutsch C, Ferrel A, Seibel B, Pörtner HO, Huey RB (2015) Climate change tightens a metabolic constraint on marine habitats. Science 348:1132–1135

Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. Science 321:926–929

Duineveld G, Lavaleye MSS, Berghuis EM, de Wilde P (2001) Activity and composition of the benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic). Oceanol Acta 24:69–83

Dunlop KM, van Oevelen D, Ruhl HA et al (2016) Carbon cycling in the deep eastern North Pacific benthic food web: investigating the effect of organic carbon input. Limnol Oceanogr 61:1956–1968

Durrieu de Madron X et al (2000) Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). Oceanol Acta 23:717–729

Emig CC, Geistdoerfer P (2004) The Mediterranean deep-sea fauna: historical evolution, bathymetric variations and geographical changes. Carnets Geol Madrid 4(A01):10. https://doi.org/10.4267/2042/3230

Fabri MC, Pedel L, Beuck L, Galgani F, Hebbeln D, Freiwald A (2014) Megafauna of vulnerable marine ecosystems in French mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep Sea Res Part II: Top Stud Oceanog 104:184–207

Fanelli E, Delbono I, Ivaldi R, Pratellesi M, Cocito S, Peirano A (2017) Cold-water coral Madrepora oculata in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquatic Conserv: Mar Freshw Ecosyst 27:965–975

Flecha S et al (2015) Trends of pH decrease in the Mediterranean Sea through high frequency observational data: indication of ocean acidification in the basin. Sci Rep 5:16770

Flexas MM, Durrieu de Madron X, Garcia MA, Canals M, Arnau P (2002) Flow variability in the Gulf of Lions during the MATER HFF experiment (March–May 1997). J Mar Syst 33–34:197–214

Flexas MM, Boyer DL, Espino M, Puigdefabregas J, Rubio A, Company JB (2008) Circulation over a submarine canyon in the NW Mediterranean. J Geophys Res Oceans 113:C12002

Fohrmann H, Backhaus JO, Blaume F, Rumohr J (1998) Sediments in bottom arrested gravity plumes: numerical case studies. J Phys Oceanogr 28:2250–2274

Font J, Puig P, Salat J, Palanques A, Emelianov M (2007) Sequence of hydrographic changes in NW Mediterranean deep water due to the exceptional winter of 2005. Sci Mar 71:339–346

Galil B, Zibrowius H (1998) First Benthos samples from Eratosthenes Seamount Eastern Mediterranean. Sencken Marit 28:111–121

Gambi C, Lampadariou N, Danovaro R (2010) Latitudinal, longitudinal and bathymetric patterns of abundance, biomass of metazoan meiofauna: importance of the rare taxa and anomalies in the deep Mediterranean Sea. Adv Oceanogr Limnol 1(1):167–197

Gambi C, Corinaldesi C, Dell'Anno A, Pusceddu A, D'Onghia G, Covazzi-Harriague A, Danovaro R (2017) Functional response to food limitation can reduce the impact of global change in the deep-sea benthos. Global Ecol Biogeogr 26:1008–1021

Hare CE, Leblanc K, Di Tullio GR, Kudela RM, Zhang Y, Lee PA, Riseman S, Hutchins DA (2007) Consequences of increased temperature and CO_2 for phytoplankton community structure in the Bering Sea. Mar Ecol Prog Ser 352:9–16

Harris PT, Whiteway T (2011) Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. Mar Geol 285:69–86

Hassoun AER et al (2015) Acidification of the Mediterranean Sea from anthropogenic carbon penetration. Deep Sea Res Part I: Oceanogr Res Papers 102:1–15

Hennige SJ, Wicks LC, Kamenos NA, Bakker DC, Findlay HS, Dumousseaud C, Roberts JM (2014) Short-term metabolic and growth responses of the cold-water coral Lophelia pertusa to ocean acidification. Deep sea Res Part II: Top Stud Oceanogr 99:27–35

Henry LA, Stehmann MFW, De Clippele L, Findlay HS, Golding N, Roberts JM (2016) Seamount egg-laying grounds of the deep-water skate *Bathyraja richardsoni*. J Fish Biol 89:1473–1481

Heussner S, Durrieu de Madron X, Calafat A, Canals M, Carbonne J, Delsaut N, Saragoni G (2006) Spatial and temporal variability of downward particle fluxes on a continental slope: lessons from an 8-yr experiment in the Gulf of Lions (NW Mediterranean). Mar Geol 234:63–92

Jones DOB, Yool A, We LC, Henson SA, Ruhl HA, Watson RA, Gehlen M (2014) Global reductions in seafloor biomass in response to climate change. Global Change Biol 20:1861–1872

Keeling RE, Körtzinger A, Gruber N (2010) Ocean deoxygenation in a warming world. Ann Rev Mar Sci 2:199–229

Kitchingman A, Lai S, Morato T, Paulay D (2007) How many seamounts are there and where are they located?'. In: Pitcher TJ et al (eds) Seamounts: ecology, fisheries and conservation. Blackwell Publishing, Oxford, pp 26–40

Kopf (2002) Significance of mud volcanism. Rev Geophys 40(2):1005. https://doi.org/10.1029/2000RG000093

Koslow JA, Goericke R, Lara-Lopez A, Watson W (2011) Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. Mar Ecol Prog Ser 436:207–218

Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol Lett 13:1419–1434

Krom MD, Kress N, Brenner S, Gordon LI (1991) Phosphorus limitation of primary productivity in the eastern Mediterranean. Limnol Oceanogr 36:424–432

Lacombe H, Tchernia P (1972) Caractères hydrologiques et circulation des eaux en Méditerranée. In: Stanley DJ (ed) The Mediterranean Sea. Dowden, Hutchinson and Ross, Stroudsberg, pp 26–36

Le Treut H, Somerville R, Cubasch U, Ding Y, Mauritzen C et al (2007) Historical overview of climate change. Cambridge University Press, Cambridge, pp 95–127

Journal : Large 12210	Article No : 725	Pages : 17	MS Code : LYNC-D-18-00035	Dispatch : 13-6-2018

Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF, Perez T (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol Evol 25:250–260

Levin LA, Le Bris N (2015) The deep ocean under climate change. Science 350:766–768

Levin LA, Sibuet M (2012) Understanding continental margin biodiversity: a new imperative. Ann Rev Mar Sci 4:79–112

Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B (2013) Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. PLoS One 8:e67737

Martin J, Palanques A, Puig P (2006) Composition and variability of downward particulate matter fluxes in the Palamo's submarine canyon (NW Mediterranean). J Mar Syst 60:75–97

Maynou F, Cartes JE (2012) Effects of trawling on fish and invertebrates from deep-sea coral facies of *Isidella elongata* in the western Mediterranean. J Mar Biol Assoc 92:1501–1507

McClain CR, Allen AP, Tittensor DP, Rex MA (2012) Energetics of life on the deep seafloor. Proc Natl Acad Sci USA 109:15366–15371

MEA. Millennium Ecosystem Assessment (2005) Ecosystems and human well-being, synthesis. Island Press, Washington (DC)

Mengerink KJ, Van Dover CL, Ardron J, Baker M, Escobar- Briones E, Gjerde K, Koslow JA, Ramirez-Llodra E, Lara- Lopez A, Squires D, Sweetman AK, Levin LA (2014) A call for deep-ocean stewardship. Science 344:696–698

Mora C, Aburto-Oropeza O, Ayala Bocos A, Ayotte PM, Banks S, Bauman AG et al (2011) Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biol 9:e1000606. https://doi.org/10.1371/journal.pbio.1000606

Mora C, Wei CL, Rollo A, Amaro T, Baco AR, Billett D et al (2013) Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. PLoS Biol 11:e1001682

Morri C, Bianchi CN, Cocito S, Peirano A, De Biase AM, Aliani S et al (1999) Biodiversity of marine sessile epifauna at an Aegean island subject to hydrothermal activity: milos, eastern Mediterranean Sea. Mar Biol 135:729–739

Naumann MS, Orejas C, Ferrier-Pages C (2014) Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. Deep-Sea Res Part II 99:36–41

Norse EA, Brooke S, Cheung WWL, Clark MR, Ekeland I, Froese R, Gjerde KM, Haedrich RL, Heppell SS, Morato T, Morgan LE, Pauly D, Sumaila R, Watson R (2012) Sustainability of deep-sea fisheries. Mar Pol 36:307–320

Nykjaer L (2009) Mediterranean Sea surface warming 1985–2006. Clim Res 39:11–17

Orr JC et al (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Painter SC, Tsimplis M (2003) Temperature and salinity trends in the upper waters of the Mediterranean Sea as determined from the MEDATLAS dataset. Cont Sci Res 23:1507–1522

Palanques A, Durrieu de Madron X, Puig P, Fabres J, Guillen J, Calafat A, Canals M, Bonnin J (2006) Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. Mar Geol 234:43–61

Palmiéri J et al (2015) Simulated anthropogenic CO2 storage and acidification of the Mediterranean Sea. Biogeosciences 12:781–802

Philippart CJ, Anadòn R, Danovaro R, Dippner JW, Drinkwater KF, Hawkins SJ, Oguz T, O'Sullivan G, Reid PC (2011) Impacts of climate change on European marine ecosystems: observations, expectations and indicators. J Exp Mar Biol Ecol 400:52–69

Pop Ristova P, Wenzhöfer F, Ramette A, Felden J, Boetius A (2015) Spatial scales of bacterial community diversity at cold seeps (Eastern Mediterranean Sea). ISME J 9:1306–1318. https://doi.org/10.1038/ismej.2014.217

Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. Fish Oceanogr 15:451–464

Psarra S, Tselepides A, Ignatiades L (2000) Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. Progr Oceanogr 46:187–204

Purkey SG, Johnson GC (2010) Warming of global abyssal and deep southern ocean waters between the 1990s and 2000s: contributions to global heat and sea level rise budgets. J Clim 23(4):6336–6351

Pusceddu A, Gambi C, Zeppilli D, Bianchelli S, Danovaro R (2009) Organic matter composition, meiofauna and nematode biodiversity in deep-sea sediments surrounding two seamounts. Deep Sea Res II 56:755–762

Pusceddu A, Mea M, Canals M, Heussner S, Durrieu De Madron X, Sanchez-Vidal A, Bianchelli S, Corinaldesi C, Dell'Anno A, Thomsen L, Danovaro R (2013) Major consequences of an intense dense shelf water cascading event on deep-sea benthic trophic conditions and meiofaunal biodiversity. Biogeosciences 10(4):2659

Pusceddu A, Carugati L, Gambi C, Mienert J, Petani B, Sanchez-Vidal A, Canals M, Hessuner S, Danovaro R (2016) Organic matter pools, C turnover and meiofaunal biodiversity in the sediments of the western Spitsbergen deep continental margin, Svalbard Archipelago. Deep Sea Res Part 1 Oceanogr Res Pap 107:48–58

Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, Escobar E, Levin LA, Menot L, Rowden AA, Smith CR et al (2011) Man and the last great wilderness: human impact on the deep sea. PLoS One 6:e22588

Rex MA, Etter RJ, Morris JS, Crouse J, McClain CR, Johnson NA, Stuart CT, Deming JW, Thies R, Avery R (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Mar Ecol Progr Ser 317:1–8

Rivetti I, Fraschetti S, Lionello P, Zambianchi E, Boero F (2014) Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. PLoS One 9(12):e115655

Rixen M, Beckers J, Levitus S, Antonov J, Boyer T, Maillard C, Fichaut M, Balopoulos E, Iona S, Dooley H, Garcia M, Manca B, Giorgetti A, Manzella G, Mikhailov N, Pinardi N, Zavatarelli M (2005) The Western Mediterranean Deep Water: a proxy for climate change. Geophys Res Lett 32(12):L12608

Roberts JM, Cairns SD (2014) Cold-water corals in a changing ocean. Curr Opin Environ Sustain 7:118–126

Robinson LF, Adkins JF, Frank N, Gagnon AC, Prouty NG, Roark EB, van de Flierdt T (2014) The geochemistry of deep-sea coral skeletons: a review of vital effects and applications for palaeoceanography. Deep Sea Res Part II: Top Stud Oceanogr 99:184–198

Rogers AD (2015) Environmental Change in the Deep Ocean. Annu Rev Environ Resour 40:1–38

Ruhl HA, Smith KL Jr (2004) Shifts in deep-sea community structure linked to climate and food supply. Science (New York, N.Y.) 305:513–515

Sánchez F, Serrano A, Parra S, Ballesteros M, Cartes JE (2008) Habitat characteristics as determinant of the structure and spatial distribution of epibenthic and demersal communities of Le Danois Bank (Cantabrian Sea, N. Spain). J Mar Syst 72:64–86

Sánchez F, González-Pola C, Druet M, García-Alegre A, Acosta J, Cristobo J, (2014) Habitat characterization of deep-water coral reefs in La Gaviera canyon (Avilés Canyon System, Cantabrian Sea). Deep Sea Res Part 2 Top Stud Oceanog 106:118–140

Sanchez-Vidal A, Pasqual C, Kerherve P, Heussner S, Calafat A, Palanques A, Durrieu de Madron X, Canals M, Puig P (2009) Across margin export of organic matter by cascading events traced by stable isotopes, northwestern Mediterranean Sea. Limnol Oceanogr 54:1488–1500

Sardà F, Calafat A, Flexas M, Tselepides A, Canals M, Espino M, Tursi A (2004) An introduction to Mediterranean deep-sea biology. Sci Mar 68 (S3):7–38

Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. Nat Clim Change 1:401–406

Skliris N, Djenidi S (2006) Plankton dynamics controlled by hydrodynamic processes near a submarine canyon off NW corsican coast: a numerical modelling study. Cont Shelf Res 26:1336–1358

Smith CR, De Leo FC, Bernardino AF, Sweetman AK, Arbizu PM (2008) Abyssal food limitation, ecosystem structure and climate change. Trends Ecol Evol 23(9):518–528

Smith KL Jr, Ruhl HA, Bett BJ, Billett DSM, Lampitt RS, Kaufmann RS (2009) Climate, carbon cycling, and deep-ocean ecosystems. Proc Natl Acad Sci USA 106:19211–19218

Smith KL Jr, Ruhl HA, Kahru M, Huffard CL, Sherman AD (2013) Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific. Proc Nat Acad Sci 110(49):19838–19841

Snelgrove PVR, Soetaert K, Solan M, Thrush S, Wei CL, Danovaro R, Fulweiler RW, Kitazato H, Ingole B, Norkko A, Parkes RJ, Volkenborn N (2017) Global carbon cycling on a heterogeneous seafloor. Trends Ecol Evol 33:96–105

Stramma L, Johnson GC, Sprintall J, Mohrholz V (2008) Expanding oxygen-minimum zones in the tropical oceans. Science 320:655–658

Stramma L, Schmidtko S, Levin LA, Johnson GC (2010) Ocean oxygen minima expansions and their biological impacts. Deep-Sea Res Part I 57:587–595

Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, Visbeck M, Wallace DWR, Brandt P, Körtzinger A (2012) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat Clim Change 2:33–37

Sweetman AK et al (2017) Major impacts of climate change on deep-sea benthic ecosystems. Elem Sci Anth 5:4

Taviani M. (2014) Chapter 5 Marine Chemosynthesis in the Mediterranean Sea in the Mediterranean Sea: its history and present challenges, pp 69–83. https://doi.org/10.1007/978-94-007-6704-1_5

Tepsich P, Rosso M, Halpin PN, Moulins A (2014) Habitat preferences of two deep-diving cetacean species in the northern Ligurian Sea. Mar Ecol Prog Ser 508:247–260

Thurber AR, Sweetman AK, Narayanaswamy BE, Jones DOB, Ingels J, Hansman RL (2013) Ecosystem function and services provided by the deep sea. Biogeosciences 10:18193–18240

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D et al (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466:1098–1101

Tselepides A, Polychronaki T, Marrale D, Akoumianaki I, Dell'Anno A, Pusceddu A, Danovaro R (2000) Organic matter composition of the continental shelf and bathyal sediments of the Cretan Sea (NE Mediterranean). Prog Oceanogr 46:311–344

UNEP-WCMC (2011) Marine and coastal ecosystem services: Valuation methods and their application. UNEP-WCMC Biodiversity. Series No. 33

Van den Hove S, Moreau V (2007) Deep-sea Biodiversity and Ecosystems: A Scoping Report on Their Socio-economy, Management and Governanace (No. 184). UNEP/Earthprint

van der Grient JMA, Rogers AD (2015) Body size versus depth: regional and Taxonomical variation in deep-sea meio- and macrofaunal organisms. Adv Mar Biol 71:71–108

Van Dover CL, Aronson J, Pendleton L, Smith S, Arnaud-Haond S, Moreno-Mateos D, Barbier E, Billett D, Bowers K, Danovaro R, Edwards A, Kellert S, Morato T, Pollard E, Rogers A, Warner R (2014) Ecological restoration in the deep sea: desiderata. Mar Pol 44:98–106

Vetter EW, Dayton PK (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep sea Res Part II: Top Stud Oceanogr 45:25–54

Wei CL, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T et al (2010) Global patterns and predictions of seafloor biomass using random forests. PLoS One 5(12):e15323

Woolley SN, Tittensor DP, Dunstan PK, Guillera-Arroita G, Lahoz-Monfort JJ, Wintle BA, Worm B, O'Hara TD (2016) Deep-sea diversity patterns are shaped by energy availability. Nature 19;533(7603):393–396

Würtz M, Rovere M (eds) (2015) Atlas of the mediterranean seamounts and seamount-like structures. IUCN, Gland, Switzerland and Málaga, Spain, p 276

Yacobi YZ, Zohary T, Kress N, Hecht A, Robarts RD, Waiser M, Wood AM (1995) Chlorophyll distribution throughout the southeastern Mediterranean in relation to the physical structure of the water mass. J Mar Syst 6(3):179–190

Yakimov MM, Giuliano L, Cappello S, Denaro R, Golyshin PN (2007) Microbial community of a hydrothermal mud vent underneath the deep-sea anoxic brine lake Urania (Eastern Mediterranean). Orig Life Evol Biosph 37:177–188

Yasuhara M, Danovaro R (2016) Temperature impacts on deep-sea biodiversity. Biol Rev 91:275–287

Zanoli R, Carlesi L, Danovaro R, Mandolesi S, Naspetti S (2015) Valuing unfamiliar Mediterranean deep-sea ecosystems using visual Q-methodology. Mar Pol 61:227–236

Journal : **Large 12210**	Article No : **725**	Pages : **17**	MS Code : **LYNC-D-18-00035**	Dispatch : **13-6-2018**