

The Portofino Promontory: 200 Years of History of Marine Biology

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Abstract: This paper outlines the history of scientific research developed in the Portofino Promontory, located in the centre of the Ligurian Sea. The chronicles span over two centuries, from the late 18th century to the present day. Portofino is now recognised as one of the best-known areas in the world regarding marine biological communities and their temporal dynamics, particularly in relation to current climate changes. In addition, since 1999, with the establishment of the Marine Protected Area, significant research related to marine environment conservation has developed in Portofino. The role of the University of Genoa, the Natural History Museum, other important institutions, and the researchers involved in the Portofino area has been outlined.

Keywords: marine sciences; historical recollection; marine protected area; Mediterranean Sea



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1. Introduction

The Portofino inlet, in ancient times *Portus Delphini*, was one of the few natural ports between La Spezia and Genoa (Figure 1a–c). The origins of the settlement are ancient, as evidenced by the mention made by Pliny the Elder and Pomponius Mela, a Roman geographer who worked in the first century CE [1]. The inlet is protected by a promontory, once known as Capodimonte, which shelters it entirely from the southerly winds. This efficient port structure has ensured that the population of Portofino has always had close ties to the sea, which means the village has always been frequented by numerous seafarers, including illustrious people, who sheltered their vessels in the inlet at times of unexpectedly rough seas. In the 19th century, this small fishing village acquired international fame and became an inescapable stop on the grand tour. A sign of this importance is attested to by the imperial decree of 1813, in which Napoleon Bonaparte, aggrieved by the tragic results of his Russian campaign, found the time to change the village's name to Porto Napoleone. However, such a toponym would have been as ephemeral as the emperor's downward spiral [1].

As early as the first half of the 19th century, the Promontory of Portofino was the subject of naturalistic research: it was in 1819 when Sarzana native Antonio Bertoloni, already the author of an essay on the zoophytes of the Gulf of La Spezia [2], published *Historia fucorum Maris*

Ligustici with the first reports of algal species gathered by Chiavari native Bernardino Turio from the rocks of Portofino [3]; this was followed in 1842 by *Algologiae Maris ligustici* specimen [4] and in 1846 by *Prospetto della Flora Ligustica e dei Zoofiti del Mare Ligustico* [5], both by Giuseppe De Notaris; the *Prospetto* was part of the three-volume work *Descrizione di Genova e del Genovesato* [6] (Figure 1d), presented at the eighth meeting of Italian scientists, which was held in Genoa under a patriotic and nationalistic fervour. The first volume included, in addition to geological and climatological notes, the bathymetric chart drawn by Rear Admiral Gen. Giuseppe Albini (Figure 1e) and the *Catalogo degli animali invertebrati marini del Golfo di Genova e Nizza osservati da Gio Batta Verany*. These works of illustrious academics explicitly reported on observations and items collected in Portofino [7]. Particularly important are the descriptions of new species and a bathymetric chart, at the time referred to using the term “*Carta di Sonde*”, which highlighted how “of the sea depths immediately along the coast, the greatest are those corresponding to the Monte di Portofino, which rises, so to say, perpendicular to the sea”.

Other marine biology studies were published in the second half of the 19th Century, including *Enumerazione delle Alghe di Liguria*, a text on seaweeds with numerous references and updates relating to the sea and coast of Portofino [8].

Towards the end of the 19th century, three researchers from the University of Turin, Lorenzo Camerano, Mario G. Peracca, and Daniele Rosa (Figure 2a–c), built a small marine biology station in Rapallo [9] (Figure 2d,e), which remained active for nearly ten years. In this period, significant efforts were made to describe the species present in an even larger area hitherto largely unknown, as demonstrated, for example, by the study on the echinoderms carried out by Pietro Marchisio [10], who worked on material gathered by Camerano and Rosa. The station also hosted foreign scientists such as Arthur W. Waters, who spent three weeks there in March of 1893 to study the bryozoans of the gulf [11].

Between 1877 and 1907, the Tigullio Gulf hosted on several occasions Ernst Haeckel, who was invited to Portofino by the British Consul, Lord Montague-Brown, who provided accommodation, vessels, and men for his marine biology research. Haeckel was, however, particularly linked to Rapallo, where he stayed many times (Figure 2f). In the same period, Carus [12], in his monumental work *Fauna del Mediterraneo*, cited Haeckel and De Notaris for some cnidarians found in the Gulf of Rapallo. In 1904, Haeckel was a guest of honour in a symposium in Genoa, which saw the participation of Corrado Parona, Giacomo Cattaneo, and Arturo Issel of the University of Genoa [13].

More contributions were later made by Raffaele Issel, professor of zoology at the University of Genoa and a pioneer of marine biology in Italy (Figure 2g). His university text on marine biology was the first Italian manual [14] (Figure 2h). It was primarily based on studies that the author conducted in the marine biology laboratory at Quarto, a locale of Genoa [15,16], but also contained numerous references to Portofino. In the introduction to this highly famous text, Issel stated that one of the reasons that motivated him to write the volume was learning that Baron von Mümm, having established himself in San Giorgio castle in 1912, was employing a zoologist from Frankfurt intending to publish a text on the marine biology of Portofino. The German project was never completed, but it proved very useful to stimulate the Italian one.

Issel, along with his colleagues Alessandro Brian and Renato Santucci, covered various issues regarding the systematics, ecology, and biology of marine organisms, studying the meadows of the seagrass (*Posidonia oceanica*) [17]. In 1912, he published a study on the benthic organisms living on the leaves of *P. oceanica*; in the same work, a description of all the shallow meadows on the western side of the Gulf of Tigullio was provided. Issel also collected material for foreign specialists. For example, Stechow [18] lists six species of hydrozoans for the Portofino coast collected by Issel, in particular naming the new species *Sertularia perpusilla* (now *Tridentata perpusilla*) for a hydrozoan frequently found on the leaves of *P. oceanica*. Subsequently, Issel also provided the first information on the commercial bathyal fauna of the Ligurian Sea, focusing more on the Gulf of Genoa [19,20].

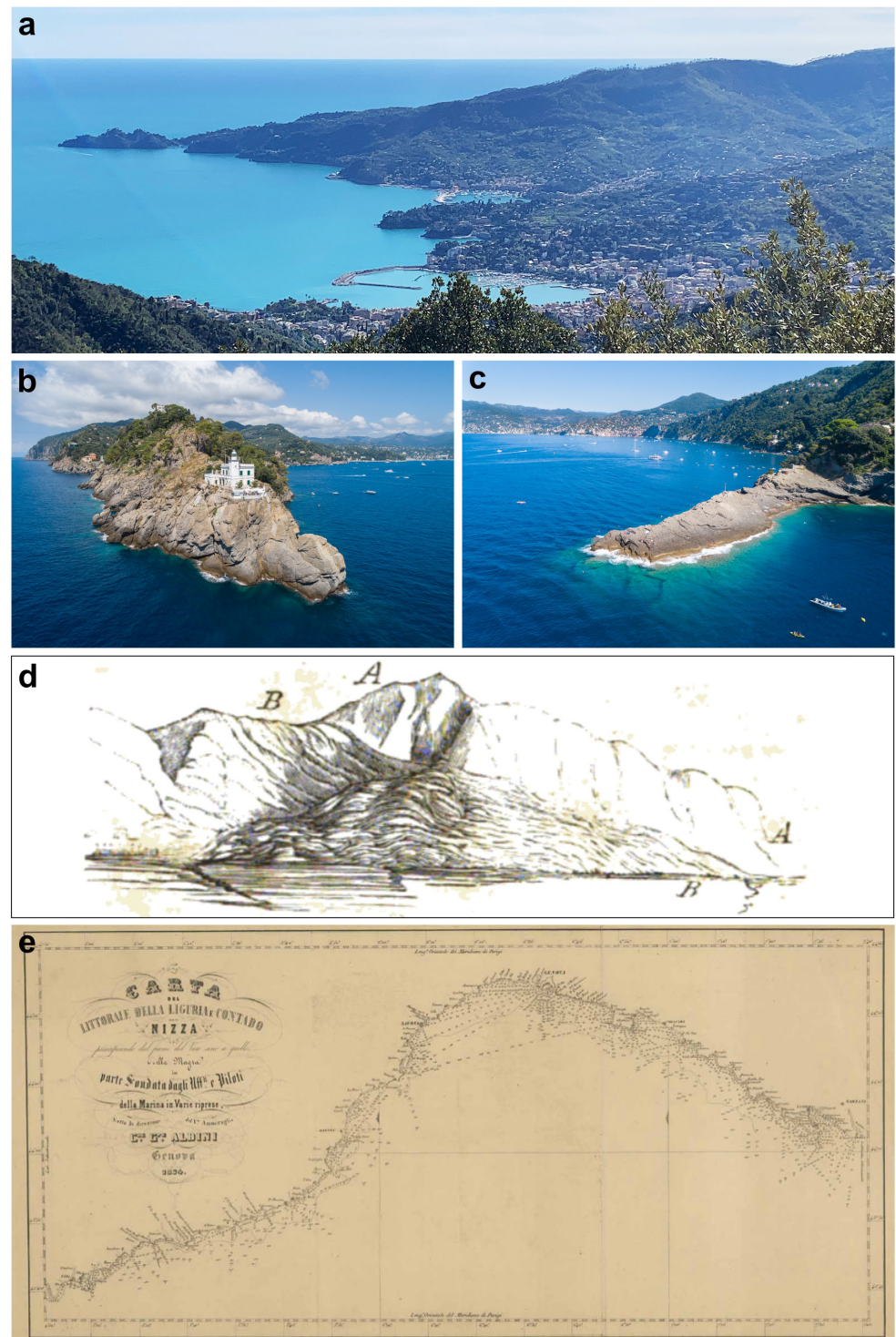


Figure 1. The Portofino Promontory. (a) View of the western side of the Gulf of Tigullio and the Portofino Promontory; (b,c) the two ends of the promontory: Punta del Faro to the east (b) and Punta Chiappa to the west (c); (d) representation of the Portofino Promontory (A, puddingstone, B, fucoid limestone) (from [6]); (e) historical nautical chart of the Gulf of Tigullio.

In 1936, a very young Enrico Tortonese (1911–1987), a native of Turin who had spent some years of his youth in Genoa, where he had frequented the Museum of Natural History Giacomo Doria and got to know the famous ichthyologist Decio Vinciguerra, published an article on the Alcyonacea of the Gulf of Genoa, in which he cited species from Portofino.



Figure 2. History. (a–c) Three young zoologists from the University of Turin, Lorenzo Camerano (a), Mario G. Peracca (b), and Daniele Rosa (c); (d,e) the marine biology laboratory in Rapallo in 1898; (f) Ernst Haeckel during his last stay in Rapallo in 1907; (g,h) Raffaele Issel and the original edition of his famous Hoepli manual of Marine Biology published in 1918.

A new impetus in research into the marine environment of this region came in the period following the Second World War, particularly in the 1950s and 1960s, with the work of the oceanographic centre Centro Talassografico Tirreno. In 1956, a marine biology observatory was founded in Santa Margherita Ligure at the initiative of the University of Parma, with the

contribution of the municipal administration. Its work was particularly fruitful up until 1962. It allowed for drafting a “planktonic calendar” and studies of the benthic biocoenoses of the Gulf of Tigullio, specifically of the area between Paraggi and Rapallo [21].

Scientific research in the Portofino area took a turn in the 1950s when two Turinese scientists, Enrico Tortonese (Figure 3a,d), director of the Giacomo Doria Museum of Natural History in Genoa since 1955, and Lucia Rossi (Figure 3b), professor of zoology at the University of Turin started working on the observations and material collected by a group of divers led by Duilio Marcante (Figure 3c), making use of the SCUBA technique patented a few years before by Cousteau and Gagnan [22,23].

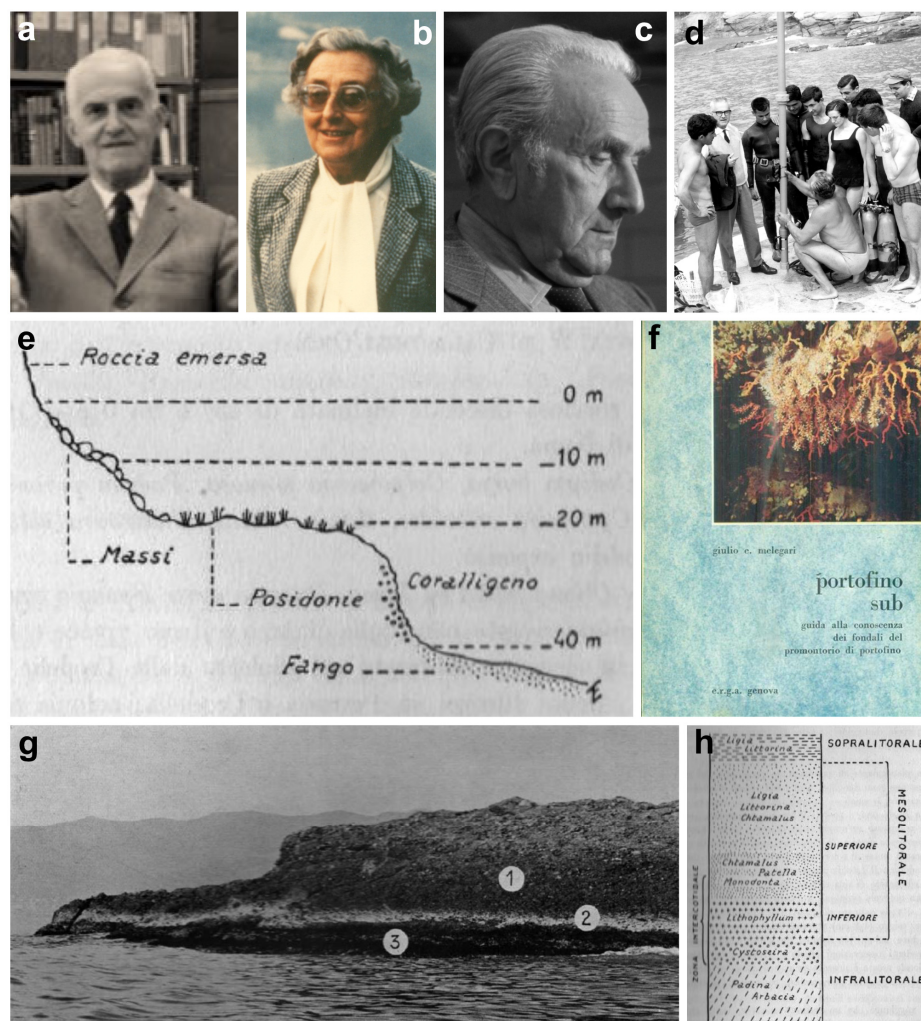


Figure 3. Marine biology, the beginnings. (a,b) Two pioneers of marine biology research on the Portofino Promontory: Enrico Tortonese (a), director of the Giacomo Doria Natural History Museum in Genoa from 1955 to 1976, and Lucia Rossi (b), professor of zoology at the University of Turin; (c) Duilio Marcante, pioneer of scuba diving; (d) Marcante (crouched) and Tortonese (second from left) with a group of divers on a Camogli dock; (e) the first zonation scheme of benthic communities along a vertical transect in Cala Dell’Oro [24]; (f) the first Italian diving guide regarding Portofino published by Giulio Melegari in 1973; (g,h) photograph of Punta Chiappa with the main shallow-water biocoenoses (1, supralittoral; 2, upper midlittoral; 3 lower midlittoral); (g) and zonation scheme (h) (from [24]).

Thanks to his partnership with the SCUBA divers, Tortonese [24,25] described the initial fundamentals of the bionomy of the promontory’s seabed and published the first vertical transect of Cala dell’Oro and Punta Carega, mapped directly during the dives (Figure 3e,g,h).

In 1959, Cino Motta [26] published the first underwater sketch of the Punta del Faro reef. Rossi's research [27–29] concentrated primarily on cnidarians. Recreational divers' interest in Portofino was definitively consecrated by the foundation in 1954 of the Centro Subacqueo Mediterraneo di Nervi, a diving centre founded on the initiative of Marcante, and the first Italian diving guide, Portofino Sub, published by Giulio Melegari [30] (Figure 3f).

In 1957, a cruise was held on the oceanographic vessel *Calypso*, which gathered samples of benthos and sediments from the soft areas of seabed between depths of 75 m and 1000 m in the Portofino area. The results are contained in a series of monographs published in the *Annales de l'Institut Océanographique*, whose title includes the phrase *Campagnes de la «Calypso» dans le Golfe de Gênes*. Tortonese himself [31] published a paper on echinoderms, while Rossi dedicated herself to anthozoans, describing the white coral communities [32]. Tortonese promoted and organised the 1957 Congress of the Commission Internationale pour l'Exploration Scientifique de la Méditerranée (CIESM), which had the concluding session of the “Sous Comité Benthos” in Santa Margherita Ligure: this event saw the finalisation of the definition of the Mediterranean benthic zonation [33], which was subsequently generalised at the worldwide level [34].

In 1964, Michele Sarà became director of the Zoology Institute of the University of Genoa (Figure 4a) and began working on the sponges of the shallow caves of the Ligurian coast, some of which were in the Portofino area [35]. Previously, in 1958, Sarà [36] had investigated the sponges of the promontory, studying an extensive collection provided by Tortonese. At the time, the sponges of Liguria were virtually unknown: 41 species were listed in 1958, of which two were new to science. Around the same time, Sarà began to take on the issue of the temporal evolution of the community of sponges. With the assistance of Gustavo Pulitzer-Finali (Figure 4b), he spent over a year mapping some groups of encrusting sponges, tracing their outlines with a pencil through a piece of transparent plexiglass (Figure 4c,d). This work was performed on the walls of the Cala dell'Olivetta, on the northern part of Punta del Faro (Figure 4e). Marine biologists' interest in this small bay is borne witness to by the book by Baron von Mümm [1], who described it as a treasure chest for researchers.

The results obtained during this research period led to the publication of one of Sarà's most interesting papers [37], in which he demonstrated that sponges are led to the occupation of space, depending on the surrounding conditions, by both competitive and cooperative phenomena.

The same period also saw the study by Aurora Corte Montemartini [38] on the marine fungi of Portofino Bay, which was dedicated to the fungal component of fouling on wooden material. Marine mycology research has been resumed in more recent years. In 2015, Garzoli et al. [39] published a study about lignicolous marine fungi in the Mediterranean Sea. Fungi found on collected wood samples were analysed using a combination of morphological and molecular techniques. Original samples were collected during the summer of 2011 in different sites along the Italian coastline, including the Marine Protected Area of Portofino. In 2019, Greco et al. [40] described the natural infection of *Chondrosia reniformis* by *Aspergillus tubingensis* for the first time, also signalling the danger represented by this fungus as a fatal opportunistic pathogen.

Since then, research in this area of the Ligurian Sea has continued with regularity: an important role was played by the programme of the Italian National Research Council (CNR) “Oceanografia e Fondi Marini” (oceanography and seafloors) (1977–1981), which committed various units primarily operating under the University of Genoa [15]. The seabed around the Promontory of Portofino thus became the most widely studied in the entire Ligurian Sea [41,42]. Much of the research that has begun in this area is continuing at the Earth, Environment and Life Sciences Department (DiSTAV) and the Interuniversity Center for Scientific Cooperation Europe—Latin America (C.I.C.S “EULA”).

In 1982, the University of Genoa acquired Villa Costa-Carmagnola in Santa Margherita Ligure, where, under the initiative of Norberto della Croce and Francesco Maria Faranda, the Marine Environmental Sciences Institute was housed, primarily engaged in ocean-

graphic research. For some years, this prestigious building was the CoNISMa's headquarters (Consorzio Nazionale di Scienze del Mare—National Consortium of Marine Sciences), founded in Genoa in 1994.

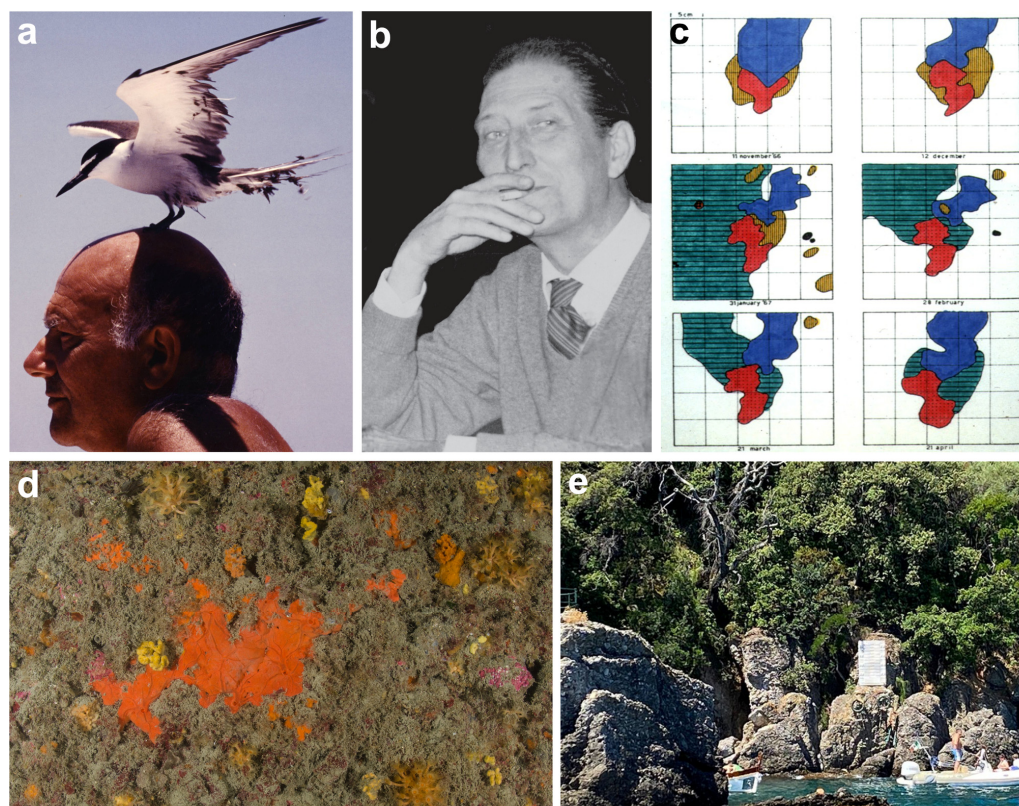


Figure 4. Genoese sponge research. (a) Michele Sarà, director of the Institute of Zoology of the University of Genoa, and (b) Gustavo Pulitzer-Finali studied the temporal changes of the shallow-water sponge communities; (c) temporal maps of the encrusting sponge communities observed on the cliffs of Cala dell'Olivetta obtained by tracing the contours of the specimens on transparent plexiglass tablets (drawing by Roberto Pronzato); (d,e) sponges (d) settled on the cliffs of Cala dell'Olivetta (e).

Since 26 April 1999, the Promontory of Portofino has been part of a Marine Protected Area (MPA), which includes the coastline of the territory of the Camogli, Santa Margherita Ligure, and Portofino municipalities.

Riccardo Cattaneo-Vietti (1949–2021), to whom this paper is dedicated, conducted much of his research in these waters. The Promontory of Portofino, with which Riccardo had deep bonds, was extensively described in the book *Mare di Liguria*, published in 1980, written with Sirigu and Tommei [41].

2. General Information

2.1. Geomorphology, Geology, and Climate

The Portofino Promontory is located on Liguria's Riviera di Levante, around 25 km from Genoa, and represents one of the areas of greatest naturalistic and environmental prestige on the Italian Riviera (Figure 1a). The topography is characterised by a ridge interrupting the continuity of the coast between Sestri Levante and Genoa, dividing the Gulf of Tigullio (or Marconi Gulf) to the east from the Paradiso Gulf to the west [43]. The promontory, sliced by tectonic action, has a roughly quadrilateral shape with a maximum elevation of 609 m, such that it features microclimates typical of the Mediterranean coast in its southerly portion and other microclimates more typical of the inland area on its northerly side [44]. One side of the promontory, in which the bays of Portofino and Paraggi open, faces eastwards. The south-facing side of the promontory extends from Punta del Faro, at

the east (Figure 1b), to Punta Chiappa, a rocky spur over 200 m long and perpendicular to the coast, on its western edge (Figure 1c). In it, two deep coves open: in the first lies the small village of San Fruttuoso di Camogli, while the second, which has always been uninhabited despite having a freshwater source, is called Cala dell'Oro. During the latter half of the 10th century, a Romanesque abbey was built in San Fruttuoso, which, with subsequent structural additions and alterations, reached its current form during the 16th century. It housed a Benedictine monastery for a long time, which had significant influence during the entire medieval period. A large room in the building was chosen to house the tombs of the Doria family.

In 1984, the Doria Pamphilj family donated the complex to the Fondo Ambientale Italiano (FAI), the National Trust of Italy, which oversaw its complete renovation. At the entrance to the cove, at a depth of around 17 m, on the initiative of diving pioneer Duilio Marcante, a statue of Christ by Guido Galletti was installed in remembrance of Dario Gonzatti and all those lost to the sea [45,46].

The climate of Portofino can be defined, using the classification of Tomaselli et al. [47], as “meso-Mediterranean type B” that features a limited arid period (in practice just one month) and relatively high annual average rainfall (over 1200 mm), concentrated above all during autumn. This is a climate specific to central–eastern Liguria. According to the worldwide bioclimatic classification system, the Promontory of Portofino falls into the sub-Mediterranean temperate macrobioclimate. It features three levels—weak (prevalent), very weak, and strong—of the sub-Mediterraneity index (Isbm), with weakly euoceanic continentality index, lower mesotemperate and upper mesotemperate thermotypes, and lower humid and upper humid ombrotypes [48,49]. Based on the recordings of the Osservatorio Meteorico e Sismico (weather and seismic observatory) in Chiavari, the dominant winds are overall those from the first quadrant (Greek), followed by southerly ones (Sirocco, Libeccio), which are most common during the summer months.

The coastline is characterised by tall, rocky cliffs interspersed with “pocket beaches”, small beaches delimited by rocky spurs [50]. The former are the dominant formations in terms of their extent and importance in the landscape and include rocks of different types [51]. The best-known and most interesting from a naturalistic point of view is undoubtedly the conglomerate of Portofino, an Oligocene puddingstone that forms the front of the promontory [52–54]. Followed by this are the calcareous–marly foothills of Monte Antola, which extend from the Punta della Cervara towards the northeast, interspersed by short plains formed by the dry riverbeds of Santa Margherita Ligure and Rapallo. Lorenzo Pareto was the first to study the geology of the Portofino area, and he exhibited and depicted it in the famous “Descrizione di Genova e del Genovesato” [6] (Figure 1e). Just two years later, Pareto had very different matters to attend to when he became the first foreign minister of Carlo Alberto of Sardinia after the proclamation of the Albertine Statute. He found himself advising his sovereign in the most dramatic moment of its existence.

Along the promontory, the reefs reach a depth of 40–50 m, giving way to large, crumbing rocks and then sands and mud, which are partially biogenic. All around the promontory, at the base of the rock face, the seabed is formed primarily from detritus deriving from the erosion of the rocky coast and enriched by the calcareous remains of the coralligenous organisms above. The seafloor is noticeably muddy in the section of the sea between Punta del Faro and Santa Margherita Ligure. In contrast, on the seafloor of the continental shelf off the promontory, one finds, still evident, the deposits of the ancient fossil beaches dating back to the Versilian transgression following the last ice age of 20,000–18,000 years ago. In this sector, the Holocene sedimentary transgression, predominantly muddy, is minimal and does not cover the coastal deposits of the last ice-eustatic cycle. A role in the spread of sediment by the currents is undoubtedly played by the protrusion of Punta del Faro, which blocks the sedimentary flow from the Gulf of Tigullio. The continental shelf east of the promontory is subject to mud sedimentation, although less abundantly so. The seafloor stratigraphy of the continental shelf retains the characteristics of the sedimentation of the last five million years, particularly the

paleo-shelf ascribable to the advances and retreats of the sea, which also sees the contribution of subsidence of the sector.

The continental escarpment is characterised by abundant sedimentation due to matter carried from the coast, transported by the contouritic currents that flow along the margin. These deposits constitute a sedimentary escarpment of significant proportions, which presents shallow and deep gravitational phenomena eroded at the base by the currents of the Levante Canyon. Another characteristic element of the escarpment, particularly in its upper portion, is the presence of pockmarks, small depressions that are circular or lengthened by the current, with an average diameter of 100–300 m and sometimes also in the shape of small volcanoes, due to the escape of gas trapped in the sediment [55–57].

The surface hydrography of the region is not particularly developed, but the Rio Boate stream in Rapallo is worth considering. The Entella River, formed by the confluence of the Lavagna, Sturla, and Graveglia streams, flows out around 10 km east of Portofino and influences the eastern flank of the promontory. The Entella is one of Liguria's largest rivers in terms of the size of its catchment area (around 370 km²) and flow, which is, on average, less than 30 m³·s⁻¹ but can exceed 450 m³·s⁻¹ during floods (data from the Italian hydrographic service). In winter, the predominance of the northerly winds induces transport towards the open sea, while in summer, a certain stagnation of the coastal waters can occur [58].

2.2. Oceanography

The general Ligurian cyclonic circuit affects the circulation along the Portofino Promontory with an NW prevailing current moving at an average surface speed of 25 cm·s⁻¹ [59]. Its effects are discernible in winter when the coastal circulation intensifies significantly, giving rise to a current that exits the Gulf of Tigullio in a SE direction, brushing the coast at Portofino [60]. In summer, the weakening of the general circulation means that, in proximity to the coast, local anemometric and barometric conditions prevail; towards the end of July, a phenomenon typical of the Portofino Promontory often occurs, caused by heating of the upper layers of the water column: the formation of a coastal current heading towards the east [61].

Waves are linked to southerly winds [62], most affecting the southern side of the promontory [24,63]. Sea storms occur most frequently in November/December and March/April, while between May and September, long periods of calm usually prevail [56]. A storm of exceptional intensity caused severe damage to the coastal infrastructure and underwater environment in late October 2018 [64,65].

The coastal marine area off the Promontory of Portofino was added to the LTER—International Long Term Ecological Research network in 2007 (Marine Area of Portofino Promontory—LTER Code: LTER EU IT 015) [66] thanks to numerous successive studies in the region since the 1980s, and in particular, since 1999, when the systematic gathering of the main physical and chemical–biological variables along the water column, and of the main weather/climate drivers, began. This site's extensive set of physical, chemical, and biological data represents a powerful tool for reconstructing the seasonal cycles and differentiating regular and recurring models from occasional and exceptional events [67]. Data analysis highlighted an increase in the average temperature along the water column in recent years compared to the decade 1985–1995 and, in particular, a progressive increase in surface temperature in spring and autumn, leading to an extension of the warm period.

The area also features substantial interannual variability: significant temperature anomalies were recorded in the summer of 2003, in the autumn and spring of 2006–2007, and in the last decade, with higher surface temperatures than the average due to significant atmospheric temperature anomalies. This variability affects plankton populations, modifying the community's responses, particularly in the late spring. The area nevertheless retains the oligotrophic characteristics typical of the Ligurian Sea: indeed, while displaying evident interannual variability, the average phytoplankton biomass in the surface layer continues to remain low, with a decreasing trend in recent years [68].

3. Study of Habitats and Biocoenoses of the Portofino Promontory

3.1. Pelagic Environment, Plankton, and Pleuston

The first research into the plankton of the Gulf of Genoa was carried out by Brian [69,70] and subsequently by a group of researchers working at the Institute of Environmental Sciences of the University of Genoa, particularly Norberto della Croce [71,72], Tecla Sertorio [73], and Anna Maria Carli [74]. More specifically, as concerns the western part of the Gulf of Tigullio and the Portofino area, the first research studied the plankton communities of the ports of the Ligurian Sea and the northern Tyrrhenian Sea [75–78]. This body of research was resumed and added to by Sei et al. [79], who compared the plankton of the tourist port of Rapallo with that of Prelo Cove. The plankton community was described thoroughly during this study, reporting some Atlantic species never collected in Italian waters. This study observed that the plankton in ports was similar to that recovered in the relatively less urbanised Prelo Cove.

From 1985 to 1995, the Gulf of Tigullio was sampled fortnightly for surface plankton. Processing these data [80] demonstrated marked seasonality in the communities. The different species were grouped based on environmental parameters, which theoretically regulate their temporal trajectories. It was observed that atmospheric pressure, the speed and direction of the current, and the temperature are the main drivers of the plankton community in this area.

The analysis of time-series data of abundance and composition for the zooplankton community off Punta Faro (LTER site) for the period 2003–2022 determined an increase in total mesozooplankton and copepod abundance since 2019, following a decrease in the first part of the series, and in correspondence of an increase in temperature. This trend is accompanied by an increase in key organisms such as *Centropages typicus*, *Temora stylifera*, and *Clausocalanus* spp., detritivore and carnivore copepods (*Oncaea* spp. and *Corycaeus* spp.), and other typical carnivore groups (Chaetognatha) and gelatinous suspension-feeders (Thaliacea). In parallel, we also observe a decrease in meroplankton, Cladocera, Appendicularia, and *Oithona* spp. [80].

An ecosystem modelling approach, coupled with a subset of the zooplankton time-series, determined sharp differences between the years 2003–2005 and 2018–2019, both in terms of community composition and the system's functionality and structure. The analyses suggested a shift from a community dominated by herbivore copepods towards a system characterised by increased trophic contributions from detritus and microbial loop, and identified increased temperature and oligotrophy as possible mechanisms explaining this shift [81,82]. A particular focus was then given to the research into meroplankton, above all larvae of decapod crustaceans, with sampling performed in the Gulf of Tigullio and along the Portofino Promontory starting from the mid-1970s [83,84]. In three expeditions conducted in 1973–1974, 1983, and 1994–1995, Pessani and Salton [85] collected 44 species of larvae of brachyuran crustaceans. Pessani [86] described the larvae of 29 species of decapods, distinguishing groups of species characterised by different seasonality. The abundant strandings of the euphausiacean *Meganyctiphanes norvegica* along the beaches of the Gulf of Tigullio allowed various studies on the chemical composition (fatty acids and heavy metals) of this important planktonic component to be carried out [87–89].

Recently, the Random Forest machine learning algorithm was used to model copepod distributions from 1985 to 1986 in the Portofino Promontory ecosystem, producing the first abundance and distribution maps of the area [88]. Five copepod genera were studied across different trophic guilds, revealing seasonal habitat preferences and ecological fluctuations. This study shed light on the ecological niches and historical spatial dynamics of this important plankton group [90].

Some studies concentrated on pleuston, those groups of organisms that spend at least part of their lifecycle floating on the surface of the water and are partially exposed to the air. Among the best-known pleustonic animals is the hydrozoan *Velella velella*, the by-the-wind sailor, characterised by floating colonies with a chitinous sail, which allows them to be transported by the wind (Figure 5a). In spring, carried by the southerly winds,

large schools of *V. verella*, at the end of their life cycle, are transported from the open seas towards the Ligurian coast, where they are often involved in huge mass strandings. The mass stranding of 2016, which affected the whole of Liguria but was particularly intense along the beaches of Santa Margherita Ligure (with peaks of almost 115,000 colonies m^{-2}), was studied and quantified to better understand and describe the lifecycle of the species and the environmental dynamics leading to these strandings [91] (Figure 5b). Studying the associated fauna also allowed the detection of the nudibranch predator *Fiona pinnata* under some colonies. The association of this nudibranch with *Verella* had previously been highlighted by Brian [92] during the stranding of the 16th of May 1923 on the eastern Genoa coast (Figure 5c,d) and by Issel [93]. In May 2017, the Ligurian coast was also affected by an exceptional stranding of the pleustonic gastropod *Janthina pallida*, a typical predator of *V. verella*. Although various species of molluscs are typically associated with the strandings of by-the-wind sailors, the event involved almost exclusively the gastropod, with peaks of over 2000 examples per m^2 (Figure 5e,f). The presence of some specimens of the Atlantic barnacle *Dosima fascicularis* (Figure 5g,h) amongst the gastropods led to the hypothesis of an Atlantic origin of the pleustonic aggregation. The beaches of Rapallo, Santa Margherita Ligure, and Paraggi were among those most interested in the phenomenon [94]. Analyses of the genetic variability of stranded *V. verella* and *J. pallida* in the springs of 2016 and 2017 at ten locations along the Ligurian and Tyrrhenian seas (including Santa Margherita Ligure) showed for the first time the existence of panmictic Mediterranean populations [95].

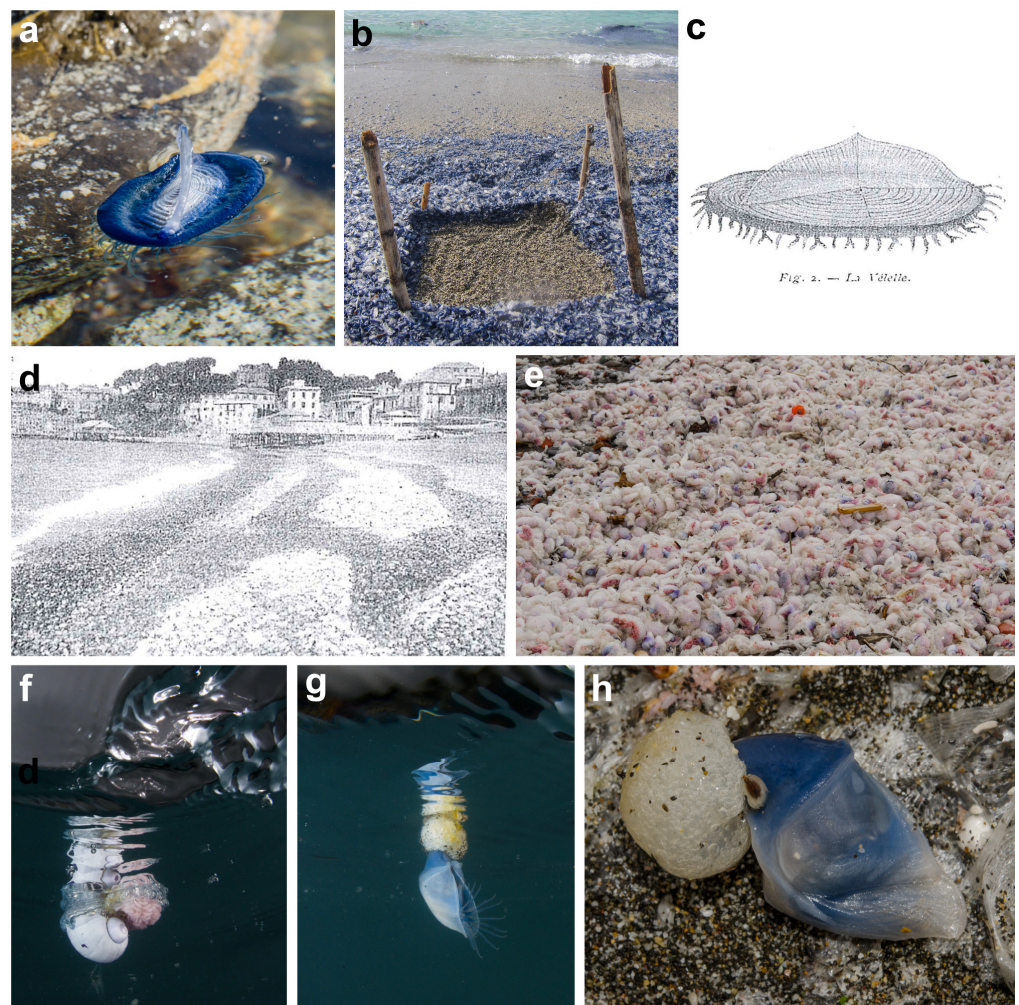


Figure 5. Pleustonic organisms. (a) A colony of the pleustonic hydrozoan *Verella verella*, known as by-the-wind sailor, photographed in front of the Portofino coast; (b) seasonal mass stranding of

V. verella along the coast of Santa Margherita Ligure; (c) drawing of a colony of *V. verella* (from [92]); (d) photograph of a huge stranding, along Sturla beach, occurred in 1923 (from [92]); (e) tens of thousands of specimens of the pleustonic gastropod *Janthina pallida* stranded on the Sturla beach in 2017; (f) a specimen of *J. pallida* and (g) the rare Atlantic goose barnacle *Dosima fascicularis* pictured in the port of Bogliasco and (h) in the 2017 stranding.

3.2. Rocky Coastal Areas

Beneath the surface, the promontory descends with sub-vertical rock walls and extensive crumbling rocks, which, below 20–25 m in depth, host coralligenous bioconstructions. The bathymetric belt closest to the surface, colonised by photophilic populations, has been subject to numerous naturalistic studies over the years.

Studies of the underwater cliffs of the Promontory of Portofino began in 1956 thanks to the partnership between the Centro Subacqueo di Nervi, led by Duilio Marcante, and the Genoa Museum of Natural History, headed by Enrico Tortonese [96], thus representing one of the first examples in Italy of the participation of recreational divers in marine scientific research [22]. The divers made observations (and collected samples) as they rose along the vertical profile of the cliffs from around 40 m depth to the surface [26], laying the foundations for the so-called vertical transects, which would become the standard for underwater bionomy research [97] and cartography [98].

Tortonese [24,25,99] dedicated himself to inventories of flora and fauna, separated by site and bathymetric zone. He investigated first-hand the populations of the foreshore and organised the information obtained by the divers into four bathymetric layers: 0–10 m, 10–20 m, 20–30 m, and 30–40 m. In the uppermost fringe of the infralittoral zone, he described a facies of *Ericaria amentacea* followed—in the first ten metres in depth—by algal populations he defined as luxuriant. *E. amentacea* still has an extensive presence in the infralittoral fringe of the Portofino Promontory (Figure 6a,b), with an average percent dominance of around 50% [100]. Between 10 m and 20 m, the gorgonian *Eunicella singularis* joined the algae. Between 20 m and 30 m, the algae were primarily represented by sciaphilous species, while there were numerous sponges, including *Calyx nicaeensis* and large numbers of the gorgonian *E. cavolini*. In the deepest layer, between 30 m and 40 m, the fauna predominated significantly over the flora, composed exclusively of sciaphilous algae; poriferans, bryozoans, and gorgonians were the most represented groups: the most eye-catching species were the poriferan *Spongia lamella*, the red coral *Corallium rubrum*, the gorgonian *Paramuricea clavata*, the bryozoans *Reteporella grimaldii* and *Smittina cervicornis*, and the starfish *Hacelia attenuata*. The same author highlighted the importance of the steepness of the substrate—as well as its depth—in conditioning the distribution of the populations. Based on Tortonese publications and his own underwater observations, Melegari [30] distinguished the following “environments”: (i) of *Codium bursa* and *Paracentrotus lividus*, between sea level and 8–10 m in depth; (ii) of *E. singularis*, from around 10 m to 20–25 m; (iii) of *Eunicella cavolini*, between 20–25 m and 30–40 m; and (iv) of *Paramuricea clavata* and *Corallium rubrum*, from 30–35 m to 40–60 m in depth.

Vertical transects like those already performed, following Tortonese instructions, by the divers of the Centro Subacqueo di Nervi in the 1950s, were repeated between 1991 and 1993 [101,102] and between 2008 and 2013 [103], and continue to be performed today to carry forward this important, and extremely rare, historical set of information. Initially, the communities proved to be similar to those described over thirty years before. Yet, species that Tortonese had not found were later reported as common, such as *Pseudochlorodesmis furcellata* and *Zanardinia typus*. On the contrary, some previously abundant species disappeared, for example, the sponge *C. nicaeensis* and the bivalve *Spondylus gaederopus*. The disappearance of the latter was probably due to disease [104], while no explanation was found for the disappearance of the sponge [102], which was still present in the late 1970s elsewhere in the region [105].

On the other hand, the 2008–2013 surveys highlighted much more dramatic changes, which continue to be observed today. In the algal populations, the large erect species belonging to the order Fucales, which were still abundant in the 1980s [56,106], gave way

to algal turfs with little vertical development: this loss of volume negatively influenced the diversity of the minute fauna, which lived amongst the algal fronds [107]. These algal turfs have been proven to favour the settlement of the alien alga *Caulerpa cylindracea*, which invaded the submerged cliffs of Portofino from the early 2000s onwards, to take root; above all in late summer, the coverage of the substrate reaches very high values (up to 25%) between 1 m and 45 m in depths, with the highest levels around 20 m [108,109]. No other species in Portofino has ever shown such abundance and ubiquitousness, although a decrease has been recently observed [110]. The infra- and circalittoral macroalgal diversity has been studied multiple times over the years, and information on the subject was gathered by Mangialajo et al. [111].



Figure 6. Algal reforestation. (a) An algal fringe dominated by *Ericaria amentacea*; (b) a close-up view of the algae; (c) one of the terracotta supports with young propagules used for the restoration.

An additional driver of change is linked to the ever more frequent explosions of mucilage on the rocky cliffs of the promontory, which are related to the increase in water temperatures [108]. During the event of 2003, the mucilage aggregates were formed by the free-living form of the Phaeophyceae *Acinetospora crinita* [112]. A severe event occurring in the summer of 2018 caused significant impacts on the composition of the benthic communities, above all below 20 m depth, where it also provoked the widespread death of various colonies of *Paramuricea clavata* [112–114].

Some species, stenothermic but relatively eurybathic, dropped to lower depths, maybe due to the increased thermal variability of shallow waters [115]: among the many ex-

amples, there is the brown alga *Dictyopteris polypodioides*, the poriferan *Spongia officinalis*, the bryozoan *Reteporella grimaldii*, and the ascidians *Halocynthia papillosa* and *Microcosmus sabatieri* [106]. Similarly, the anthozoan *Alcyonium coralloides*, which has now disappeared from depths reachable by recreational divers, is still present at 70–150 m [116]. The same may be true for the catshark *Scyliorhinus canicula*, which in the 1970s was relatively common at depths of 30–40 m, and its eggs could easily be seen attached to the branches of gorgonians; since the 1990s, it has not been sighted by recreational SCUBA divers, but can still, although rarely, be found at greater depths [106].

Corriero et al. [117] compared samples of the bivalve *Arca noae* collected in Portofino with samples from Sicily, aiming to understand the symbiosis between the bivalve and the sponge *Crambe crambe*. Betti et al. [118] analysed specimens belonging to eighteen species of heterobranchs, aiming to determine the presence of biofluorescence in these animals and the ecological role of the phenomenon. Galli et al. [119] recently studied the sea spider fauna between the surface and 5 m depth.

Schiaparelli et al. [120] studied the penetration of boring bivalves, particularly *Gastrochaena dubia*, in the different types of calcareous substrates, both mineral and biogenic, present in the Portofino cliffs. Regarding the intertidal portion of the rocks, Pannacciulli and Relini [121] studied the *Chthamalus* populations of Punta Chiappa within the European project (EUROROCK MASS-CT95-0012). They provided information on the vertical distribution of *Chthamalus stellatus* and *C. montagui*, comparing them with data from other areas of Liguria and the Gulf of Trieste.

The MPA was recently the setting for a conservation and environmental restoration project focused on the introduction of the rare *Patella ferruginea*. The project, in addition to allowing the development and application of a controlled reproduction protocol of the species [122], allowed numerous wild individuals to be found along the Ligurian coast, including a dozen specimens found along the Portofino Promontory [123]. The findings are of great relevance because the species was long considered extinct in the area and, more generally, along the peninsular coastline of Italy. Once again, from the Portofino reef, algal thalli of *Ericaria amentacea* were gathered, which, appropriately propagated in the laboratory, were used for reforestation in the Cinque Terre MPA [124,125] (Figure 6c). The Outdoor Portofino Society conducted Citizen Science activities in partnership with the University of Genoa to sensitise and allow outdoor tourists to participate in the monitoring activities of the ecological restoration of *E. amentacea*. A demonstration was set up on the cliffs of Paraggi Castle for the purpose.

For several years, the seafloor of Cala dell'Oro, in the strictly protected zone of the MPA, hosted an experimental commercial sponge farm [126].

3.3. Seagrass Meadows

Posidonia oceanica is the most widespread seagrass along the Portofino Promontory (Figure 7a,b), holding a crucial ecological role and was already considered by scientists at the end of the 19th century (Figure 7d). When Issel [14,17] studied the meadows of *P. oceanica* on the eastern flank of the Portofino Promontory for the first time, he hoped that a map of what he called the “green belt” along the entire Ligurian coast would be created. Thanks to technological advances, his wish was realised only seventy years later [127].

The maps created in 1990 showed that the underwater seagrass meadows of the Portofino Promontory were made up of *P. oceanica* and *Cymodocea nodosa* (Figure 7c). All three sides of the promontory contain *P. oceanica* meadows. The most extensive area borders the western flank: it runs from the section below San Rocco to Porto Pidocchio for over 25 ha. Prior information on the presence of this meadow is contained in Pastorino and Canu [128], Melegari [30], and Morri et al. [58]. More limited formations of *P. oceanica* can be found on the southerly front of the promontory and are found (1) in the cove to the east of Punta della Chiappa, (2) in Cala dell'Oro, and (3) in Cala di San Fruttuoso; elsewhere, much less prominent stands of this seagrass appear, often on rocks [30]. The San Fruttuoso meadow, previously mentioned by Tortonese [25], is the largest but does

not exceed 3 ha. The small meadow of Cala dell'Oro is mentioned by Tortonese [24], Matricardi [129], and Boyer et al. [130].

On the eastern side of the Portofino Promontory, a tiny *P. oceanica* meadow is found in Cala Niasca, on the southern side of Paraggi Cove. The central part of the cove is, on the other hand, occupied by a small *C. nodosa* meadow. Between Cervara Abbey and Punta del Pedale, a *P. oceanica* meadow extends for around 13 ha. This meadow was probably part of a continuous belt that ran parallel to the coast along the entire western side of the Gulf of Tigullio. Between the tip of Portofino and Santa Margherita, Issel enumerated seven of these meadows: (1) Cala dell'Oliva (or Cala dell'Olivetta); (2) the southern extremity of the port of Portofino; (3) the cove below the Piccolo Hotel in Portofino; (4) Cala Niasca; (5) the inlet to the north of Cervara Abbey; (6) the coast to the south of Punta del Pedale; and (7) the inlet to the north of Punta Bagno delle Donne. From his brief descriptions, we can deduce that the meadows were luxuriant (above all that of Niasca), with leaves 80–120 cm in length and with frequent blooming “in late summer”; from the description that he gave of the term “surface”, it derives that their upper limit was relatively near to the coast and probably gave rise to surfacing formations that have now disappeared.

Between December 1982 and May 1983, Bavestrello [131] made a new series of observations during dives to the same meadows described by Issel to be able to assess any modifications (Figure 7e). Comparing the results obtained with Issel's notes, Bavestrello [131] and Balduzzi et al. [132] reported, first and foremost, that all the meadows listed in 1912 still existed. Considerable retreats were reported in the meadows located in the port of Portofino and the cove below the Piccolo Hotel. Similarly, the Cala Niasca meadow did not rise beyond 2 m in depth, while Issel (1912) [17] described the leaves, reaching the surface of the water, as “longer and more luxuriant than in other nearby locations”. The meadows of Punta del Pedale and Punta Bagno delle Donne were suffocated in their shallow-water range by dumped sediment [133], and, as such, their upper limit was lowered by around 3 m. Bavestrello [131] found that the meadows near Punta del Pedale and Punta Bagno delle Donne, which Issel considered distinct, were the extremities of a single meadow that ran parallel to the coast. A small meadow of *C. nodosa*, of no more than 7 ha, was present in the natural harbour of Santa Margherita Ligure. On the seabed between Punta Pagana, which delimits the entry to the port of Santa Margherita Ligure to the northeast, and the start of the jetty of the tourist port of Rapallo, there is a *P. oceanica* meadow of around 16 ha. The meadow covers the seafloor of Prelo Cove almost uniformly (Figure 7a,f,g). In San Michele di Pagana Cove, the meadow is split by a channel perpendicular to the beach. The upper limit nearly reaches the shore in the Prelo Cove and is kept inshore in the two portions of meadow in the cove of San Michele to the east. Almost 3 ha of dead matte are found at 18 m off Punta Pagana. The first bibliographic mention of this meadow is found in Tortonese [99], who stated that in the Gulf of Tigullio, “*Posidonia oceanica* . . . forms rather thick meadows, for example, in the Prelo Cove”. The author also states that in 1959, the population of the meadows was gathered by dredging performed between 2 and 22 m (which allows us to assume that the lower depth corresponded to the lower limit of the meadow at the time). A few lines later, he added, “Old fishermen say that the *Posidonia* meadows were once much more extensive”. According to Bavestrello [131], the Prelo meadow is the largest on the eastern coast of the Portofino Promontory. The most noteworthy part comprises two vast areas of matte located between 0.5 and 1 m in depth: the leaves of the plants touch the surface of the water at low tide in summer; the lower limit is at a depth of 9 m.

Both the mapping carried out in 1990 and the underwater observations made by [131] and subsequent authors highlighted the regressive status of the promontory's meadows. This regression, however, was difficult to quantify on maps of a scale of 1:25,000. A 1:2000 scale map was made in 2005 [134] and, combined with the application of reference models [135], allowed us to describe the regression state of these meadows adequately. In total, *P. oceanica* covers an area of 43 ha around the Promontory of Portofino, corresponding to 30% of the entire area. In the southern part of the promontory, the meadow between

Camogli and Porto Pidocchio extends for 29.8 ha, from 3 m down to a maximum depth of 33 m, with a lower limit gradually retreating towards Camogli and clearly in retreat towards Porto Pidocchio. The area of dead matte, present primarily around the lower limits, covers a surface of around 3 ha (10% of the total surface area of the meadow) and bears witness to an average linear retreat of the lower limit of around 20 m. The small meadows on the southern side of the promontory, between Punta Chiappa and Cala dell'Oro inclusive, do not show any sign of regression. In the eastern portion of the promontory, the largest meadow is located between Punta del Pedale and Punta Cervara (8.5 ha); more limited formations are found between the cove of Paraggi and Cala del Prato (3.8 ha) and between Cala del Prato and Punta Torretta (1.2 ha). The meadow between Punta del Pedale and Punta Cervara extends from 8 m down to a maximum depth of 15 m, with a lower limit in clear regression, characterised by areas of dead matte (2.2 ha, 26% of the seagrass meadow), which bears witness to an average linear retreat of this limit of around 40 m. Around the upper limit, the areas of dead matte surveyed (1.2 ha, 14% of the meadow) suggest a linear retreat of around 125 m towards Punta del Pedale and around 35 m towards Punta Cervara. In general, the meadow of the western side of the Portofino Promontory shows better health than that of the eastern side: in the western portion, around 3 ha (10%) of the original surface area of the Neptune grass meadow were lost, corresponding only to the lower limit, while in the eastern portion around 3.2 ha (26.2%) were lost at the lower limit and 2.5 ha (20.4%) at the upper limit. The main causes of the regression of the lower limits on both sides of the promontory are ascribable to the increased turbidity of the waters and the mechanical damages inflicted by the anchoring of recreational vessels.

The regression of the upper limits, recorded in the meadows on the eastern side, is essentially ascribable to the annual beach nourishment and coastal works [136–143]. The adoption of specific ecological indicators and indices allowed for the evaluation of the health status of these meadows and to follow their evolution over time [139,144–148]. The flowering of *P. oceanica* was observed several times [58,130,131,149] (Figure 7b); Montefalcone et al. [150] determined an interval of around ten years, coinciding with that of sunspots: autumn 1973, 1983, 1994, 2003, and 2012 (the latter following fruiting in May 2013). Although the sexual reproduction of this plant seems to be highly variable, both in terms of space and time, the prediction of Montefalcone et al. [150] of a future mass flowering event in the northwestern Mediterranean in 2022 turned out to be correct, with mass flowering reported from September 2022 in most Ligurian meadows (including those of the Portofino Promontory) and the meadows of the northwestern Mediterranean Sea.

The meadow of Prelo is the most extensively studied (Figure 7a,f,g). Various organisms associated with the *P. oceanica* meadows were investigated (Figure 7h): poriferans [151], hydrozoans [152,153], bryozoans [154,155], and the entire epiphyte community [156–158]. Change in meadow conditions was documented over time [104,130,136,137,154,159–162]. Its regression began a few years after the observations of Issel [14,17] due to the construction of a 12 m long jetty for pleasure vessels, which altered the hydrodynamic conditions of the entire inlet, generating strong backflow currents that caused erosion of the matte and altered the sediment balance [162]. Towards the end of the 1950s, the areas of dead matte were colonised by the green alga *Caulerpa prolifera*. *C. prolifera* disappeared in 1979, making way for *Cymodocea nodosa* [131], which persisted at least until 1986 [58]. In this phase, the dynamics of the meadow apparently followed a secondary succession, suggesting a possible recovery in the following years.

In 1991, however, the situation reversed: *C. nodosa* disappeared, and *C. prolifera* reappeared [163]. Being a thermophilic species, *C. prolifera* may have been encouraged by the warming of the waters in the 1980s and 1990s, remaining abundant until at least 2004 [164]. Despite the persistence of high temperatures, the investigations of recent years have not found *C. prolifera* again but rather the invasive species of the same genus, *C. cylindracea* [165], as predicted by the phase shift model of Montefalcone et al. [144] and contrary to both the successional and warming hypotheses [104]. Since the early 1970s, in the Prelo Cove and San Michele di Pagana Cove, at the beginning of June each year,

an extensive system of chains is laid on the seabed, which is then removed again in early October, covering a total surface area of over 10 m² in each cove with various surface buoys allowing for mooring of recreational vessels. This system of chains, which is not fastened to the seafloor and so was free to move and drag the plants, caused the most recent regression in both areas; in the Prelo Cove alone, it was estimated that over 2800 m² of meadow was destroyed in the last few decades [164]. Each year, every linear metre of chain laid on the seabed causes the loss of 2.5–3 m² of meadow. The exceptional storm of October 2018 severely damaged the Prelo meadow, causing erosion and burial, halving the seafloor cover, and further worsening its already precarious health status [165].

Working on core samples of sediment entrapped in the mat of this meadow, Bertolino et al. [166] evaluated the number of spicules of poriferans present at the different levels, hypothesising that the number of spicules in the sediment was proportional to the biomass of sponges existing in the surrounding area. These data suggested that the Prelo Bay sponge community had remained constant for a long time. At the same time, a significant reduction was evident in conjunction with the rapid urban development that occurred along the Ligurian coast following the Second World War, particularly in the 1960s.

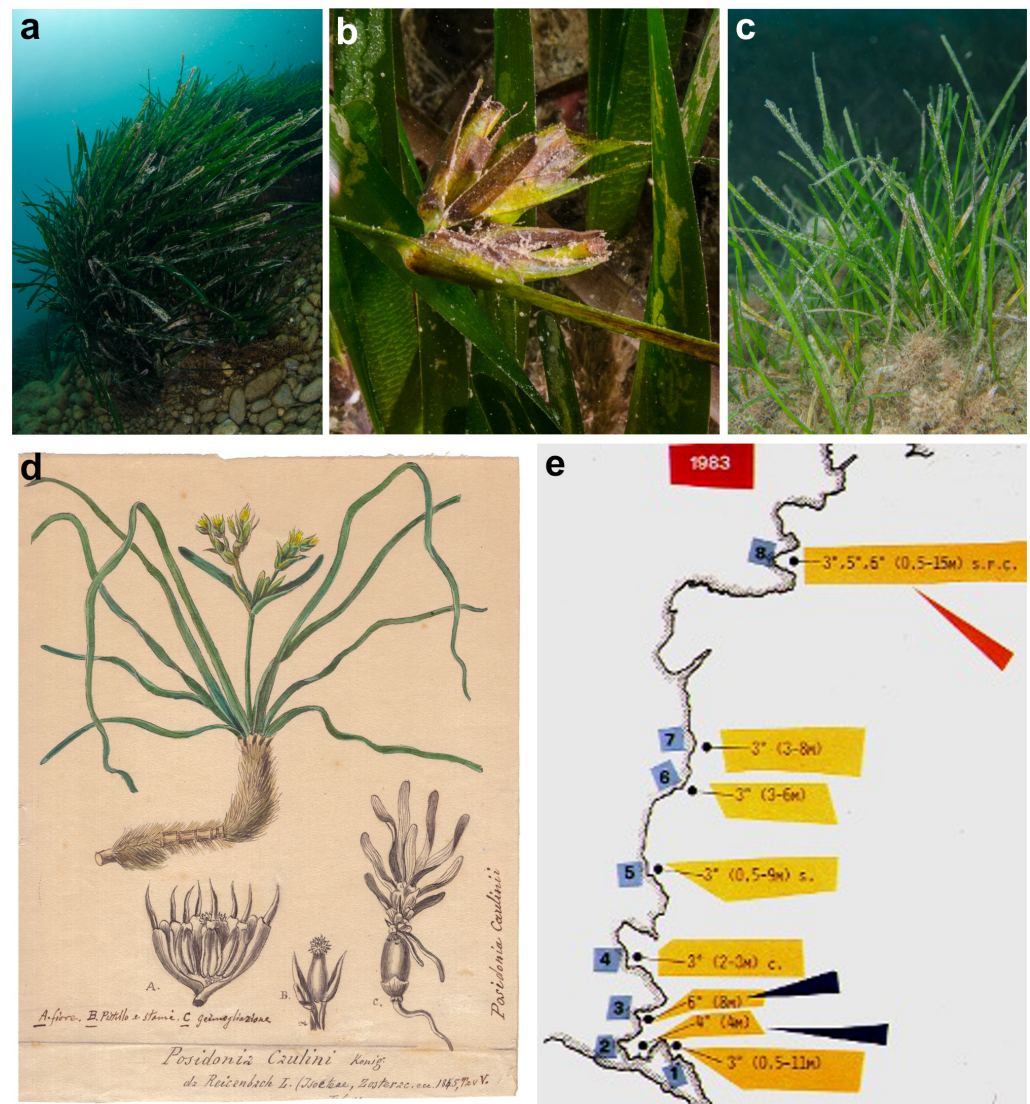


Figure 7. Cont.

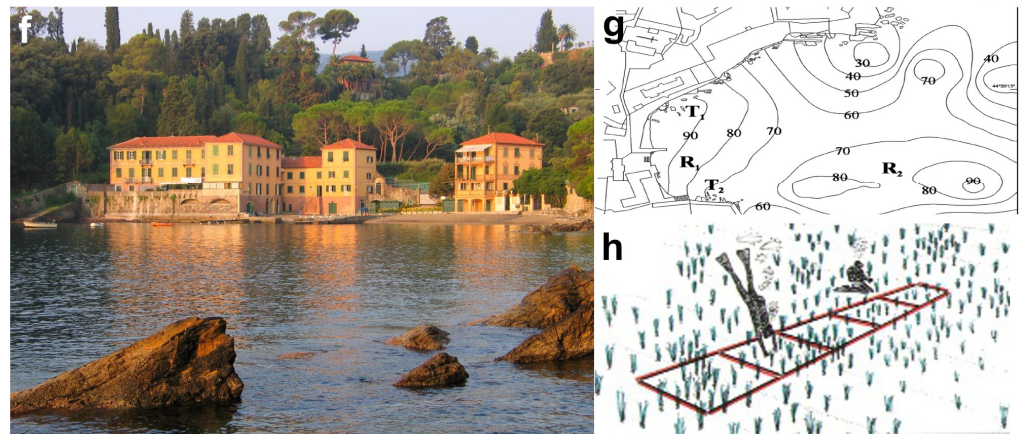


Figure 7. *Posidonia* meadows. (a) *Posidonia oceanica* in Paraggi Bay; (b) detail of an inflorescence; (c) *Cymodocea nodosa* along the eastern front of the promontory; (d) water–colour drawing of *P. oceanica* by C. Parona (e) diagram of the *P. oceanica* meadows visited by Issel [17] on the western side of the Tigullio Gulf and studied again by Bavestrello [131]; (f) the Bay of Prelo, home to a long-studied meadow; (g) isolines of the cover of *P. oceanica* in the Prelo Bay (T, matte terraces and R, high cover areas) (from [136]); (h) scheme by Roberto Pronzato illustrating the semi-quantitative method used to study the fauna associated with rhizomes and leaves.

In June 2022, a regressing portion of the meadow of Punta del Pedale, between 9 and 13 m, underwent a reforestation project (Figure 8a,b). This project restored 100 m² of seabed covered with dead matte, with around 2000 shoots found free on the seafloor (likely uprooted by anchoring). The shoots were anchored onto a biomatte made from natural coconut fibre using a modern technique (Figure 8a,b).



Figure 8. *Cont.*



Figure 8. *Posidonia oceanica* reforestation. (a) Reforestation activities of the *Posidonia oceanica* meadow in Punta Pedale; (b) anchoring the cuttings to the biomattes.

3.4. Caves

Marine caves are priority habitats that must be protected under the European Union Habitats Directive and the Mediterranean Action Plan of the United Nations Environment Programme [167]. The rocky cliffs of the Portofino Promontory house numerous marine caves. These are essentially cavities formed by rockfalls and/or marine erosion, while speleothems are very limited or absent due to the geological nature of the rock. Most of the sea caves of Liguria are located in karst areas and originate from the ingress of the sea into pre-existing terrestrial cavities [168].

Some of Portofino's caves reach the surface and include an aerial portion; almost all of them are listed in the Ligurian Cave Registry and are cited in the volume by Bixio [169]. Among the best-known semi-submerged caves are the Cala dell'Olivetta Tunnel, the Chiesa di S. Giorgio Cave, and the Colombara Cave, also known as Tortonese Cave. Punta Carega hosts, in addition to the Tortonese Cave mentioned above, the Armato Cave and the Marcante Cave; on the eastern side of Punta Chiappa is the spectacular Gamberi Cave; on the north side of Punta di Paraggi are the Castello di Paraggi Cave and Presepe Grotto; at the site named Roccia del Dragone is the Dragone Tunnel; other underwater caves well known to divers are found at Testa del Leone and Scoglio del Raviolo, but ravines, ceilings, passages, and cavities of smaller size are spread all around the promontory.

These caves have yet to be the subject of detailed studies. Tortonese [24,25] mentioned the Marcante Cave, illustrating its location thanks to a model of Punta Carega made by Duilio Marcante (Figure 9a). Bavestrello et al. [170] studied the population of red coral (*Corallium rubrum*) covering this cave's vault. Sarà [37,171] studied the poriferans of the Cala dell'Olivetta Tunnel, providing a general description of the cavity (which the author refers to as a "corridor") with a plan and a perspective view. Bianchi and Morri [172] carried out a topographical and bionomic survey of the Castello di Paraggi Cave and

described it. The cave consisted of a large vertical split in the rock cliff below Castello di Paraggi, in which, at around 7 m depth, a narrow passage was wedged for 280° N, terminating in a funnel-shaped chamber that reached around 15 m. The wall before the entrance featured a population of coralligenous affinity, dominated by *Eunicella cavolini*; following this, there was a narrow belt with large sponges, ascidians, and hydrozoans, and one with encrusting sponges, while most of the cavity showed virtually bare walls, essentially colonised by serpulids. The fish *Sciaena umbra* and *Apogon imberbis* and the decapod crustaceans *Plesionika narval* and *Palaemon serratus* were among the motile fauna. In these cavities, Bavestrello and Sarà [173] studied the different morphologies of the sponge *Petrosia ficiformis* along the hydrodynamic and light gradients.

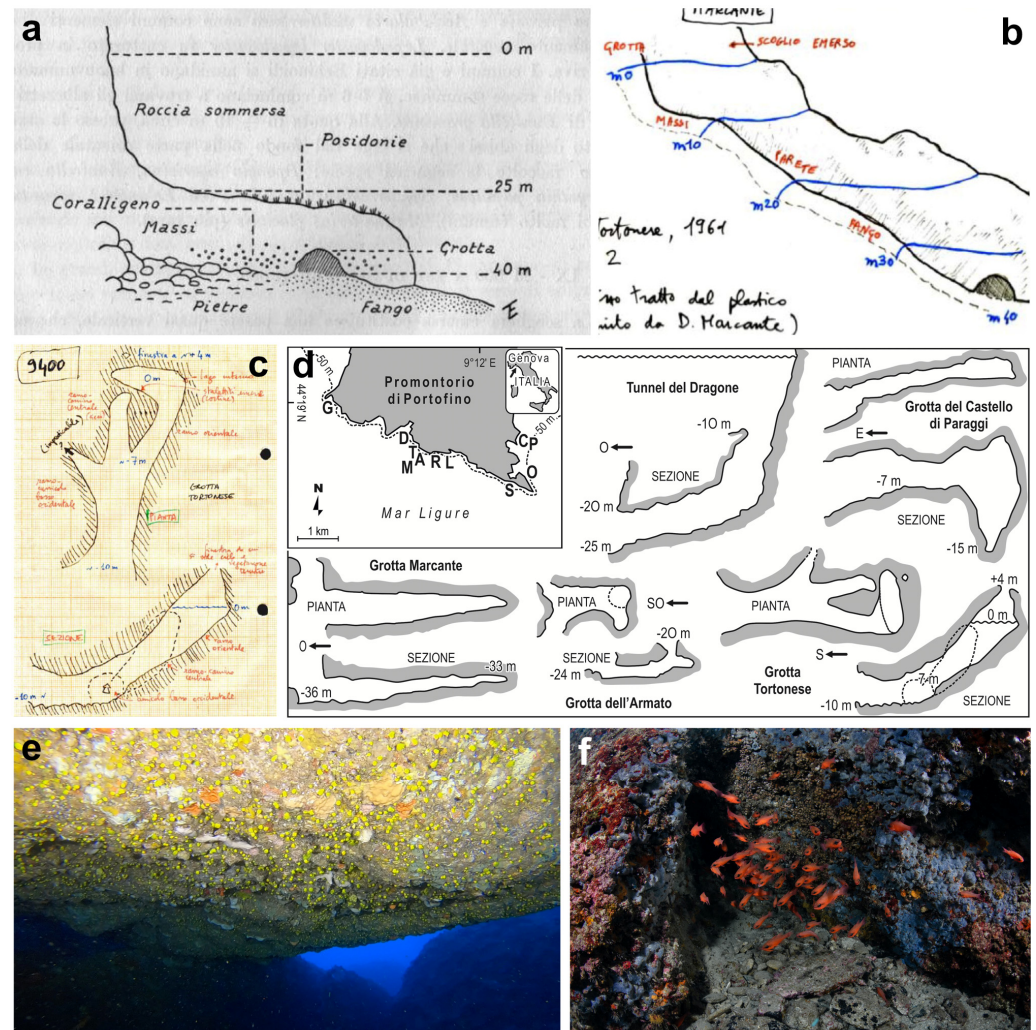


Figure 9. Caves. (a) Diagram of a portion of Punta Carega with the Marcante Cave [24]; (b) profile of the Marcante Cave from [25] re-drawn by Carlo Nike Bianchi; (c) survey carried out by Carlo Nike Bianchi of the Tortonese Cave; (d) location of the main marine caves of the Portofino Promontory, and diagrams of some of them (from [174]); (e) the Dragone Tunnel and some typical sciaphilic organisms, such as the scleractinians *Leptopsammia pruvoti* and *Madracis pharensis*, and (f) the cardinal fish *Apogon imberbis*.

Bianchi and Morri [172] concisely described also the Presepe Grotto in Paraggi, which is close to the preceding one. It is a small cavity that opens at about 20 m depth into a wall dominated by *Flabellia petiolata* and other sciaphilous algae. Despite much fine sediment, most of the cave did not appear confined and hosted abundant large sponges of various species; only in some small terminal niches did the biological coverage decrease significantly. Amongst the mobile fauna, the decapods *P. narval* and *Stenopus spinosus*

and the fish *Thorogobius ephippiatus* stood out due to their abundance. Visits from squids (*Loligo vulgaris*) were evidenced by the typical oothecae hanging from the ceiling.

Recent information on some of the underwater sea caves of the Portofino Promontory can be found in Bianchi et al. [174] and Montefalcone et al. [175] (Figure 9b–d). The Marcante Cave opens at around 36 m on the western side of Punta Carega. It is a wedge-shaped cavity about 20 m long with a floor sloping upward to about 33 m. The portion closest to the entrance hosted a facies of *C. rubrum* and *Leptopsammia pruvoti*, while the terminal section featured virtually bare rock, with just a few serpulids. The Armato Cave is a tunnel-like passage between rocks, proceeding first horizontally and then vertically, for a total length of around 12 m, and was found between 24 m and 20 m in depth. The entrance, facing southwest, was characterised by the hydrozoan *Eudendrium armatum*, while most of the cavity was populated by large and encrusting sponges; a facies of confined cave, with bare rock and serpulids, was observed in a niche on the eastern side of the tunnel. Moray eels (*Muraena helena*) and shrimps (*Lysmata seticaudata*) were common near the entrance. The Tortonese Cave opens at around 10 m on the west Punta Carega, continuing northward for around 10 m inside the split in the rock, rising to around 7 m in depth. Here, the cave splits into three branches: the western one soon becomes impenetrable, the central one has a dead end, while the eastern one rises to an internal “lake” with a vast air chamber with a window on the vault (at a height of around 4 m), through which terrestrial vegetation can be seen. The walls of this chamber present some modest speleothems due to the percolation of meteoric water. The fauna of the cave was very limited, and the rock was almost bare: the initial part was characterised by the zoanthid *Parazoanthus axinellae* and the calcareous sponge *Ascandra contorta*.

Dragone Tunnel opens towards the west at a depth of 20–25 m and then rises obliquely up to around 10 m (Figure 9e,f). Various species were encountered: the sponge *P. ficiformis*, the red coral *C. rubrum*, the scleractinians *L. pruvoti*, *Polycyathus muellerae*, and *Madracis pharensis*, and the forkbeard *Phycis phycis*. Gamberi Cave opens at a depth of around 37 m and penetrates obliquely into the rock for around 15 m. The floor is muddy, and sponges and serpulids colonise the walls. The cavity runs north–south and terminates at a dead end. The name (“Shrimp Cave”) derives from the extraordinary abundance of the shrimp *P. narval*. Spiny lobsters (*Palinurus elephas*), clawed or common lobsters (*Homarus gammarus*), and forkbeards (*P. phycis*) can also be found there.

The other caves of the promontory have never been investigated, although many have been documented by Ferrari [176]. At the Scoglio del Raviolo cliffs, there is a tunnel between 33 m and 27 m, formed by a passage between large rock masses, and a dead-end cavity at 35 m; both are around 10 m long. Further west, near the site known as Testa del Leone, a small wide and low cavity develops between 7 m and 5 m populated by demosponges (*Chondrosia reniformis* and *P. ficiformis*) on the rocky floor, encrusting sponges on the walls, and the scleractinian *L. pruvoti* on the ceiling; towards the dead end, the percolation of meteoric water creates a characteristic permanent halocline, with a layer of fresh water floating on the seawater. In the rocks below Chiesa di San Giorgio, a cave opens at a depth of around 10 m, featuring a large entrance partly blocked by a rock fall: about 15 m long, it continues to the surface.

In 2020, the Marine Protected Area of Portofino and DiSTAV monitored the impact of divers in 6 of the Portofino Promontory’s caves, characterising the biocoenoses through a visual census and identifying a high level of vulnerability.

3.5. Coralligenous Reefs

Coralligenous reefs are bioconstructions formed by coralline algae and animals with calcareous skeletons in low-light conditions [177] (Figure 10a). These bioconstructions significantly increase the three-dimensional nature of the substrate and, under the action of boring organisms, are full of cavities of various sizes. This structural complexity favours biodiversity, making the algal reef one of the most interesting from the point of view of scientific research and recreational diving. Bertolino et al. [178] described the population

of sponges of some blocks of coralligenous collected in the Portofino MPA (Figure 10b), finding 71 species, including either large or encrusting sponges and boring and infiltrating ones. It was demonstrated that the number of species and the biomass of the endobiotic community is 6–10 times greater than that of the epibiotic community [179]. In addition, thanks to the study conducted in Portofino on substrate preferences of the various species of boring sponges, it has been suggested that the action of these organisms determines the prevalence of carbonate of algal origin in the bioconstructions [180]. In 2002, Schiaparelli described the new genus *Petalopoma* and the new species *Petalopoma elisabettae* of siliquariid molluscs that were found to live in deep crevices of the coralligenous bioconstructions off Punta del Faro, embedded in the sponge *Haliclona* sp. [181].

The study of the siliceous spicules left inside the coralligenous structure (Figure 10c) by dead endolithic sponges allowed us to trace the evolution of sponge populations along a time scale of thousands of years [182].

On the coralligenous cliff of Paraggi and the southern front of the promontory, Bavestrello et al. [183,184] assessed the slow crumbling of the bioconstruction, which rolls down along the cliff and enriches the seabed detritus. This study was carried out via special sediment traps adhering to the rock wall (Figure 10d,e), which, besides detritus, also capture various mobile organisms. The data obtained allowed us to describe the seasonal variations of some small hermit crabs of the genus *Pagurus* [185].

Although the spatial distribution of the coralligenous reef and its bathymetric extension on the promontory had been identified as far back as the late 1950s [24,25] and subsequently updated by the regional bionomic cartography [186], specific studies for the Portofino area have only been carried out this century under the impetus of the Marine Strategy Framework Directive (MSFD 2008/56/EC), which introduced the concept of “seafloor integrity”, meaning integrity at a level that guarantees the safeguarding of the structure and the function of the ecosystems. The mapping of the Ligurian coralligenous reefs based on acoustic methods and diving surveys highlighted four facies for the Portofino Promontory characterised by various species of gorgonians: *Paramuricea clavata*, *Corallium rubrum*, *Eunicella cavolini*, and *Leptogorgia sarmentosa* [187]; the coralligenous community was then compared with that of other four Italian locations by Valisano et al. [188], who showed its noteworthy structure, high evenness and, at the same time, the high level of impact by fishing gears.

The recent application of ecological indices has allowed the assessment of the health status of the Portofino coralligenous reefs, which exhibit values of environmental quality ranging from high (e.g., Altare, Torretta) to moderate (e.g., Secca Gonzatti, Punta del Faro) [189–193].

Oprandi et al. [194] highlighted that the percent cover of habitat-forming organisms in the basal layer of the coralligenous reefs was significantly lower in zones of partial protection compared to the strictly protected zones. Nevertheless, the level of sedimentation, rather than the level of protection, was the main factor that influenced bioconstruction in this habitat.

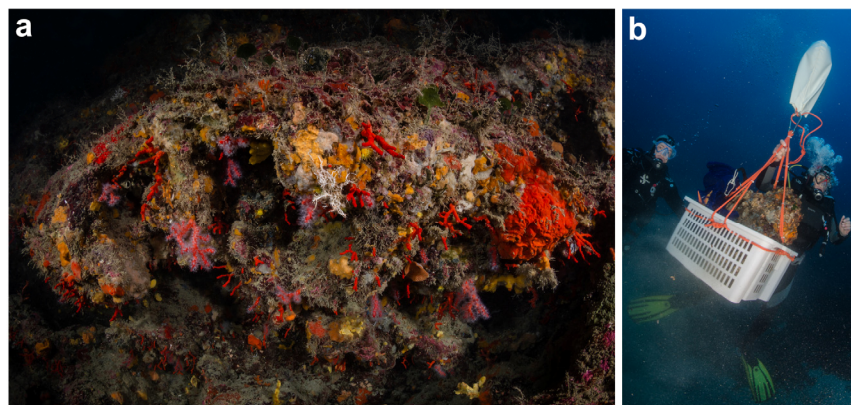


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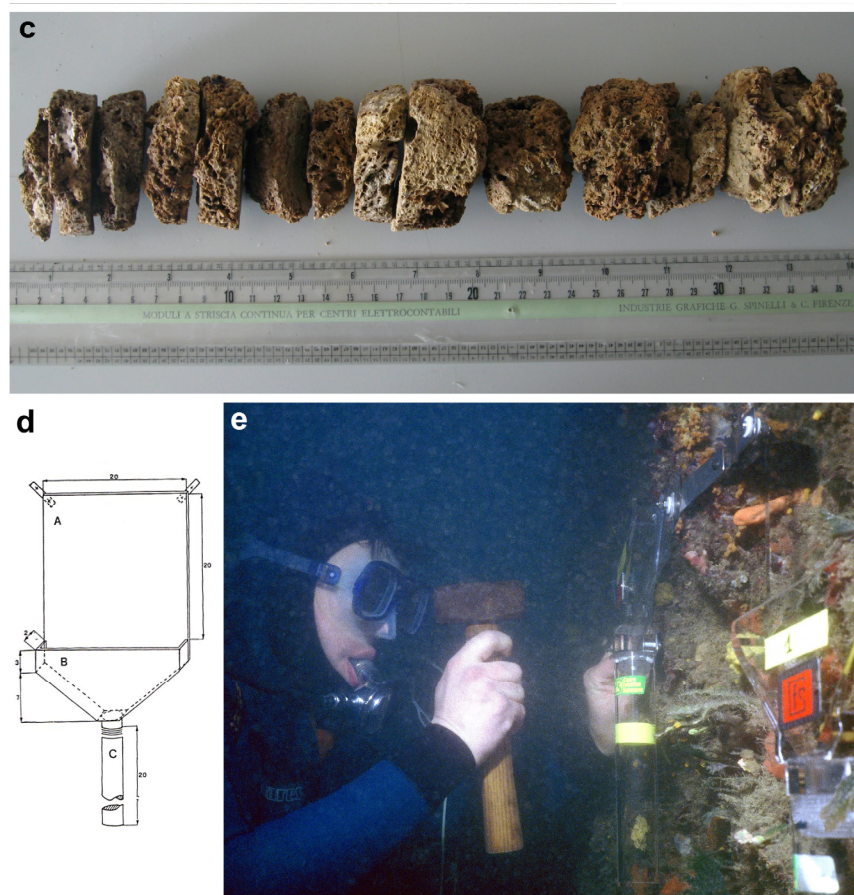


Figure 10. Coralligenous reefs: past and present. (a) Coralligenous shelf from the Altare dive spot at 35 m; (b) Marco Bertolino and Giorgio Bavestrello sampling coralligenous blocks for the study of paleospicules; (c) core of the coralligenous bioconstruction; (d) diagram of the sediment trap used to study the detritus rolling down along the Paraggi coralligenous cliff (from [183]); (e) Giorgio Bavestrello during the installation of the traps.

Multidisciplinary approaches and models for the large-scale identification of the coralligenous habitat and caves were recently applied to the Portofino Promontory, providing important indications for implementing the Marine Strategy protocols [195].

3.6. Red Coral: A Key Species

The relationship between the inhabitants of Portofino and red coral is very old, above all because the collection of this precious resource has always been a traditional activity of the inhabitants, up to at least the latter half of the 19th century, as demonstrated by the church of San Giorgio, built thanks to donations from the “corallari” (coral fishermen) [196]. The native coral populations of the promontory probably never represented an economically attractive resource, even though they were sporadically exploited, according to ancient documents. For example, in 1757, a Genoese official prohibited fishermen from using a tool known as *bronzino* to harvest the coral because it damaged the seafloor.

A few years later, the captain of Rapallo was warned by the inhabitants of Portofino that four Catalan boats were harvesting coral from the promontory, complaining that they “come to fish coral in these waters using rasps, and with them, they uproot the rocks where the coral is born, to the detriment of the people of this community” [197]. It took 230 years for coral-harvesting dredges to be banned across the Mediterranean Sea.

Issel [198] and Parona [199] reported coral populations in different locations along the Ligurian coasts, including the Portofino Promontory.

From the point of view of scientific research, starting from the mid-1960s, a group of underwater zoologists from the University and Aquarium of Milan began a series of research on the cliffs of the promontory to study *C. rubrum*, which would then be strongly developed some decades later. Marchetti [200] assessed the biomass and structure of the populations in a series of 40 stations down to a depth of 40 m between Punta Chiappa and the Portofino lighthouse (Punta del Faro). This work demonstrated that the Portofino coral was largely present on the southern front, with populations suffering greatly, probably due to the harvesting performed by divers over the previous decade. Barletta and Vighi [201] dedicated themselves to a pioneering study on the boring poriferans of the skeleton of the coral colonies. These studies had important developments in the 1990s thanks to the collaboration between Riccardo Cattaneo-Vietti, then a researcher at the Zoology Institute (Figure 11a), and Fabio Cicogna, a Milanese living in Massa Lubrense and a great enthusiast of marine biology, especially of coral. This partnership was particularly fruitful and led to two volumes published by the Ministry of Agricultural and Forestry Resources [202,203] (Figure 11b,c). The coral populations of Portofino were studied again in this period, and the population structure was evaluated. In particular, the relationship between red coral and other benthic organisms was investigated through photography (Figure 11d). This research highlighted that the coral populations disturbed by harvesting became progressively denser and dominated by very small colonies, similar to coppiced woodlands. This hypothesis was confirmed 20 years later when the coral populations of Portofino were studied again, and a reduction in the density was observed alongside an impressive increase in size [196] (Figure 11e,f). These were the first data from a Mediterranean MPA that demonstrated coral populations' recovery. In the meantime, the Portofino coral had undergone various investigations, in particular, those linked to the estimation of ages and growth rates of the colonies [204], to the genetic structure of surface and deep-water populations [205], and to transplant experiments [206].

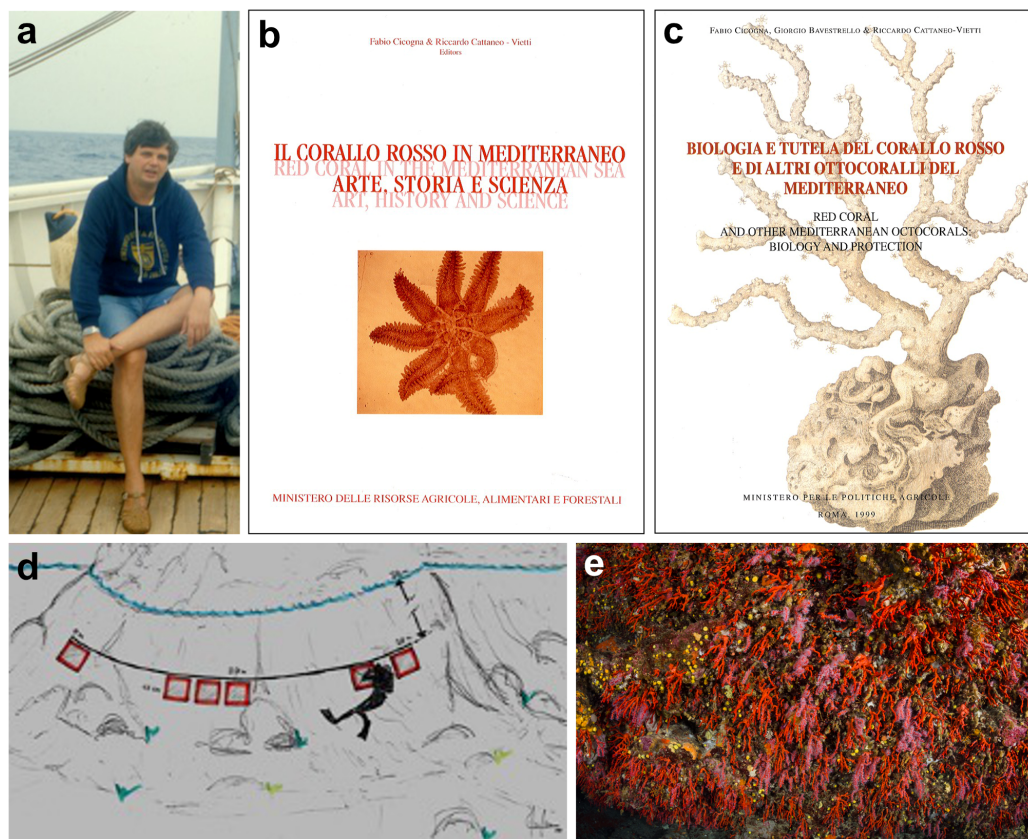


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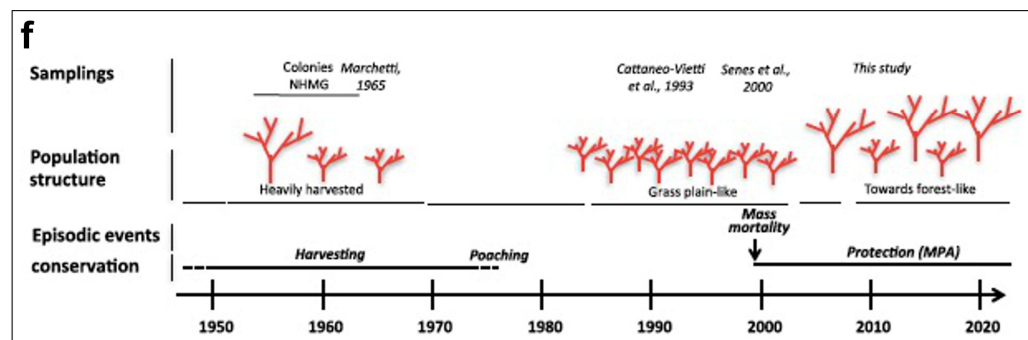


Figure 11. Red coral: a key species. (a) Riccardo Cattaneo-Vietti, who stimulated the study of *Corallium rubrum* in Portofino and to whom this paper is dedicated; (b,c) the two volumes on red coral published by the Ministry of Agricultural and Forestry Resources [202,203]; (d) diagram by Roberto Pronzato illustrating the method used to study the relationship between red coral and the scleractinian *Leptopsammia pruvoti* at Punta Torretta; (e) population of *C. rubrum* on the Altare cliff at 35 m; (f) evolution of the population structure of *C. rubrum* on the Portofino Promontory from the 1950s to today (from [196]).

3.7. Soft Bottoms

At the time of the pioneering research of Enrico Tortonese and Duilio Marcante [24,25,99], the only information available on the seafloor of the Portofino Promontory was that contained in fishing maps, such as those of Mancini [207] and Santi [208], both at 1:100,000 scale, and Fusco [209], at 1:120,000 scale. The small scale and the specific scopes partially compromise the usefulness of these maps, which nevertheless demonstrated to be sufficiently reliable about the presence and extent of certain types of seafloors [210]. Increased research efforts in the 1980s allowed the first seabed maps of the area to be produced based on scientific criteria on a scale of 1:30,000 [58]. The creation of the MPA in 1999 encouraged and finalised further investigation, which allowed for a more detailed seabed map on a 1:10,000 scale [211].

The seafloor surrounding the Promontory of Portofino presents a sedimentary coverage that, inshore, comes primarily from biogenic debris deriving from the rocky cliffs above while, offshore, mainly derives from the Entella River transporting fine matter [212] (Figure 12a). The dominant coastal currents transport the terrigenous sedimentary material from Entella towards the western part of the Gulf of Tigullio, from which they tend to exit southwards, brushing Punta del Faro and, to some extent, accumulating inshore: an inverse sediment gradient is thus established along the eastern flank of the promontory, with deposition of fine material near the shore. The sandy bottoms are represented by limited coastal areas and clearings within seagrass meadows [213]. The sand and gravel below the front of the promontory, partially biodetritic, extend to greater depths [214]. The rest of the shelf is occupied by terrigenous mud composed of varying proportions of silt [215], while at greater depths, a viscous yellow mud is recognised from which the original volcanic substrate locally emerges [214].

The sandy coastal seafloor of the eastern flank of the promontory, below 10 m, hosts a rich community (Figure 12b–f) dominated by infaunal species such as the amphipod *Centraloecetes dellavallei* and the bivalve *Laevicardium crassum*. Other important species are the polychaetes *Aricidea cerrutii*, *Paradoneis ilvana* and *Protodorvillea kefersteini*, the bivalve *Lucinella divaricata* (Figure 12b), and sipunculids [213]. Further offshore, the typical bio-coenosis of coastal terrigenous mud is recognisable, particularly the facies of the polychaete *Sternaspis scutata* (Figure 12c) and the gastropod *Turritellinella tricarinata* [216,217].

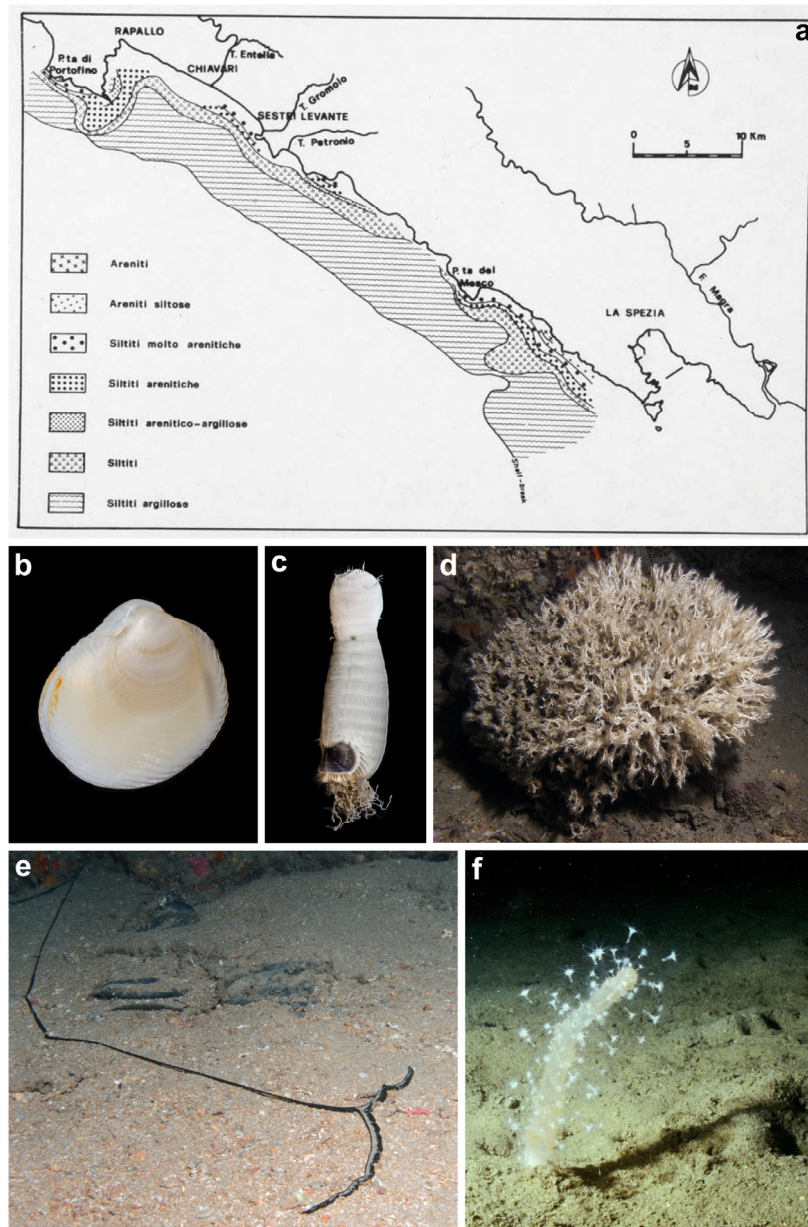


Figure 12. Soft bottoms. (a) Distribution map of surface sediments between Portofino and La Spezia (from [212]); (b,c) two of the main representatives of the burrowing macrofauna of Portofino, the bivalve *Lucinella divaricata* (b) and the polychaete *Sternaspis scutata* (c); (d) the serpulid *Filograna implexa*; (e) the echiuran *Bonellia viridis*; (f) the pennatulacean *Veretillum cynomorium*.

The detritic bottom on the southern front, starting from 40 m, features an abundance of erect, branched, calcified bryozoans belonging to different species. *Turbicellepora incassata* is constantly present, and other common species include *Fron dipora verrucosa*, *Pentapora fascialis*, *Rhynchozoon neapolitanum*, and *Smittina cervicornis*. As mentioned by Blanc [214], the bryozoans can form the first nuclei of a bioconcretion alongside calcareous algae (rhodoliths), with whom they can coexist (loose nodules of *Rhynchozoon* are common, probably starting from the encrustation of debris). Amongst the components that can usually be found in this habitat, there are masses of the serpulid *Filograna implexa* (Figure 12d), the bivalve *Pecten jacobaeus*, the irregular urchins *Brissus unicolor* and *Spatangus purpureus*, the echiuran *Bonellia viridis* (Figure 12e), the sabellid *Bispira viola*, etc. In clear waters, a dense canopy of erect algae (*Sporochnus pedunculatus*, *Arthrocladia villosa*, *Osmundaria volubilis*) and the gorgonian *Eunicella singularis* can develop, especially when stones and pebbles are

present. *E. singularis* can be replaced first by *E. verrucosa* and then by *Leptogorgia sarmentosa* with increased turbidity and siltation [218]. When the detritus becomes noticeably muddier, around 60 m, the ophiuroid *Ophiothrix quinquemaculata* becomes dominant, forming a well-developed facies, followed by the bivalve *Solecurtus candidus* and the sea pen *Veretillum cynomorium* (Figure 12f).

Further offshore, near the edge of the continental shelf, a facies of the crinoid *Leptometra phalangium* characterises the transition with the bathyal zone, where (at least until the 1970s) facies of the poriferan *Thenea muricata*, the sea pen *Funiculina quadrangularis* and the alcyonacean *Isidella elongata* were found [99,219].

3.8. The Deep Sea

Much scientific literature ascribable to the Portofino Promontory concentrates on relatively shallow waters explored through traditional SCUBA diving techniques. Nevertheless, numerous environments are found beyond the 50 m isobath, which marks the bathymetric border of the Marine Protected Area, and these environments have attracted scientific interest for over a century. The promontory's steep rocky cliffs extend to 50 m, where rocky outcrops surrounded by organogenic detritus give way to a muddy slope that continues to 150 m, at around two nautical miles from the coast. Here, the continental shelf quickly becomes steeper. At around three nautical miles, the depths touch 800 m, reaching a tortuous zone of ancient inactive muddy canyons that extend downwards towards the bathyal zone (Figure 13a).

The first works on the deep seafloor around the Promontory of Portofino were ichthyological studies. From the mid-20th century, trawling began on the Ligurian continental shelf, particularly in the Gulf of Genoa and nearby areas [20]. Operations along the coast of Portofino became particularly intense in the 1960s and 1970s: in this zone, indeed, is the most famous shrimping haul in Liguria, the so-called Cala di Terra le Rame [220,221] (Figure 13b). Commercial and scientific trawling, aside from providing data on commercial species between 200 and 750 m (e.g., *Aristeus antennatus*, *Nephrops norvegicus*), provided an important source of deep fauna also for numerous other taxa not of commercial interest, such as sponges, cnidarians, molluscs, and echinoderms, studied here extensively by numerous Genoese authors for nearly 60 years [19,20,32,216,219,222–229]. Still today, the deep-water bycatch collected around Portofino provides surprises, such as the very recent report of the rare bathyal gorgonian *Placogorgia coronata* in the scleractinian thanatocoenosis adjacent to the red shrimp haul [221] (Figure 13c).

Pioneering biological and geological observations in the mesophotic and epibathyal zones were carried out in the Portofino area during the research voyages of the vessel *Calypso* in November 1957. A dense network of sampling stations was located between the promontory, Chiavari, and the St. Lucia Bank [214] (Figure 13d). Topographic and sedimentological surveys were performed in the area, including a bathymetric characterisation of the living and fossils populations of foraminifera [214]. Sampling in the Portofino area targeted numerous taxa, primarily of soft bottoms, including polychaetes (73–730 m) [230,231], echinoderms (15–900 m) [31], and bryozoans (15–146 m) [232]. During the *Calypso* cruise, dead white coral was dredged between 700 and 800 for the first time in Portofino [214] (Figure 13e). The thanatocoenosis was described as strongly micritised and covered by a layer of iron and manganese. The original bioconstruction, of uncertain age, is located on a siliceous substrate at a lower depth than the current one. It is believed that during a phase of marine regression, detritus and microfauna from the continental shelf (60–100 m) covered the formations, crystallising as interstitial calcitic cement. The corals were subsequently brought to the current depth (770 m) under the influence of a marine transgression or an inclined movement of the rocky substrate due to continental flexion caused by the canyon formation [233].

However, trawling nets and dredges remain destructive sampling methods that do not allow an organism to be precisely located in the environment or to study the species in their natural habitat. This is why, in the last 20 years, other technologies have seen widespread

use in the scientific field for deep-sea studies, such as technical diving (down to 120 m), bathyscaphes, and remotely operated vehicles, also known as ROVs. In the Portofino area, in 1994, Leonardo Tunesi and Giovanni Diviacco, on board the oceanographic vessel *Le Suroit*, carried out dives at three sites off the Gulf of Tigullio using the bathyscaph *Cyana* of IFREMER (French Research Institute for Exploitation of the Sea) in search of living white corals [234] (Figure 13f–h). This prospecting involved the seafloor off Punta Chiappa (between 140 and 280 m) and Punta del Faro (from 138 to 300 m, approximately), and the canyon facing the outlet of the Entella River, off the coast of Chiavari (from 100 down to 570 m). Information was gathered on the biocoenosis of offshore detritus and deep mud. The bathyscaph also allowed direct observations of the deep-water ichthyofauna in environments that were difficult to sample by other means [234] (Figure 13h).

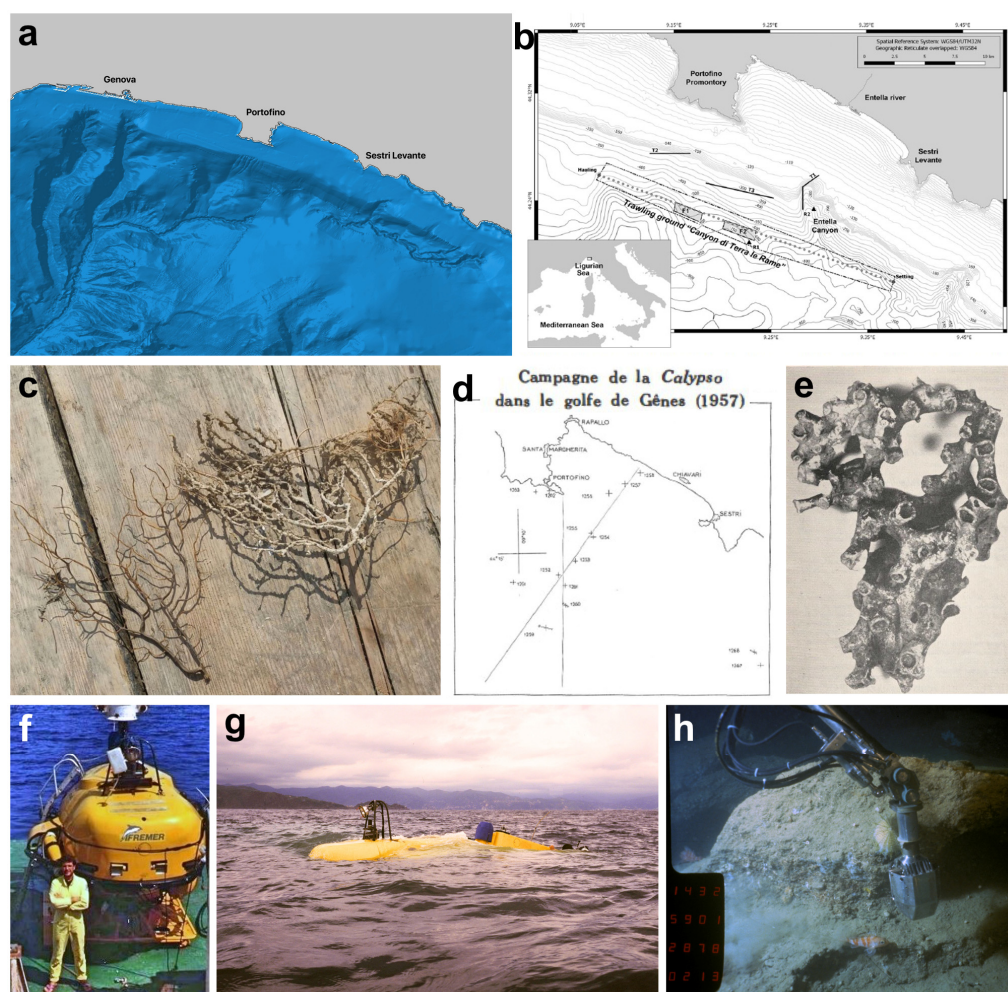


Figure 13. Deep sea: first explorations. (a) Bathymorphology of the seabed of the central–eastern Ligurian Sea (from EMODNET); (b) map of the seabed in front of Portofino and Sestri Levante, with the trawl track Di Terra Le Rame (from [221]); (c) specimens of the rare gorgonian *Placogorgia coronata* found in the trawling discard (from [221]); (d) map of the sampling stations visited during the oceanographic campaign carried out by the *Calypso* in the Gulf of Genoa [214]; (e) dead fragment of *Desmophyllum pertusum* from the Portofino thanatocoenosis [32]; (f) Leonardo Tunesi together with Ifremer’s bathyscaph *Cyana* on the deck of the oceanographic vessel *Le Suroit*, about to dive in front of Punta del Faro; (g) bathyscaph *Cyana* about to dive; (h) sample collection filmed by the on–board camera.

Schiaparelli et al. [235] used remote sampling to study the structure of the bathyal communities in the Portofino area. The comparison of samples performed at a distance of 15 years showed a significant difference in the specific composition of the communities,

above all in terms of the trophic structure of the community, with an increase in the necrophage and carnivore components compared to detritivores, possibly due to the intense trawling activity.

More recently, Carlo Cerrano started to investigate the mesophotic environments using the most recent diving techniques (Figure 14a), leading to numerous deep biocoenotic characterisations and complex manipulation experiments. The first results in this field for the Portofino area involved the description using technical diving of a facies of the zoanthid *Savalia savaglia* at around 70 m near Punta del Faro [236]. This study highlighted the three-dimensional nature of these environments, identified as coral forests, and their role in increasing diversity at all levels. Various studies conducted in the MPA highlighted the role of the circalittoral gorgonian forests and the effects of their removal on the benthic community [237–239]. Similar investigations were also carried out in heterogeneous seafloor environments to characterise and study the ecological role of the forests of the hydrozoan *Lytocarpia myriophyllum* at 70 m at the base of the rocky cliff of Punta del Faro [240,241]. The gorgonian forests of Portofino also underwent studies focusing on innovative monitoring technologies such as photogrammetry and “Structure from Motion” (SfM) models to obtain important metrics relating to the population (e.g., morphometry, biomass, and three-dimensional structure) starting from a sequence of images [242]. The same approach was also used to monitor morphological plasticity in the sponge *Sarcotragus foetidus* [243].

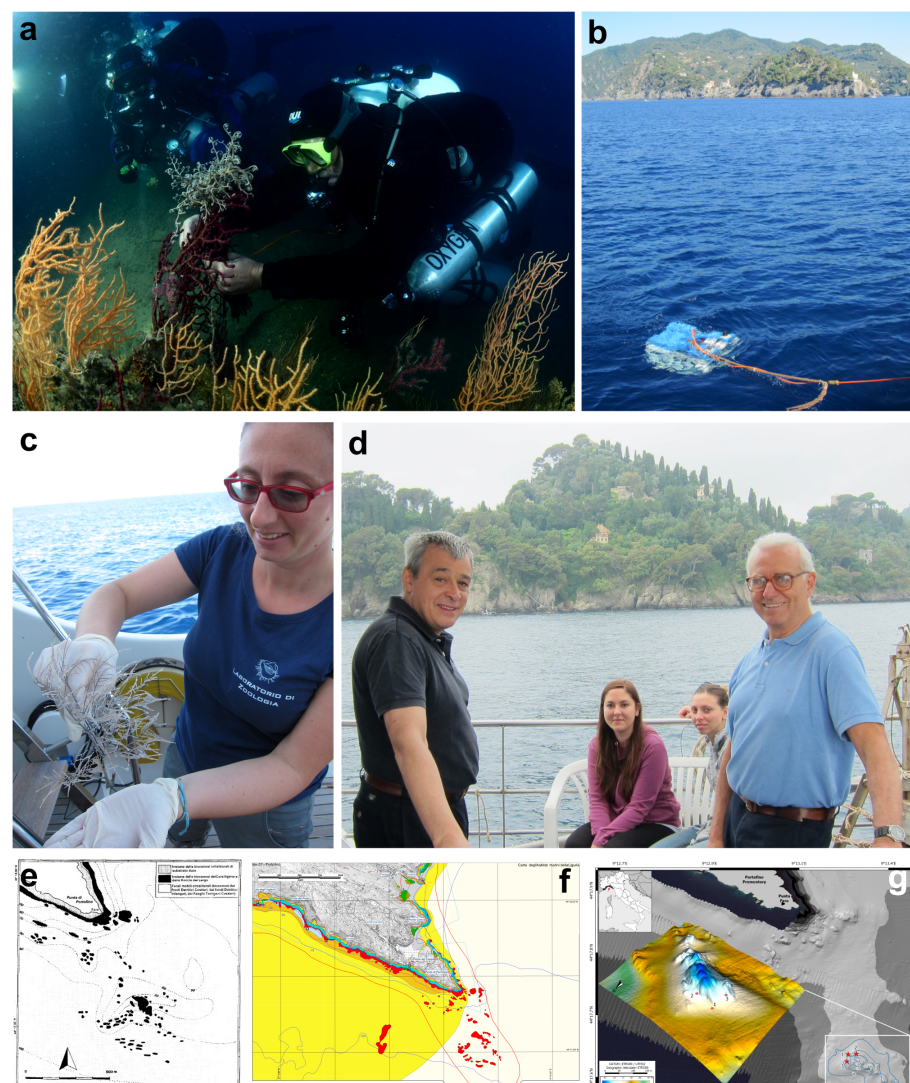


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Figure 14. Deep shoal of Portofino. (a) Carlo Cerrano sampling anthozoans during a technical dive on the deep shoal of Portofino; (b) the ROV Pollux off Punta del Faro; (c) Marzia Bo with a sample of *Antipathella subpinnata* just collected by ROV; (d) Giorgio Bavestrello (left) and Maurizio Pansini (right) on the ISPRA oceanographic vessel *Astrea* in June 2012; (e) biocoenotic cartography of the deep rocky outcrops of Punta del Faro (from [234]), updated in 2021 (f) (by [244]); (g) three-dimensional bathymorphology of the deep shoal of Punta del Faro obtained through multi-beam echo sounder (from [245]); (h) first photograph of the black coral *A. subpinnata* from Portofino (from [246]); (i) a colony of Ligurian *A. subpinnata* (from [41]); (j) the same species photographed in Portofino by ISPRAs ROV Pollux in June 2012.

Also falling into this context is the work performed within the scope of the Marine Strategy (MSFD 2008/56/EC) exploration programme, directed in Liguria by ARPAL (Agenzia Regionale per la Protezione dell’Ambiente Ligure—Regional Agency for the Protection of the Ligurian Environment), and other studies of the University of Genoa along the entire Ligurian coast and some offshore zones, with a total of nearly 180 dives between 40 and 1820 m. These studies have significantly expanded the knowledge of the spatial and bathymetric distribution of Ligurian mesophotic and bathyal habitats and biocoenoses in the last decade. Firstly, with regard to Portofino, the multibeam mapping performed during the expedition was used by the region of Liguria to update the cartography of the promontory, expanding it with high-resolution geomorphological data from 40 to 100 m and delineating the boundaries of the coralligenous and rocky environments of the deep circalittoral area [244]. The ROV exploration programme of the promontory, conducted with the contribution of ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale—Italian Institute for Environmental Protection and Research) and the use of the ROV Pollux and the oceanographic vessel *Astrea* focused on five sites between 2012 and 2016 (Punta del Faro, Secche di San Giorgio, Cala degli Inglesi, Isuela, and Punta Chiappa) for a total of 12 dives between 40 and 110 m (Figure 14b–d). These studies allowed mapping of the megabenthic communities of the mesophotic zone, with a particular focus on those dominated by structuring species able to form three-dimensional forests [247–249]. Of the 12 communities identified for Liguria, nine were also encountered along the promontory, six of which were dominated by structuring species such as sponges, anthozoans, and bryozoans of high ecological value and high vulnerability [247]. At the same time, the mapping of waste of anthropogenic origin identified the main sources of impact on the mesophotic environments of the promontory, with an average of around 1500 objects per hectare in the MPA, primarily ascribable to artisan and recreational fishing [250]. To assess the ecological state of the mesophotic environment and implement management measures capable of attaining Good Environmental Status, multi-parametric ecological indices were developed exploiting the ROV archives and using structuring anthozoans as indicator species (MAES Index [184]; MACS Index [251]). These indices, tested within the MPA of Portofino, have identified a moderate environmental status for Punta del Faro. ARPAL and the University of Genoa started the Marine Strategy monitoring programme in the area in 2018, focusing on previously acquired ROV transects. The first result of this monitoring regarded the basket-star *Astrospartus mediterraneus*, associated with dense aggregations of massive sponges and gorgonians between 20 and 120 m and especially abundant in Punta del Faro (0.45 specimens m^{-2}). This study found a strong correlation between the basket-star density and rainfall amounts that, in oligotrophic waters, such as those of the Ligurian Sea, represent an important input of organic matter for these passive filter feeders, especially in the summertime [252].

Concerning the mesophotic coral forests, a particular focus was placed on the deep shoal of Punta del Faro (Figure 14e–g), a rocky elevation 200 m long and around 15 m high, surrounded by organogenic detritus, which had already undergone pioneering studies with ROVs in the 1990s. In July 1994, Cattaneo-Vietti, Bavestrello, and Cerrano carried out the first exploration of the shoal on board the vessel *Tetilla* using an ROV (ROBY2) provided by the Veruggio Operating Unit of the Italian Research Council (CNR) Institute for Naval Automation [246]. Three dives between 58 and 120 m were made to detail the presence and distribution of deep red coral. Photographs were also taken of the arborescent black coral *Antipathella subpinnata*, which had always been considered an enigmatic presence in Liguria, as in the rest of the Mediterranean Sea [41] (Figure 14h,i). The first photographic documentation of the populations of the shoal was also produced, and the first evidence regarding the impact of artisanal fishing was provided. Subsequently, Diviacco and Tunesi produced a biocoenotic cartography of the populations of the shoal based on the investigations performed using Side Scan Sonar and ROV (Achille) in December 1996 [253]. The investigation confirmed the presence of the black coral facies and 29 megafaunal taxa in the zone. The deep shoal of Portofino was the target site for various multidisciplinary studies that used the arborescent black coral *A. subpinnata* as a model species (Figure 14j). This species was found in great abundance between 65 and 75 m. In 2016–2017, thanks to the aid of technical divers, tagging experiments coupled with various collections of material were performed to investigate the diet and reproductive cycle of this species. At the same time, thanks to data gathered by the Biological Oceanographic Laboratory of DiSTAV, the seasonal temperature, salinity, and chlorophyll-a profile in the area were obtained, measuring the influence of the later summer water plume at 16 °C down to a depth of 70 m. Within the scope of these investigations, the trophic seasonality of this coral [245], the microbiome variability based on the site and season [254], and the level of genetic connectivity with other Italian populations were studied for the first time [255]. Moreover, individuals kept alive in the tanks of the Genoa Aquarium revealed interesting reproductive traits of this species, such as the ability to fragment as well as to produce asexual propagules in a process known as “bail-out” [256,257]. A recent study using a habitat predictive model of this site emphasised the high conservation value and vulnerability of the deep shoal at this site, highlighting the importance of its protection through its inclusion in the MPA, whose external perimeter is currently 200 m from the study area [258].

Amongst the deep-water ecosystems of greatest naturalistic and ecological relevance are the bathyal coral systems dominated by scleractinian bioconstructions. The first information on the existence of this biogenic habitat in the area overlooking the promontory came from trawling bycatch [32,259] and the explorations of the *Calypso* [211]. Fossil samples of *Madrepora oculata* and *Lophelia pertusa* (= *Desmophyllum pertusum*) from Portofino are also preserved in the Museum of Zoology of the University of Genoa (donation from Lidia Orsi-Relini). However, it was only with Fusco’s cartographic work [209], requested by the Merchant Shipping Ministry, that two frameworks were mapped in proximity to the red shrimp trawling grounds to highlight the danger to fishers. Around 20 years after the explorations of the *Cyana* [234], new ROV studies were conducted in 2017 on board the catamaran *Daedalus* (Fondazione Azione Mare) with the use of the MultiPluto (Gaymarine Srl, Lomazzo, Italy) between 400 and 800 m within the project BioMount (Figure 15a,b); these studies revealed the extent and the elevation of the subfossil bioconstruction in the area further to the east [221] (Figure 15c). The framework was also investigated in a recent ROV exploration campaign financed by the University of Genoa (Curiosity Driven Project, Lost Coral Bioherms, 2020–2021), which also shed light on important bathyal gorgonian forests associated with the bioconstruction [260] (Figure 15d). The study reported a dead coral framework of 7.4 km² but also provided the first evidence of living *D. pertusum* in the Ligurian Sea (Figure 15e,f). The complexity of the structure guarantees a substrate and refuge to numerous species, and the Levantine Intermediate Current, coming from the east, flows through the site, ensuring food and oxygen to the benthic communities. Trawlers occasionally operate near this site, breaking off portions of coral [221], undermining the structure’s integrity, and leaving vast quantities of debris on the seafloor. Only now do we

fully understand the importance of this site, which emerged as part of a more complex bathyal coral region embracing the entire eastern Ligurian Sea and identified as the ninth white coral province of the Mediterranean Sea [260].

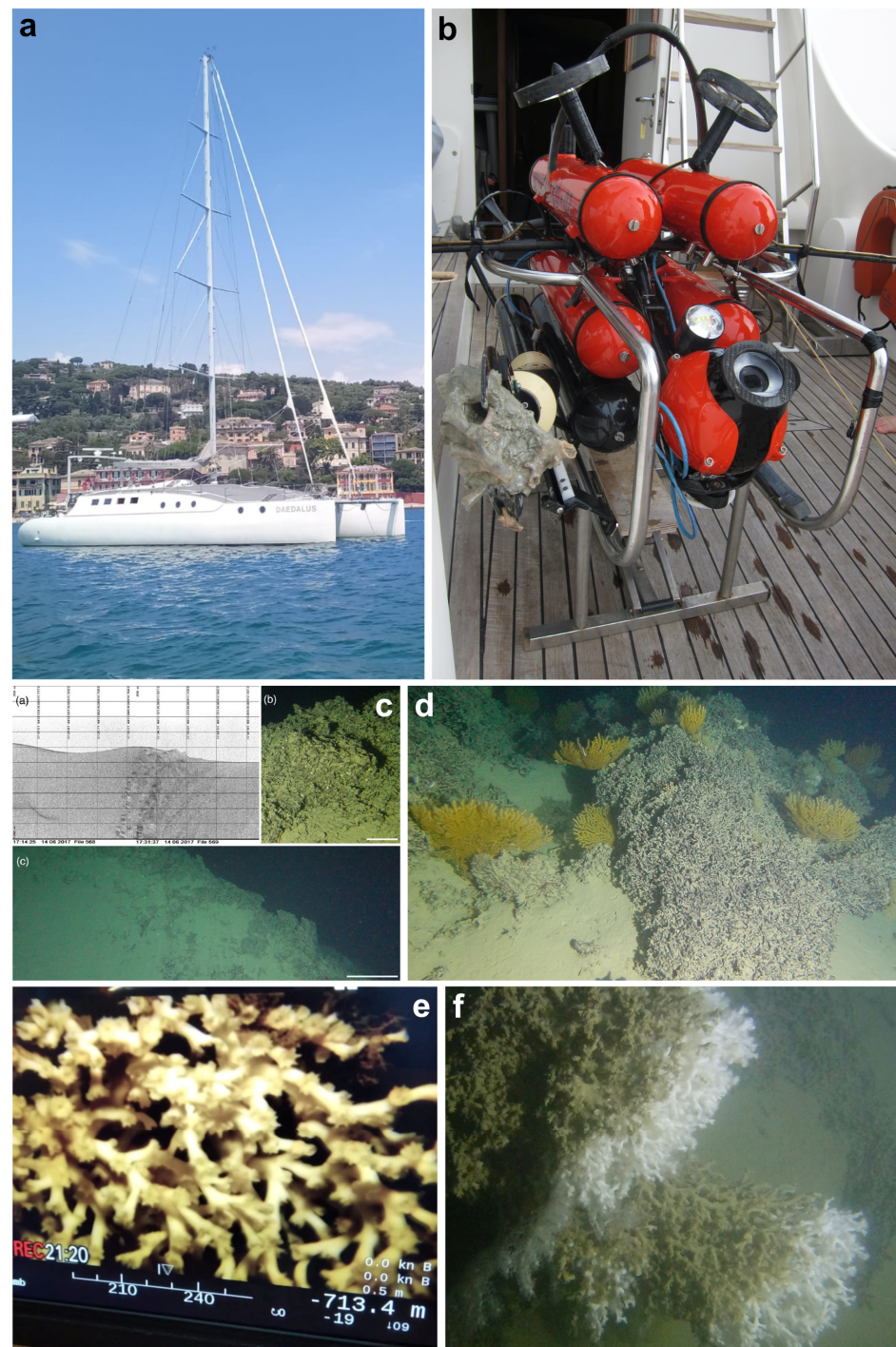


Figure 15. Portofino bioherm. (a) The catamaran *Daedalus* of engineer Guido Gay, operational base for numerous explorations in the Ligurian Sea through the use of the ROV Multipluto designed by Gay himself; (b) close-up view of the ROV Multipluto; (c) Side Scan Sonar map (a) and ROV footage of the Portofino bioherm (b–c) (from [221]); (d) a forest of large colonies of the gorgonian *Placogorgia coronata* on the white coral thanatocoenosis in front of the promontory (from [260]); (e) a colony of the white coral *Desmophyllum pertusum* taken by the ROV at over 700 m depth in Portofino; (f) large living colonies of the white coral *Desmophyllum pertusum* (from [260]).

From a conservationist point of view, it is undoubtedly necessary to continue exploring these environments since it is impossible to protect what is not known [249], and this is particularly true for deep-sea ecosystems. The conservation measures applied to the coastal MPA and SAC (Special Area of Conservation) are challenging in offshore sites. In the past, multiple Genoese authors suggested the creation of protected zones to safeguard deep-water biocoenoses from the impacts of trawling [223]. Today, various institutional tools are available for this goal (e.g., Marine Protected Areas, Sites of Community Importance, and Fisheries Restricted Areas), and the scientific knowledge and the interest to monitor their health status exist; we only have to implement the measures.

4. Study of the Benthic Communities: Bathymetric and Temporal Trends

The 1970s were a period of intense scientific work on the Portofino Promontory (Figure 16a–f). The publication of the “Nouveau manuel de bionomie benthique de la Mer Méditerranée” by Pérès and Picard [33] emphasised the environmental factors driving the zonation of the benthic biocoenoses. A group of young underwater researchers, under the supervision of Michele Sarà, obtained a boat (Figure 16a) and carried out numerous underwater investigations along the promontory (Figure 16b–f). In particular, they began to sample along a vertical transect located on the northern front of the promontory, known as Transect Aurora [60,261], below the terrace of the Aurora Restaurant (Figure 17a–c).

The cliff of the Transect Aurora is located on the northern side of the promontory, about 100 m from Punta del Faro (Figure 17a). It is a sub-vertical wall terminating at about 25 m on the detritic slope, with northeasterly exposure subject to moderate wave action and dominant currents in the easterly direction. At the time of the research, the waters of the area were not subject to significant pollution (total nitrogen was, on average, $48 \mu\text{g}\cdot\text{L}^{-1}$, total phosphorous $26 \mu\text{g}\cdot\text{L}^{-1}$), and the water exchange was good; transparency was poor, above all during the winter months, due to the turbidity of the waters of the Gulf of Tigullio flowing offshore [262]. The average values of the light reaching the cliff ranged from $3.6 \text{ mW}\cdot\text{h}^{-1}$ at a depth of 1 m to $0.5 \text{ mW}\cdot\text{h}^{-1}$ at 20 m. Wave action was particularly intense in the first metre of depth, but at 3 m, it was already 40% of the incident one; at 15 m and 20 m, it was below 20%. Sedimentation phenomena were evident from 10 to 15 m. At the surface, a minimum temperature of $12 \text{ }^\circ\text{C}$ (February) and a maximum of $25.5 \text{ }^\circ\text{C}$ (August) were recorded, with a summer thermocline oscillating between 10 and 15 m; below 15 m, the temperature ranged from around $14 \text{ }^\circ\text{C}$ (February) to $17.5 \text{ }^\circ\text{C}$ (August). The salinity was constant, around 37 psu [60].

The community of the cliff was overall sciaphilous and characterised by a thick algal bed of *Dictyopteris polypodioides*. Below 10 m, a concreted substrate rich in encrusting coralline algae, serpulids, poriferans, and bryozoans developed. The gorgonian *E. cavolini*, although limited overall, also appeared at shallower depths (5–7 m), and large hydrozoans of the genus *Eudendrium* were particularly abundant in winter. Around 20 m, the algal component was reduced, but the rhodophyte *Phyllophora crispa* appeared, and the ascidian *Microcosmus sabatieri* became frequent [263,264].

The variation in environmental parameters (light and hydrodynamics) was studied, along with the bathymetric distribution of the species of the different groups (Pronzato and Pansini, poriferans; Pessani, anthozoans; Balduzzi, bryozoans; Boero, hydrozoans). During the same period, Bianchi [10] described the communities of serpulids.

The goal was to verify the two benthic zonation models in vogue at the time to describe the bathymetric distribution of the communities: one based on the reduction in light [33] and the other on changes in water movement [265]. It should be noted that two researchers from the Zoological Station in Naples, Eugenio Fresi and Francesco Cinelli, participated in this research, or at least in its initial phases; they had already taken on the issue while studying the Mago Cave on the island of Ischia [266].

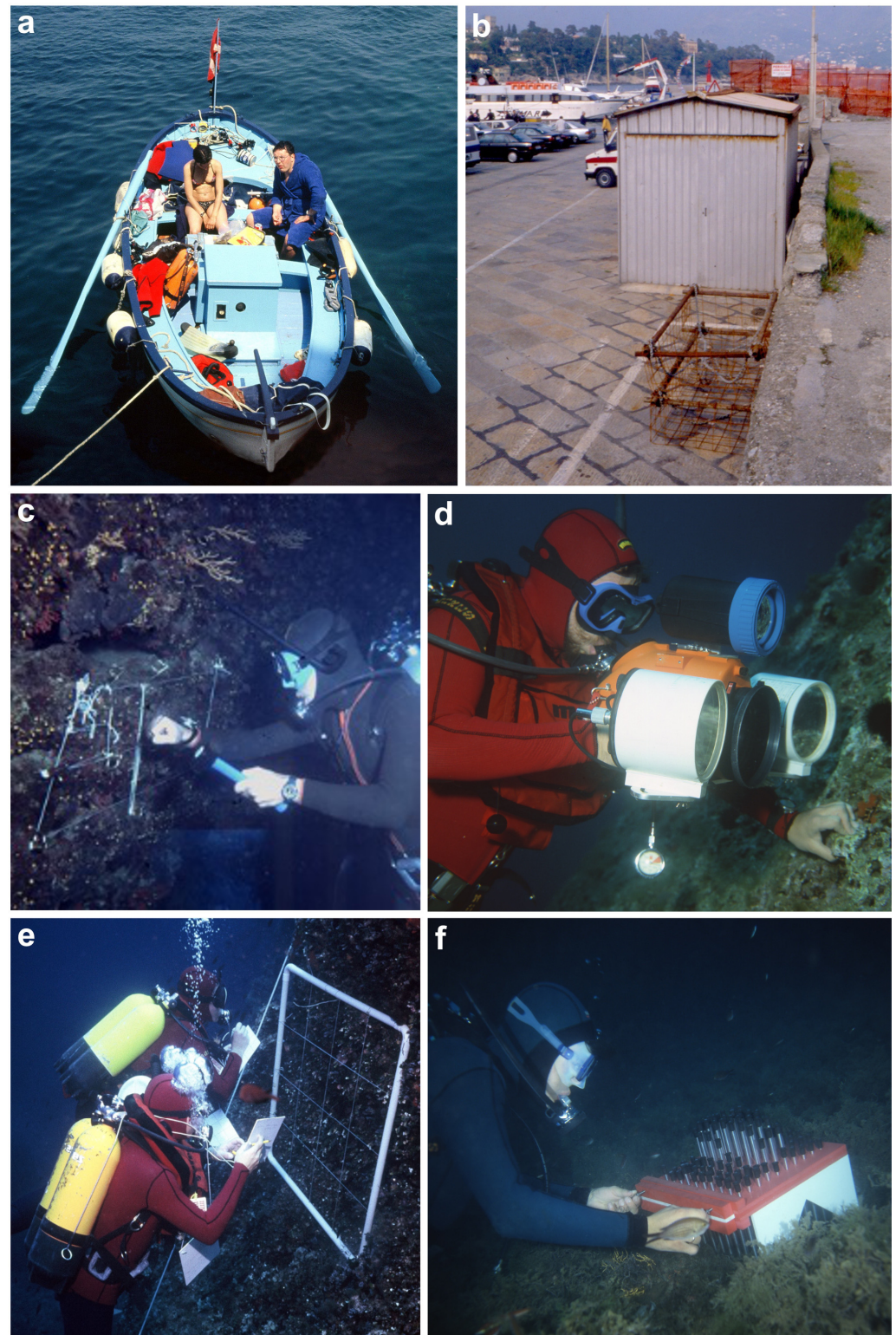


Figure 16. Underwater group of the University of Genoa. (a) Carlo Nike Bianchi and Carla Morri on board the first vessel of the diving group of the Institute of Zoology; (b) the first operational base of the diving team in the port of Santa Margherita Ligure since 1983; (c) Ferdinando Boero working on the minimum sampling area on the Portofino coralligenous cliff; (d) Roberto Pronzato during a photographic sampling with the famous Hasselmar 500 C/M (Hasselblad, Göteborg, Sweden); (e) Roberto Pronzato and Renata Manconi analyse the diversity of the coralligenous; (f) Giorgio Bavestrello evaluates the volume of a massive sponge with a specially built instrument.

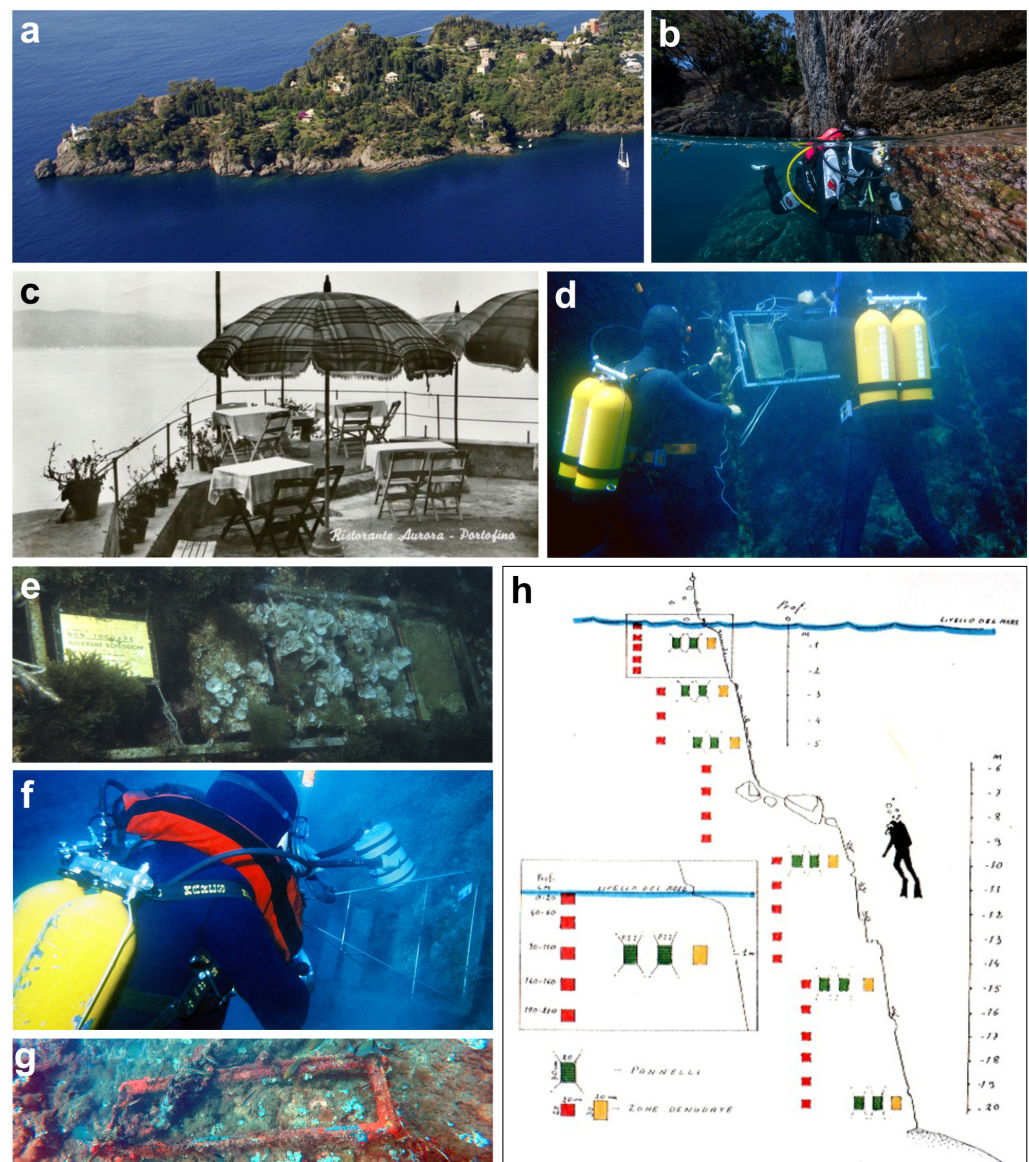


Figure 17. Study of the benthic communities: the Aurora Transect. (a) The northern side of the Portofino Promontory where the Aurora Transect is located; (b) Federico Betti sampling hydrozoans in 2018 along the historic transect (photo by Alessandro Grasso); (c) the restaurant Aurora above the cliff where the homonymous transect is located; (d) two researchers position the panels on the steel frame; (e) the panels in position; (f) Carlo Nike Bianchi photographs the panels; (g) the frame still visible today on the bottom; (h) diagram by Roberto Pronzato showing the distribution of the panels along the transect.

The Aurora Transect followed a rocky wall that, with a couple of gaps, reached the detritic seafloor at 25 m, and its position was marked by a catenary that supported steel frames on which panels prepared for the study of the initial settlement phases and the subsequent development of the communities, could be inserted (Figure 17d–h). Giulio Relini developed this technique to study the benthic communities of the port of Genoa and subsequently applied it to the underwater hardbottom communities of Portofino [263,264]. Although partially destroyed, the catenaries and steel frames are still perfectly identifiable along the transect (Figure 17g).

In those years, in addition to the bathymetric distribution, there was interest in the idea of the temporal evolution of marine communities. In Portofino, the topic was approached at two different levels. During the period 1981–1982, Boero gathered all species of hydrozoans

present along the Aurora Transect every 5 m in depth with a monthly frequency. This work led to the identification of around 100 species. The annual cycle was identified for each species, making the hydrozoan community of the Aurora Transect the best-known in the world [267]. Until then, only Lucia Rossi had worked on the hydrozoans in the area [29]. A particular focus was dedicated to one of the largest colonial species of the Mediterranean Sea, *Eudendrium glomeratum*, which, in 1982, was followed for a year within a standard area of 1 m² [268] (Figure 18a,b). One of the most fruitful research fields at the time was combining the polyp and medusa phases thanks to laboratory rearing. The most interesting discovery was that of a thecate hydroid, *Anthohebella parasitica*, which produced a medusa with gonads on the manubrium instead of the radial canals [269] (Figure 18c). Some years later, Bavestrello et al. [270] described the medusa *Turritopsis dohrnii*, which sinks on the seafloor after emitting the gametes and transforms again into a polyp, bypassing sexual reproduction (Figure 18d). Thanks to later developments in other papers, e.g., [271], this discovery resonated worldwide in subsequent decades, and the species was nick-named “the immortal medusa”.

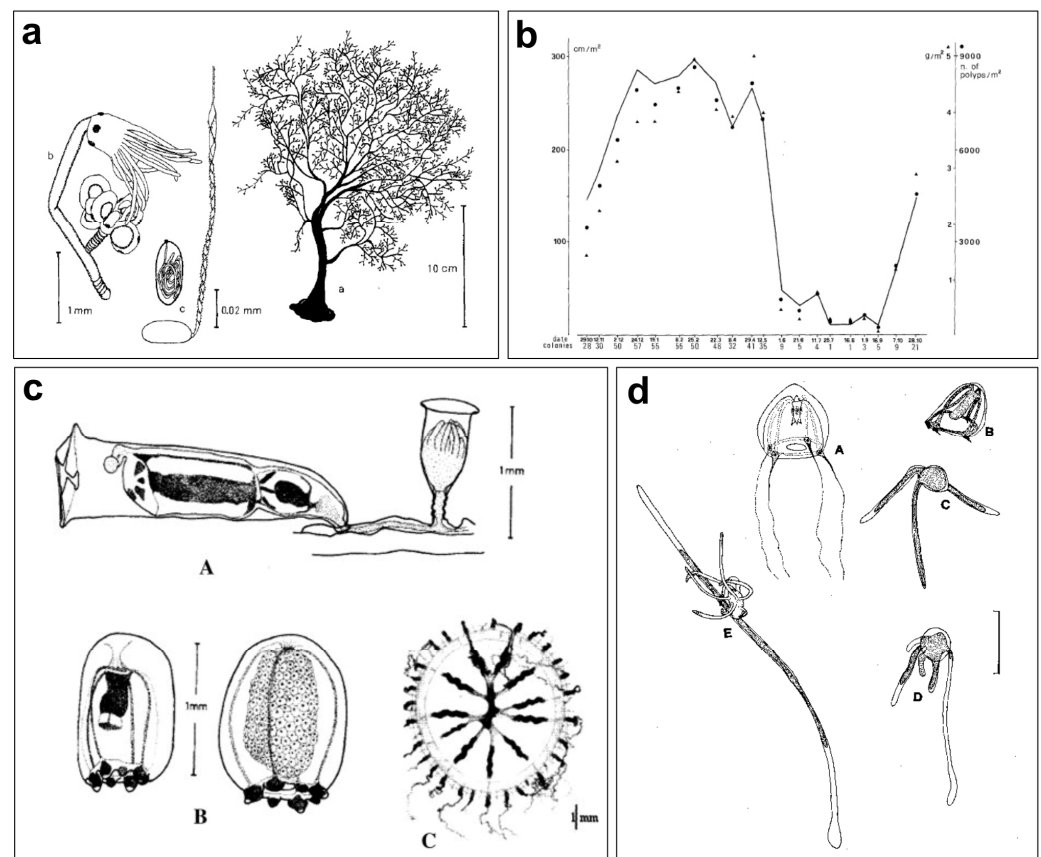


Figure 18. Temporal dynamics of the benthic communities: the hydrozoans. (a,b) Drawings of the polyp and the colony of the hydrozoan *Eudendrium glomeratum* (a) and its seasonal trend (b) (from [268]); (c) polyp and medusa of the thecate hydrozoan *Anthohebella parasitica* (from [269]); (d) polyp and medusa of the athecate hydrozoan *Turritopsis dohrnii*. The jellyfish, at the end of the cycle, transforms back into a polyp (from [270]).

Similar to the hydrozoans, the serpulids of the Aurora Transect were also investigated in some detail [272,273]. These studies took into consideration species taken from the natural substrate (the Oligocene puddingstone of the promontory) at six different depths (1, 3, 5, 10, 15, and 20 m) and species settled on artificial substrates immersed at the same depths for 1, 2, 4, 6, and 12 months) [263,274].

In total, 32 species of serpulids were identified (around half of those known in the Mediterranean basin), some of which at the time had not been reported in the Ligurian Sea yet (*Hydroides helmata*, *H. nigra*, *Pileolaria heteropoma*, *Placostegus crystallinus*, *Proto-laespira striata*, and *Spiraserpula massiliensis*). The most abundant species were *Filograna implexa*, *Josephella marenzelleri*, *Spirobranchus polytrema*, and *S. triqueter*, all species common in the infralittoral associations of hard substrate. *S. polytrema*, in particular, is an important component, alongside *Serpula concharum* and *Vermiliopsis striaticeps* (also relatively abundant), of those serpulid concretions establishing themselves within the infralittoral algal assemblages [275].

Most species were collected on both substrate types, six only on the natural substrate and four only on the artificial substrate; the latter were essentially pioneer species, above all spirorbids. The temporal analysis of the serpulid communities highlighted a gradual dynamic, although initially slow. The number of species and individuals grew as the immersion time of the artificial substrate increased. A relatively more marked change was observed starting from the sixth month. These dynamics were interpreted as a primary ecological succession, with a settlement phase after the first six months as a prelude to reaching a more mature community.

Nevertheless, even after 12 months, the community of serpulids on the artificial substrate still appeared significantly different from that of the natural substrate. The main cause of the difference between the two types of substrates was the algal conditioning and roughness of the natural substrate, which allowed crevice-dwelling species typical of coralligenous reefs and caves to occur. In contrast, developing a comparable micro-biogenic relief on the artificial substrate similar to that of the natural substrate would have taken not less than three years.

Both on the natural and the artificial substrate (independently from the duration of immersion), two different communities were recognised: one more superficial (characterised by *Spirobranchus lamarcki* and *Simplaria pseudomilitaris*) and a deeper one (characterised by *Hydroides norvegica*, *Serpula lobiancoi*, and *Semivermilia crenata*). The change occurred between 5 m and 10 m, where other species (*Vinearia koehleri*, *Vermiliopsis labiata*, and *Spirorbis cuneatus*) exhibited their greatest abundance. This zonation could be explained by the environmental topography: the vertical wall indeed terminated at around 10 m, giving way to a series of sloping terraces, with a change in inclination of the substrate and the conditions of sedimentation, hydrodynamics, and light. The presence of typical circalittoral species above 20 m was a clear example of the phenomenon of the ascent of deep-water species, which characterised the Portofino cliffs in the 1970s.

Most species were present at all examined depths on the artificial substrate, while the replacement of species with depth was more marked on the natural substrate. Within the genus *Vermiliopsis*, bathymetric vicariance was observed: *V. striaticeps* was abundant at 1–3 m, *V. labiata* at 10 m, and *V. infundibulum* at 20 m. The number of species was greater at 10–15 m and lower at 1–3 m. On the contrary, the highest number of individuals was found at 3 m and secondarily at 15 m, and the lowest number at 5 m and 10 m.

Using artificial substrates also allowed the evaluation of the biomass accumulation of the sessile benthic organisms along the bathymetric gradient [264]. The biomass was measured as wet weight after drip-drying and with no decalcification. The maximum biomass production was recorded at 3 m, with values of $2.4 \pm 1.59 \text{ kg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (with an absolute maximum of $4.2 \text{ kg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), while the minimum was recorded at 20 m, with $0.5 \pm 0.17 \text{ kg}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$. The difference was such that the maximum annual accumulation of biomass at 20 m ($0.7 \text{ kg}\cdot\text{m}^{-2}$) was less than that obtained at 3 m in just two months ($0.9 \text{ kg}\cdot\text{m}^{-2}$, April–May 1979). The decrease in biomass between 3 m and 20 m was gradual, but low values were also encountered at 1 m, probably due to the intense wave action. The difference in production in the sub-surface zone (3–5 m) and the deeper one was accentuated over time. In general, the increase in biomass was exponential in the initial phase, followed by a slowdown in the accretion rate. The environmental factor that determined this slowdown was the progressive decrease in surface area available

for the settlement of new organisms. Assuming that the increase in biomass follows a sigmoidal curve as in the logistic function, it was hypothesised that production would stabilise after 3 or 4 years.

In the same years, thanks to the use of underwater photography, a long-term study of the temporal study of sponge populations was realised [276–278] (Figure 19a,b). Michele Sarà's old idea of the temporal development of the populations was verified by monitoring sponges at different depths for seven years [278] (Figure 19c). The study of temporal trends was also applied to a group of motile species like the heterobranchs [279] (Figure 19d), the study of which started in Portofino by Barletta and Melone [280]. A large portion of the Portofino studies on heterobranchs was incorporated by Cattaneo-Vietti in the atlas he published together with Chemello and Giannuzzi-Savelli in 1990 [281]. The development of a time-lapse camera by Pronzato and Cicogna (Figure 19e) allowed short-term dynamic studies, for example, the monitoring of the opening and closing rhythms of polyps in the gorgonian *Eunicella cavolini* [282] (Figure 19f).

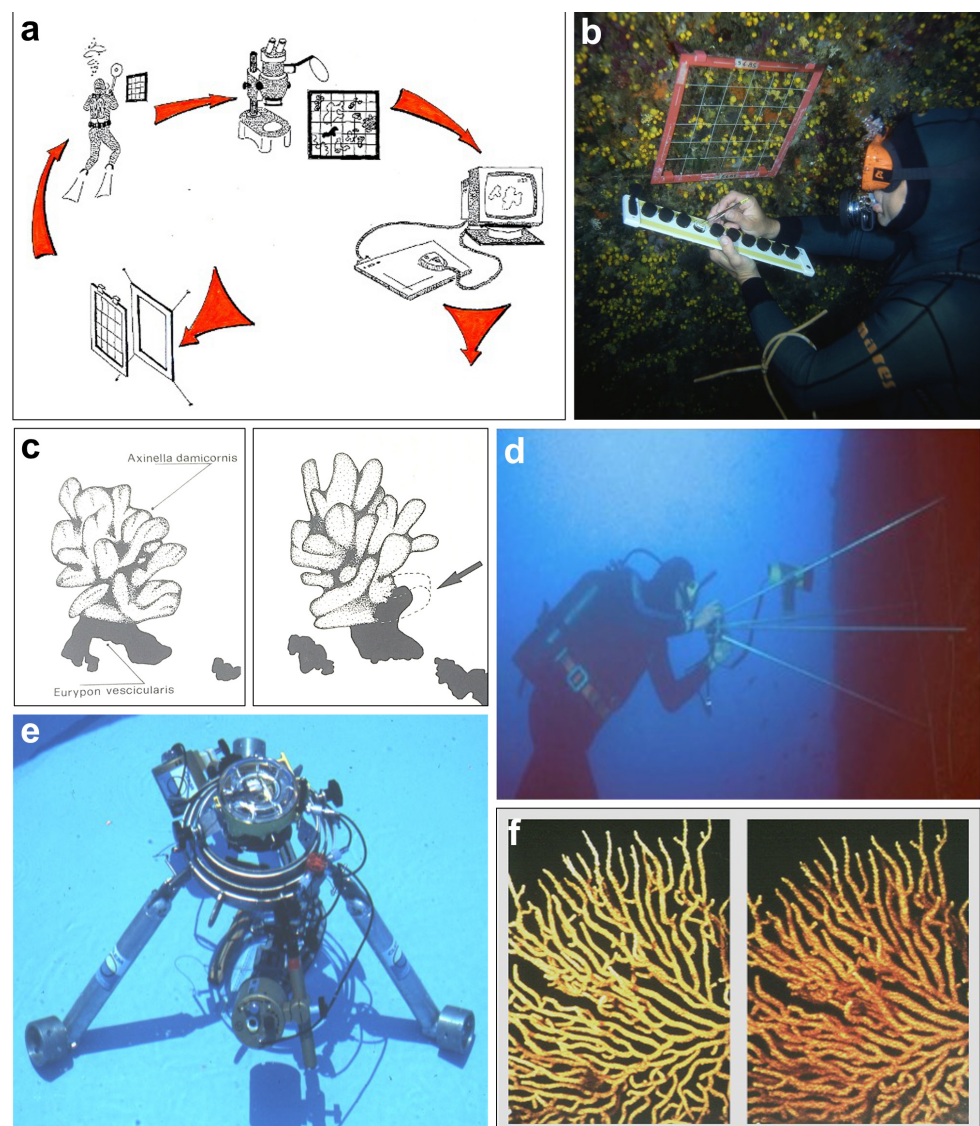


Figure 19. Underwater photography. (a) Scheme by Roberto Pronzato illustrating the methodology for studying the temporal variations of the sponge communities; (b) Maurizio Pansini collecting all

the sponge specimens present within a standard surface; (c) two drawings by Roberto Pronzato showing the dimensional changes of two sponges, one year apart (from [278]); (d) Riccardo Cattaneo-Vietti carries out a photographic survey in Paraggi; (e) the underwater time-lapse camera built by Roberto Pronzato and Fabio Cicogna used to study the opening rhythms of the polyps of the gorgonian *Eunicella cavolini*; (f) the same colony with contracted (**left**) and expanded (**right**) polyps (from [282]).

5. Fishing Biology

5.1. From Its Beginnings to Modern Studies

The Società Ligure-Sarda per la Protezione della Pesca (Sardinian-Ligurian Society for the Protection of Fishing) was founded in Genoa in September 1910 to aid, protect, develop, and improve the maritime and freshwater fishing industry, promoting, amongst other things, the formation of fishing co-operatives and also the creation of Issel, Mackenzie and Brian's famous marine laboratory [16]. Members included Benedetto Rappini, President of the Società Armatori Marinai e Pescatori of Santa Margherita Ligure as councillor, and Decio Vinciguerra, sole scientific exponent of the first board of directors, in virtue of his undoubted expertise in the ichthyological field [16].

Between 1928 and 1932, the society was already dealing with hot topics from the point of view of fishery management and conservation of resources, especially in light of the young age of commercial fishing activities in the region. In a letter regarding the condition of the Riviera's fisheries drafted by the society's president, attorney at law Edoardo Devoto, with the fishermen's representative of Rapallo (Luigi Sanguineti), overfishing of juveniles by trawlers was already an issue [283]. Establishing a repopulation area (the "experiment zone") between the promontory and Punta Manara was advocated. Some rules were proposed, of which the following stood out for their paradoxical actuality: prohibit the landing of whitebait, reform the mesh size of nets, respect the reproductive season and sizes of spiny lobsters, suspend fishing with drift nets during the reproductive periods, prohibit fishing with light sources, use of minimum size tables, and prohibit sales by those without professional licences. A further contribution in this area was provided 125 years in advance, in 1806, by the prefect of the seventh maritime district of Genoa by order of the Marine Minister [16], who implemented, with a penalty of imprisonment, a prohibition of catching juvenile fish, listing it as "a clear threat to the population of fish" in the Ligurian Sea. This in virtue of the "unlimited freedom that Ligurian mariners have heretofore enjoyed to fish during any season of the year, and with any sort of net, without obstacles nor restrictions", referring to the use of "nets of very tight mesh, which, in dragging along the seafloor, carry away everything, and that, for a tenuous and instantaneous benefit, remove all resources and hope for the future".

In 1932, the legal headquarters of the society moved to the Zoology Institute of the University of Genoa, and a ministerial circular reminded it to keep its activities limited to the scientific investigations and studies relating to fishing, ruling out practical and support work in the field [16]. The society would carry out its mandate by combining its activities with the scientific ones of the marine laboratory, already part of the institute. In 1935, the two entities merged to form the Società Ligure per gli Studi di Biologia Marina attinenti alla Pesca (Ligurian Society for the Study of Marine Biology relating to Fishing).

The main topics of study of the marine laboratory were the monitoring of plankton, the oceanographic characteristics of the water, the shrimp's biology, which at the time was fished between 150 and 300 m, but also fish parasites and mackerel feeding preferences [19,20,222]. A system of tanks kept alive some species collected with deep-water trawling, including the decapods *Polycheles typhlops* and *Nephrops norvegicus* and the flying gurnard *Dactylopterus volitans*. In 1933, Renato Santucci, director of the society, held a cycle of conferences for the fishermen of Santa Margherita Ligure on the biology of the Ligurian fauna. The first collaborations with fishermen spontaneously provided material for study dates to this period [16]. Much work was made from samples collected in the Gulf of Genoa, but the contribution from the promontory is also undoubted. The society and the laboratory were definitively dissolved in the 1970s, the latter partially replaced in 2011 by the operational base in the port of Santa Margherita Ligure, a structure able to house equipment for numerous studies on the benthos carried out along the promontory [16] (Figure 16b).

Starting in the 1970s, Lidia Orsi Relini and Giulio Relini, along with their colleagues, carried forward numerous studies on fish biology in Liguria, working with, amongst others, the fishermen of the promontory, above all, those of Santa Margherita Ligure (in particular between 1987 and 1998) [284]. Two vessels that saw the widest use in these years were the *Lavoratore II* (Figure 20a) and *Papà Baicin*. The collaboration of Benedetto Paccagnella, boat owner and fishing master of Santa Margherita Ligure, was vital for this work [220] (Figure 20b). Dozens of publications were produced regarding catches of great naturalistic interest, stomach contents analyses, trophic net, zonation, adaptations to environmental gradients, reproductive strategies, recruitment, growth models and age, seasonality of catches, population structure, nocturnal populations, nycthemeral migrations, hourly production and management measures (for full coverage of the bibliography on bathyal fishing, see [220,285]) (Figure 20c,d). The main targets were decapod crustaceans, cephalopods, cartilaginous, and bony fishes. Although data from studies using passive gear (trammel nets, gillnets, pots, longlines) were gathered, most of the scientific production was based on data collected by commercial and experimental trawling, with a particular focus on deep-water trawling [220,224,225,285–287]. The experimental trawling was widely used within standardised long-term monitoring projects, some financed by the EU's Maritime Affairs and Fisheries Department (GRUND, MEDITIS, CAMPBIOL). These projects were anticipated between 1977 and 1981 by the CNR project "Oceanografia e Fondi Marini, Risorse Biologiche" (oceanography and seafloors, biological resources).

Bathyal fishing developed in Liguria (in particular in Genoa and Santa Margherita Ligure) from 1925 onwards with the advent of steam-powered fishing boats and, later, motor fishing boats replacing sailing vessels, which were able to operate at 200 m depth along the bathyal escarpment [20,287]. Two deep-water fishing areas were identified in front of the promontory, the epibathyal and mesobathyal hauls Cala di Terra le Rame, of which the second, dedicated to shrimp fishing (*Aristeus antennatus* and *Aristaeomorpha foliacea*), received significant attention for obvious reasons linked to the prestige of the target species (Figures 13b and 20e–g). The catch trend, with some variations, showed a progressive decrease in the post-war period from as early as 1950 (from 1 t per boat per day in 1948 to 18 kg in 1995), with the almost complete disappearance of the red shrimp from the 1970s and with major shifts in the bathymetric distribution and sizes of the species [210] (Figure 20g). While in the late 1940s, there were 26 boats, today, fewer than 10 boats exploit the deep-water fishing ground [221,288].

More recently, various studies have been carried out to characterise the diversity and fishing efforts of artisanal and recreational coastal fishing within the Portofino MPA for conservation purposes. This area traditionally hosted a well-developed fleet of artisanal fishing boats, which, despite the natural decline due to the retirement of elderly fishermen, is still active today [289–292]. The artisanal fleet consists of around 20 vessels <10 m TL, and activities are permitted in the zones of partial protection for residents of the three municipalities of the area [292]. The fishing activity features numerous *métiers* and target species: with the exclusion of the *tonnarella* tuna trap and gillnets (restricted to Zone C and to specific times of the year), most of the equipment used in the zone consists of fixed nets and traps, followed by longlines and seiners [293]. Recreational fishing, which numbers over 350 operators, is permitted in the zone of general protection to residents only, while it is also allowed for non-residents in the zone of partial protection, with authorisation. Specific regulations, including a ban on trawling within the boundaries, are laid out in the MPA's 2008 execution and organisation regulations [291]. The MPA recently implemented monitoring programmes, with personnel on board the vessels to characterise the artisanal and recreational fishing efforts in the 18 fishing areas identified along the promontory, reporting maximum efforts (from 140 to 160 fishing days per year) at the two capes of Punta del Faro and Punta Chiappa, in large part due to recreational fishers operating from land [294–296]. The fishing monitoring estimated a total catch of around 8–9 t per year of fish caught by rod and reel, of which the greater amberjack *Seriola dumerili* and the dolphinfish *Coryphæna hippurus* represent the most frequent catches.

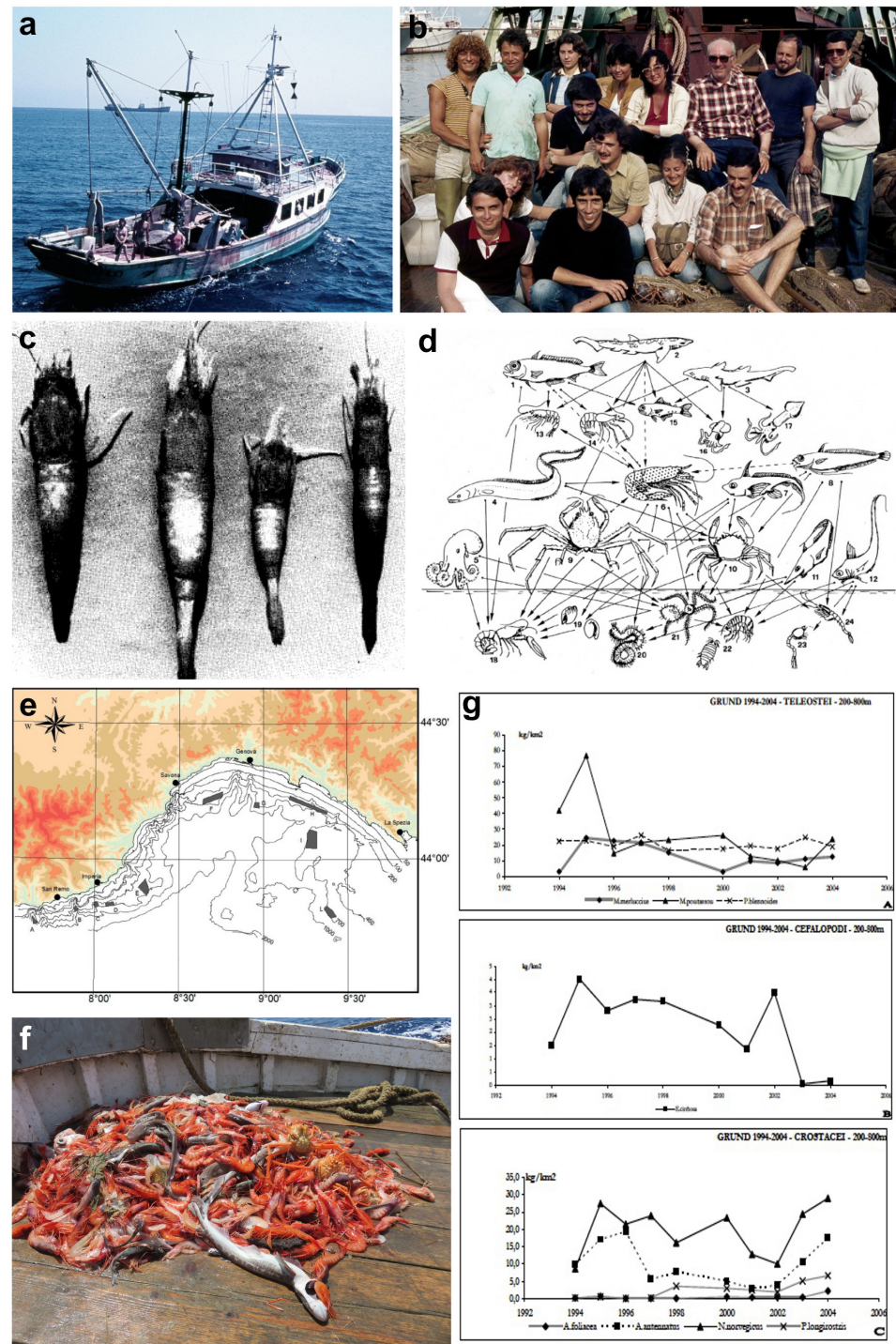


Figure 20. Fishing biology. (a) The trawling vessel *Lavoratore II* of Benedetto Paccagnella used for a long time by Giulio Relini and Lidia Orsi Relini to study the shrimp fishing grounds; (b) Benedetto Paccagnella surrounded by students from the University of Genoa, some of whom continued their scientific careers in marine biology (Mario Mori, Mario Petrillo, Paolo Povero, Leonardo Tunesi); (c) some crustaceans obtained during scientific fishing campaigns (from [225]); (d) deep-water food web scheme for the Ligurian trawling grounds (from [223]); (e) bathymetric map of the Ligurian Sea showing the main trawling fishing areas of the purple shrimp *Aristeus antennatus* (from [220]); (f) a shrimp haul (in the foreground a blackmouth catshark, *Galeus melastomus*); (g) graphs showing the quantities (kg/km²) of the trawl target species detected during the GRUND scientific fishing campaigns (from [220]).

5.2. The Tonnarella of Camogli

Two tuna traps (*tonnare*) once delimited the section of the coast currently falling under the Portofino MPA. Both were historically documented from the early 17th century, although they are certainly older. The first tuna fishery was located in the area of Santa Margherita Ligure and was abandoned in 1875; the memory of it remains in the toponym of Punta Pedale. The second (*tonnarella*) was situated immediately to the west of Punta Chiappa, within the municipality of Camogli, and operated until 2023 (Figure 21a–d).



Figure 21. The tuna trap of Camogli. (a) Preparation of the nets used in the *tonnarella*; (b) the *tonnarella* in action; (c,d) historical and recent hauling of the nets; (e) school of bullet tunas *Auxis rochei* inside the death chamber; (f–i) historical photographs of exceptional catches of large pelagic animals: (f) great white shark, *Carcharodon carcharias*, (g) great white shark photographed on the pier of the port of Portofino by Baron von Mümm, (h) devil fish, *Mobula mobular*, and (i) leatherback turtle, *Dermochelys coriacea* (from [297]).

The fishing system, smaller than that of an authentic Sicilian or Sardinian *tonnara* and used primarily for catching pelagic species other than bluefin tuna (*Thunnus thynnus*), was cast every year from April to the end of August and was composed of coconut fibre material (Figure 21a). This was woven partially in Camogli, partially in the hamlet of S. Fruttuoso, along a strip next to the famous abbey of the Italian National Trust, the FAI (Fondo Ambiente Italiano). In the last few decades, coconut fibre replaced cordage manufactured with rope grass (*Ampelodesmos mauritanicus*), produced in San Fruttuoso until the mid-20th century. The coconut cordage selected a rather particular community of benthic organisms dominated by the tube-dwelling amphipod *Jassa* [298,299]. Over the years, the fishers tried using different materials. Still, they observed that the one able to generate the most attraction for some fish species was precisely that on which this crustacean settled [300]. The first quantitative data on the catches from the *tonnarella* were published by Parona [199], while since 1940, data from the Camogli fishermen's cooperative have been available, noted daily, and divided into three daily catches. In the mid-1970s, these data were tallied, generating a series of works on the catch's temporal trends [301,302].

The data on catches between 1959 and 1974, listed by Balestra et al. [301], were analysed by Morri and Bianchi [102]. While the total catch remained relatively constant over time [303], the species composition changed sharply from a fish community dominated by the bullet tuna (*Auxis rochei*) (Figure 21e) in the 1950s to one dominated by the salema (*Sarpa salpa*). Balestra et al. [301] explained the decrease in abundance of the bullet tuna with overfishing and the increase in abundance of the salema as the consequence of replacing the hemp or nylon nets with coconut fibre nets: the algae attracting herbivorous fish such as the salema settled more easily on the latter. Nevertheless, the minimum temperatures of the tuna-dominated years were less cold than the salema-dominated ones. Consistent with this, the bullet tuna is a warm-water species with a wide distribution across tropical and subtropical seas, while the salema is a species of temperate waters typical of the Atlantic–Mediterranean region [102,302,304].

Boero and Carli [298] concentrated on the elasmobranch catches, highlighting the progressive numerical decrease of this group but also reporting a series of exceptional catches. These latter included great white sharks *Carcharodon carcharias*, such as a 1.5 t specimen caught in May 1954 [305] (Figure 21f) and the large specimen pictured on the pier of the port of Portofino [1] (Figure 21g), and, above all, the first catch in the Mediterranean Sea of a large specimen of the great hammerhead, *Sphyrna mokarran*, which occurred in 1969. In the same set-up, specimens of the basking shark, *Cetorhinus maximus*, and devilfish *Mobula mobular* (Figure 21h) were caught with a particular frequency [297]. Other specimens of *Mobula* have been caught relatively frequently in recent years. In addition to the elasmobranchs, the *tonnarella* held other surprises in store, such as the only Mediterranean catch of black marlin (*Makaira indica*), a specimen of around 180 kg caught in September 1986 [306]. Finally, two specimens of white marlin (*Tetrapturus albidus*), male and female, were trapped in the nets in 2009.

In 1935, the *tonnarella* caught the only specimen of the Mediterranean monk seal (*Monachus monachus*) documented in the Ligurian Sea, which is now on display at the Natural History Museum Giacomo Doria in Genoa [307]. Underwater sightings of this mammal also occurred in July 2010 and May 2015, the latter documented by a photograph.

More recently, the *tonnarella's* catch has once again undergone study [303], demonstrating that, around the turn of the millennium, a change in the qualitative composition of the catches was seen with an evident decline in the Atlantic mackerel *Scomber scombrus*, a species of northern affinity, replaced by the Chub mackerel, *Scomber japonicus*, which has a greater affinity for warm waters; in addition to this, Cattaneo Vietti et al. [293] highlighted a simultaneous increase in greater amberjacks and horse mackerels (*Seriola dumerili* and *Trachurus* spp.) and other species of warm water affinity such as the dolphinfish *Coryphaena hippurus* and the barracuda *Sphyrna viridensis*. This change in catches seems consistent with the warming of the waters of the Mediterranean basin [293,308]. The history of the

tonnarella, the fishing techniques, and the catch trends were summarised in a volume by Riccardo Cattaneo-Vietti and Simone Bava [297], revised in 2021.

In their revision of the catches of great white sharks in the Ligurian Sea, De Maddalena and Heim [309] highlighted that most occurred in the Portofino area. Some of the caught specimens enriched the collections of various Italian Natural History Museums, such as those in Genoa (cat. N. CE 27517), Modena (cat. N. 045/91), and Milan (cat. N. 2142). The stories surrounding the encounters and catches are various and fascinating. In 1961, a spearfisher encountered a great white shark of around 5 m during a fishing trip between Camogli and Punta Chiappa but survived it. In 1991, at the site of Covo di Nord-Est (Santa Margherita Ligure), a great white shark attacked a woman tanning on a surfboard a few metres from the shore. The shark bit the board, leaving a bite mark. Finally, in February 2015, some fishers from Camogli recovered a common thresher (*Alopias vulpinus*) of around 3 m from a longline, whose body had been sliced clean through behind the pectoral fins, very likely by a large shark [310].

The catch from the *tonnarella* was also peculiar due to the large quantity of ocean sunfish (*Mola mola*). Parona, who visited the set-up in 1906, described a catch of around 500 individuals of this species. The ocean sunfish was sold as fillets for a long time, but its catch is currently prohibited by the European Union [311]. The Promontory of Portofino is one of the Mediterranean areas with the greatest abundance of these huge medusivorous fish, and this suggests the presence of still-unknown trophic chains able to support its extremely high biomass. An increase in the abundance of jellyfish and their predators in the last decade has been hypothesised as a direct consequence of overfishing in the Mediterranean Sea [312]. A high concentration of gelatinous plankton in the area can also be correlated to capturing an enormous specimen of the leatherback sea turtle *Dermochelys coriacea*, weighing 450 kg in 1945 (Figure 21i). The specimen is now preserved in the Museum of Natural History in Genoa [205].

In addition to the *tonnarella*, other traditional fishing *métiers*, which are still carried out on the promontory, have been described [313]. A very particular type of net, still used today in Camogli, is the mugginara. This bag-shaped net is lowered open like a large mouth between two fishing boats and suddenly let out at a sign from a lookout stationed at an elevated point on the coast [297]. Another fishing activity practised for centuries on the promontory targets the transparent goby *Aphia minuta* (rossetto) [314–317] and whitebait (young anchovies and sardines) (bianchetti). *Aphia minuta* is a goby that is almost entirely transparent and reaches a maximum length of 50 mm; it has been reported in Italy only in the Gulf of Naples and the Ligurian Sea [315]. The fishing of the two targets, which is performed using seines, is allowed within the special management plan for GSA 9 (Geographic Sub-Area defined by the General Fisheries Commission for the Mediterranean—GFCM including the Ligurian Sea and the Northern and Central Tyrrhenian Sea), adopted nationally on the 19th of May 2011 in dispensation to regulation (EC) no. 1967/2006. This type of fishing has been monitored in Portofino for a long time [315], clearly demonstrating that a sharp decline in the resource could also be due to the climatic changes that have occurred in the Ligurian Sea [316,317].

A catch unique to Portofino is that of the bottom-dwelling whitebait, the crystal goby *Crystallogobius linearis*, first reported in Liguria in 1977 but present since ancient times. This catch occurs between December and March in well-delineated areas of the coast of the Portofino Promontory, the location of which is handed down from generation to generation of fishermen. The fishing is performed in the first hours of the day, preferably after a storm surge, when the water is still slightly turbid. A modestly powered motorboat drags a small, narrow mesh seine. It is worth remembering that during reproduction, this species presents strong adaptations to benthic life because it lays its eggs inside tubes of large polychaetes, such as, for example, *Protula tubularia*. The eggs, almost claviform, are taken care of by the male, which, due to its small size, can enter the tubes of the polychaetes used as nests.

6. Conservation

6.1. The Marine Protected Area of Portofino

The Portofino Marine Protected Area (MPA) was set up by decree of the Minister of the Environment, Edo Ronchi, in agreement with the Treasury Minister, Carlo Azeglio Ciampi, on the 6th of June 1998 (Official Journal no. 188, 13 August 1998) (Figure 22a). The consultation for this act began on the 16th of June 1992, when, a few months from the Framework Law on Protected Areas (no. 394, 6 December 1991), the Marine Protection Council advanced the preparatory proposal. ICRAM (Istituto Centrale per la Ricerca Applicata al Mare—Central Institute for Research Applied to the Sea) and the municipalities of Camogli, Portofino, and Santa Margherita Ligure then expressed a positive opinion of this proposal. On the 8th of September 1997, the Liguria region sent the Ministry of the Environment a note (no. 98830/1134) requesting some modifications to the original proposal, then adopted by the council.

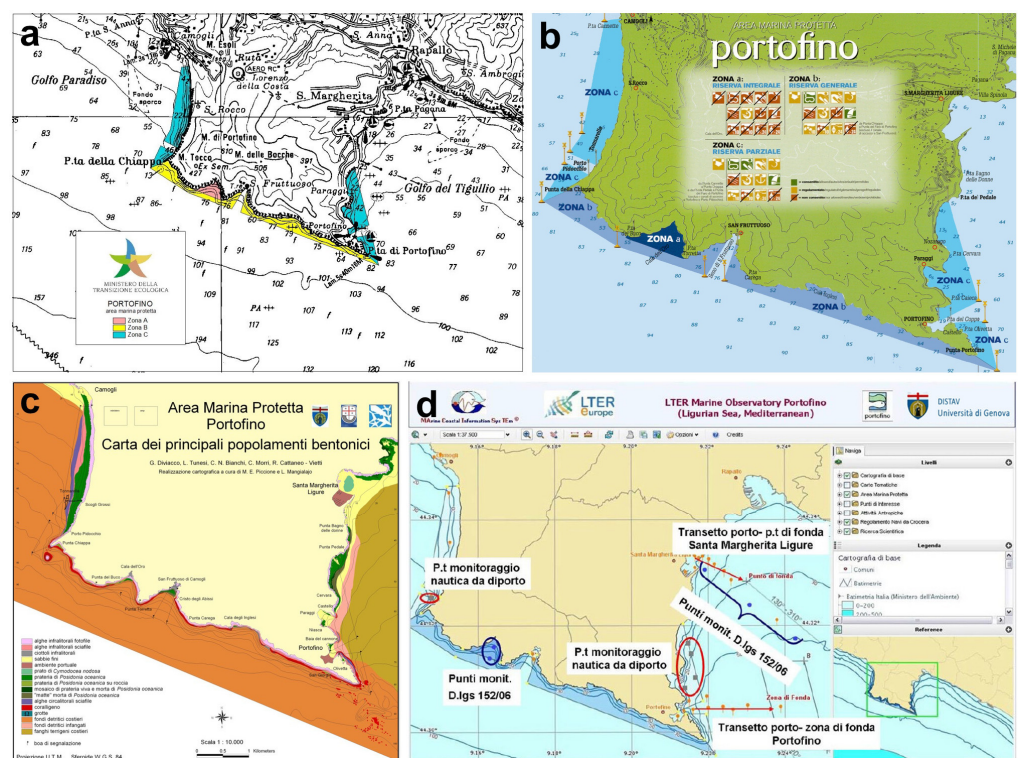


Figure 22. Portofino Marine Protected Area. (a) Ministerial map indicating the boundaries of the Portofino Marine Protected Area; (b) map indicating the zonation and regulation of the activities; (c) map of the main benthic biocoenoses (from [253]); (d) map of the area extrapolated from the WebGIS Maciste.

In reality, before the consultation period, the protection of the marine environment had already started in regulatory terms with Article 15 of Italian Law 963/1965 and Article 98 of the relative implementing regulation (Italian Presidential Decree 1639/1968). In 1998, the establishment seemed to catch everyone by surprise. The truth is that the idea of a marine park completed a long journey since in 1971, Ghisotti and Fanelli and later on in 1974, Michele Sarà and Enrico Tortonese already proposed an underwater park around the Portofino Promontory in various conventions organised by the Genoese provincial administration.

Moreover, the “Portofino Gulf” was included in the 20 areas listed in Article 31 of the “Provisions for Defence of the Sea” Law no. 979 of 31 December 1982, for which the Council for Defence of the Sea against Pollution had to perform some checks for the purposes of establishing “Marine Reserves”; these checks involved investigations relating to the following: (a) natural situations of the places and surfaces to be protected; (b) scientific, ecological, cultural, educational and economic goals with which the protection was to be

coordinated; (c) any study and research programmes as well as exploitation; (d) reflections on protection with regards to maritime navigation and economic exploitation of the sea and the marine state property; (e) easily foreseeable effects of the establishment of the marine reserve on the natural marine and coastal environment, and of the economic and social situation of the involved territory and populations; and (f) plan of restrictions and protection and exploitation measures considered necessary for implementing the goals of the marine reserve. Concretely, the timeframes for protection of the “Portofino Gulf” were also extended by the appeals against Law 979/1982 put forward in 1983 by the regions of Friuli-Venezia Giulia and Liguria through recourse to the constitutional court, as well as the transfer of some competences from the Merchant Shipping Ministry to the Environment Ministry, implemented with Law 349/1986. The appeals were deemed inadmissible by the constitutional court with its judgement no. 1031 issued on 27 October 1988. In 1986, the first bionomic map of the area [58] was produced, which, when subsequently implemented, formed the foundations for the MPA cartography. Further delays probably also derived from the time necessary for discussion, approval, and application of the Framework Law on Protected Areas, no. 349/1991, which, concerning the Portofino Gulf, acknowledged the provisions of Law 979/1982, confirming it to be among the applicable marine areas in which “marine parks or reserves could be established”.

The approval of the Framework Law on Protected Areas nevertheless provided impetus to studies and proposals: the first draft of a structured proposal for the establishment of an MPA in Portofino was attributed to Diviacco et al. [318] and Diviacco and Tunesi [253]. Some years would still pass before the proposal could be rendered effective. On 13 September 1997, the Official Journal no. 214 published the decision with which, on 2 December 1996, the Committee for Protected Natural Areas approved the update to the first three-year programme in 1994–1996: the Ministry of the Environment established seven marine reserves within the first three months of publication, including the Portofino Gulf Marine Reserve. In the months that passed between the decision and its publication, public debate was not lacking. On 9 July 1997, Senator Roberto Avogadro presented an interrogation to the Minister for the Environment: “Given that the proposal to establish a marine reserve in Portofino has been floated; that this choice has been made not following the involvement of local bodies, but rather on a centralist initiative; that the community of the Portofino park expressed itself against this proposal on the 19 June 1997; I would like to know the following: whether the proposal for the establishment of the Portofino Marine Reserve is true; if so, is this method of managing things not anachronistic, without the involvement of the local bodies who should play a leading role in these choices; what is intended to be done to re-establish respect for the rights of those in Portofino who live and work and know the situation close-hand, rather than interfering with an improvident measure”. On 18 November 1997, the minister responded, “With the interrogation in question, the issue of the establishment of the Portofino marine reserve is brought to the attention of this Ministry. In this regard, attention is drawn to the fact that the Committee for the Defence of the Sea against Pollution formulated its proposal for the establishment of the Gulf of Portofino Marine Protected Area as far back as 16 June 1992 and that the interministerial Committee for Protected Areas decreed its establishment in the session of 6 December 1996. We are awaiting the Region of Liguria, in consideration of the request for further information on the socio-economic aspects and repercussions of the Marine Protected Area, to give a definitive response to the proposal for establishing an area of national interest which cannot, therefore, be subject to specific local interest which, even if legitimate, must fall within the composition of the wider framework offered precisely by the regional authority”.

The implementing decree of 1998 was the subject of an intense debate between the central administration and the local organisations involving not just Portofino but also various other protected areas and local bodies, including associations and ad hoc groups supporting different ways of thinking: those who considered the protected area as an issue to be avoided entirely, those who saw it as a potential economic resource, and those who saw it as an ethical requirement for protecting biodiversity. Within this context, on

9 December 1998, the Italian Law no. 426 on “New Interventions in the Environmental Field” was approved, which modified some of the Laws 979/1982 and 394/1991 provisions. Following additional modifications requested by the Liguria region, and after hearing the opinion expressed on 22 April 1999 by the Joint Conference of State, Regions, Cities and Local Authorities, on 26 April 1999, the Ministry for the Environment, in agreement with the Treasury Minister, approved a new decree (published on the Official Journal no. 131 of 7 June 1999) that superseded the original decree. The main differences compared to the original decree were the explicit exclusion from the MPA and the relative restrictions of the access channels and natural harbours of Portofino, S. Fruttuoso, and Porto Pidocchio and, consequently, the division of the MPA into four segments; more permissive navigation and anchoring rules, both in Zones “B” and “C”; the reduction from 1000 m to 500 m of the buffer zone bordering the MPA where navigation was only permitted at speeds not exceeding 10 knots.

Therefore, the current MPA corresponds to that established by the Ministerial Decree of 26 April 1999. It includes the sea and seabed (including the corresponding coastal territories belonging to the marine state property) off Camogli, Santa Margherita Ligure, and Portofino [289].

The MPA covers an area of 346 ha and is divided into zones with different levels of protection (Figure 22a,b). Zone A (Integral Reserve) includes the creek of Cala dell’Oro, delimited by Punta Torretta and Punta del Buco. Here, navigation, anchoring, access, bathing, sports or professional fishing, and SCUBA diving are prohibited, and only authorised research and monitoring activities are permitted. Zone B (General Reserve) ranges from Punta del Faro to Punta Chiappa. In this zone, sport fishing is allowed, with regulations, to residents only; SCUBA diving is permitted for diving centres (associations and companies) and authorised private individuals, while free diving and bathing are allowed. Zone C (Partial Reserve) extends to the two sides of the Portofino Promontory. Here, diving and bathing are unrestricted; recreational fishing is also permitted to non-residents, although regulated. In addition to these zones, as previously mentioned, the MPA is surrounded by a 500 m wide buffer zone in which the maximum navigation speed is 10 knots.

The MPA is managed through the application of executive and organisational regulations, the current version of which was approved by the Minister for the Environment on 4 August 2008 (G.U. N °181).

Since 2005, the area has acquired the status of Specially Protected Area of Mediterranean Importance (SPAMI), which was assigned by the Regional Activity Centre for Specially Protected Areas (RAC/SPA) of Tunis. This centre operates on behalf of UNEP (United Nations Environment Program) in applying the Barcelona Convention (1975). Currently, the list of SPAMIs consists of 34 sites, of which 11 are Italian Marine Protected Areas. A detailed cartography of the habitats and biocoenoses of the MPA was later produced and updated by the region of Liguria (Figure 22c) together with an online public GIS cartography of the area (WebGIS Maciste, University of Genova) (Figure 22d).

More recently, the Portofino MPA has been considered for inclusion in a newly created Portofino Natural Park, incorporating both sea and land. The 2018 Budget Law (no. 205 of 27 December 2017) was added to Article 34, paragraph 1, of the Framework Law no. 394/91. The same budget law was provided to finance the Portofino National Park with EUR 1,000,000 from 2019 onwards. The controversy around this park is well known and was featured in television and media debates and events. The controversy derives from the existence of three different boundary proposals: the ministerial proposal (following the prompting of the Lazio TAR, or Regional Administrative Tribunal) with provisional boundaries including 11 municipalities for a total of 5363 hectares; the proposal of ANCI Liguria (Association of Italian Municipalities, Regional section), which includes seven towns for a total of 2940 hectares; and the proposal of the Liguria region, which consists of three municipalities (the same as the MPA) for a total of 1700 hectares. The process turned into a flurry of judicial decisions following various appeals, including that of the Liguria region at the Liguria TAR (Regional Administrative Court), against

the boundaries proposed by the Ministry of the Ecological Transition. The Liguria TAR cancelled the ministerial decree of provisional boundaries, but subsequently, the Council of State conceded the suspension of the TAR's decision and found that the Liguria TAR did not have standing for a question of national interest, such as the establishment of the boundary of a national park. The Decree of the Minister of the Environment and Energy Security no. 331 of 10 October 2023 established a new provisional perimeter (reduced to only three municipalities) and new provisional safeguard measures for the Portofino National Park (annulling the previous ministerial decrees of 2021). The same minister, with a decree of 6.11.2023, established a new Provisional Management Committee. The TAR of Liguria, with sentences no. 372 and no. 373 of 21 May 2024 annulled these last ministerial decrees, restoring the initial provisional perimeter involving 11 municipalities. However, this is still a provisional and not definitive perimeter. In 2023, the Portofino MPA turned 25 years old, and even though it is sufficiently active in pursuing its goals, a period of uncertainty has reigned for around two years, caused precisely by the proposal to incorporate it into a national park whose boundaries and organisation appear rather vague. The role, professionalism, and image acquired internationally by the Portofino MPA in recent years should continue to be consolidated without further delay.

6.2. The Special Area of Conservation

The establishment of the MPA was preceded in June 1995 by the proposal for Site of Community Importance "IT1332674 Fondali Monte Portofino" in applying Directive 43/92/EEC "Habitats". The site, part of the European ecological network Natura 2000, extends for 544 hectares. Its boundaries were designated within a national-scale phase of investigations and verifications of the project "Progetto BioItaly". This project, financed by the European Union, was started by the Ministry of the Environment through the Natura Conservation Service, specifically in implementing the Habitats Directive and in virtue of the provisions of Law 394/91. The project allowed for collecting, organising, and systematising information on the environment, particularly the biotopes and natural or semi-natural habitats of greatest interest, to address specific forms of safeguarding and management. The project led to the identification within the Liguria region of numerous sites of community (SCIs), national (SNIs), and regional (SRIs) importance, and special protection areas (SPAs), with habitats, flora, and fauna of exceptional naturalistic value that were worthy of conservation.

The boundaries of the "Fondali Monte Portofino" site were traced with the main scope of preserving four habitats listed in Annex I of Directive 43/92/EEC and one species listed in Annex II: (a) 1110 sandbanks, which are slightly covered by seawater all the time; (b) 1120* *Posidonia* beds (*Posidonia oceanica*) priority habitat; (c) 1170 reefs; (d) 8310 submerged or partially submerged sea caves; and (e) common bottlenose dolphin (*Tursiops truncatus*). The outline of the species to protect is completed by the long-spined urchin (*Centrostephanus longispinus*) and the Mediterranean slipper lobster (*Scyllarides latus*), listed in Annex IV of the directive, and by red coral (*Corallium rubrum*), included in Annex V, in addition to other species included in the Red Lists of fauna that are threatened or protected by international conventions.

With a decree dated 13 October 2016 (Official Journal 28/10/2016 n. 253), the Minister of the Environment and for the Protection of Land and Sea designated the "Fondali Monte Portofino" site as a Special Conservation Area (SAC) of the biogeographic Mediterranean region, subject to the conservation measures drafted in 2014 by the regional government of Liguria, as well as to the MPA regulations. The SAC designation represented a critical step in contributing to the full implementation of the Nature 2000 Network. It guaranteed specific conservation measures and offered greater security for managing the network and its strategic role in stopping the loss of biodiversity in Europe. The SAC status involves greater responsibility and cautiousness in using terrestrial and marine resources, including preventive procedures assessing the effect that the plans, programmes, projects, interventions, and activities could have on the state of conservation of habitats and species under protection.

6.3. Pelagos: The Cetaceans Sanctuary

The Portofino Promontory is part of the Pelagos Sanctuary, established in 1999 thanks to an agreement between Italy, France, and the Principality of Monaco. The primary goal of the sanctuary is to “guarantee the positive conservation status of marine mammals by protecting them and their habitat from the direct or indirect negative impacts of anthropogenic activities” [319–321]. In 2001, the Barcelona Convention recognised its importance, adding it to the SPAMI (Specially Protected Areas of Mediterranean Importance) list; only in 2002 did the sanctuary effectively come into force, and in 2004, a management plan shared by the three states was adopted to make the protection of cetaceans more effective through participative management of the area.

The origin of the toponym Portofino derives, according to Pliny the Elder, from *Portus Delphini*. According to an anonymous text mentioned by Da Prato [322], the ancient name is linked to the “multitude of dolphins which inhabit this sea”. In addition to dolphins (*Delphinus delphis*, *Stenella coeruleoalba*, *Grampus griseus*, and *Tursiops truncatus*), the Portofino coast has been visited by numerous other cetaceans that, in some cases, were captured. Many are preserved in the Museum of Natural History Giacomo Doria [323]. Among these is the common minke whale (*Balenoptera acutorostrata*) captured in Camogli in 1916. In February 1983, a long-finned pilot whale (*Globicephala melas*) was captured in Punta Chiappa, and its internal organs were donated to the University of Genoa’s museum. The dried stomach and a portion of the intestine with acanthocephalan parasitic worms (*Bolbosoma capitatum*) remain in the collections of the Department of Earth, Environment and Life Sciences. Finally, a rare example of a false killer whale (*Pseudorca crassidens*) was captured in Camogli in February 1893.

Among the species of cetaceans present in the sanctuary, the common bottlenose dolphin *Tursiops truncatus* is the most coastal species, and one of its resident populations frequents the waters of the Portofino Promontory [324]. Starting in 2013, a permanent automated passive acoustic monitoring system, able to detect and track dolphins in real time, was tested in the area within the frame of the ARION Life+ Nature project activities [325–327]. Bottlenose dolphins were acoustically monitored by two fixed units, each equipped with four hydrophones, placed on two beacons located off two sites on the southern front of the promontory, namely Punta Carega and Casa del Sindaco [328]. The analysis of the recordings demonstrated that the Portofino MPA is highly frequented by common bottlenose dolphins, which were detected in 37% of the recording days. *Tursiops* are present year-round but are more common in the spring and partially in summer, and the research highlighted the use of the promontory zone for transit and feeding. Their reduced presence in summer was linked to the disturbance caused by recreational vessel traffic [327].

Meliadò et al. [329] recently studied the dolphins captured in Italy from 1927 to 1937. In the Gulf of Genoa, 347 specimens were caught in that decade, concentrated primarily in the port of Camogli, whose fishing community mainly practised harpoon fishing. Artisanal production of a dolphin meat speciality called “*musciamme*” (from an Arabic word meaning dry and tough) continued until the 1980s. The *musciamme* was salted in 20–25% brine for two weeks and then air-dried [330,331].

6.4. Environmental Accounting

Coastal marine ecosystems are high-value systems that provide services and benefits such as high productivity, commercial and non-commercial fishing, stabilisation of sediment, and numerous recreational and cultural services. Nevertheless, the intense urbanistic, industrial, and tourism development in coastal areas, combined with a limited perception of the link between the health of the ecosystems and human well-being, is threatening marine ecosystems worldwide.

The coastal area of the Portofino Promontory, especially that relative to the MPA, is characterised by a particularly anthropised environment, including numerous activities (nautical tourism, diving, fishing) and developed urban areas; a particular focus has

therefore been placed on the studies of the main ecosystem services of the site, from the point of view of the creation of management models aiming for sustainable development of the entire study area, in which a context of high naturalistic prestige is combined with the potential growth of the anthropogenic pressure requiring careful management.

Ecosystems' capacity to produce services and generate benefits is based on maintaining natural capital, defined as the stock of natural resources supporting ecosystem goods and services. Effective ecosystem management will then rest on correctly assessing the natural capital.

In this context, environmental accounting represents a fundamental tool for summarising the ecological complexity and assigning a value to the natural capital.

The assessment of the natural capital of an MPA requires keeping in mind the fact that an MPA contains a variety of habitats that provide different types and quantities of ecosystem services, which are subject to various pressures and respond differently to stresses. The heterogeneous nature of these habitats makes it fundamental to know the location of each habitat to evaluate appropriate conservation goals and manage anthropogenic pressures. Consequently, habitat mapping became an effective tool for implementing the decisions of the MPAs and summarising the essential spatial information for monitoring and further managing the MPAs.

The environmental accounting of the Portofino MPA is estimated at over €10 million in its natural capital [143,332,333]. The assessment also allowed us to identify its spatial distribution, obtain a quantification of the value of the ecosystem services generated and the benefit that humans draw from them, and develop a decision-supporting system for the managers of the area. The decision-supporting system, based on a cost/benefit analysis through an ecological approach, allows the assessment of how effective the management and protection measures are in maintaining human capital while continuing to offer ecosystem services to the users and well-being of the population.

6.5. Anthropogenic Impacts and Conservation Status Assessment

The establishment and activities of the MPA have led to the production of many studies regarding the characterisation of the benthic and fish communities, as well as numerous management works regarding the impact of human activities on marine communities. Three main categories have been considered regarding this latter aspect: the impact of fishing gear, the impact of diving activities, and the impact of recreational vessels, above all, concerning anchoring.

Even before the establishment of the MPA, a study demonstrated for the first time the effect of lost fishing lines on the condition of the large red gorgonian *Paramuricea clavata*. At the time, line fishing was considered the lowest impact gear due to its selectivity regulated by the size of the hooks. However, lost lines remain trapped in the coralligenous substrate, which is highly heterogeneous, and on the arborescent colonies, destroying the coenenchyme and allowing epibionts to settle on the skeleton, thus ultimately leading to the death of the organisms [334] (Figure 23a–c). The impact of fishing on the colonies was re-evaluated in 2016, demonstrating that over 50% of the *P. clavata* colonies and 36% of the *Eunicella cavolini* colonies exhibited portions of tissue destroyed from the contact with fishing gear, ascribable both to artisanal and recreational fishing [296] (Figure 23d–f). The impact also interested *Corallium rubrum* (Figure 23g). The seriousness of the situation can be determined by considering that inside the Medes Islands MPA, this type of impact does not exceed 10% [335]. Nylon was also found trapped within the coralligenous matrix, confirming the persistence of the material in the environment. To this end, a study was conducted within the MPA to determine whether the temporal succession of fouling on the nylon lines could be used as an indirect reference to estimate the age of the fishing litter, providing important management implications [336]. Faced with a growing number of reports of lost gear within its boundaries and based on the research performed, the MPA supplemented its management plan with measures designed to reduce the impact, prohibiting shore fishing for some periods in specific sites and implementing monitoring of fishing through catch monitoring and censuses, also including non-commercial vessels.

Some studies, in particular, shed light on the relationship between small-scale artisanal fishing and recreational fishing within the boundaries of the MPA [292]. Moreover, in recent years, the local diving community became a promoter of seafloor cleaning initiatives, and these activities have been supplemented with Citizen Science projects carried out in partnership with the Reef Alert Network made up of aware divers aiming to train SCUBA divers to monitor lost fishing gear and impacts on organisms.

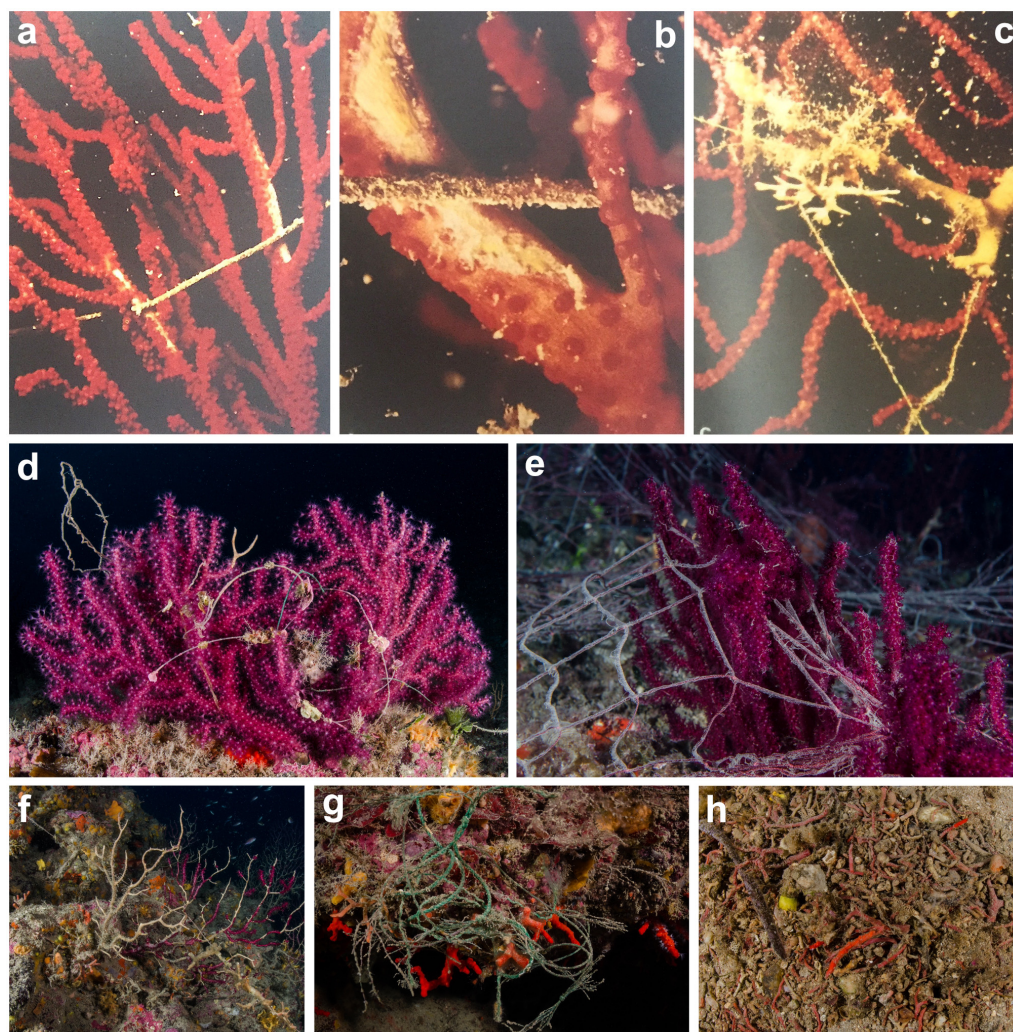


Figure 23. Anthropic impacts on the benthic communities. (a–c) Effects of entangled fishing lines on the gorgonians: the lines, moved by the current, scrape the coenenchyma (a,b), enhancing the settlement of epibiotic organisms on the denuded portions (c) (from [334]); (d–f) the monitoring activity of the health status of the gorgonians carried out in 2016 shows numerous colonies of *Paramuricea clavata* enveloped by lost gear, lines (d), and nets (e), which cause abrasion of the living tissues of the gorgonians, sometimes leading to the death of the colonies (f) ((d,f), from [296]); (g) the same survey showed *Corallium rubrum* colonies entangled in lost fishing gear; (h) accumulation of fragments of benthic organisms, including *C. rubrum*, at the base of cliffs with high diving frequentation.

Various studies have been conducted on the fish communities present in the MPA and the impact that fishing has on them. The most relevant data is that, after 15 years of protection, the fish biomass in the MPA significantly increased, promoting a positive spill-over effect. Simultaneously, it has been demonstrated that fishing removes around 100 tonnes per year from the MPA, of which 8% are by the hands of recreational fishers [337,338].

The high intensity of diving activities determines another significant source of impact for the benthic communities of Portofino. About 40,000 dives are performed annually along

the 6 km coastline of Zone B. While the conservation knowledge of the divers has markedly increased, it has been shown that the impact is significant in sensitive environments, like those featuring a significant vertical development of calcified organisms. Characterisation of the divers entering the waters of the Portofino MPA and studies of their direct contact with the seafloor were analysed by Lucrezi et al. [338–340]. By comparing similar sites with different levels of frequentation, it was possible to measure up to ten times greater quantities of broken red coral colonies in sites featuring a high presence of divers [341] (Figure 23h). Based on this evidence, during the summer of 2020, a vulnerability assessment was carried out regarding diving activities for all the diving sites of the MPA between 10 and 40 m. In particular, the sensitivity of the benthic species present in each site to the impacts generated by diving was assessed to provide a tool that would allow the management of diving to be optimised within the MPA. This study evidenced the particular vulnerability of the bathymetric zones below 20 m and the highest level of vulnerability of sites such as Grotta della Colombara, Punta Torretta, Secca dell’Isuela, and Cristo degli Abissi, featuring a great abundance of fragile species such as *Corallium rubrum*, *Leptopsammia pruvoti*, and various species of calcified erect bryozoans [342]. This research promoted the establishment, commencing in the spring of 2022, of courses for environmental diving supervisors aiming to promote sustainable diving and encouraged the adoption of MPA rules regarding the maximum number of divers permitted in the most vulnerable sites.

The Portofino MPA is also widely frequented by recreational boats, with numbers higher than what is reported in the other Ligurian MPAs, with peaks during summer months and holidays of over 200 vessels per day. These can generate impacts, especially during anchoring, which is prohibited in Zones A and B but permitted in Zone C; since 2006, various monitoring efforts have been made to understand the issue and encourage its correct management [343,344]. The zone is also highly frequented by tourist cruises, whose economic and environmental impact can be significant, above all for the small village of Portofino [345].

The most evident effect of the MPA’s protection has probably been the significant increase in the populations of the dusky grouper *Epinephelus marginatus* [346]. In the 2014 edition of Cernia Day, organised by the Portofino MPA, a census was taken at 23 diving sites, resulting in 269 dusky groupers and ten golden groupers *Epinephelus costae*. Today, the mottled grouper *Mycteroperca rubra* is also certain [347].

Regarding the effects of the protection regime on the benthic communities, in addition to the previously mentioned effects on the red coral populations, Montefalcone et al. [134,139] and Lasagna et al. [136] evaluated the state of the *P. oceanica* meadows a few years after the establishment of the MPA. These studies demonstrate regression phenomena in the eastern section of Zone C. At the same time, the meadows remain substantially stable in the areas of greater protection to the west, although exhibiting a certain stress level.

Thibaut et al. [348] analysed the changes in the environmental status of the algal ecosystem of the rocky reefs of Portofino before and after the establishment of the MPA, using the multimetric biotic index EBQI (Ecosystem-Based Quality Index). Portofino is the only Marine Protected Area in the Mediterranean Sea for which comparable information is available both for the period before (1990–1993) and after (2008–2014) the establishment of the MPA. The ecological status was assessed as being “moderate” for both periods, with minimal variations in the value of the index (4.98 in 1990–1993 versus 5.43 in 2008–2014); the confidence level of the index was similar in both cases (8.30 in 1990–1993, 9.10 in 2008–2014). Nevertheless, a significant decrease in macroalgae occurred, although counterbalanced by an increased abundance of fish. The protection was, therefore, effective for fish but did not prevent the degradation of the structure of the habitat [106]. This result is not surprising since in MPAs, particularly when fishing restrictions are rigorously applied, fish respond more clearly and directly to the protection measures [349]. This highlighted the need for administrators not to consider only the index’s total value: the scores of the individual components must always be checked to evaluate better which management actions are most appropriate [350]. As an example, the ecological quality assessed for the macroalgal communities of the intertidal fringe using the CARLIT index [351] showed high values

for the Portofino MPA from the first surveys in 2004/2005 [352], remaining substantially unchanged over the following decade [353].

Scianna et al. [354,355] recently assessed the effectiveness of the Portofino MPA applying organisation science. Results indicated a moderate management performance with respect to a great organisational size (ratio between full-time equivalent positions and surface area), which suggests the need for improvement in management: the MPA conducts appropriate projects but invests little in assessing, planning and accomplishing their activities (e.g., monitoring the effect of educational programmes).

6.6. Diseases and Mass Mortalities

The first signals of climate change, the study of which would represent one of the most interesting lines of research in the decades to come, were perceived in February 1986 when a disease affecting the colonies of *Eunicella cavolini* was noticed on the rocky cliff of Paraggi, destroying their tissues and leaving their skeleton bare [356] (Figure 24a). The following year, an intense mass mortality of sponges, in particular *Spongia officinalis*, was observed across the entire promontory. Gaino and Pronzato [357] described the phenomenon, being the first to suggest that it was due to some bacteria able to destroy the spongin that forms the skeleton of these sponges. In 1993, mass mortality struck the red gorgonian *Paramuricea clavata*, with around 10,000 colonies dying along the promontory between 20 and 35 m [358] (Figure 24b,c). The study of benthic mass mortality events would reach its peak in 1999, when a mass of warm water crossed a large part of the Ligurian coast from east to west, from Livorno to Marseille, causing intense mortality of many benthic invertebrates, with gorgonians hit particularly hard. It was the largest mass mortality event ever recorded in the Mediterranean Sea [359]. This episode gave rise to numerous studies on the recovery of the affected populations, the differential impact of the disease on males and females [360], and the involvement of pathogenic microorganisms [361]. Although smaller in scale, other mass mortality events were observed in 2002 and 2006 [362–364]. Summer 2022 again saw peak temperatures similar to, if not even higher, than 1999's, with surface water temperatures over three degrees higher than the seasonal average and positive temperature anomalies recorded down to 35 m, which continued until October. Observations carried out in Portofino in September 2022 highlighted mass mortalities of *P. clavata* and *E. cavolini* in many sites of the Portofino Promontory (Montefalcone, pers. obs.) (Figure 24d,e) and altered reproductive potential of the brown alga *Ericaria amentacea* (Chiantore, pers. obs.).

More recently, Corinaldesi et al. [365], while studying variations in the microbiome of *P. clavata*, *E. cavolini*, and *Corallium rubrum* at the same time as the temperature anomalies recorded on the Portofino Promontory in August 2011, observed that, while the studied alcyonaceans did not show visible signs of necrosis, the abundance of associated bacteria and archaea became greater as the temperature increased. This was explained by the decline of the dominant bacteria and the increase in new rare and opportunistic taxa, including pathogens, which determined a direct effect of the alteration of the microbiomes induced by the heatwave. Nowadays, Portofino Promontory is listed among the many Mediterranean sites that provide valuable information regarding marine heatwaves and mass mortality events [366,367].

In addition to the damage caused by heatwaves, the Portofino red coral was tested to determine the variations in the rates of biocalcification, growth rates, and polyp feeding activity in various scenarios of increasing acidification of the waters. The data obtained demonstrated a significant reduction in these parameters with the pCO₂ forecast for the end of this century (pH reduction of 0.2). This research suggested that the acidification of the oceans expected by 2100 will significantly increase the risk of extinction of the current populations [368].

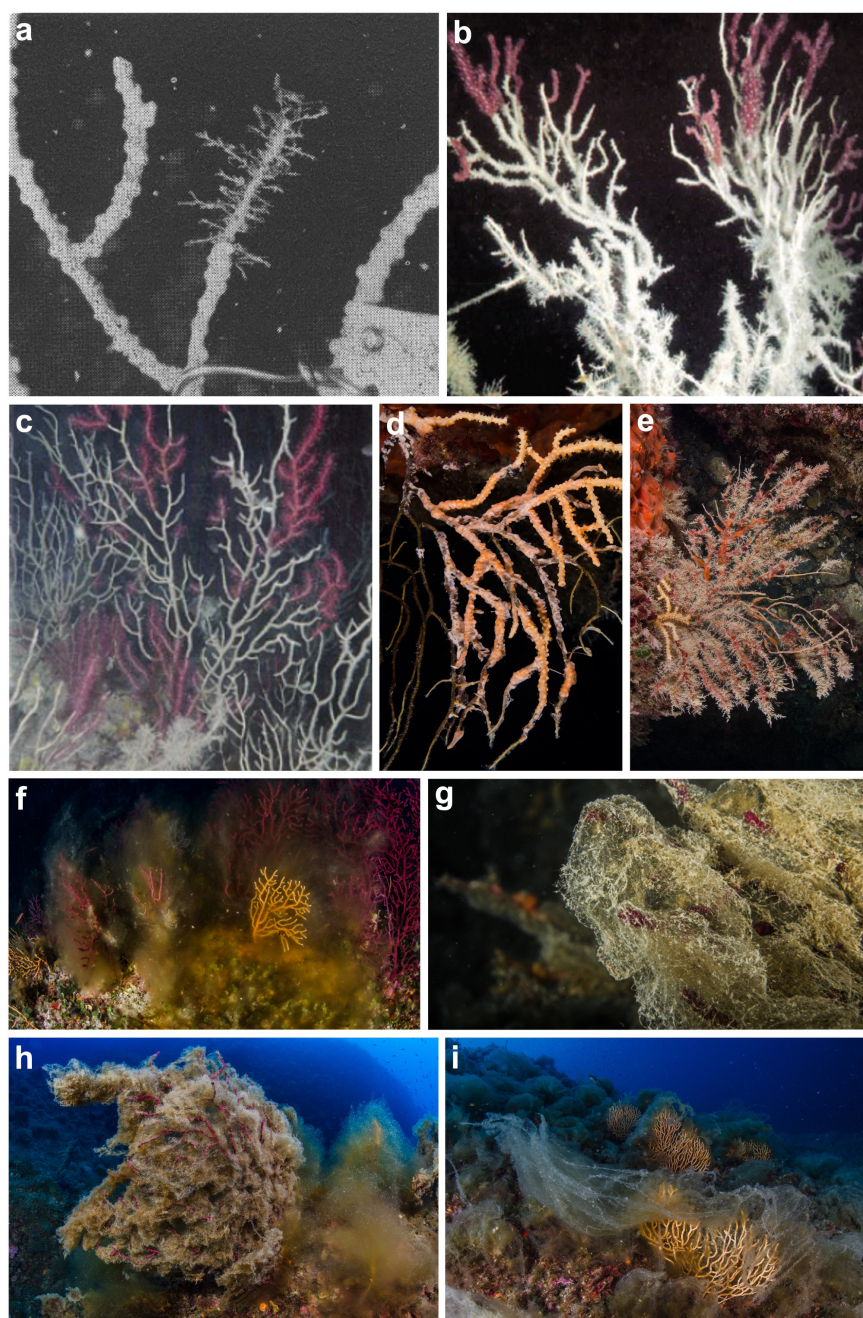


Figure 24. Diseases and mass mortalities. (a) The first Mediterranean report of a disease of *Eunicella cavolini* occurred in 1985 on the cliff of Castello di Paraggi (from [356]); (b) mass mortality of the gorgonian *Paramuricea clavata* observed at the end of summer 1993 on the Punta del Faro cliff (from [358]); (c) colonies of *P. clavata* affected by the mass mortality event of 1999 (from [359]); (d) necrosis in the gorgonian *Eunicella cavolini* during an episode of mass mortality; (e) high coverage of epibionts on *E. cavolini* following the loss of coenenchyme; (f,g) significant quantities of mucilage covering the seabed of the promontory and enveloping the colonies of *P. clavata* and *E. cavolini*; (h) detail of on a branch of *P. clavata* covered by mucilage; (i) colonies of *E. cavolini* covered in mucilage.

Red coral is also sensitive to the concentration of microplastics in the water [369]. The polyps preferentially ingest polypropylene, which has numerous biological effects, from compromised feeding to mucus production and altered genetic expression. Microplastics can also directly and indirectly change the microbiome associated with red coral, causing tissue abrasions that allow opportunistic bacteria to proliferate.

Another source of stress for the benthic populations of Portofino is mucilage, which forms on the seafloor during the summer and accumulates on the branches of the gorgonians, suffocating the polyps [112] (Figure 24f–i). A major mucilage event occurred in Portofino in the summer of 2003, affecting macroalgae, sponges, and scleractinians [112,370]. An even larger event was observed in the summer of 2018 [104,113,114]. The mucilaginous aggregates began to form just below the summer thermocline in June and completely covered the seafloor in July and August. A period of calm in August caused anomalous heating of the surface layer (as previously described by Sparnocchia et al., [371]), leading to the formation of a second thermocline and the development of mucilaginous aggregates even in shallow waters. The filaments in deeper waters (down to 40 m) entangled in the branches of the gorgonians, causing necrosis as observed in other regions of the western Mediterranean Sea [372,373]. In a recent study conducted in partnership between DiSTAV and the University of Milan-Bicocca, it was demonstrated how the climate stress of 2018, with the consequent occurrence of mucilaginous aggregates, caused oxidative damage to the cell membranes of the *P. clavata* polyps in Portofino [374].

The toxic microalga *Ostreopsis ovata*, which can also produce mucilaginous matrices, must be mentioned among the recently arrived species due to seawater warming. This species is present in the Portofino MPA and produces blooms in the surface waters in the hottest periods between July and August but with significantly less abundance compared to more anthropogenic environments characterised by less intense hydrodynamics. A correlation was found between the abundance of the toxic microalga and the presence of structuring algae of the genus *Ericaria* [375]: the integrity of the *Ericaria* populations seems to contribute to reducing the onset of blooms of this toxic microalga.

Finally, monitoring performed from 2012 onwards highlighted, at the end of 2018, the complete disappearance of *Pinna nobilis*, the largest known Mediterranean bivalve, from the waters of the promontory, following mass mortality caused by the protozoa *Haplosporidium* [376] and reported for the first time in 2016 along the Spanish coastline [377]. The species, now in critical danger of extinction, has no longer been observed in the area, leaving space for the southern congeneric *Pinna rudis* [378].

6.7. Climate Change

Studies of the effects of climate change and the long-term impact of anthropogenic activities were made possible after the first decade of this century thanks to the large mass of data deriving from the work of the last 30–40 years. Puce et al. [379] studied the community of hydrozoans of the Aurora Transect 25 years after the study of Boero and Fresi [267].

The comparison highlighted a reduction in species diversity, mainly in the summer months, a shift in the life cycle towards the colder period for numerous summer species, and the descent to lower depths of some surface-dwelling species. These trends are in accordance with the increase in water temperatures. Subsequent studies performed in 2018 confirmed the severe reduction in the diversity of the hydrozoans, the arrival or longer permanence of thermophilic species, and the anticipation of the life cycles in terms of peaks of abundance and fertility [380]. Parravicini et al. [106] highlighted a significant reduction in the large frondose brown algae occupying the shallower rocks of Portofino, thus reducing the three-dimensionality of the habitat.

Similar results were obtained by comparing the community present on 6 m² of cliff in Paraggi between 15 and 20 m at a distance of 25 years [381] (Figure 25a,b). The results showed a sharp reduction in the algal cover, particularly in the frondose algal component. The results were more complex for the poriferans, with some species decreasing while others, particularly encrusting ones such as *Spirastrella cunctatrix*, showed significant increases over time. Similarly, comparisons performed at a distance of 10 years inside Zones A and B of the MPA demonstrated a reduction in the three-dimensionality of the benthic environment due to reductions in erect macroalgae. Homogenisation of the communities was observed at different depths together with variations in the species composition, with an increase in thermophilic and non-indigenous species [108,382,383].

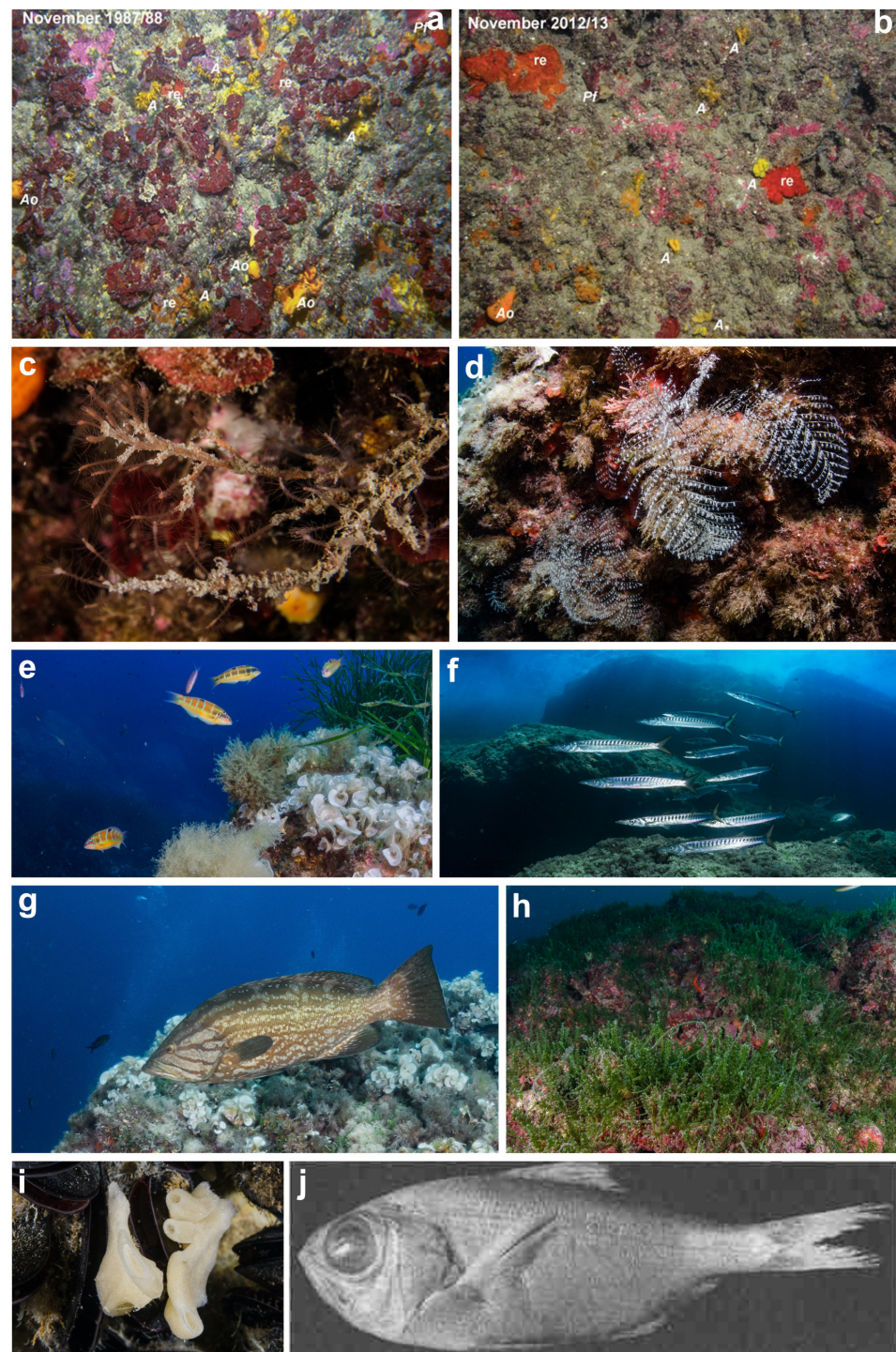


Figure 25. Effects of climate changes on the benthic and fish communities. (a,b) Change in benthic coverage recorded on the Paraggi cliff from November 1987–1988 (a) to November 2012–2013 (b) (from [381]); (c,d) the thermophilic hydrozoans *Corydendrium parasiticum* (c) and *Pennaria disticha* (d) increasingly observed during the summer months along the cliffs of the promontory; (e–g) thermophilic species expanding their geographic distribution in the Ligurian Sea: the ornate wrasse *Thalassoma pavo* (e), the yellow-mouth barracuda *Sphyrna viridensis* (f), and the mottled grouper *Mycteroperca rubra* (g); (h–j) non-indigenous species recorded in Portofino including the algae *Caulerpa cylindracea* (h), the calcareous sponge *Paraleucilla magna* (i), and the splendid Alfonsino *Beryx splendens* (the latter from [384]).

Gatti et al. [103] reconstructed a historical series of observations of the sessile benthic communities along vertical transects from the surface to 40 m, revisiting sites investigated by Enrico Tortonese and Duilio Marcante in the 1950s. Information was drawn from nine scientific publications, five pieces of grey literature, and a technical report covering 112 diving surveys. Three investigation periods were distinguished: (1) from 1956 to 1979, (2) from 1980 to 1999, and (3) from 2000 to 2013. Overall, it was possible to reconstruct over 50 years of history of the rocky cliffs of Portofino: an unprecedented record in the Mediterranean Sea. The most significant changes in the sessile communities were observed in the second period, coinciding with rapid water warming. Human pressure (tourism and related economic activity) grew strikingly, especially after establishing the MPA in 1999. The species composition of the communities changed: some species disappeared or became rarer, many found refuge at greater depths, and new taxa arrived, including non-indigenous species (NIS). This study demonstrated the importance of descriptive historical data in understanding the extent and modality of change in the long-term evolution of marine ecosystems.

Although the Promontory of Portofino is located in one of the most northern portions of the Mediterranean basin, the presence of thermophilic species has become ever more important in recent decades (Figure 25c–g). These include the hydrozoans *Corydendrium parasiticum* (Figure 25c) and *Pennaria disticha* (Figure 25d), and the fish *Thalassoma pavo* (Figure 25e), *Sphyræna viridensis* (Figure 25f) and *Mycteroperca rubra* (Figure 25g) [104,347]. At the same time, non-indigenous species have also appeared in the waters of the promontory (Figure 25h–j), including the calcareous sponge *Paraleucilla magna* (Figure 25i), the splendid alfonso *Beryx splendens* (Figure 25j) and above all, the green alga *Caulerpa cylindracea* (Figure 25h), whose expansion strongly contributed to the change in the zonation of the benthic communities [94,103,104,108,165,384–386]. This latter species was the target of a Citizen Science project promoted by Reef Check Italia Onlus, which involved numerous divers and was conducted in the Portofino MPA [387]. The goal of the project, in addition to reporting the alien alga, was also to make a census and estimate the abundance of protected or ecologically relevant species.

In 2015, the Portofino MPA joined the international climate-change monitoring network TMednet (<https://t-mednet.org/>, accessed on 15 September 2024), which allowed it to participate in two Interreg Med projects coordinated by the Barcelona CSIC (Consejo Superior de Investigaciones Científicas) and, in 2019, in the national project “Mare Caldo” (Warm Sea), coordinated by Greenpeace and DiSTAV. All these projects aimed at monitoring the effects of climate change on the rocky ecosystems through two main tools: (1) continuous monitoring of the temperature of the water column with sensors positioned along the rocky reef in Cala dell’Oro from 5 m to 40 m, allowing any temperature anomalies to be recorded; and (2) monitoring of the thermophilic species present in Portofino and mass mortality events of benthic species, thanks also to Citizen Science contributions.

Finally, extreme meteorological phenomena are also often the consequence of global climate change and can profoundly influence the structure of the benthic communities. On the night between 29 and 30 October 2018, Liguria was struck by a particularly intense storm with southeasterly strong winds (with peaks of over 130 km/h), torrential rain, and waves over 10 m high. The storm caused severe damage to anthropogenic coastal structures, such as the partial destruction of the ports of Rapallo and Santa Margherita Ligure (with the sinking of around 250 boats) and the collapse of the road connecting the latter towns to Portofino, among many others. Moreover, the storm modified the shape of the coast, breaking down rocky cliffs and moving large quantities of sediment, with evident repercussions on the benthic communities, overturning large, submerged masses and eradicating numerous sessile organisms; in particular, the severe effects on *P. oceanica* meadows and *P. clavata* forests were studied in detail [64,65] (Figure 26a–d).

During the month of October, the seawater temperature from the surface down to about 50 m depth showed a strong anomaly in comparison to previous years (Figure 26e,f).

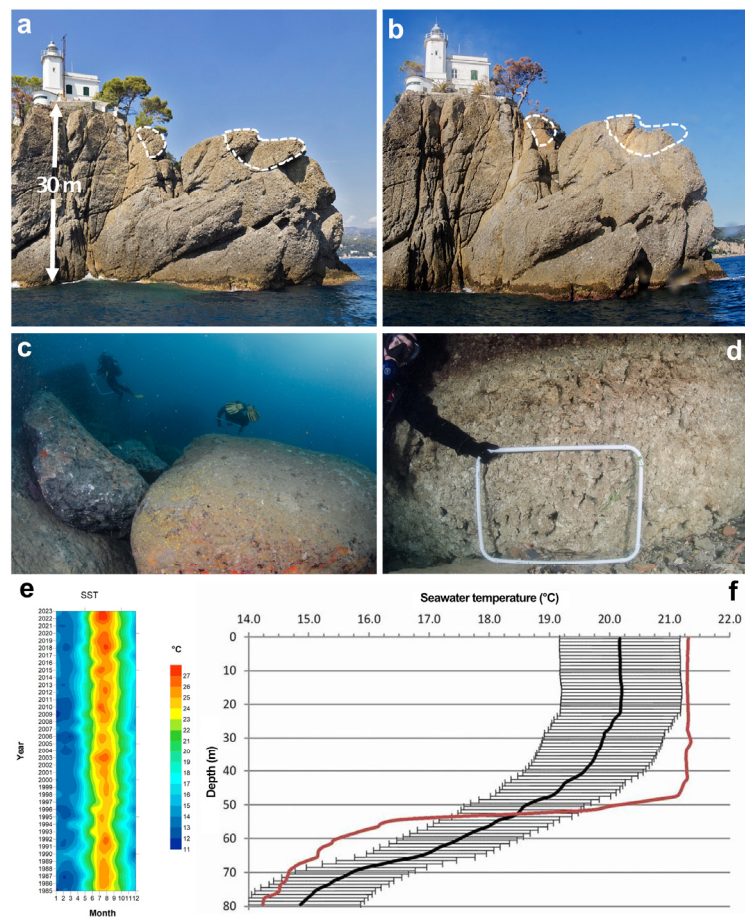


Figure 26. The storm of 29–30 October 2018. (a,b) Punta del Faro before (a) and after (b) the storm showing evident changes in the cliff morphology (dotted parts); (c) large rocky boulders fallen from the cliff or overturned by the storm waves; (d) the sandy seafloor of Paraggi lowered more than a metre by the waves (all images from [64]); (e) temperature ($^{\circ}\text{C}$) profile in Lighthouse Cape station on 25 October 2018 (in red) compared to the average profiles of the second half of October from 2000 to 2017 (in black; horizontal bars denote standard deviations) (from [377]); (f) annual trend of the seawater surface temperature showing the progressive increase.

7. Conclusions

In his vast 1884 monograph on the Mediterranean fauna, Julius Victor Carus listed numerous species for which he provided the known distribution [12]. To provide some examples, in this work, the toponym Nice recurs 2455 times, Naples 1278 times, Messina 340 times, Genoa 154 times, and Rapallo 3 times, while Portofino is never mentioned. In the latter half of the 19th century, the Gulf of Genoa was little known compared to the large Mediterranean centres of marine biology. The Gulf of Tigullio and the Portofino Promontory remained unknown within this large area.

Since then, research in this area has rapidly increased, thanks to the collaboration of various institutions, first and foremost the Museum of Natural History Giacomo Doria and the University of Genoa, which were joined, at the beginning of this century, by the newly established Marine Protected Area of Portofino.

A census performed by the Marine Protected Area, which lists about 380 publications between 1889 and 2007, illustrates the increased knowledge of the area. Until the 1960s, the frequency of studies remained constant (1–5 per decade), while from the 1970s, this increased linearly, reaching 140 works in the period 2000–2007. In this anthology for the period 2008–2024, 143 works were cited, surpassing a total of over 500 publications.

The numerous new taxa described from Portofino point to the importance of this area for the natural history of the Mediterranean Sea. The list presented here (Table 1) probably

needs to be completed, but it indicates the extensive efforts made over the years to gain knowledge of the biodiversity of this marine region.

Table 1. Species described on type material coming from Portofino Promontory.

New Taxa	Authority	Locality	Type Material
<i>Petalopoma</i>	Schiaparelli, 2002 [181]	Portofino	
<i>Axinella vacoleti</i>	Pansini, 1984 [12]	Portofino	Holotype
<i>Calthropella inopinata</i>	Pulitzer-Finali, 1983 [388]	Camogli	Holotype
<i>Eurypon gracile</i>	Bertolino, Calcinai, and Pansini, 2013 [178]	Portofino	Holotype
<i>Delectona madreporica</i>	Bavestrello, Calcinai, Cerrano, and Sarà, 1997 [389]	Paraggi	Holotype
<i>Paratimea loricata</i>	Sarà, 1958 [36]	Punta Chiappa	Holotype
<i>Ircinia retidermata</i>	Pulitzer-Finali and Pronzato, 1981 [390]	Portofino	Holotype
<i>Spiroxya corallophila</i>	(Calcinai, Cerrano, and Bavestrello, 2002) [391]	Portofino	Paratype
<i>Thoosa tortonesei</i>	Sarà, 1958 [36]	Punta Chiappa	Holotype
<i>Perarella propagulata</i>	Bavestrello, 1987 [392]	Cala Niasca	Holotype
<i>Sertularia perpusilla</i>	(Stechow, 1919) [18]	Portofino	Holotype
<i>Anthoplana antipathellae</i>	Bo and Betti, 2019 [393]	Portofino	Paratype
<i>Petalopoma elisabettae</i>	Schiaparelli, 2002 [181]	Portofino	Holotype
<i>Hincksina synchysia</i>	Berning, Spencer Jones, and Vieira, 2021 [394]	Portofino	Holotype

Within the National Recovery and Resilience Plan (2021–2027), Italy established the National Biodiversity Future Centre (NBFC) to monitor, conserve, and restore Italian biodiversity, enhancing the shift towards sustainable use of biodiversity-derived resources. Within this context, the Ligurian Sea has been identified by the NBFC as a key area of interest. The vast amount of data on marine communities and species obtained from the Portofino Promontory offers enormous potential for understanding the effect of multiple stressors and refinement of biodiversity conservation tools.

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