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Consequences of the marine climate and ecosystem shift of the 1980-90s on the Ligurian Sea biodiversity (NW Mediterranean)

C. N. BIANCHI ¹, A. AZZOLA¹, M. BERTOLINO ¹, F. BETTI ¹, M. BO ¹,
R. CATTANEO-VIETTI ¹, S. COCITO ², M. MONTEFALCONE ¹, C. MORRI ¹,
A. OPRANDI¹, A. PEIRANO ², & G. BAVESTRELLO ¹*

¹DiSTAV (Department of Earth, Environmental and Life Sciences), University of Genoa, Genova, Italy, and ²ENEA (Italian Agency for New Technologies, Energy and Sustainable Economic Development), Marine Environment Research Centre, La Spezia, Italy

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Abstract

A rapid temperature increase in the 1980-90s has been accompanied by dramatic and unprecedented changes in the biota and communities of the Ligurian Sea. This review uses existing historical series (a few of which have been purposely updated) to assess extent and consequences of such changes. A number of warm-water species, previously absent or occasional in the comparatively cold Ligurian Sea, has recently established thanks to warmer winters. Occurrence among them of invasive alien species is causing concern because of their capacity of outcompeting autochthonous species. Summer heatwaves, on the other hand, caused mass mortalities in marine organisms, some of which found refuge at depth. New marine diseases appeared, as well as other dysfunctions such as the formation of mucilage aggregates that suffocated and entangled benthic organisms. Human pressures have combined with climate change to cause phase shifts (i.e., abrupt variations in species composition and community structure) in different habitats, such as the pelagic environment, seagrass meadows, rocky reefs, and marine caves. These phase shifts implied biotic homogenization, reduction of diversity, and dominance by invasive aliens, and may be detrimental to the resilience of Ligurian Sea ecosystems. Another phase of rapid warming has possibly started in the 2010s and there are clues pointing to a further series of biological changes, but data are too scarce to date for proper assessment. Only well addressed long-term studies will help understanding the future dynamics of Ligurian Sea ecosystems and their possibilities of recovery.

Keywords: *Sea water warming, depth refugia hypothesis, historical series, phase shift, Ligurian Sea*

Introduction

The first evidences of anthropogenic global warming date back to the 1970s (Broecker 1975), and the temperature increase of ocean waters is now amply documented (Lima & Wethey 2012). Climate change is modifying the properties of the world's ocean at a fast rate (Gattuso et al. 2015), leading to unprecedented biological shifts (Beaugrand et al. 2019). Change threatens all components of biodiversity, from individual organisms to the biological communities providing ecosystem services (Hooper et al. 2005; Bellard et al. 2012). The climate-induced loss

of biodiversity has thus become a major scientific and societal issue (Cardinale et al. 2012; Urban et al. 2016). Contrarily to a diffuse opinion in the past (Boudouresque & Bianchi 2013, and references therein), recent studies indicate that marine species may be more vulnerable to warming than are terrestrial ones (Richardson & Schoeman 2019).

The semi-enclosed nature of the Mediterranean Sea, together with its smaller inertia due to the relative short residence time of its water masses, makes it highly reactive to climate change (Durrieu de Madron et al. 2011), so that it ranks among the

*Correspondence: G. Bavestrello, DiSTAV, (Department of Earth, Environmental and Life Sciences), University of Genoa, Corso Europa 26, Genova I-16132, Italy. Tel: +39 010 35358031. Fax: +39 010 352169. Email: giorgio.bavestrello@unige.it

world's regions for which the strongest warming rates are predicted (Giorgi 2006). The Mediterranean Sea is also a biodiversity hotspot (Bianchi & Morri 2000a; Coll et al. 2010), threatened by many anthropogenic forcings (Claudet & Fraschetti 2010; Lejeune et al. 2010; Fraschetti et al. 2011). In addition to direct human impacts, climate change is driving the sensitive Mediterranean Sea ecosystems towards an unpredictable future (Turley 1999; Bianchi et al. 2012; Boero 2015a, 2015b).

The ongoing increase of water temperature is influencing the Mediterranean marine biota by a combination of direct (survival, reproduction, recruitment, etc.) and indirect effects, mediated by biotic interactions (predation, parasitism, diseases, etc) or the altered emphasis of marine current fluxes between adjacent basins (Bianchi 1997). Species distribution within the Mediterranean Sea is modifying in response to climate change (Gambi et al. 2008; Bianchi et al. 2013), with tropical taxa taking over communities, thus triggering - together with sea water warming - a process of "tropicalization" (Bianchi & Morri 2003; Bianchi 2007; Raitzos et al. 2010).

The Ligurian Sea (Figure 1) is one of the northern and colder sectors of the Mediterranean Sea, and its biota is somewhat different from that of the rest of the basin, with a dearth of thermophilic species and the comparative abundance of cold temperate boreal species (Bianchi et al. 2012). The Ligurian Sea is also one of the most anthropized parts of the Mediterranean Sea, due to huge urban, touristic and industrial development, harbour activities and construction of artificial structures, building of coastal roads and railways, dumping and drainages,

professional and recreational fisheries, and beach replenishments (Mangialajo et al. 2007; Mistic et al. 2011; Parravicini et al. 2012, 2013; Prato et al. 2016; Cánovas-Molina et al. 2016a; Venturini et al. 2017, 2019; Enrichetti et al. 2019a, 2019b).

There is a wealth of studies, spanning over a century, on the Ligurian Sea ecology (Bianchi et al. 1987), which altogether offer a baseline to evaluate the footprint of global change on its ecosystems (Cattaneo-Vietti et al. 2010). It has therefore been possible to describe the modifications undergone by the biodiversity of Ligurian Sea in the last decades (Morri & Bianchi 2001; Cattaneo-Vietti 2018). There is growing evidence that a major shift in Ligurian Sea climate and ecosystem regime occurred around the 1980-90s (Gatti et al. 2015, 2017), in coincidence with similar change observed in other European seas and perhaps globally (Conversi et al. 2010; Reid et al. 2016). A proper evaluation of ecosystem change requires the availability of long-time series (Hampton et al. 2019), which are unfortunately rare (Bianchi & Morri 2004a; Boero et al. 2015). The Italian part of the Ligurian Sea, facing the coast of Liguria (an administrative region in NW Italy), represents a partial exception, as historical data are available for a number of taxa and habitats.

This review aims at describing the most important consequences of the 1980-90s shift on the marine biodiversity of Liguria, searching for common patterns of change through the comparative analysis of existing data series, a few of which have been purposely updated for this review using unpublished information. Some of these data series span several



Figure 1. Geographical setting of the Ligurian Sea, with its position within the Mediterranean (inset). Localities cited in the text are indicated.

decades (Morri et al. 2001; Bavestrello et al. 2015; Cattaneo-Vietti et al. 2015; Gatti et al. 2015, 2017; Parravicini et al. 2015; Burgos-Juan et al. 2016; Betti et al. 2017a; Costa et al. 2018; Montefalcone et al. 2018), and a few use retrospective techniques to reconstruct trends for up the last 3000 years (Peirano et al. 2004; Bertolino et al. 2012, 2014a, 2017).

Ligurian Sea water warming

Since the second half of the 1980s, clues of Mediterranean Sea water warming came from both temperature measurements and, even more clearly, biological indicators (Bianchi & Morri 1993; Francour et al. 1994). A major climatic event has been the so-called Eastern Mediterranean Transient (EMT), which started in the mid 1980s and spanned the whole 1990s, implying important changes in water circulation (Malanotte-Rizzoli et al. 1999; Beuvier et al. 2010). The effects of the EMT had been especially observed in the Levant and Ionian seas, but the consequences extended over the adjacent basins (Manca 2000) to reach the Western Mediterranean (Gasparini et al. 2005; Schröder et al. 2006). Starting from the mid 1990s, hydrological changes were detected in the Ligurian Sea (Marty & Chiavérini 2010).

Series of water temperature data in the Ligurian Sea have been recently analysed by Parravicini et al. (2015) and Bianchi et al. (2018a), among others. Parravicini et al. (2015) used data collected fortnightly off Villefranche-sur-Mer (43°41.10' N, 7°18.94' E) at 0 m, 10 m, 20 m, 30 m, 50 m and 75 m depth between January 1958 and December 2010. An increase in water temperature over the whole period was observed at all depths, but while at 75 m this increase appeared

continuous and gradual, at the shallowest depths warming showed three main phases: a cooling phase between 1958 and the 1980s, a phase of rapid warming from the 1980s to the 1990s, and a phase of more gentle warming from the 1990s to 2010. The existence of the break in the 1980-90s, representing a shift between a comparatively cool and a warm period, had already been documented by studies that analysed either air temperature (Astraldi et al. 1995; Morri & Bianchi 2001) or sea surface temperature (SST) data (Lelieveld et al. 2002). The rapid warming phase of the 1980-90s mostly coincided with the EMT (Lejeusne et al. 2010). The findings of Parravicini et al. (2015) were consistent with these earlier results and indicated that water warming did not concern the sea surface alone, but the entire water column down to at least 75 m depth.

Bianchi et al. (2018a) examined SST data derived from NOAA satellite records at 42°54' N and 9°24' E (freely available at www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl), calibrated with field measurements (Bianchi & Morri 2004b). Despite calibration, these data were considered as representative mostly of offshore conditions, whilst in shallow coastal waters air temperature data are often better climatic proxies than ocean temperature data (Morri & Bianchi 2001). Thus, the annual means of air temperature obtained from the Meteorological Observatory of Genoa were also used. Both air temperature and SST raised in the last decades, mean temperatures in the 2000s being up to half a degree higher than in the 1970s (Gatti et al. 2017). At Portofino, where detailed sea truth data are available, SST increased of 0.1°C on annual average between 2002 and 2013 (Cattaneo-Vietti et al. 2015). As a consequence, the surface isotherms of February (the coldest month in the year) in

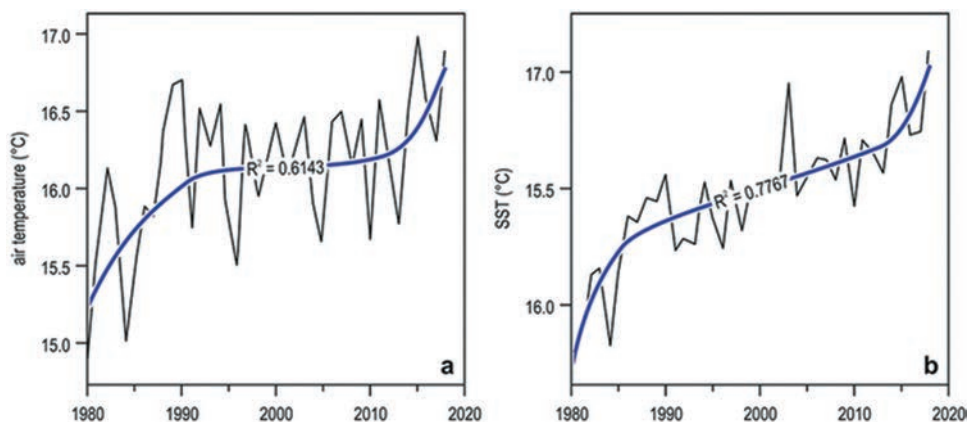


Figure 2. Multidecadal (1980–2018) trends of yearly averages of temperatures in Liguria. (a) Air temperature, measured at the meteorological observatory of Genoa university. (b) Sea surface temperature (SST), from NOAA satellite data (www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl). In both graphs, the smoothed thick lines depict the 6th degree polynomial fit.

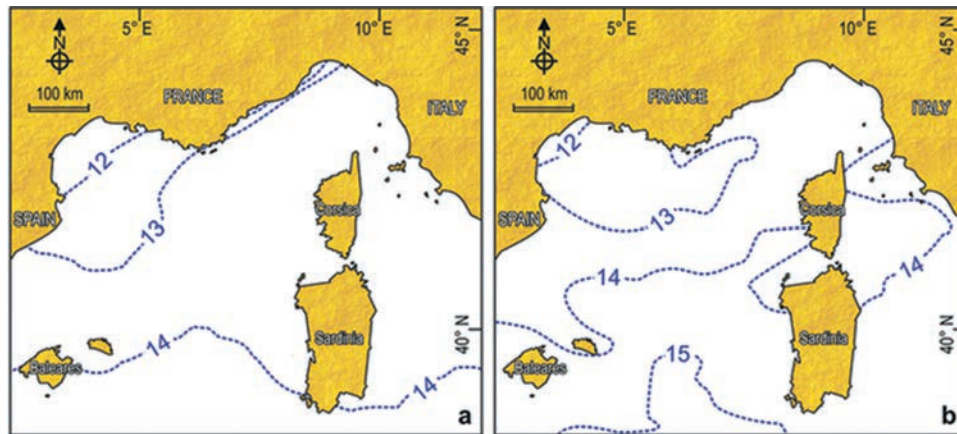


Figure 3. Surface isotherms of February in the Ligurian Sea. (a) Climatological means from the historical dataset 1906–1985. (b) Means for 1985–2006. Redrawn and modified from Bianchi et al. (2012).

the Ligurian Sea moved northward (Figure 2), causing warmer winters. Bianchi et al. (2018a), however, observed that the rise of temperature was not regular with time and four main phases were distinguished, notwithstanding large year-to-year variability: 1) a comparatively cold phase from the late 1960s to the early 1980s; 2) a rapid warming phase in the second half of the 1980s; 3) a warmer, stabilized phase since the 1990s; 4) another apparent rapid temperature rise after 2010. The recent update to 2018 of both air temperature and SST data confirms the existence of this fourth phase, 2014 to 2018 having been the warmest years on records (Figure 3) and thus conforming to the expected further rapid warming over the whole Mediterranean Sea (Shaltout & Omstedt 2014). Numerical experiments suggest that the future Mediterranean thermohaline circulation will replicate the EMT (Adloff et al. 2015).

Changes in the marine biota

The biota of the Ligurian Sea has been the object of studies since the second half of the XVIII century, when the famous biologist Lazzaro Spallanzani (1729–1799) carried out observations in the Gulf of La Spezia. The well-known feather-duster worm *Sabella spallanzani*, described in 1791, has been dedicated to him by Johann Friedrich Gmelin (1748–1804). In the XIX century, the monumental work “Descrizione di Genova e del Genovesato”, published in 1846, contained the first organic lists of the marine fauna and flora of Liguria (Tortonese 1971). In the XX century, the marine biota has been studied extensively, allowing Rossi (1969) to outline the zoogeography of the Ligurian Sea.

In the last decades, however, the Ligurian Sea has witnessed unprecedented modifications in the composition of its biota due to a combination of human impacts and climate change (Morri & Bianchi 2001; Bianchi & Morri 2004b; Parravicini et al. 2013). Three main processes can be recognized: i) the arrival and establishment of southern species; ii) mass mortalities; and iii) increased incidence of diseases and other dysfunctions (Boero 2011; Cattaneo-Vietti 2018).

Southern species

Occasional records of warm-water species, whose range was normally restricted to the Tyrrhenian Sea and other southern sectors of the Mediterranean, had been explained in the past with the occurrence of “thermophilic oases” along the Ligurian coasts (Sarà 1985). These alleged thermophilic oases may derive from eddies created along the coast by the current circulation in the Ligurian Sea (Casella et al. 2011). The comparatively stable Ligurian Circuit pushes against the coast the much more variable Tyrrhenian Current (Figure 4) so that in certain years lens of warm water may persist along the Ligurian coast (Astraldi et al. 1995; Vignudelli et al. 2000): here, southern organisms whose motile stages are transported by the Tyrrhenian Current (Aliani & Meloni 1999; Aliani & Molcard 2003) can settle and withstand winter conditions. Such a process explains the historical variability of southern species records in the Ligurian Sea.

Starting from the late 1980s, records of southern species have become more frequent and numerous (Bianchi & Morri 1993, 1994a). Reduced winter cooling and increased average temperature have

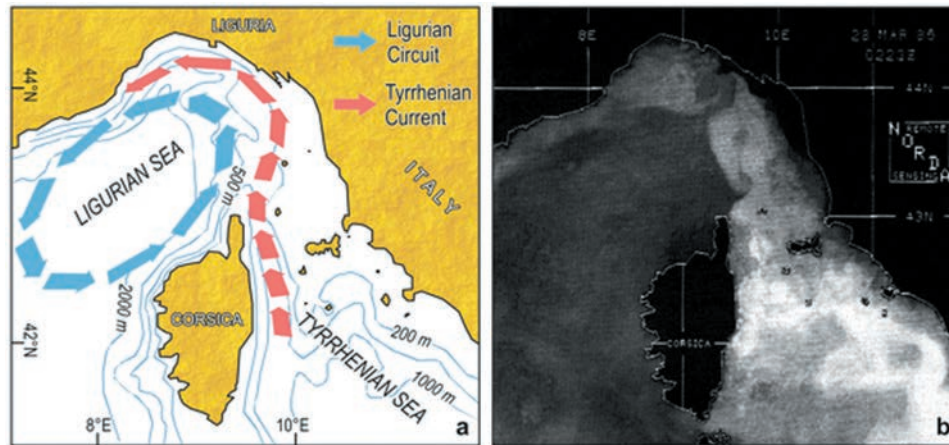


Figure 4. Surface circulation in the Ligurian Sea. (a) Scheme of the main current systems, with the steady Ligurian Circuit (colder) and the inflowing Tyrrhenian Current (warmer). (b) Satellite infra-red thermal imagery (AVHRR NOAA 9): the whitest areas are the warmest.

allowed these southern species to establish and diffuse in the Ligurian Sea (Parravicini et al. 2015; Bianchi et al. 2018a). The ornate wrasse *Thalassoma pavo*, for example, has been proved to reproduce in the Ligurian Sea (Vacchi et al. 1999, 2001; Sara et al. 2005), even if it does not reach population densities comparable to those observed in the warmer Tyrrhenian Sea (Guidetti et al. 2002). Several other fish species of southern origin are now to be considered as established in the Ligurian Sea, such as the zebra seabream *Diplodus cervinus*, the pearly razorfish *Xyrichtys novacula*, the Atlantic lizardfish *Synodus saurus*, the yellowmouth barracuda *Sphyrna viridensis*, the parrotfish *Sparisoma cretense* and the cryptobenthic Molly Miller combtooth blenny *Scartella cristata* (Parravicini et al. 2008; Bianchi et al. 2018a; Cattaneo-Vietti 2018). The same holds for a larger number of algae and invertebrates (Parravicini et al. 2015; Bianchi et al. 2018a).

All the above-mentioned southern species are native of the Mediterranean Sea. Together with them, however, came also numerous species of extra-Mediterranean origin. The arrival of these non-indigenous species (NIS) has been directly or indirectly favoured by human activities, but their successful establishment has once again been made possible by sea water warming (Bianchi et al. 2018a). Both the fish NIS, such as the bluespotted cornetfish *Fistularia commersonii* and the blunthead pufferfish *Sphoeroides pachygaster* (Orsi Relini 2010), and the invertebrate NIS, such as the calcisponge *Paraleucilla magna* (Bertolino et al. 2014b; Ulman et al. 2017), the four-colour nudibranch *Godiva quadricolor* (Betti et al. 2015), the sabellid polychaete *Branchiomma luctuosum* (Betti et al. 2018), and the crab *Percnon gibbesi* (Bianchi et al. 2018a), have been

recorded irregularly (both in space and time) to date. On the contrary, the algal NIS, such as the rhodophytes *Acrothamnion preissii*, *Asparagopsis armata* and *Womersleyella setacea*, and the chlorophytes *Caulerpa cylindracea* and *Caulerpa taxifolia* (Gatti et al. 2015; Montefalcone et al. 2015; Parravicini et al. 2015) are causing concern because of their fast spreading and wide distribution. Fishermen have been harmed by the abundance of these algae, which clog their traps and nets, but have also involuntarily contributed to their diffusion by cleaning their fishing gears at sea. Due to its impact on native ecosystems since the mid 1980s, especially along the French tract of the Ligurian Sea, *C. taxifolia* gained the nickname of “killer alga” (Meinesz 1999). However, by 2000 its dispersal rate slowed down and the species did not persist in areas formerly colonized (Montefalcone et al. 2015). In contrast, *C. cylindracea*, first recorded in 1996 in the Ligurian Sea (Bussotti et al. 1996; Modena et al. 2000), exhibited an impressive and constant expansion of its range, becoming invasive in most coastal habitats of the Ligurian Sea, marine protected areas included (Morri et al. 2019).

The numbers of both native southerners and NIS have increased in recent times, but with a different trend (Bianchi et al. 2018a). Collating information from scuba diving records indicated that the number of the former somehow fluctuated with climate variability, whereas that of the latter increased steadily, with an apparent acceleration after the 2000s (Figure 5(a)). Regular monitoring at Genoa between 2009 and 2015 evidenced that the number of the native southerners increased linearly, that of the NIS increased exponentially (Figure 5(b)). The ever growing incidence of warm-water species,

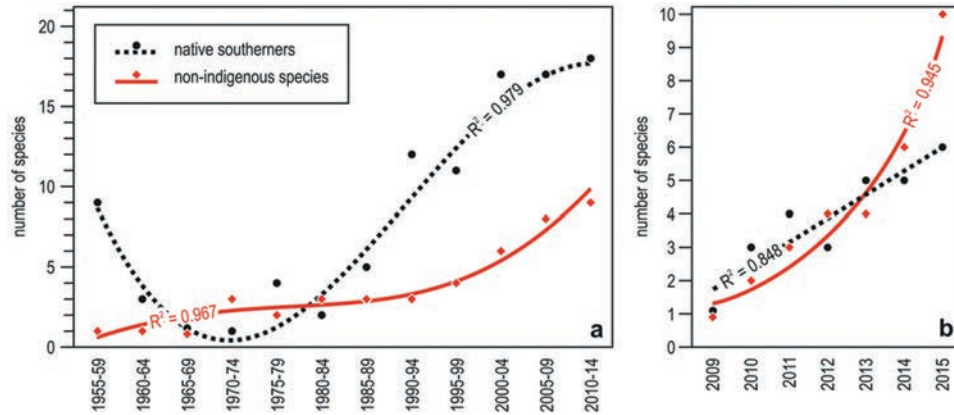


Figure 5. Trends in southern species occurrence in the Ligurian Sea. (a) Number of native or non-indigenous southern species recorded by diving in several localities of Liguria per 5-year period; the curves represent the second degree polynomial fits. (b) Yearly trends in the number of native or non-indigenous southern species in Genoa sites regularly monitored. The best fit is linear for native southerners and exponential for non-indigenous species. Redrawn and modified from Bianchi et al. (2018a).

either native or non-indigenous, is changing the biogeography of the Ligurian Sea (Bianchi et al. 2013).

Mass mortalities

While allochthonous warm-water species made their way into the Ligurian Sea, many autochthonous benthic invertebrates suffered mass mortalities correlated with summer heatwaves (Cerrano & Bavestrello 2009a; Rivetti et al. 2014). Increased frequency of marine heatwaves (discrete periods of

extreme local sea water warming) is concurrent with long-term persistent warming, and is having deleterious impacts on many species in the world's ocean (Smale et al. 2019).

In the Ligurian Sea, the first documented mass mortality episodes occurred in the 1980s. The red coral *Corallium rubrum* and the gorgonians *Eunicella cavolini* and *Paramuricea clavata* were heavily struck (Bavestrello & Boero 1986; Rivoire 1991; Bavestrello et al. 1994; Harmelin & Marinopoulos 1994; Garrabou et al. 2001), as well as *Spongia officinalis* and other sponges (Gaino et al. 1992). In

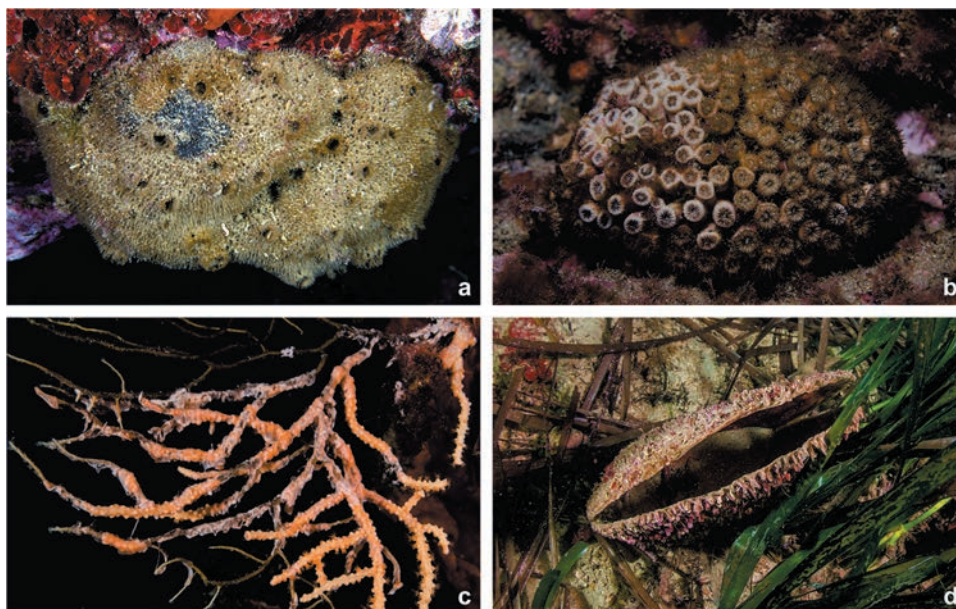


Figure 6. Examples of invertebrate mortality in the Ligurian Sea. (a) Necrosis in the sponge *Spongia officinalis* (Portofino, 5 m depth). (b) Partial mortality of the scleractinian coral *Cladocora caespitosa* (Portofino, 10 m depth). (c) Branch necrosis in the gorgonian *Eunicella cavolini* (Portofino, 30 m depth). (d) Empty shell, still in living position, of the bivalve *Pinna nobilis* killed by the pathogen *Mycobacterium* (Berpeggi, 15 m depth).

the second half of the 1990s, mass mortalities were observed in the bivalve *Spondylus gaederopus*, in the scleractinian corals *Balanophyllia europaea*, *Cladocora caespitosa* (Figure 6(b)) and *Oculina patagonica* (Rodolfo-Metalpa et al. 2000, 2005) and in the sponge *Petrosia ficiformis* (Cerrano et al. 2001).

The most severe and widespread episode of mass mortality ever recorded occurred at the end of the summer 1999, and affected 27 species of sessile invertebrates including sponges, gorgonians, corals, bryozoans and ascidians, from the Tuscan Archipelago, Italy, to Marseille, France (Cerrano et al. 2000; Pérez et al. 2000; Garrabou et al. 2001). Quantitative data on gorgonians (*Eunicella cavolini*, *E. singularis*, *Paramuricea clavata*) indicated that the proportion of colonies affected ranged from 60% to 100%, which implied that millions of gorgonians died in the Ligurian Sea (Figure 7(b)). Mortality did not similarly hit all colonies. Small colonies (<10 cm) were less affected than larger ones, and females more intensely than males, causing a shift in sex ratio in favour of males of about 3:1, in contrast with the original ratio of 1:1 (Cerrano et al. 2005). The mortality followed an unusual meteorological period, with a decrease of the NW winds from July to October 1999 and an anomalous increase of the sea water temperature of up to 2–5°C for several weeks, with a major peak at the end of August in surface waters and at the end of September at 32 m depth (Figure 7(a)); the mixed layer deepened to 40 m, instead of the normal 20–25 m (Romano et al. 2000; Laubier 2001).

Another well documented case of mass mortality, which involved not less than 25 rocky benthic macroinvertebrates (mainly sponges and gorgonians), took place in summer 2003. The heatwave of June to September 2003 in Europe caused an anomalous warming of sea water, which reached between 1° and

3°C above the climatic values (Sparnocchia et al. 2006), causing mortality in up to 80% of the Ligurian Sea gorgonian colonies (Garrabou et al. 2009).

The effects of these catastrophic heatwaves remained evident for years. Recovery of populations was slow, with most species showing only partial recovery (Linares et al. 2005; Cupido et al. 2008; Cerrano & Bavestrello 2009b). Notwithstanding high recruitment rates (Sara et al. 2003), gorgonian populations attained only half their previous density and remained far from their original size/age structure (Cupido et al. 2009). The reproductive output fell dramatically (Cupido et al. 2012) and biomass values remained low for several years, mainly because new colonies were small and the survived ones reduced their sizes due to the breaking of necrotic branches (Cerrano et al. 2005). Loss or reduction of the gorgonian canopies and of the assemblages dominated by long-lived macroinvertebrates led to the dominance of turf-forming species, which in turn facilitated the proliferation and spread of the invasive alga *Caulerpa cylindracea* (Gatti et al. 2015; Verdura et al. 2019).

Quantitative data on the precious coral *Corallium rubrum* collected in 1964 (Marchetti 1965), 1990 and 2012 (Bavestrello et al. 2015) at Portofino indicated a dramatic shift in population structure. This species had been subjected to strong harvesting pressure from the 1950s to the early 1970s, but recent protection measures allowed for an increase in colony weight (from 3 g to 8 g on average). Thus, the red coral population switched from a “grass plain-like” towards a “forest-like” appearance.

The population of the bryozoan *Pentapora fascialis*, a large erect and perennial species, was monitored since 1997 in the Gulf of La Spezia (Cocito et al. 1998), thus allowing evaluating the impacts

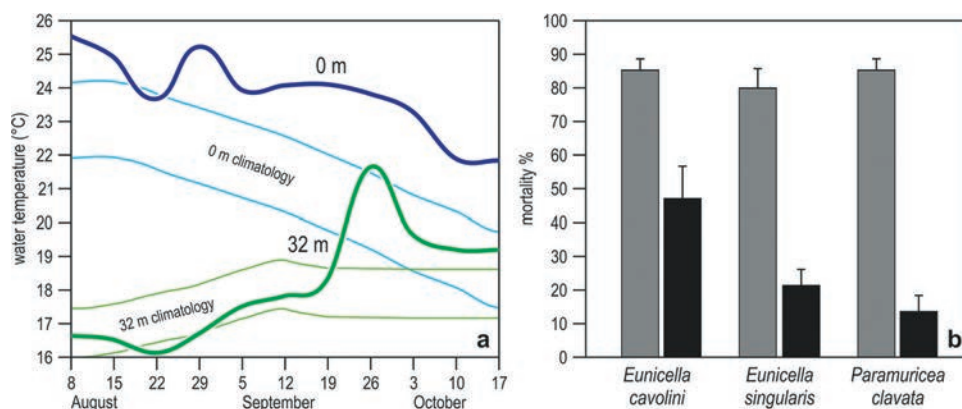


Figure 7. The heatwave of summer 1999 and gorgonian mortality in the Ligurian Sea. (a) Trend in sea water temperature at 0 m and 32 m depth, between August and October. Lines are weekly averages, bands the confidence limits ($\pm 95\%$) obtained from the secular (1909–1987) trend calculated on Ligurian Sea records. (b) Percentage of partially (grey) and totally (black) dead colonies in three common gorgonian species. Redrawn and modified from Cerrano et al. (2000).

and consequences of the 1999 and 2003 warming events (Cocito & Sgorbini 2013). Cover declined rapidly, with larger colonies being the most affected. Deeper colonies recovered to pre-disturbance levels, while shallower colonies underwent necrosis and algal epibiosis.

Diseases and other dysfunctions

Marine disease outbreaks caused by opportunistic pathogens are increasing in frequency and severity worldwide and there is a growing body of evidence that points to links with climatic change (Harvell et al. 1999; Hayes et al. 2001; Burge et al. 2014; Cohen et al. 2018). Thermal stress may reduce the resistance of animals and plants to microorganisms (virus, bacteria, protozoans, fungi) that otherwise would have remained non virulent (Cerrano & Bavestrello 2009a).

No etiological agent was unequivocally identified in the mass mortalities of invertebrates observed in the Ligurian Sea, but the bacterium *Vibrio coralliilyticus*, originating from warmer seas, possibly played a role in the death of the gorgonian *Paramuricea clavata* (Martin et al. 2002; Bally & Garrabou 2007; Vezzulli et al. 2010). Summer mortality events of the scleractinian coral *Oculina patagonica* (Rodolfo-Metalpa et al. 2006) were demonstrated as due to the combined effect of high temperature and infection by the bacterium *Vibrio shiloi* (Rosenberg & Falkovitz 2004). The abundance of several other species of *Vibrio*, such as *V. cholerae*, *V. vulnificus* and *V. parahaemolyticus* (potentially pathogenic to humans), has been recently observed in the Ligurian Sea when the sea surface temperature exceeded 25°C (Vezzulli et al. 2009). *Aspergillus sydowii*, a fungus that has been responsible for the mass destruction of coral in the Caribbean Sea over the last 15 years, has been recently recorded in the Port of Genoa and may represent a risk for Ligurian corals, gorgonians and sponges (Greco et al. 2017).

A microbial infection had been invoked as the causal agent of mortality in the bivalve *Spondylus gaederopus* (Meinesz & Mercier 1983) and in the sea urchins *Arbacia lixula*, *Paracentrotus lividus* and *Sphaerechinus granularis* (Boudouresque et al. 1980). The populations of the giant pen shell *Pinna nobilis* living in Bergeggi and Portofino were infected in late summer 2018 by a species of *Mycobacterium* (Carella et al. 2019), with 30-100% animals dead (Figure 6(d)). The Ligurian Sea populations of the zoanthid *Parazoanthus axinellae* have been suffering from a summer disease since 2000: from June to October, the polyps became covered with dense mats of the

filamentous cyanobacterium *Porphyrosiphon*, which compromised polyp activity (Cerrano et al. 2006). Scuba diving observations at Bergeggi and Portofino in late summer 2018 evidenced that diseased colonies were localized above the thermocline, whereas those living below the thermocline were healthy, suggesting the combined action between microbial attack and elevated temperature.

Diseases in sponges have been studied in detail. The sponges most seriously affected were those characterized by a skeleton of spongin fibres, and a spongin fibre-perforating bacterium was hypothesized to be the causative agent of the disease (Gaino & Pronzato 1989; Cerrano et al. 2000). Generally, the disease started as small necrotic areas on the surface of the sponge (Figure 6(a)), which increased in size until they affected the whole sponge. The progression of the disease was influenced by the growth form, with massive sponges damaged faster than the branching forms. Rates of tissue regeneration depended on the species and amount of damage. Recovery was facilitated when individual sponges were able to isolate the necrotic tissue by means of a layer of new pinacoderm between healthy and necrotic tissue, as seen in *Petrosia ficiformis* (Cerrano et al. 2001).

The list of tropical species whose range expansion in the Ligurian Sea has been favoured by climate warming also includes the toxic dinophyte *Ostreopsis ovata*. It produces ovatoxin-a, a form of palytoxin, one of the most toxic non-proteic molecules occurring in nature (Ciminiello et al. 2008). Ovatoxin-a causes disease in the marine fauna (Faimali et al. 2012; Privitera et al. 2012) and irritations by contact or cough, fever and respiratory problems by inhalation of marine aerosols in humans (Abbate et al. 2012, and references therein). The first massive bloom of *O. ovata* in the Ligurian Sea occurred in August 1998 (Abbate et al. 2007). Since then, blooms were reported almost every summer (with a major episode in 2005) in shallow waters during periods of warm and calm weather (Mangialajo et al. 2008a, 2010; Cohu et al. 2013; Bianchi et al. 2018a). Urbanized areas and degraded habitats have been shown to be more prone to its proliferation (Meroni et al. 2018).

Blooms of mucilaginous aggregates of filamentous algae have been another dysfunction linked to hot summers in the last decades. The algae producing these aggregates included both Phaeophyceae and Chrysophyceae, but in the Ligurian Sea the former were dominant, with the species *Acinetospora cimita*. The mucilage aggregates were able to cover wide extents of the sea floor, suffocating benthic organisms.

A major mucilaginous event occurred at Portofino in summer 2003, affecting macroalgae, sponges and scleractinian corals (Schiaparelli et al. 2007). A possibly stronger event was observed in summer 2018. Aggregates started forming just below the summer thermocline in June (Figure 8(a)) and arrived at covering completely the sea floor in July and August (Figure 8(b)). A period of calm weather in August caused an anomalous warming of the surface layer (as already described by Sparnocchia et al. 2006), leading to the formation of a second thermocline and to the development of mucilage aggregates also in shallow water (Figure 8(a)). Filaments sunk to deeper water (down to more than 40 m) entangled gorgonians (Figure 8(c, d)), causing their necrosis (Figure 6(c)) as observed in other regions of the Western Mediterranean (Giuliani et al. 2005; Piazzì et al. 2018).

Modification of marine habitats

All marine habitats of Liguria have been thoroughly investigated during the XX century, so that it was possible to produce a comprehensive compendium in the 1980s (Cattaneo-Vietti et al. 1988). A comparative dearth of information on deep rocky reefs has been partially remedied in recent years

(Cánovas-Molina et al. 2016a; Enrichetti et al. 2019c). However, historical data-series that encompass the climate change of the last decades are available for only four habitats: the pelagic environment; seagrass meadows; rocky reefs; and marine caves.

The pelagic environment

The disappearance of some species and the arrival of others, even of commercial interest, have characterized the pelagic fish assemblages of the Ligurian Sea in the last decades. Inter-annual variations in sea surface temperatures affected the abundance of anchovies: in 1985, 1986 and 1993, high egg productivities were observed, together with temperature trends exhibiting a fast increase of sea surface temperature in May and a reduced temperature variability during the reproductive period, June to August (Petrillo et al. 1998). On the contrary, in 1991, a year with low temperature increase in spring and high temperatures in the following summer, the lowest abundances of anchovy eggs were reported. Also the increased abundance of the round sardinella *Sardinella aurita*, a thermophilic species, could be related to temperature increase in the Ligurian Sea (Cattaneo-Vietti et al. 2010).

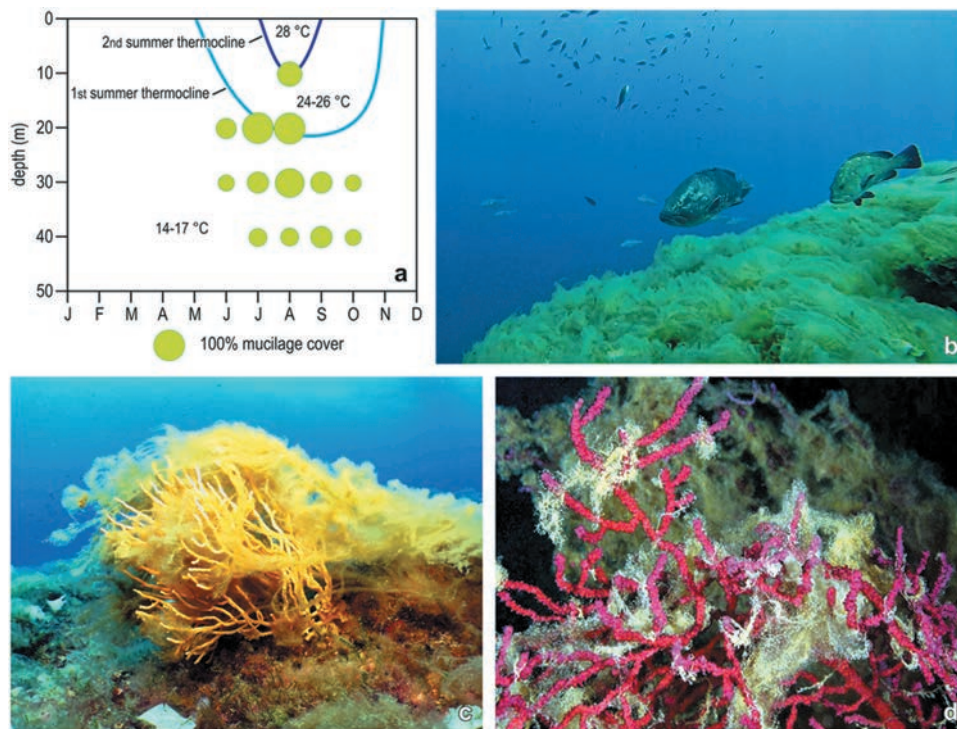


Figure 8. Phenology of the mucilage event of 2018 at Portofino. (a) Abundance of mucilage aggregated according to time and depth. Circles are roughly proportional to mucilage cover. Approximate positions of summer thermoclines are also indicated. (b) 100% cover of mucilage aggregates at about 20 m depth in July. (c) Mucilage filaments entangling the gorgonian *Eunicella cavolini* at about 30 m depth in August. (d) Mucilage filaments entangling the gorgonian *Paramuricea clavata* at about 40 m depth in September.

The long period of activity of a small tuna trap, the “tonnarella” of Camogli (Balestra et al. 1976; Cattaneo-Vietti & Bava 2009), allowed analysing the yearly differences in the fish catches in comparison with change in sea surface temperature (Morri & Bianchi 2001; Cattaneo-Vietti et al. 2015). A number of thermophilic species, such as the dolphinfish *Coryphaena hippurus*, the yellowmouth barracuda *Sphyræna viridensis* and the greater amberjack *Seriola dumerili* (Figure 9(a)), have numerically increased, while boreal species, such as the bullet tuna *Auxis rochei* (Figure 9(b)), have decreased. Large pelagic predators, such as sharks and in particular the blue shark *Prionace glauca*, once frequent in the Ligurian Sea, also decreased. Sharks have become increasingly rare everywhere in the Mediterranean Sea (Ferretti et al. 2008; Britten et al. 2014) due to overfishing, intense use of pelagic longlines or impoverishment of their prey, but their reduced occurrence in the Ligurian Sea has been probably also due to the noise disturbance caused by boat traffic during summer (Cattaneo-Vietti 2018).

Regarding cetaceans, MacLeod (2009) predicted that, at world level, the distribution of 88% of the species may be affected by changes in water temperature. In the Ligurian Sea, now included in the Pelagos Sanctuary for marine mammals (Notarbartolo Di Sciara et al. 2008), the striped dolphin *Stenella coeruleoalba* has increased in abundance, while the common dolphin *Delphinus delphis* has decreased in the last decades (Meliadò et al. 2019) but the relationships of these evidences with the variations of SST are not clear. However, a study conducted in this area (Azzellino et al. 2008) evidenced that fin whales and striped dolphins respond to the spatial variability of the SST and are both attracted by thermal anomalies. On the contrary, sperm whales show a lower preference for the thermal anomalies.

The abundance of jellyfish, and especially of the stinging scyphozoan *Pelagia noctiluca*, in the Ligurian

Sea has increased starting from the 1980s, with major peaks in 1981–1985 and 1994–2008 (Bernard et al. 2011). Outbreaks were possibly linked to the climatic variability of the Ligurian Current, which may push *P. noctiluca* swarms towards the coast (Ferraris et al. 2012). Similarly, the strandings of the by-the-wind sailor *Velella velella*, known in the Ligurian Sea since at least 1923 (Pellerano 2016), have apparently increased in recent years (Betti et al. 2017b). In 2009, a bloom of the alien combjelly *Mnemiopsis leidyi* was recorded in the eastern Ligurian Sea, but the species apparently did not get established (Boero et al. 2009).

Seagrass meadows

Seagrass meadows are important coastal ecosystems in tropical and temperate seas worldwide, providing essential ecosystem services (Cullen-Unsworth et al. 2014). The Mediterranean endemic species *Posidonia oceanica* represents a most valuable example of natural capital (Vassallo et al. 2013) and is protected by several international initiatives and national laws, which call for its management and monitoring for conservation (Montefalcone 2009). Despite its importance as foundation species, its meadows are experiencing a well-documented regression in the Mediterranean due to multiple anthropogenic pressures and invasive species, worsened by the effect of climate change (Chefaoui et al. 2018, and references therein).

The first studies on *P. oceanica* meadows of Liguria date back to the beginning of the XX century (Issel 1918) but the first detailed maps of their distribution became available only in the mid 1990s (Bianchi & Peirano 1995), evidencing a generalized regressive condition of the meadows. Combining a morphodynamic model, which predicts the extent of *P. oceanica* meadows in absence of any human influence (Vacchi et al. 2014, 2017, and references therein), with the available historical data (Burgos-



Figure 9. Two examples of fish species caught in the tuna trap (“tonnarella”) of Camogli. (a) The greater amberjack *Seriola dumerili* has been first recorded in the 1990s. (b) The bullet tuna *Auxis rochei* has halved in abundance with respect to the 1950s.

Juan et al. 2016; Burgos et al. 2017), it has been possible to estimate that more than 50% of the original surface of the meadows of Liguria has been lost under the influence of human impacts (Peirano & Bianchi 1997; Peirano et al. 2005; Montefalcone et al. 2006a, 2006b, 2007a, 2008a, 2008b, 2009, 2010a). A similar trend has been observed in the French part of the Ligurian Sea (Holon et al. 2015).

In the last decades, possibly thanks to the adoption of protection measures, regression apparently halted, with even some signs of recovery (Figure 10(a)), as observed also in other regions (Carmen et al. 2019). Regular monitoring activities on the *P. oceanica* meadow of Monterosso-al-Mare from 1991 to 2007 (Peirano et al. 2001, 2011) and occasional surveys

between 1991 and 2017 showed a sudden and lasting increase of cover and shoot density, respectively, in coincidence with the sea water warming of the 1980-90s (Figure 11). The relationship between sea water warming and *P. oceanica* growth, however, is controversial (Montefalcone et al. 2013; Pergent et al. 2014).

Decline of *P. oceanica* in Liguria has often been coupled with its replacement by the more tolerant seagrass *Cymodocea nodosa* (Bianchi & Peirano 1995; Montefalcone et al. 2006a; Barsanti et al. 2007): such a replacement might be favoured by sea water warming (Ontoria et al. 2019), but showed an obvious positive relationship with the increased artificialization of the coastline (Figure 10(b)). In recent years, *C. nodosa* was in turn partly replaced first by the native green alga *Caulerpa prolifera* and then by

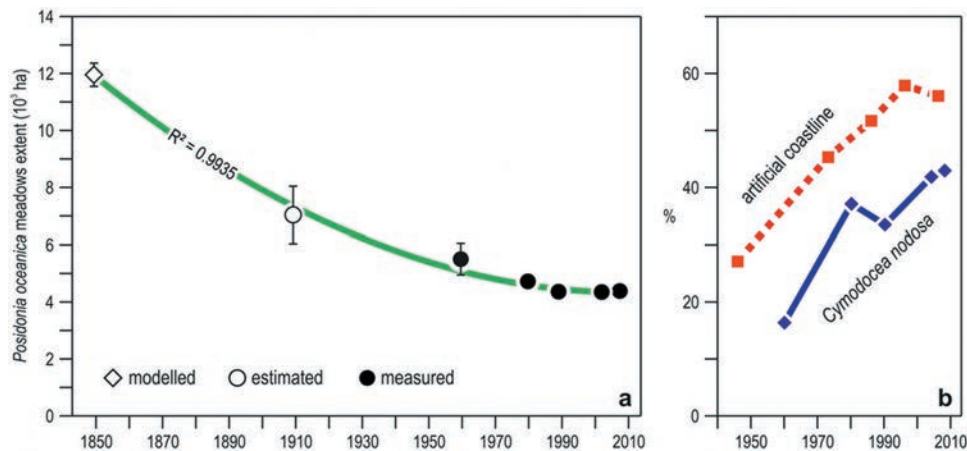


Figure 10. Changes in seagrass meadows of Liguria. (a) Time trend of *Posidonia oceanica* meadow extent since the mid of the XIX century, combining modelling, estimations, and quantitative cartographic measurements. The curve depicts the second degree polynomial fit of the data. (b) Time trend of the proportion of *Cymodocea nodosa* out of the total areal extent of seagrass meadows, and of the proportion of the linear extent of artificial structures on the coastline.

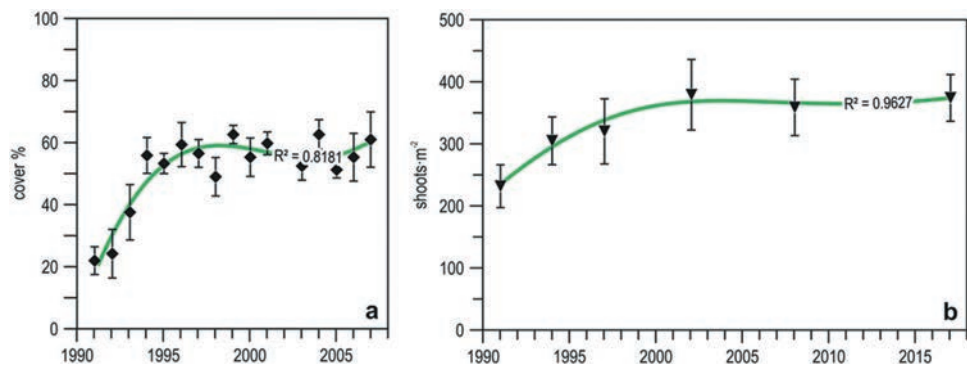


Figure 11. Trends in the *Posidonia oceanica* meadow at Monterosso. The curves depict the third degree polynomial fit of the data. (a) Yearly means (\pm se) of cover values, 1991–2006. (b) Discontinuous measures of mean shoot density (\pm se), 1991–2017. Data from Peirano et al. (2011) and Regione Liguria (http://www.cartografiar.liguria.it/SiraQualMare/script/PubRetePuntoParam.asp?_ga=2.97453724.2042002155.1518772812-601063746.1517569932&fbclid=IwAR00qk1ShUaKXOXg0Hdi3ITtzAjMvUir-ryolOenpw9-v_yTP4wcl3wI2yk).

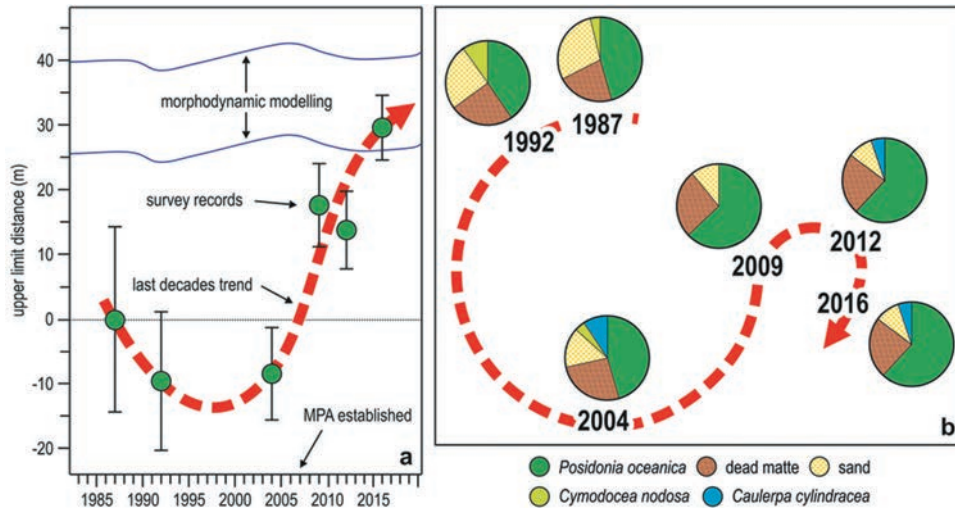


Figure 12. Changes in the *Posidonia oceanica* meadow of Bergeggi in 25 years. (a) Position of the meadow upper limit with respect to 1987. (b) Time trajectory of the meadow in the MDS ordination plane; pie diagrams illustrate the quantitative meadow composition. Redrawn and updated from Oprandi et al. (2014a, 2014b).

its two alien congeneric *C. taxifolia* and, especially, *C. cylindracea* (Montefalcone et al. 2007c, 2010b, 2015).

The modifications underwent by the meadow of Prelo Cove in the last century represent a good example of such a series of substitutions. In the 1930s, the meadow of Prelo Cove had been severely impacted by the building of a jetty for pleasure craft (Lasagna et al. 2006a, 2006b, 2011). By the late 1950s, the areas of the cove's sea floor deprived of *P. oceanica* were colonized by *C. prolifera* (Tortonese 1962). By 1979, *C. prolifera* disappeared to leave place to *C. nodosa*, which lasted there to at least 1986 (Morri et al. 1986). At this stage, the regressed meadow was therefore apparently following the secondary successional pattern envisaged by Molinier and Picard (1952), suggesting the possibility of recovery in the following years. By 1991, however, the pattern was reverted: *C. nodosa* was not found anymore, whilst *C. prolifera* was back again (Tunesi & Vacchi 1994). Being a thermophilic species, *C. prolifera* had been possibly favoured by the water warming of the 1980-90s, to remain abundant till at least 2004 (Montefalcone et al. 2006b). Notwithstanding persisting warm-water conditions, recent surveys in the 2010s did not find *C. prolifera* but *C. cylindracea* (Montefalcone et al. 2015), as predicted by the phase-shift model of Montefalcone et al. (2007c) and contrarily to both the successional and the warming hypotheses. The multidecadal change observed in the Prelo meadow was mirrored in the modifications of the associated sponge fauna, as reconstructed through the analysis of the

siliceous spicules trapped within the matte (Bertolino et al. 2012).

The longest data series available on a Ligurian seagrass meadow, that of Bergeggi (Montefalcone et al. 2007b; Oprandi et al. 2014a, 2014b), illustrates well the present dualism of the health state of Ligurian *P. oceanica* meadows: on the one hand, the meadow has been recovering (in term of areal extent) since 2009 (Figure 12(a)); on the other hand, it has been suffering from substitution by *C. cylindracea*, which is deviating the recovery trajectory of the ecosystem towards a different basin of attraction (Figure 12(b)). Thus, information collected to date indicates hysteresis, rather than resilience (Montefalcone et al. 2011). Similarly, the resilience of seagrass ecosystems worldwide is becoming compromised by a range of local to global stressors (Unsworth et al. 2015).

Rocky reefs

Rocky reefs are a quantitatively trivial fraction of the marine environment but hold a great scientific and economic importance (Bianchi et al. 2004), as they represent a major reservoir of marine biodiversity and provide ecosystem services especially for fishery and tourism (Sala et al. 2012; Paoli et al. 2017). It is not a coincidence that virtually all the Mediterranean marine protected areas are established in correspondence with rocky coasts (Sala et al. 2002). Reefs are listed in the European Habitats Directive among the marine habitats of interest (Thibaut et al. 2017) and

are defined, according to the European Nature Information System (EUNIS, <http://eunis.eea.europa.eu>), as “submarine, or exposed at low tide, rocky substrates and biogenic concretions, which arise from the sea floor in the sublittoral zone but may extend into the littoral zone where there is an uninterrupted zonation of plant and animal communities. These reefs generally support a zonation of benthic communities of algae and animal species including concretions, encrustations and corallogenic concretions”.

The coasts bordering the Ligurian Sea are rocky for the most part, and many studies exist on the benthic communities thriving there, especially in the sublittoral (Cánovas-Molina et al. 2016b). On the contrary, and notwithstanding easier access, littoral communities have received little and discontinuous attention (Morri et al. 1986, and references therein). Betti et al. (2017a) reconstructed a 59-year-long time series of occurrence of the hydroid *Paracoryne huvei*, an encrusting species typical of the intertidal zone, where it may cover wide expanses in late winter and early spring (February to April). Once considered rare (Boero 1984), *P. huvei* has recently increased its abundance and habitat occupancy. This stenothermal species possibly took advantage of the present phase of reduced winter cooling; the recent slow but progressive improvement of water quality (Asnaghi et al. 2009; De La Fuente et al. 2018) might also have played a role.

Sublittoral communities have been more extensively studied since the dawn of scuba diving, the Ligurian Sea having been the cradle of two major pioneer studies (Bianchi & Morri 2000b). Enrico Tortonese undertook fundamental research on the

benthos of Portofino reefs in the late 1950s, using descriptions and samples taken by the divers of the Centro Subacqueo of Genova-Nervi, directed by Duilio Marcante (Tortonese 1958, 1962). Lucia Rossi did the same a few years later at Punta Mesco, describing the subtidal reef communities on the basis of still-frame underwater photographs taken by the diver Gianni Roghi (Rossi 1965). The sites studied by Tortonese-Marcante and Rossi-Roghi were revisited in the following decades, so that long-term series have become available for both Portofino and Mesco.

Gatti et al. (2017) collated all the available information on Portofino reefs, starting from the pioneer studies of Tortonese, to build a large dataset of descriptive and semi-quantitative data, which allowed exploring the evolution of the rocky reef sessile assemblages across nearly 60 years. A major change of community composition was evidenced in the 1980-90s, under the combined effects of climate warming and increased human pressures, especially diving tourism (Lucrezi et al. 2017). Some species disappeared or got rarer, many found refuge at depth, and among the newcomers there were recently introduced alien species. The general trend included the loss of canopy-forming algae (Mangialajo et al. 2008b) in favour of algal turfs (Figure 13).

A detailed study on hydroids, first collected in 1980 (Boero & Fresi 1986) and then resampled in 2004 (Puce et al. 2009) and 2018 (Betti et al. 2019) with the same technique and in the same stations, evidenced changes in species composition (due to the appearance of southern species), seasonality, and depth distribution. Species richness, in particular,



Figure 13. Change in the rocky reef communities of Portofino at about 10 m depth. (a) *Sargassum vulgare* and *Dictyopterus polypodioides* canopy in 1981. (b) *Sarpa salpa* grazing in a turf-dominated environment in 2009. Modified from Parravicini et al. (2013).

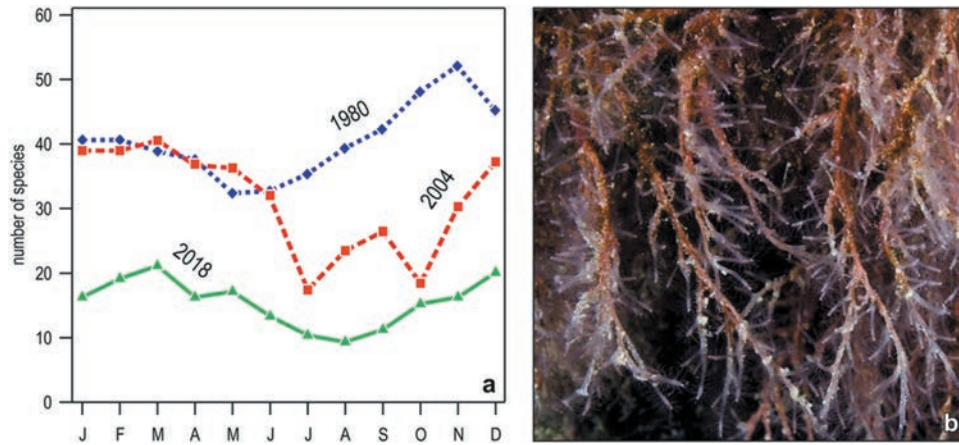


Figure 14. Change in the hydroid assemblage of Portofino reef. (a) Monthly variations in the total number of species in three years. (b) *Corydendrium parasiticum*, a species first recorded in 2018 in shallow waters (<5 m).

increased from Spring to Autumn in 1980 but exhibited the opposite trend in 2004, and remained low all year round in 2018 (Figure 14(a)). *Corydendrium parasiticum*, a conspicuous species with warm-water affinity, was first recorded in 2018 in shallow water (Figure 14(b)).

The comparison of quantitative data (still-frame underwater photographs) collected in 1987–1988 and 2012–2013 on the whole sessile community confirmed the severe depletion of macroalgal cover, while the total cover of sponges remained almost unvaried notwithstanding species substitutions (Bertolino et al. 2016). Photographs taken in 2002–2003 (i.e., few years after the establishment of the Marine Protected Area in 1999) and in 2013 (Betti et al. 2017c; Longobardi et al. 2017) illustrated a continued trend of modifications: frondose macroalgae (such as species of *Cystoseira* and *Sargassum*) decreased further, resulting in a significant reduction of habitat complexity and three-dimensional structure, which might affect in turn the small associate fauna (Losi et al. 2018; De La Fuente et al. 2019; Marchini et al. 2019). Further changes included the increased abundance of the bryozoan *Bugula fulva*; the decreased abundance of the barnacle *Perforatus perforatus* and the mussel *Mytilus galloprovincialis*; and the appearance of alien species (*Asparagopsis armata*, *Caulerpa cylindracea* and *Paraleucilla magna*).

Comparison of still-frame underwater photographs (Peirano & Sassarini 1992; Peirano et al. 2000; Bianchi et al. 2001; Roghi et al. 2010) was also used to explore change in the communities of the rocky shoal of Punta Mesco. These

communities remained qualitatively and quantitatively stable from 1961 to 1990. The same result was obtained by the analysis of descriptive studies since 1937, which suggested that there had been no major modification for more than 50 years (Gatti et al. 2015, and references therein). Between 1990 and 1996, the communities changed dramatically, to remain subsequently stable in a new configuration to 2017. The communities passed from highly structured assemblages with a dense canopy of the gorgonian *Paramuricea clavata*, an understory dominated by the long-lived calcified bryozoan *Cellaria fistulosa* and a basal layer of encrusting corallines, such as *Lithophyllum stictiforme*, to a homogenized community with a reduced canopy, an understory with large hydroids and a basal layer of filamentous algae dominated by the alien species *Womersleyella setacea* and *Caulerpa cylindracea* (Figure 15). Reduced canopy and scarcer calcified organisms implied loss of structural complexity, with likely consequences on the whole associate biota and ecosystem services. The two alternative states showed comparatively stable for decades (1961–1990 and 1996–2017, respectively), while the transition between them has been abrupt (1990–1996) and marked by the quantitative exuberance of a number of species that acted as “passengers” of change. Boudouresque (1970) described as “Riou effect” (from the name of an island near Marseilles, France) the outburst of generalist species at the transition between two distinct species assemblages along a spatial gradient. What has been observed at Punta Mesco was apparently a Riou effect along a temporal gradient. While the drop in similarity was rapid, requiring only six

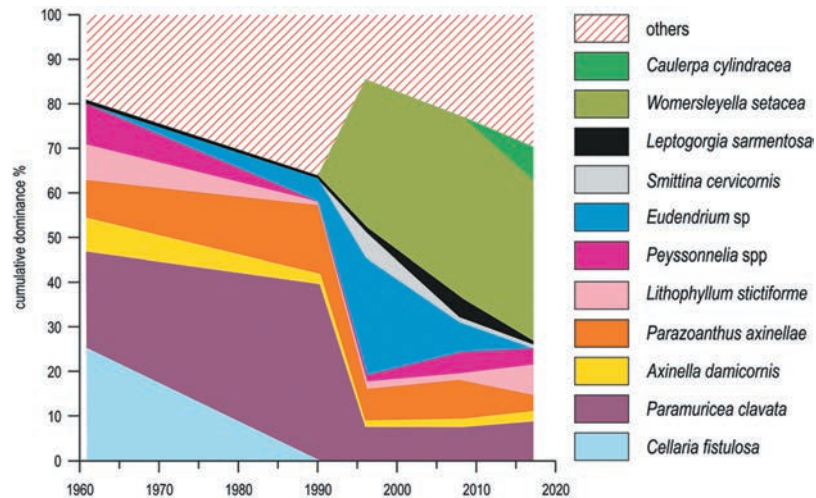


Figure 15. Compositional change in the rocky reef community of Mesco Shoal. Others include species whose cover has always been <5%.

years, homogenization increased continuously and gradually (Gatti et al. 2015).

A 25-year-long data series from Gallinara Island (1991–2016) evidenced a reduction in the three-dimensional structure of the epibenthic communities and a severe decrease in species diversity (Bianchi et al. 2018b). Beside biodiversity loss, the most impressive outcome was biotic homogenization: deep (23–35 m) and shallow (2–9 m) communities were clearly different in 1991, but merged into an indistinct unique assemblage in 2009 and 2016 (Figure 16). In this case, the modifications observed have been attributed mostly to local human impacts rather than to sea water warming, the sea floor having been littered with derelict fishing gear and other waste from boats.

There were striking parallels in the biotic changes observed at Portofino, Punta Mesco and Gallinara Island. Based on the quantitative information available, species were classified as “losers” if

they decreased their percent cover or disappeared over time, and as “winners” if they conversely increased or newly appeared (Figure 17). The losers included the algae *Cystoseira* spp, *Flabellia petiolata* and *Sargassum vulgare*, the sponge *Axinella damicornis*, the cnidarian *Alcyonium coralloides*, and the bryozoan *Cellaria fistulosa*; some species (such as the sponges *Agelas oroides* and *Petrosia ficiformis* and the cnidarians *Eumicella singularis* and *Parazoanthus axinellae*) recovered, at least partially. The winners were represented only by the alien algae *Caulerpa cylindracea* and *Womersleyella setacea*, thus conforming to the paradigm that a few winners will replace many losers in a frame of biotic homogenization (McKinney & Lockwood 1999; but see Dornelas et al. 2019). Among the losers, stenothermal but eurybathic species found refuge at depth, to avoid the increased temperature variability in shallow waters (Morri et al. 2017): so did, for instance, the

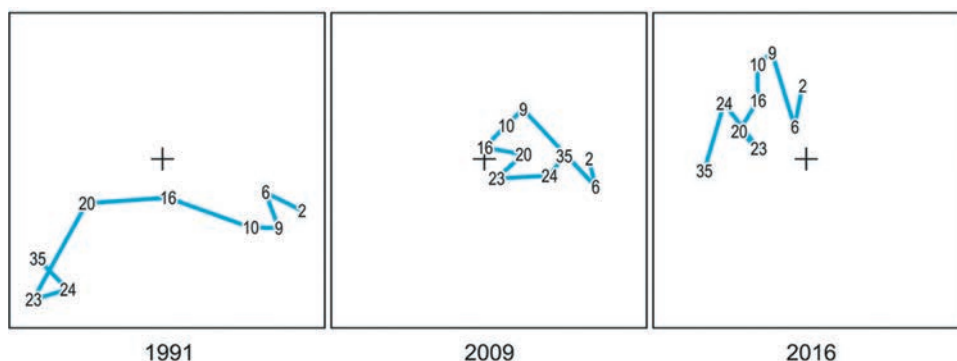


Figure 16. Ordination plot on the first two axes from Correspondence Analysis of epibenthic species cover data (82 species \times 78 sampling quadrats) of Gallinara Island, in 1991, 2009, and 2016. Variance explained: 47.0%. All diagrams are in the same plane and have been split for ease of reading. Station-point centroids are identified by their depth (in meters). Lines illustrate the depth gradient.

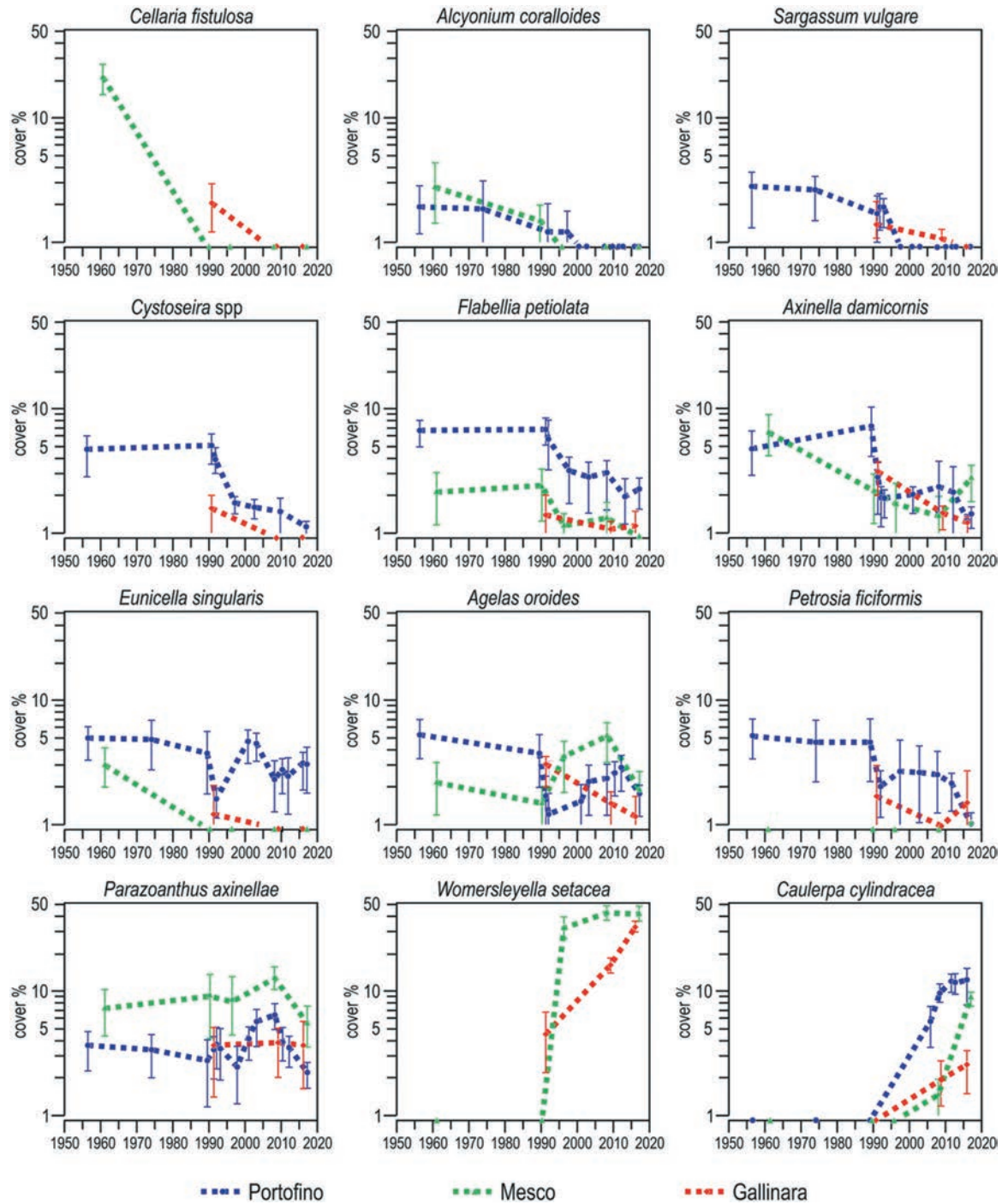


Figure 17. Selected examples of epibenthic species that changed their mean cover (\pm se) with time in Ligurian rocky reefs. Note logarithmic scale on y axis.

brown alga *Dictyopteris polypodioides*, the sponge *Spongia officinalis*, the bivalve *Pinna nobilis*, the bryozoan *Reteporella grimaldii*, and the ascidians *Halocynthia papillosa* and *Microcosmus sabatieri* at Portofino (Figure 18). *A. coralloides*, disappeared from scuba depths (Figure 17), is still found at

70–150 m (Bo et al. 2014). The same might be true for the small-spotted catshark *Scyliorhinus canicula*: although quantitative data are not available, it was frequently observed at scuba depths in the 1970s and its egg cases attached to gorgonian branches were a common sight; by the 1990s, it

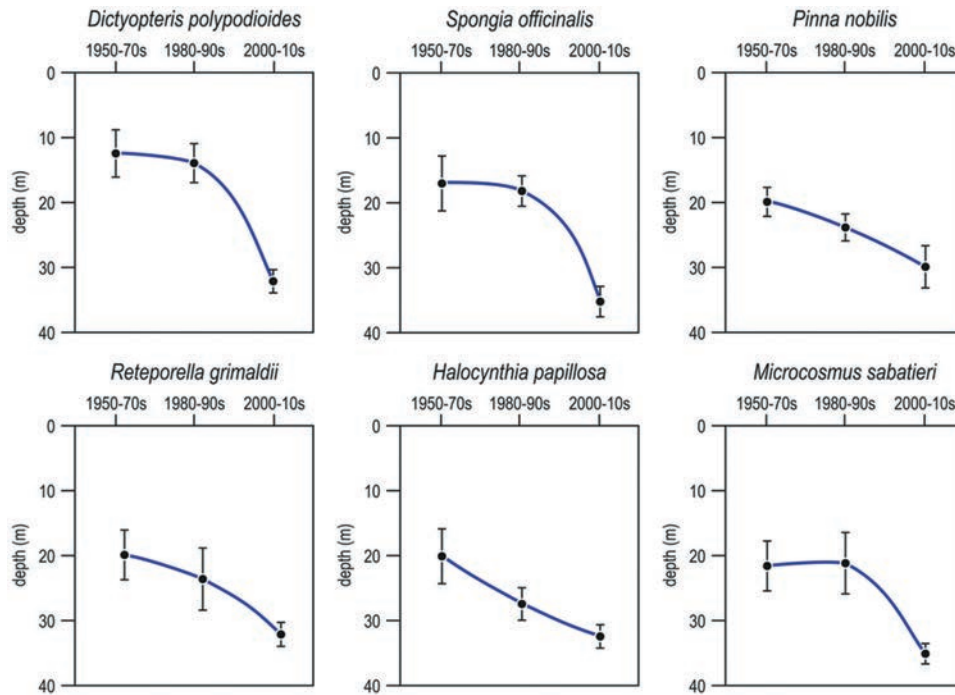


Figure 18. Selected examples of species that changed their depth range preference (mean \pm se), going deeper with time, in Portofino rocky reefs.

disappeared from scuba depths but was still found, although rarer, in deeper waters (Ferretti et al. 2005). Studies on larval dispersal of the gorgonian *Paramuricea clavata* in the Eastern Ligurian Sea (Pilczynska et al. 2016) detected larval exchange between different depth zones, supporting the hypothesis that deep water colonies unaffected by the surface heatwaves may provide larvae for shallow waters, thus helping population recovery.

Bertolino et al. (2014a, 2017) studied the dynamics of a sponge assemblage at decennial and millennial temporal scales analysing the siliceous spicules entrapped in the biogenic concretions of coralligenous reefs at Santo Stefano, Bogliasco, Portofino and Punta Manara. Notwithstanding changes in diversity and abundance that coincided with Holocene climate variations, the sponge assemblage remained rather stable during 3000 years. On the contrary, between 1973 and 2014 species richness decreased of about 45% on average. The decrease involved mainly massive and erect species, while encrusting, boring and cavity-dwelling species were less affected.

Marine caves

Marine caves are unique and vulnerable habitats with high aesthetic value (Rovere et al. 2011). The cave communities of the Mediterranean Sea are rich in biological peculiarities (including specialized

organisms and deep-sea species), are poorly resilient, and act as refuges for ancestral forms (Cattaneo & Pastorino 1974; Bianchi et al. 1996). Their scientific interest made marine caves to be listed in the EU Habitats Directive and the Barcelona Convention, and calls for study and monitoring (Rastorgueff et al. 2015). After more than five decades of research, however, knowledge on marine caves remains fragmentary (Cicogna et al. 2003).

About 76 marine caves are known to exist along the Ligurian coast (Canessa et al. 2014), but information on their biological communities is available for only a dozen of them (Bianchi & Morri 1994b; Ugolini et al. 2003; Nepote et al. 2017). The sponge fauna of two semi-submerged cavities at Bonassola and Zoagli were first studied in 1961–63 (Sarà 1964) and again in 2015–16 (Costa et al. 2018). A still undetermined species of *Aplysina*, previously absent from the caves, was found common in the intertidal zone. The comparative analysis also evidenced an increase in species richness (Figure 19(a)) and a significant change of growth forms (Figure 19(b)), massive sponges having been replaced by encrusting forms.

Similar results had been obtained by Parravicini et al. (2010), who compared the sessile assemblages of the marine cave of Bergoggi in 1986 and 2004, i.e. before and after the summer heatwaves of 1999 and 2003: these positive thermal anomalies (with peaks up to 4°C above the climatological mean)

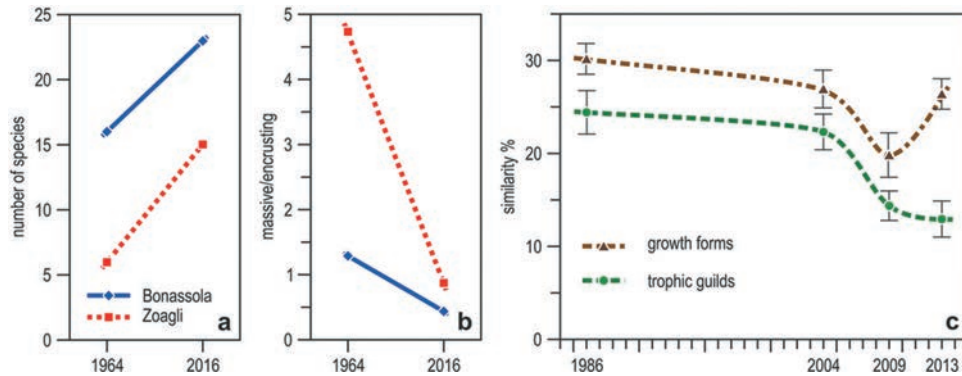


Figure 19. Change with time in the communities of Ligurian marine caves. (a) Number of sponge species in the two semi-submerged caves of Bonassola and Zoagli in 1964 and 2016. (b) Percent ratio of massive to encrusting sponge species in the same caves and in the same years. (c) Trends of average (\pm se) Bray-Curtis similarity among the sessile communities of the Bergeggi marine cave from 1986–2013, using morpho-functional descriptors. (a) and (b) from data in Costa et al. (2018), (c) redrawn and modified from Montefalcone et al. (2018).

were thought to have selectively killed erect and massive organisms (such as the sponge *Petrosia fici-formis*) and caused their replacement by encrusting organisms.

The marine cave of Bergeggi is unique in the Ligurian Sea – and perhaps in the whole Mediterranean – as it has been studied more or less regularly since the late 1970s (Bianchi et al. 1986; Sgorbini et al. 1988; Morri et al. 1994). Increased sea water temperature induced the substitution of the warm-water mysid *Hemimysis margalefi* for the cold-water species *H. speluncola* in the marine cave of Bergeggi, as well in other marine caves of the north-western Mediterranean (Chevaldonné & Lejeusne 2003). Such a species shift is likely to exert great influence on the energy budget of cave ecosystems (Bianchi 2007). Mysids stay in caves during the day but move outside at night to feed. In so doing, they import organic matter from outside into the oligotrophic cave ecosystem, but *H. speluncola* typically forms huge swarms while *H. margalefi* small groups. Thanks to the availability of a 30-year-long series of quantitative data (substratum cover from wire-frame photographs) on the sessile communities of the marine cave of Bergeggi, Montefalcone et al. (2018) evaluated change in both the structural (growth forms) and functional (feeding guilds) aspects of the cave ecosystem. The most important rate of change was observed after the climate events mentioned above and coincided with major beach nourishments and the extension of a neighbouring commercial harbour. Structural aspects, but not functional ones, have been showing some recovery in recent years (Figure 19(c)).

Concluding remarks

The present review of historical and recent data on climate and marine biodiversity of the Ligurian Sea allowed novel understanding about the nature, magnitude and direction of change in recent decades. The sea water temperature increase has been accompanied by an impressive change in the marine biota, and especially by the establishment of warm-water species of various origins and by episodes of mass mortality of sessile organisms. The most dramatic changes occurred around the 1980–90s, in correspondence with a phase of more rapid warming. Another phase of rapid warming has possibly started in the 2010s and there are clues pointing to a further series of biological changes, as already observed in other warm-temperate regions of the globe (Caputi et al. 2019); Ligurian Sea data, however, are too scarce to date for proper assessment.

The effects of climate change on Mediterranean marine ecosystems are multifarious (Calvo et al. 2011). Beside the establishment of southern species (aliens included), the most commonly effects observed in Liguria include native species finding refugia at depth, to avoid the heatwaves of shallow waters (Sparnocchia et al. 2006), and the biotic homogenization of the communities. Both phenomena have been observed in other Mediterranean regions and elsewhere (Bianchi et al. 2014; Assis et al. 2016; Morri et al. 2017). The availability of a number of historical data series allowed describing trajectories of change that have the 1980–90s as a turning point. An ecosystem shift in the same years has been recorded in other regions of the world's ocean (Conversi et al. 2010; Defriez et al. 2016; Reid et al. 2016). Linking global to regional trends is a basic step for understanding the

ecological impacts of marine climate change (Popova et al. 2016).

Perhaps coincidentally, major changes in both climate and human pressures took place in roughly the same period (Parravicini et al. 2013; Gatti et al. 2015, 2017). Global climate warming and local human pressures are known to combine their effects on the marine biota (Bianchi et al. 2014). Local anthropogenic stressors, such as habitat degradation or destruction, pollution, sedimentation, and overfishing, together with a gradual history of changes in environmental conditions (climate, habitat quality, resource availability), can potentially exacerbate biodiversity decline and habitat loss, thus eroding the ability of ecosystems to absorb and recover from additive or synergic affectors (Montefalcone et al. 2011). Local and global pressures may interact in a complex way (Bianchi 1997), favouring, for example, the biological invasion by alien species in habitats already stressed by warming and human activities (Occhipinti-Ambrogi & Savini 2003; Montefalcone et al. 2010b). Distinguishing the modifications caused by climate change from those caused by local human disturbance is often difficult (Morri & Bianchi 2001). For instance, the loss of habitat-forming macroalgae (e.g., species of *Cystoseira* and *Sargassum*) observed in the Ligurian Sea (Mangialajo et al. 2008b; Gatti et al. 2017) – as well as in other regions of the Mediterranean Sea (Thibaut et al. 2005; Bianchi et al. 2014; Blanfuné et al. 2016; Capdevila et al. 2019; Catra et al. 2019) – has been considered by different authors as due to either climate or human impact. Similarly, the reduction of gorgonian canopies caused by sea water warming might have been enhanced by the impact of fishing, and in particular by the lost fishing gears that entangle their colonies (Bavestrello et al. 1997).

Mass mortalities caused by heatwaves may be equated to pulse disturbances, whereas most human pressures (e.g., pollution, turbidity) may be assimilated to a continuous stress. Despite the conceptual and practical difficulty in differentiating between disturbance and stress, the two terms, which are often used interchangeably by different authors, bear different ecological meanings: both are external agents, but the former causes subtraction of biomass, the latter reduces productivity (Montefalcone et al. 2011). Montefalcone et al. (2017) devised two distinct indices to differentiate between the effects of disturbance and stress on marine ecosystems. Applying the two indices to a Ligurian coralligenous reef suggested that recovery following a disturbance may be rapid, while the effects of anthropogenic stress are more persistent.

The combined action of sea water warming and increased human pressure led to a phase shift in most Ligurian Sea habitats, with abrupt changes in species composition and community structure. A phase shift normally results from a regime shift, i.e., a large-scale and long-lasting change in the nature, intensity, and/or frequency of the factors that govern the dynamics of the ecosystem (Montefalcone et al. 2011; van Putten et al. 2019). A regime shift has been documented since the 1980s, when the whole Mediterranean Sea underwent a major change that encompassed atmospheric, hydrological, and ecological systems (Conversi et al. 2010). The phase shifts observed in Ligurian Sea communities suggest a link between basin-wide and local changes in climate and direct human pressures, to which added the absolute novelty of the invasion by alien species. Stressed ecosystems are said to be more prone to the establishment of alien invasive species (MacDougall & Turkington 2005). *Womersleyella setacea* and *Caulerpa cylindracea*, two of the “worst invasive species” in the Mediterranean Sea (Zenetos et al. 2005), were first recorded in the Ligurian Sea in the 1990s (Airoldi et al. 1995; Bussotti et al. 1996), and have recently become dominant in different habitats. The success of both invaders is favoured by sea water warming and coastal anthropization (Bianchi et al. 2018a). Urbanization has been proved to increase sediment delivery to Ligurian coastal waters (Mateos-Molina et al. 2015), and the filamentous turf formed by *W. setacea* is known to be favoured by high sedimentation rates (Airoldi et al. 1995). In turn, turf retains sediment and facilitates colonisation by *C. cylindracea* (Bulleri & Benedetti-Cecchi 2008). Such a cascade of facilitation effects likely depicts a paroxysmal positive feedback that drove the Ligurian Sea communities into an alternative state. Although some recovery from the warming-induced mass mortalities of the 1990s has been recorded, the habitat alteration caused by the invasion of the alien species leaves little scope for a reversal of the phase shift experienced by Ligurian Sea communities. Persistence of the phase shift may be detrimental to the resilience of Ligurian Sea ecosystems. Protection measures might help the return of the species that used to characterize the Ligurian Sea communities in historical times; however, they will hardly eradicate the aliens (Montefalcone et al. 2010b). Current management efforts to maintain or reach “good ecological status” (GES) for marine ecosystems (Boero 2014) should therefore consider that future marine habitats will probably lose their original peculiarities and acquire a different and unprecedented configuration partly shaped by alien species (Bianchi 2007). Only

properly addressed long-term studies (Hampton et al. 2019) will help understanding the future dynamics of Ligurian Sea ecosystems and their possibility of recovery.











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ORCID

C. N. Bianchi  <http://orcid.org/0000-0003-1071-3285>
 M. Bertolino  <http://orcid.org/0000-0003-3233-303X>
 F. Betti  <http://orcid.org/0000-0002-5492-2655>
 M. Bo  <http://orcid.org/0000-0001-8400-6722>
 R. Cattaneo-Vietti  <http://orcid.org/0000-0002-3991-9116>
 S. Cocito  <http://orcid.org/0000-0002-5607-7002>
 M. Montefalcone  <http://orcid.org/0000-0002-3851-1880>
 C. Morri  <http://orcid.org/0000-0003-4520-2741>
 A. Peirano  <http://orcid.org/0000-0001-8847-1760>
 G. Bavestrello  <http://orcid.org/0000-0002-5428-2344>

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