The Mediterranean Sea in the Era of Global Change 1

Series Editor
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30 Years of Multidisciplinary Study of the Ligurian Sea

Edited by

Christophe Migon
Paul Nival
Antoine Sciandra

iSTE
WILEY

First published 2020 in Great Britain and the United States by ISTE Ltd and John Wiley & Sons, Inc.

ISTE Ltd
27-37 St George's Road
London SW19 4EU
UK

www.iste.co.uk

John Wiley & Sons, Inc.
111 River Street
Hoboken, NJ 07030
USA

www.wiley.com

Library of Congress Control Number: 2019953879

British Library Cataloguing-in-Publication Data
A CIP record for this book is available from the British Library
ISBN 978-1-78630-428-5

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Preface

"Mediterranean" is a name steeped in history – cradle of civilization or a land of conflict, a surface of storms or dizzying calms. The Mediterranean is a semi-enclosed sea made up of several basins separated by straits, thresholds or only administrative boundaries. Its dynamics depend on exchanges of water, matter and also on living beings, with neighboring seas. Are these exchanges negligible or decisive in annual or long-term evolution of the Mediterranean? Within the Mediterranean, evaporation is not compensated by river inflows; as a result, increases in density, combined with decreases in temperature in winter, lead to surface waters sinking to the bottom in some areas of the Mediterranean. Outside the polar zones, this phenomenon of deep-water formation is found only in the Mediterranean where the thermohaline cell reproduces the global circulation process in miniature. For the Mediterranean basin, this results in a reverse estuarine circulation, which is characterized at Gibraltar by incoming Atlantic waters at the surface and outgoing Mediterranean waters at depth. The Atlantic water flow is therefore crucial. Its slightly salty water leaves a trace as far away as the Ligurian Sea, far from Gibraltar. However, the Atlantic flow is, above all, involved in the eastern basin in the formation of new water that will then irrigate all the regions of the Mediterranean, before mixing in specific places, into the deep water that will finally emerge in the Atlantic Ocean. Entry and exit imply a budget of non-living material, and also of living beings. As the open sea is never further than 300 km from the coast, the impact of continental inputs on pelagic areas is particularly significant. It must be taken into account that the shores of the Mediterranean are heavily populated and are the focus of important touristic, agricultural and industrial interests; continental emission sources are intense and also varied with, overall, the North responsible for anthropogenic influences and the South responsible for detritic (Saharan) natural influences. While African or European winds lift the sea, mix and carry away the surface layer, they also bring loads of matter that disrupt surface marine ecosystems. This sea, and each basin as well, appear to be the complex drivers ensuring the annual dynamics of marine ecosystems. Hydrodynamics, biology and chemistry combine locally and are subject to near or distant, rapid or long-term regulations, which are not yet fully known or predictable.

For several areas of the Mediterranean Sea, knowledge has been accumulated and attempts have been made to generalize it. The Ligurian Sea is a basin in which the topography of the coasts and bottoms produces simple situations. It is an “ocean model” as described by early hydrologists. Cyclonic water circulation and central divergence result from topography. The absence of a continental shelf provides access to the deep sea, and the absence of large tides simplifies temporal dynamics. These simple conditions are the main elements of the “model”. The Ligurian Sea was a laboratory to test methods and analyze different phenomena. However, with the advent of recent apparatus and research techniques, new instruments, new research strategies and new properties have been discovered. The various examples of the dynamics of offshore ecosystems, more or less enriched by the nutrient resources stored at the sea bottom, illustrate the situations encountered in vast territories of the world ocean.

The continuation and amplification of regular observations of water and planktonic populations, which began around 1895, have made it possible to identify long-term effects, particularly on a climatic scale for the entire Mediterranean basin. Knowledge about the Ligurian Sea has generally been obtained independently by laboratories, by young established researchers, during oceanographic campaigns and now, using autonomous instruments. This sea has been a training and teaching ground. The accumulation of data over time has allowed long-term series of its properties. International research programs and cooperation with other institutions have resulted in the creation of new scientific teams and large, well-equipped research vessels. It was a good opportunity to export oceanic knowledge, on the dynamics and “know-how”, capitalized in the Ligurian Sea, to the whole world. Although these snapshots on various areas are important because they are tests of hypotheses and theories, they are complementary to the exploration of all aspects of marine ecosystems, on the neighboring body of water that is easy to sample frequently, such as the Ligurian Sea. However, these distant expeditions have made it possible to define the relative place of the dynamics of the Ligurian Sea in the context of the world ocean, and to observe the amplitude of variations in the variables measured locally, with respect to those possible elsewhere. Now, the coverage capacity of all oceans with satellites and autonomous vehicles allows the continuous acquisition of new variables that must be identified and validated. The Ligurian Sea then becomes an area of testing and calibration, a kind of field laboratory giving access to the open sea. This knowledge has gradually been accumulated under various influences, within the framework of French university work, theses, master reports, or under the impetus of research agencies including CNRS, CNEXO, and also by Italian CNR, or international universities, EURATOM and IAEA. All this work and all these results deserve to be consolidated. This book is then a first step in presenting the functioning of an oceanic region, from the perspective of forming or identifying particularities and similarities with other regions of the world ocean. It also highlights the research effort that has been devoted to this part of the Mediterranean for more than 150 years. In addition to the evolution of data acquisition, we must also take into account the environmental, climatic and meteorological changes of the last three decades. Climate and meteorological changes have most likely affected the physical ocean pump. Furthermore, the supply of nutrients through external inputs has undergone significant changes, yielding modifications in plankton dynamics. A shift in phytoplankton populations in favor of species adapted to oligotrophy has indeed been observed in the Ligurian Sea.

It is within this framework that the ambitions of this book are set.

Christophe MIGON
Paul NIVAL
Antoine SCIANDRA
November 2019

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The Development of Knowledge of the Ligurian Sea

1.1. The first naturalists on the shores of the Ligurian Sea

The mild winter climate on the shores of the Mediterranean attracted not only the European aristocracy but also wealthy naturalists who discovered a host of unknown living creatures under the blue surface of the sea. In the 17th Century, learned societies became passionate about this world of animals without vertebrae. A few distant expeditions allowed some scientists to collect, draw or describe many marine and terrestrial species. However, many people explored the marine world only with the help of local fishermen.

Lazzaro Spallanzani, a professor in Bologna, but a frequent traveler, traveled the coasts of the Riviera of the Levant and Ponant to study marine animals and illustrate his lectures. In the 1780s, he even set up a small laboratory in Porto Venere, near La Spezia, which is considered the first marine station [TOD 97]. The Earl of Marsilli made an inventory of marine animals, and measured the temperature and density of the water. The report he made to the Paris Academy of Sciences, of which he was a corresponding member, opened the way for discoveries by naturalists who would frequent the shores of the Ligurian Sea in the 19th Century and even constitutes the outline of an "oceanography" [MAR 25].

Among the naturalists who explored the Ligurian Sea, it is worth noting Péron and Lesueur, who described and named some jellyfish, including

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Chapter written by Paul NIVAL.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

Pelagia noctiluca [PER 10]. Antoine Risso collected, described and detailed many marine fish species [RIS 13], nudibranchs as well as crustaceans, and attracted European naturalists to Nice and Villefranche. Some, such as Owens, Edwards, Vogt, Haeckel, Leuckart, Gegenbaur and Fol stayed for a few days or months.

The establishment of marine stations on the seaside at the end of the 19th Century satisfied the interest of zoologists for marine fauna, acalephs or other unknown zoophytes. In 1882, a laboratory of the École des Hautes Études was set up in Villefranche-sur-Mer by Jules Barrois and Hermann Fol. Alexis Korotneff and many Europeans came to study planktonic and benthic organisms. The anatomy and embryology of marine species was developed under these conditions. Some species even become biological "models" such as sea urchins and their larvae. The laboratory became the Russian zoological station, on the model of the Naples zoological station, under the direction of A. Korotneff.

On their part, the zoologists of the University of Genoa, attracted by the sea, in particular Raphael Issel and Alexandre Briand, created a marine laboratory finally located in Quarto dei Mille [REL 00a].

The marine laboratory, an essential tool for biologists, even became a laboratory for other disciplines. Fol and his colleague E. Sarasin, a physicist in Geneva, came to Villefranche in 1884 to study the penetration of light into the sea, as Forel had done in Lake Geneva. In 1903, Idrac installed a device in the Bay of Villefranche that would give the first recordings of the water temperature variation under the effect of the Mistral wind. In the 1960s, other disciplines, physicists and chemists came to work on the Ligurian Sea.

Following the round-the-world voyage of the English ship, *HMS Challenger*, designed to search for animals capable of living in the deep sea, A. Milne-Edwards and other zoologists, including A.F. Marion, a teacher at the Faculty of Science in Marseille, organized a deep-dredging mission in the Mediterranean. In 1881, they dredged at different points on a line from Villefranche-sur-Mer to Ajaccio. They noted the poverty of the macrofauna at the bottom of the Ligurian Sea and diverted their exploration towards the Atlantic. It was not until bathyscaphe dives of the 1950s [PER 64] and then 1990 that the exploration of life on the bottom was again addressed, and cores in deep sediments were taken [GUI 02] that it was quantified. Macrobenthos are rare, but sediments are populated by meiobenthic species.

In fact, oceanography, a multidisciplinary study of the sea, became a reality in the Mediterranean owing to Prince Albert I of Monaco, who, from 1886 onwards, began missions on a specially equipped ship, had original devices manufactured for physics and chemistry, for the capture of pelagic or benthic animals, and invited chemists, physicists, zoologists or physiologists to participate in his expeditions. Finally, he created a museum in Monaco to house his collections, which would become a laboratory for the study of the Sea of Monaco. He organized conferences at the Sorbonne and set up an Institute in Paris for public education, oceanographic research and teaching. In addition, Prince Albert I favored international action to produce a world map of the ocean floor and encouraged the formation of an International Commission for the Scientific Exploration of the Mediterranean Sea, similar to the International Commission for the Exploitation of the Sea created in Copenhagen by the countries of Northern Europe (ICES). While he favored the Atlantic and Arctic for his summer expeditions, he commissioned the director, Jules Richard, of the Oceanographic Museum, to launch a research program on the sea off Monaco.

The strategy of regular measurements and observations without *a priori*, as meteorologists did at the time, was introduced in 1896 at the Russian Zoological Station in Villefranche-sur-Mer (seawater temperature and presence of macroplanktonic species). This series of observations was interrupted in 1917 by the revolution in Russia.

In 1909, the prince of Monaco assigned the *Eider*, which was equipped with a winch, to a complete study of the sea off Monaco. The museum’s scientists regularly carried out hydrological measurements, water and plankton sampling on a transect extending offshore to 1000 m depths. Unfortunately, this time series was interrupted by World War I. The variations in hydrology (temperature and salinity) from surface to bottom suggested coastal mixing in winter. The study of nanoplankton revealed the existence of different species of coccolithophores in Mediterranean waters [BER 39], and other curious species of phytoplankton, alongside diatoms and dinoflagellates [PAV 37], and temporal variation in zooplankton. Monitoring of the sea was resumed in Monaco and the ship *Winnaretta Singer* allowed more distant studies in the Ligurian Sea.

The Monaco site and the Bay of Villefranche became privileged coastal water monitoring sites. Halim [HAL 60] described the annual cycle of dinoflagellates in the bay and, to explain it, introduced a strategy of regular measurements of temperature and salinity at different depths during the year, following the example of the Monaco series. He once again showed the importance of vertical hydrological structure by sampling the deep water off Cap de Nice.

Weekly measurements at a permanent station in the Bay of Villefranche (Point B) were carried out from 1957 by P. Bougis. This long series, subsequently enriched by additional variables (zooplankton, nutrients, pH), became a basis for the study of long-term variations in coastal waters due to variations in hydrodynamic and climatic forcings in the Ligurian Sea.

The temperature in deep Mediterranean waters (12.4–13°C) was measured as early as the end of the 19th Century [NIE 12]. The values much higher than those encountered in the oceans at the same depths have intrigued oceanographers, but the mechanisms responsible were only demonstrated in the 1960s.

1.2. Vertical structure of the Mediterranean and hydrodynamics

During the dredging of the *Travailleur* in 1881, A. Milne-Edwards, considering the temperature measurements in the deep layers, noted that “sa constance parfaite fait supposer qu’il y a donc une nappe d’eau presque immobile en profondeur”[1]. However, the measurement method was not perfect with a conventional thermometer. Aimé [AIM 45] proposed using a “reversing thermometer” that he used in Algiers and Toulon. This type of thermometer then replaced the ordinary Saussure thermometer in all shipments until the appearance of thermal probes (thermistors).

The *Thor* mission in the Mediterranean (1908–1910) described the spatial characteristics of the Mediterranean in summer and winter in its two basins. The vertical, three-layer hydrological structure, superficial, intermediate and deep, has been recognized [NIE 12]. Net phytoplankton, zooplankton, mesopelagic fish and fish larvae were also collected during these campaigns. However, the crossing of the Ligurian Sea in a few transects with stations too far apart does not reveal the typical spatial structures that would be discovered later.

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[1] “Its perfect constancy suggests that there is therefore an almost motionless water mass at depth”.

The contrast between the high seasonal variability of surface water and the stability of intermediate and deep waters, represented on a TS (Temperature–Salinity) diagram, leads Tchernia [TCH 60] to consider them as "typical waters" with reference value. To characterize deep water in the Mediterranean, Lacombe and Tchernia [LAC 58] compiled an inventory of existing measures. A transect South of Toulon, and stations in the Ligurian Sea, were completed by a few stations in the South of the Western basin, in the Tyrrhenian and in the Eastern basin. They highlighted three "deep waters types", kinds of references (Crete Sea, Eastern Mediterranean, Western Mediterranean) and suggested that the Mediterranean basins no longer communicate with each other at depths greater than 2000 m.

While there has been a hypothesis for the formation of deep water since Aimé ("précipitation des couches de surface en hiver"[2] [AIM 45]), the mechanism itself was not described. Gostan [GOS 62] resumed the study of hydrology off Monaco (between 1959 and 1962) and recorded a deep mixed profile in the winter of 1961. With the help of the Oceanographic Museum of Monaco *Winnaretta Singer*, he described the dynamics of hydrology on the Villefranche–Calvi transect crossing the Ligurian Sea, from August 1962 to July 1964; he carried out surface profiles at 2000 m in eight stations. In the winter of 1963, he noted once more the homogeneity of the water from surface to bottom. He suggested that the mechanism of deep water formation in winter is based on the interaction of cold and dry continental air masses with water masses at the surface of the Ligurian Sea [GOS 67b]. The increase in density of surface water by cooling and evaporation creates the density imbalance and mixing. The many measurements made later on the transect and now at the DYFAMED station show that complete mixing to the bottom does not occur every winter in the Ligurian Sea. This observation will trigger work in the Provençal Sea, South of Marseille and off the Gulf of Lion. In this region, a vast multi-vessel operation was carried out in winter (MEDOC group, [MED 70]) to estimate the effects induced by the atmosphere–ocean interaction in the Northern Western Basin. Later numerous observations were done in this area [TES 06].

During missions on the Villefranche–Calvi transect, measurements of oxygen, phosphates and chlorophyll were added to those of temperature and salinity [GOS 67]. The enrichment of the surface layer by nutrients was highlighted in the central dome produced by the divergence due to the

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[2] "precipitation of surface layers in winter".

cyclonic current flowing through the Ligurian Sea [GOS 67]. The MEDIPROD missions provided new information on the vertical structure of the North Western Mediterranean and illustrated the dynamics of nutrient salts, phytoplankton and zooplankton at the end of winter. Further regular transects from Villefranche to Calvi (Hydrokor data), from the coast offshore from Villefranche, and also from Calvi [GOF 95], made it possible to specify the variations in time and space of the vertical structure of the Ligurian Sea.

By examining several temperature measurements made since 1959 in the deep water of the Ligurian Sea, the “type waters” appeared not to be fixed references. A continuous and significant increase in deep water temperature was documented [BET 90]. A continued observation strategy of the Ligurian Sea waters appeared necessary to understand the trends that are emerging. Monitoring with regular ship stations, buoys and profiling floats has been done in the Gulf of Genoa since 1970 (ODAS Buoy, [CAN 15, REL 00b]) and in offshore waters (DYFAMED station and BOUSSOLE buoy). Coastal water is monitored at the station (Point B) located at the mouth of the Bay of Villefranche, and data were recorded for a few years (1974–1977) by the stations of the French National Observation Network (RNO, [ANO 77]) in the Ligurian Sea.

At the same time, a “laboratory buoy” was designed by J.Y. Cousteau to host scientists as a marine laboratory. During the test period in the Bay of Villefranche, he described the dynamics of oxygen and microphytoplankton and gave an estimate of primary production in coastal water [MIN 64], using the ^{14}C method. The “Lab-Buoy” was fixed in the central waters of Ligurian Sea (42°47’N, 7°29’E). Different projects were done on board: hydrodynamics of surface waters [GON 69], microphytoplankton annual cycle [LEG 71, TRA 65], oxygen budget and primary production [MIN 68, MIN 70][3].

Several campaigns in the North Western Mediterranean were designed in the Northern part of the Western Mediterranean Sea, on board of a new oceanographic ship *Jean Charcot*, within the framework of a cooperative scientific group MEDIPROD to study simultaneously, during the spring of 1967, spatial distribution of hydrology, nutrients, phytoplankton,

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[3] The buoy, refurbished after a fire on board and renamed BOHRA, was moved South of Marseille where the program MEDOC 70 took place.

zooplankton and primary production. A budget of primary production and nutrients consumption was produced for the first time [MIN 71]. During the summer of 1972, the same group described the deep chlorophyll maximum of phytoplankton in the Ligurian divergence and revealed the dominance of nanophytoplankton [JAC 76].

Following the work done for three years by Gostan and Nival on the Villefranche–Calvi transect, which revealed the dome of nutritive salts (phosphates) in the central area and the productive area it produces [GOS 67], it was deemed necessary to monitor its variability through monthly missions thanks to the vessel *Korotneff.* In parallel to hydrology, the optical properties of seawater were measured on monthly missions (Program HYDROKOR; 1973). Later, the Northern half of the transect was sampled regularly from Villefranche. The Southern half was also sampled from Calvi [GOF 95]. The symmetry of variable distribution on a meridian section across the Ligurian basin is a crude approximation. It appears in several studies that the current and temperature patterns are not symmetrical. The Northern Current field is relatively narrow compared to the Southern Current one (North Western Corsican Current). The divergence line, which is approximately the place where the 15°C isotherm is the shallowest, is North of the geographical axis of Ligurian Sea [HEL 63], reminiscent of the transects explored off Corsica.

Several hypotheses have been put forward to explain this circulation in the Ligurian Sea, based on internal forcing [BET 82] or external forcing from the Western Basin [BET 83].

Numerical simulation based on the series of observations made it possible to understand the consequences of hydrological events and to suggest mechanisms responsible for the driving forces of chemical and biological dynamics in the Ligurian Sea.

The numerous hydrological profiles have made it possible to validate winter mixing models [LEV 98], the annual cycle of the pelagic system [LAC 98] and to test data assimilation methods in a model. Circulation models (3D) have now become an efficient tool for assessing the consequences of hydrodynamics on the other variables in the sea (e.g. [LEV 03]).

1.3. Flow rate of the Ligurian Current

The Ligurian Sea is not a still and isolated body of water, at least in surface layers. The North-Western Corsican Current brings in water from the Western basin, while the Corsican Canal Current imports water from the Tyrrhenian Sea. The Westward outgoing Current along the North coast depends on both currents.

Gostan [GOS 67a] calculated the geostrophic current on the Villefranche–Calvi section. The current that is relatively slow at the coast is at its maximum between 10 and 30 miles offshore. It is slower and variable in direction in the Southern half of the section. Below 300 m, the current is low. The water flow in the Ligurian Current in the North East is of the order of 1.6 Sv (Sverdrup: $1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$). The flow was reassessed by Béthoux *et al.* [BET 82] and its variability was associated with that of incoming flows through the Corsican Channel and on the West coast of Corsica. Operation DYOME, involving current meters and drifting buoys, made it possible to describe the variability of the current in the Ligurian Sea [TAU 86].

Furnestin and Alain [FUR 62] described the hydrological structure in the Northern part of the Western Mediterranean basin. They illustrated the divergence dome on the meridian sections of the Ligurian Sea. They showed, on a longitudinal section in the Corsican Channel, that the flow of intermediate water (Eastern origin) introduced into the Gulf of Genoa is low because it is limited by the presence of a 350 m sill.

Some measurements were made in the Corsican canal to estimate the supply of Tyrrhenian water to the Ligurian basin, by Trotti [TRO 54] and Le Floch [LEF 63]. However, Astraldi *et al.* [AST 90] provided a clear description of the spatial structures in the Corsican Canal and calculated their water flows. The transport of Tyrrhenian water in the Ligurian Sea increases from 0.3 Sv in late autumn to 1.3 Sv in winter. Most of this water flow is surface water, because of a sill at 450 m that limits the intermediate water passage.

The water flow on the Northern coast of the Ligurian Sea is therefore the sum of the flows of the two Corsican Currents and varies according to the season.

1.4. Mesoscale structures in the Ligurian Sea: hydrodynamic front and the search for spatial precision

Close-up sampling on a transect off the Bay of Villefranche in the spring of 1967 on the *Korotneff* by Dallot and Nival revealed a rapid variation in water characteristics over less than a mile. Several cruises on this rapid transition zone based on continuous measurements of physical, chemical and biological variables on the ship track confirmed the presence of a boundary between coastal and offshore water [BOU 87, MOL 08]. A hydrodynamic front bordering the Ligurian Current on its left is the cause of this phenomenon. However, the various recordings revealed that the position of this gradient relative to the coast fluctuated. This variability was due to meanders in the Ligurian Current flow.

This periodic spatial structure of meanders was suggested by a hydrodynamic model of a cyclonic eddy [CRE 87], and a thermal image of the Ligurian Sea in December 1977 [CRE 82]. The Prolig-2 and Pros-6, DYOME missions devoted to the topography of the front, highlighted these meanders. The extreme complexity of the spatial structure of different variables in current flow appeared with different sampling strategies [TIB 85] and without any obvious statistical law [BEL 81]. Spatial observations show a Westward flow, vertically structured and forming horizontal meanders that move slowly Westward. Sub-mesoscale structures of eddies and filaments accompany them.

The current flow through a network of current meters set offshore Nice made it possible to calculate the Westward movement of the frontal structure (phase velocity of 10 km d-1) and also its fluctuation perpendicular to the coast, which is greater offshore than on the coast side [SAM 95].

Conditions in this hydrodynamic front lead to considerable variability in the distribution of mesoplankton species, such as copepods [BOU 87, MOL 08] or macroplankton, or species *Calanus helgolandicus* [BOU 84] or *Centropages typicus* [MOL 03]. The front appears to be an almost impassable frontier for pelagic larvae of coastal and benthic species such as sea urchins that are dragged offshore [PED 93].

In a plane perpendicular to the main flow, the Coriolis effect induces a secondary circulation able to upwell and downwell some water masses in offshore water. Nutrient-rich water rises slowly to the euphotic layer along isopycnal surfaces. These conditions are favorable for primary production. Associated downwellings carry particulate matter to the depth coastward [BOU 87, ZAK 94, ZAK 98]. Local production conditions on the left edge of the Ligurian Current should be favorable for the reproduction of planktonic species. It explains the distribution of *Pelagia* jellyfish larvae [MOR 92].

Recent studies at sea and numerical simulations produced a finer description of the hydrodynamical landscape. Mesoscale eddies appear, generated by baroclinic instabilities along the main current, and especially in the area where the two Corsican Currents join. Marullo *et al.* [MAR 85] described a 6 km radius eddy created in the Eastern Ligurian Sea by the instability of the West Corsican and East Corsican Currents, up-lifting isotherms by 2 to 3 tens of meters in the euphotic layer. Anticyclonic eddies in the Gulf of Genoa have been examined in detail on the right side of the main flow [BOR 16] and appear in 3D simulations of the Ligurian Sea [CAS 11].

The complexity of spatial structures makes it difficult to identify those that are important in the dynamics of pelagic populations and in the processes of transformation of particulate matter. Layers of zooplankton accumulation and layers of maximum phytoplankton concentration can be detected but have to be related to physical and chemical vertical gradient dynamics. Patchiness in plankton horizontal distribution has been related to sub-mesoscale hydrodynamical structure [BEL 81, IBA 73]. Spatial structures of plankton communities were investigated in Ligurian Sea and the whole Mediterranean Sea by Ayata *et al.* [AYA 18], emphasizing mesoscale grain and limits of space.

The development of continuous sampling and measurement systems, such as Towed HydroElectric System (THES) on a ship cruise track [PRI 93], has revealed the spatial discretization of the environment [PRI 81, TIB 85]. An important part of the spatial variability of chemical and biological parameters can be related to the hydrodynamical landscape.

The recent implementation in the Ligurian Sea of autonomous vehicles (gliders) equipped with sensors providing information on the characteristics of the environment, hydrology (temperature and salinity), illumination, total particles, photosynthetic particles (chlorophyll) and dissolved organic carbon (CDOM) has provided small scale pictures of the sea, showing mesoscale (10–100 km) and even sub-mesoscale (1–10 km) structures [NIE 08]. These tools, such as profiling floats, provide access to scales of spaces that are consistent with the time scales of biological processes [ZAK 98].

1.5. The seabed and living species

From the 1950s onwards, work on the underwater topography and sediments of the continental margin was carried out in the Villefranche area by Bourcart and his students ([GEN 12], see Chapter 2). A precise survey off the coast illustrated the shape of the continental Mediterranean slope. The properties of sediments have been studied (the regeneration of chemical elements [FER 96], the production of carbonates [LAL 57]).

The mapping of continental margins done in cooperation with the Monaco Oceanographic Museum revealed a hierarchy of canyons and a highly accurate bathymetric map was published. The sedimentary structure of the seabed was revealed by seismic methods introduced in the Mediterranean in the 1960s. Coastal or structural seismic geology work led to a description of the bottom at the deepest depths. The structure of the walls and bottom of the Ligurian Sea was then precisely established (canyons; salt dome, sedimentary cover, long-distance sediment transport channels), and also discovered thanatocoenoses reveal significant variations in sea level in the past.

Researchers from the Endoume Marine Station (Marseille), the Oceanographic Museum in Monaco and, later, from Nice University conducted research to study benthic ecosystems from the shore to the deepest environment. Their activity was mainly concentrated in shallow coastal environments where most of the benthic biomass is concentrated. The benthic populations of coastal and deep zones, explored by Italian scientists [REL 86], appear to be similar to those of the Provençal region. The transport of larvae of benthic species is likely the reason. It has been shown that benthic species can colonize floating objects (buoys for instance, ODAS Italia 1) several miles offshore [REL 00b]. The strong interaction of human activities and benthic ecosystems has led to the creation of Marine Protected Areas (MPA) all along the Ligurian continental shelf [FRA 10].

However, the use of dredges as well as scuba diving was useful to carry out inventories and quantify stands. Carpine [CAR 70] described the bathyal settlements with the ship *Winnaretta Singer*. The bathyal bottoms were explored during dives of the FNRS bathyscaphe [PER 64]. A towed vehicle, designed to photograph the sea bottom, was used from the *Calypso*. The development of remote operated vehicles (ROV) provided powerful equipment in the study of benthic environments.

1.6. Study of chemical substances in the Ligurian Sea

Several chemical substances of continental origin, natural or artificial, are introduced through rivers or atmospheric deposition from air masses.

In the 1950s, EURATOM set up a laboratory in Fiascherino (La Spezia) to study the dynamics of contaminants in the sea. Some studies focused on temporal variations in marine organisms (phyto- and zooplankton) [BER 67, NAS 69] and exogenous chemicals in the marine environment and living organisms.

In 1961, the IAEA created, in agreement with the Oceanographic Museum of Monaco, a laboratory to study the fate of radioactive elements in the sea. Using the Museum's nautical resources, a site for studying the sedimentation of biogenic particles off the Ligurian Sea was equipped with a line of particle traps. Traps that are set at 200 m and 1000 m are periodically retrieved. A long-term time series from the material flux to the bottom of the sea (see Volume 2, Chapter 2 of this book series) was obtained. For instance, trace metals in zooplankton and particles were estimated [FOW 77].

In addition, the laboratory measures natural or artificial radioactive elements in the sea (Lead 210, Polonium 210, etc.) [HEY 82]. Some naturally occurring radioactive elements in the sea (Uranium 234, Thorium 230) have been used to estimate the flow of particulate matter to the bottom, particularly at the DYFAMED site [SCH 02]. The study of particulate flux to the deep water was an important contribution to the understanding of matter transfer from the productive surface layer to deep layers [MIQ 11].

The variation in concentrations of heavy metals such as Pb, Cd, Cu, Zn in water, zooplankton and also in benthic organisms was addressed in the 1980s [CAP 83, HAR 80, LAU 84].

The development of a physics and chemistry laboratory in Villefranche (part of LPCM from Paris University) led to the studies of the seasonal dynamics and the role of several chemical elements in the sea, such as carbon, nitrogen and oxygen. Copin-Montégut and Copin-Montégut (1983) [COP 83] made it possible to address the dynamics of dissolved carbon, pCO_2. Other chemical parameters were also evaluated: oxygen, trace metals and chlorophyll pigments.

Offshore waters have been sampled since 1962, for O_2 and PO_4 [GOS 68], and later for several other chemical variables [MAR 02].

The sedimentation of biogenic particles or inert particles was estimated with a line of sediment traps located during one year (1987–1988) in the vicinity of Calvi [MIQ 94], and, since 1988, relocated close to the reference station DYFAMED [MIG 02]. There the useful variables for understanding the flow of biogenic particles were regularly measured.

Ongoing observations in offshore water from 1993 onwards (the DYFAMED site) addressed almost all aspects of chemical and biological physical dynamics and provide a considerable database on an annual and interannual scale [MAR 02].

The importance of the day–night cycle on the dynamics of biological processes led to measurements at the DYFAMED site at high temporal frequency (3 h) offshore (DYNAPROC projects, [AND 00]). Several other projects were coupled with routine hydrological observation at this station (Exchange of gas through sea surface [HOO 01]). There, Copin-Montégut and Avril [COP 93] showed that high amounts of dissolved organic matter accumulate in the surface layer during the oligotrophic season in the Ligurian Sea. Dissolved organic matter may then be transformed into sedimenting particles or directly transferred to depth by the winter mixing.

1.7. Towards a synoptic vision of the Ligurian Sea. Remote sensing

Few oceanographic campaigns have provided a synoptic description of the Ligurian Sea [FUR 62, HEL 63, LIC 09, MCG 04, PIN 95]. Different properties were emphasized depending on the spatial resolution of the network of stations. For instance, doming in the central region of the Ligurian Sea was shown [FUR 62], as well as on the maps of 15°C isotherm given by Hela [HEL 63]. A few transects in North West Mediterranean depicted the cyclonic pattern of currents in the Ligurian Sea (Lacombe and Tchernia unpublished data from the *Elie Monier* cruise in February–March 1960, in [CRE 82]).

Remote sensing provided oceanographers a way to get synoptic descriptions of the sea surface properties. Developments of data processing methods and integration of results from different parameters measured at sea provided methods to estimate derived variables (for instance, phytoplankton biomass estimations, estimation of taxonomic groups or functional types).

Another approach for spatial description of surface current velocity is based on microwave Radar sensors. This technology has been used in the North West part of the Ligurian Sea to validate circulation models that suggest meander and eddy formation [GUI 13].

Aside from the main cyclonic gyre, the circulation pattern in the Tuscan area and the Gulf of Genoa appears to be variable and to generate anticyclonic gyres [CAS 11]. These sub-mesoscale hydrodynamical structures which are observed in field data became important in the understanding of the spatial distribution and dynamics of biological factors and planktonic species [LEV 12].

Measurement of sea temperature by satellite sensors, although limited to the surface layer, corresponds, in fact, to that of surface mixed layer (shallow during summer but deep during autumn and winter). Wald [WAL 80] produced thermal pictures of the whole Ligurian Sea revealing some current patterns. Connection with the Tyrrhenian Sea is illustrated and periodic structures are also highlighted. These structures are considered as clues for meanders in the Ligurian Current [CRE 82].

Morel [MOR 91] developed a spectral light–photosynthesis model to estimate the primary production rate using pigment concentration derived from satellite data [BRI 87]. This “bio-optical” model, using photosynthetic radiation reaching the surface of the sea and empirical relations of vertical biomass distribution [MOR 89], was used to estimate the biomass and primary production in the Mediterranean Sea.

Morel and André [MOR 91] illustrated the spatial distribution of primary producers and production rate all over Mediterranean Sea this way. Primary production data obtained in the Ligurian Sea [ROD 73] were among those used to validate computations. This method was later extended to the global ocean.

The concentration of various pigments associated with the photosynthetic system of primary producers estimated by HPLC was used to estimate biomass of different taxonomic or functional groups of phytoplankton [BUS 95, VID 96]. Size groups of primary producers, pico- (mainly cyanobacteria), nano- (mainly prymnesiophyceae) and micro-phytoplankton (mainly diatoms, dinoflagellates) were quantified. Along this line, the signature of these phytoplankton groups was assessed in remote sensing data by Uitz [UIT 12] and spatial distributions were produced.

1.8. Towards continuous observation and environmental monitoring

Originally designed to facilitate the understanding of environmental fluctuations, in support of other work, particularly thesis work, continuous observation stations are now becoming long-term reference, calibration and monitoring tools. Continuous observation for monitoring the environment (temperature) or animals (macro-zooplankton) began in the Bay of Villefranche in 1894 at the Russian Zoological Station. Then a series of measurements were made from 1909 to 1914 in Monaco. Temperature and salinity measurements have been maintained in coastal waters in Villefranche since 1957. The coupling of biological and chemical variables makes it possible to have a complete vision of the state of the pelagic ecosystem, to monitor and even anticipate events of at least low frequency. These series can be combined with very specific, short-term research operations.

Time series have also been acquired in Calvi Bay [HEC 09] and in the Gulf of Trujillo [LIC 00] with the same monitoring objective.

The continuous sampling from coastal to central waters offered a description of water masses properties at different sites in the Ligurian Sea. The profiles of hydrological variables (temperature, salinity) were obtained from 1962 to 1964 [GOS 68] at different stations on a transect across the Ligurian Sea (Villefranche to Calvi). It was continued from 1969 to 1971 (HYDROKOR 1973) and later on the Northern half of the transect [NYF 73].

In order to understand, first, the transfer of the particles produced by primary production and food web activity to the deep water (dead organisms, fecal pellets, aggregates, colloids and transparent polymers, as well as atmospheric particles transported by air masses), and second, the dynamics of consumption–production of this sinking matter, sediment traps are deployed in the sea. The optimal location is close to a station where regular measurement of water mass properties is done. The site was the most offshore station on the North half of Nice–Calvi transect, 27 miles from Nice (52 km from Cap Ferrat – 43°25’N, 7°52’E). A line of particles traps was deployed by the IAEA laboratory and different variables have been measured monthly since January 1991. To differentiate this station, which was receiving much attention, from the other on the transect, it received the name DYFAMED (DYnamique des Flux Atmosphériques en MEDiterranée) in reference to the study of atmosphere and sea.

Measurements of temperature, salinity, oxygen, carbonates, pH, nutrients, phytoplankton pigments and dissolved organic carbon were made at different depths [MAR 02]. This station became soon a place where different research projects could be efficiently developed (exchange of gas through sea surface [HOO 01], short-term variation of zooplankton community in DYNAPROC project [AND 00], MedFlux experiment, contribution from the French JGOFS program [WAK 09]. DYFAMED is now considered as a reference for the World Ocean and seas as are BATS, HOT and some other stations.

In coastal waters (Point B site, the Bay of Villefranche) and offshore waters (DYFAMED site), long-time series now make it possible to go beyond the simple comparison of annual cycles and highlight very long-term trends or shifts in Mediterranean characteristics.

1.9. References

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2

The Ligurian Basin: A Geomorphologic and Geological Background

2.1. Introduction

It may look somewhat strange to start a book, chiefly dedicated to multidisciplinary oceanographic studies and global changes within the Ligurian Sea, with a chapter on the origin and geological evolution of this basin. We, however, hope to stress that the knowledge of the geological background of this small oceanic space, and of its bordering continental margin, is quite relevant and necessary to better understand, and interpret, several of the oceanographic characteristics of the north-eastern corner of the western Mediterranean Sea. The present-day morphology of the Ligurian basin is the direct consequence of its geological evolution and of the sedimentary mechanisms operating on its margins and in the deep sea. Both have direct impacts on the surface and deep seawater circulations as well as on the distribution and behavior of the various chemical and biological components of the Ligurian Sea waters.

2.2. Geographic and geological boundaries

The Ligurian basin, or Ligurian Sea, extends at the north-eastern corner of the western Mediterranean Sea (Figure 2.1) and as such its geological history is closely linked to the evolution of the Mediterranean basin. To the northwest, the Ligurian basin is bounded by the south-eastern coasts of France (approximately up to Toulon) and the Italian coasts of Liguria (up to

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Chapter written by Jean MASCLE, Sébastien MIGEON and Virginie HASSOUN.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

Genoa); to the south-east, the Ligurian Sea borders the coasts of western Corsica and partly of north-western Tuscany. The main bordering geological units include, to the north, the Variscan Maures massif, the Southern Alps and parts of the Northern Apennines; to the east, its geological boundaries include the Corsica Alpine and Hercynian domains (Figure 2.2).

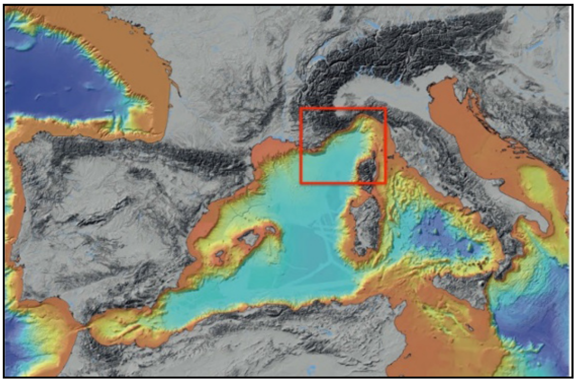

Figure 2.1. *Location of the Ligurian Sea in the north-eastern corner of the western Mediterranean Sea; map extracted from morpho-bathymetry of the Mediterranean Sea [BRO 12]. For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

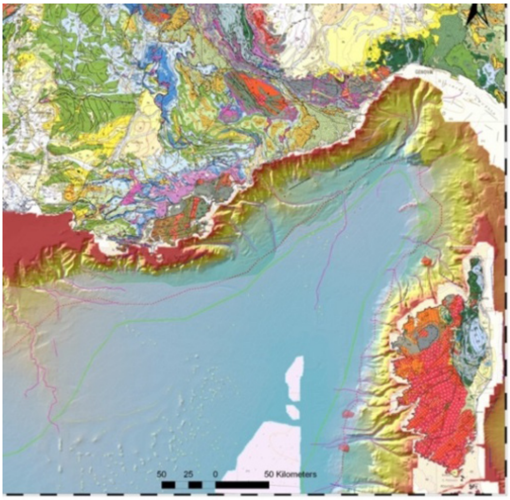

Figure 2.2. *The Ligurian basin within its geological environment. Two Hercynian massifs (Maures and central Corsica), the Southern Alps and parts of the Northern Apennines constitute most of the geological environment of the Ligurian Sea. For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

2.3. Origin and geological evolution of the Ligurian basin and of its margins: a brief review

2.3.1. *Birth of the Ligurian basin*

The creation of the deep Ligurian basin is a direct consequence of the two main geotectonic events themselves at the origin of the entire western Mediterranean Sea:

– the progressive stretching and thinning (= rifting) of the southern Europe continental crust. This relatively long episode has initiated around 35 Million years ago –Ma (in Oligocene times) and ended around 20 Ma (in Burdigalian, lower Miocene). This rifting, across still active mountain chains (Southern Alps and Northern Apennines), has resulted in the creation of the Ligurian continental margins;

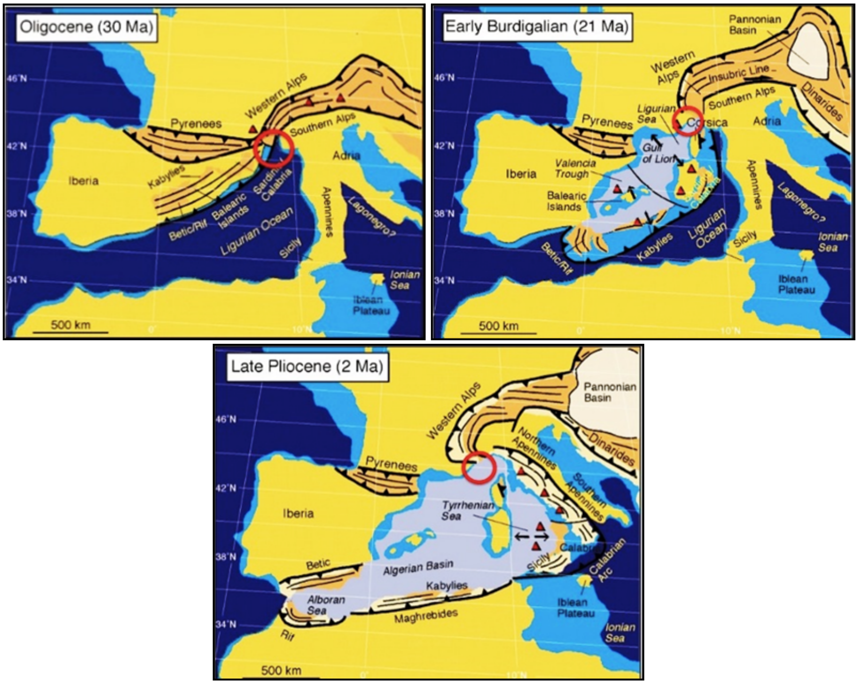

Figure 2.3. *Hypothetic evolution of the north-western Mediterranean basin since Oligocene (around -35 to 30 Ma): rifting and continental crustal thinning followed, in lower-middle Miocene times, by oceanic crust creation (–20 to –15 Ma) emplaced across the Alpine domain. By late Pliocene (–2 Ma), the western Mediterranean Sea looks like today, while the Tyrrhenian Sea is still opening (after Rosenbaum* et al. *[ROS 02]). For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

– a shorter period of oceanic accretion, active between 20 and 15 Ma ago (middle Miocene) and during which an oceanic-type crust was progressively emplaced between several drifting continental pieces from southern Europe mainland. This mechanism has resulted in the creation of a small oceanic basin, the western Mediterranean Sea, and in the dispersion of various continental fragments such as the Balearic, Corsica and Sardinia islands, the Calabria block and the two Kabylia massifs (now incorporated to northern Africa), within and around the western Mediterranean basin.

The rifting event was in fact one of the consequences of the subduction of the African plate beneath southern Europe itself a result of the long-term convergence between the two lithospheric mega-plates which initiated some 80 Ma ago (Figure 2.3).

In addition to crustal thinning (accommodated by extensional faulting), to high heat anomalies, and to regional volcanisms (whose outcrops are still exposed in several areas of the French Riviera and in Sardinia), the northward subduction of the African lithosphere has induced a progressive and continuous south-eastern-directed retreat ("roll back" effect) of the breaking European continental border.

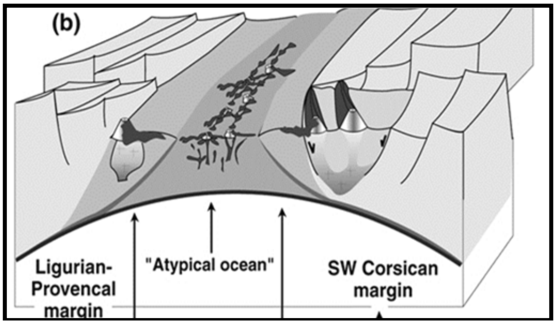

Figure 2.4. *Crustal sketch of the Ligurian Sea (after Rollet* et al. *[ROL 02, ROL 99]); the deep Ligurian basin rests on an atypical oceanic crust (dark gray) emplaced between two stretched and block-faulted continental margin domains (light gray), Provence and Liguria (on the left) and Corsica (on the right). The various magmatic bodies are represented in black*

Oceanic crust creation processes initiated when the two stretched continental blocks were finally ruptured and separated by hot mantle intrusive bodies (Figure 2.4). The upper mantle differentiated itself in various volcanic rock types (gabbros and chiefly basalts) progressively emplaced in an oceanic accretionary center creating a somewhat "atypical" oceanic crust.

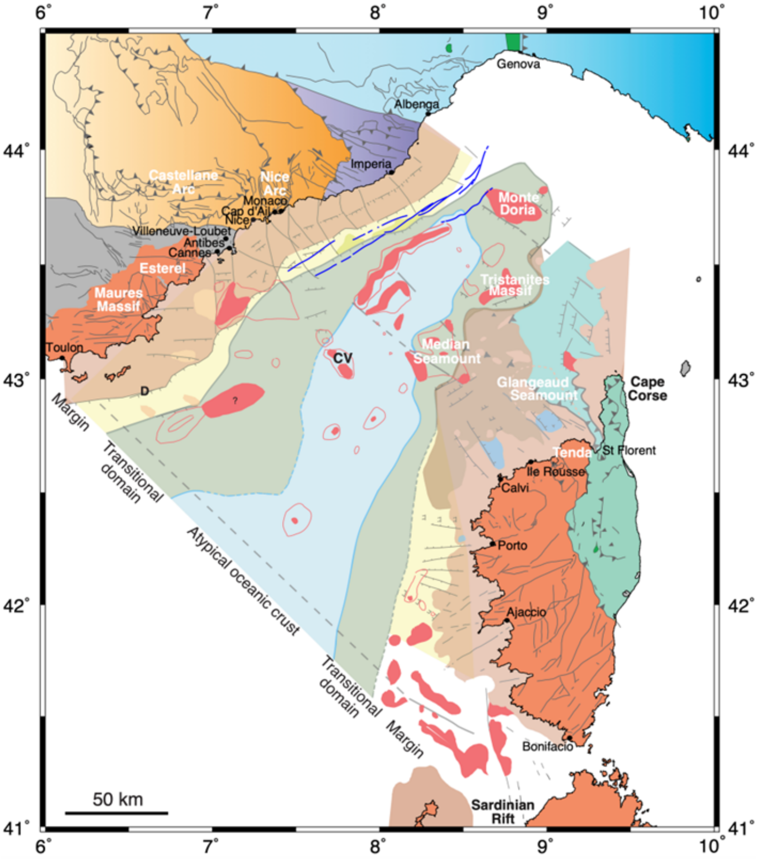

Figure 2.5. *The main crustal and structural domains of the Ligurian Sea and of its margin (modified after Rollet [ROL 99] and Rollet et al. [ROL 02]). In light blue: atypical oceanic crust; light green: transitional crust; yellow and brown: lower and upper continental margins; in red: volcanism; in dark blue the various active faults detected at the basis of the Ligurian continental margin; in green: upper Alpine nappes covered by Miocene sediments (see Rollet [ROL 99] and Dessa et al. [DES 19] for details). For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

Today, such geodynamic mechanisms are still active but, as a consequence of the "roll back" effect, have been transferred within the nearby south-eastern Tyrrhenian Sea, which can be considered as a recent mini western Mediterranean Sea. There, the south-eastern retreat of the subduction, now active beneath Calabria, has induced during the last 4 Ma, the creation of two small oceanic basins, Vavilov and Marsili basins (Figures 2.1–2.3).

The Ligurian Sea can be interpreted as a segment of oceanic "back-arc" type basin opening in response to subduction processes [ROL 02]. The basin was created in a relatively short period of time (less than 5 Ma) between two domains of breaking continental crusts, Corsica/Sardinia on its south-eastern border and an area of southern Europe previously strongly deformed by two collisions (Alps and Apennines) (Figure 2.5). It is important to keep in mind such geological setting since this heritage has exerted a strong control on the morphology of the two continental borders of the Ligurian Sea: the Riviera/Liguria continental margin on the one side, and the Corsica continental margin on the other side.

2.3.2. *Creation and evolution of the Ligurian Sea continental margins*

Based on the analysis of numerous geophysical data recorded during the last 30 years along the French Riviera margin, Sage *et al.* [SAG 11] proposed and discussed a synthetic evolution of the northern Ligurian margins in six main episodes (Figures 2.6 and 2.7). Such scenario can easily be generalised to the entire continental margins bounding the deep basin:

– during the early stages, abundant clastites resulting chiefly from the erosion of Corsica and from the nearby Alpine collision was deposited in a series of new basins created in the context of the Alpine collision; parts of these depocenters were progressively affected by rifting processes occurring between Corsica and Southern Europe;

– during the subsequent stages 2–3 (between 28 and 20.5 Ma ago), the future Ligurian continental slopes were created as a response to increasing continental thinning, increasing fault activity and increasing synrift sedimentation (S2 and S3 units that may reach up to 1,500 m in thickness); tectonic and thermal subsidence (= crustal sinking) participate to the progressive deepening of the area (Figure 2.8);

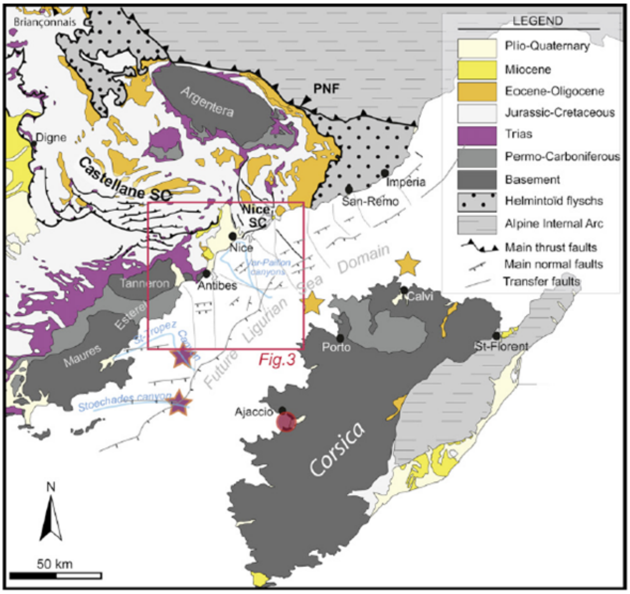

Figure 2.6. *Kinematic reconstruction of the Ligurian basin at the beginning of rifting (–35 Ma ago). Corsica has been replaced in its initial location before basin opening according to several kinematic reconstructions; the main offshore structural features are from Rollet* et al. *[ROL 02]; stars indicate the location of various samples collected during scientific dives (see Sage* et al. *[SAG 11] for details). For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

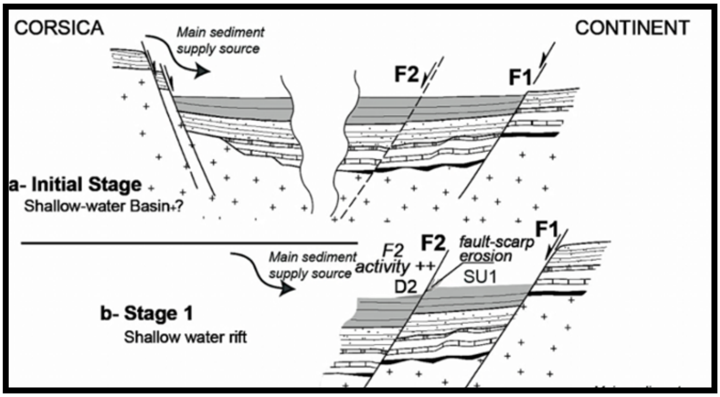

Figure 2.7. *NW-SE section showing the early stages of the Ligurian margin creation in upper Oligocene (between 35 and 30 Ma ago): fault initiation (F1 and F2) and clastic sedimentation in developing graben structures; deposition of the first synrift units originating mainly from the southern domains (Corsica); D2 and SU1 indicate the drifting and synrift sedimentary sequences (adapted from Sage* et al. *[SAG 11])*

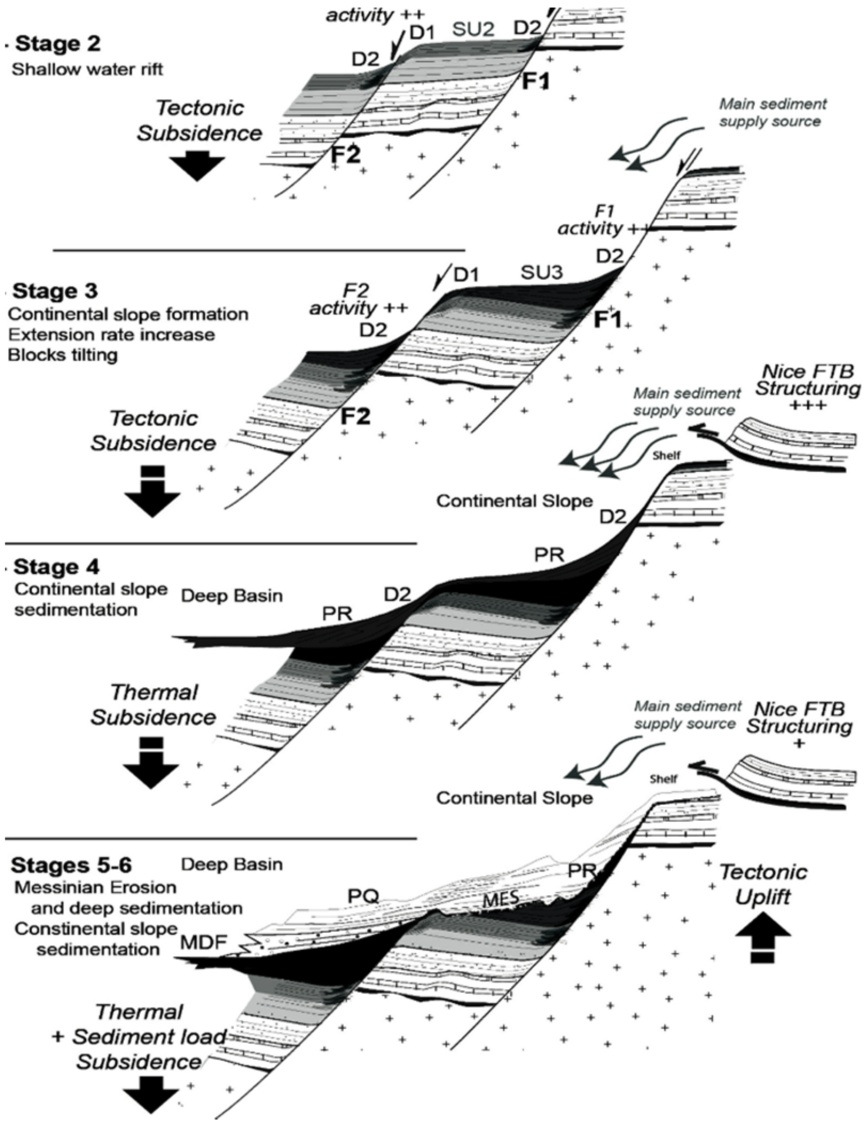

Figure 2.8. *Sketch illustrating the evolution of the geological structures, sedimentary cover and morphology of the Ligurian continental slopes during the last 20 Ma. Stages 2 and 3 illustrate the evolution during rifting episode; stage 4 illustrates the evolution during, and just after the creation of the deep oceanic crust-floored basin; stages 5–6 refer to the effects of the Messinian crisis (5) and to the various sedimentary processes active during Pliocene and Quaternary (6); F indicates the successive fault, and S and D indicate the successive synrift and drifting sedimentation (from Sage* et al. *[SAG 11])*

– during stage 4 (between 20 Ma ago and 7 Ma ago), continental breakup was finally completed, new oceanic crust emplaced on the floors of the Ligurian basin, and abundant post-rift sediments, bypassing the upper slope, participated to the construction of thick continental margin wedges, smoothing the continental slope reliefs;

– during stage 5 (roughly between 6.5 and 5.3 Ma), the Ligurian margin was strongly affected by the effects of a tectonic-driven climate crisis impacting the entire Mediterranean Sea, the Messinian salinity crisis. This event may have induced, for a short period of time, a sea level drop near its end on the order of 1,500 m and consequently, the upper and middle continental slopes were submitted to large-scale erosional processes in sub-aerial environmental conditions. On the uppermost margin areas, the morphologies of fault-bounded tilted blocks were partly rejuvenated and on the deep slope, sedimentary wedges – including thick Messinian terrigenous fans – were constructed, thus participating to partly erase the rift-inherited features;

– during stage 6 (Pliocene to Quaternary, i.e. the last 5.3 Ma), the progressive sedimentary smoothing of the margin morphology increased, although numerous internal sedimentary discontinuities detected within the sediment cover reveal numerous slope instabilities likely resulting from the combined effects of a rejuvenated seismic/tectonic activity and of steep slope gradient [MIG 11];

Various geotectonic, sedimentary and climate controls active during the last 30 Ma have hence altogether strongly controlled the Ligurian Sea morphological evolution and impacted its present-time physiographic characteristics, particularly on its continental borders.

2.4. Morphology of the Ligurian Sea

2.4.1. *General morphology*

Figure 2.9 shows the most recent synthesis of the morpho-bathymetry of the Ligurian Sea recently compiled by Migeon *et al.* [MIG 16] from a set of various swath bathymetric data recorded during the last 15 years and reprocessed to provide a map with a 30-meter Digital Terrain Model.

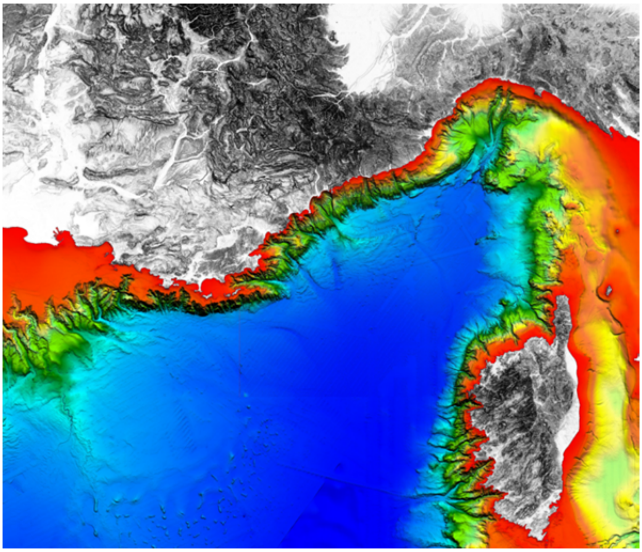

Figure 2.9. *Shaded bathymetric map of north-eastern Mediterranean Sea at a 30-m DTM [MIG 16]. The Ligurian Sea characterizes as a narrow deep basin (in blue), extending between Corsica and eastern Provence/Ligurian, and bounded by steep and narrow continental slopes (yellow to green) themselves in continuity with a narrow continental shelf. For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

All along the French Riviera and Liguria, from Toulon to Genoa, as well as off western Corsica, the Ligurian Sea is characterized by a very narrow continental margin (in red to green on the map), 20 km in width on average and only widening off north-western Tuscany. Its northern (off eastern Provence to Liguria) and southern continental slopes (off Corsica) overhang a deep (2,200–2,400 m) and almost flat basin (in light and dark blue on the map), which can be interpreted as an abyssal plain. As previously indicated, this morphology is the direct consequence of two successive geodynamics episodes: rifting, which has created the continental margins, and oceanic accretion leading to the deep basin. The domain has, however, also been morphologically shaped by various sedimentary processes operating during the last 30 Ma. For example, the flat floor of the deep basin is the consequence of a constant sediment supply, since the last 15 Ma when the basin was finally created. An interesting comparison may be made with a similar deep and small oceanic basin, the central Tyrrhenian Sea (Figure 2.1), created during the last 4 Ma, and where most of the magmatic features generated by oceanic accretion can still be observed merging from the surrounding sediment being, yet not totally covered by thick clastic sedimentation [KAS 88].

2.4.2. *Submarine canyons*

Beside its extreme narrowness and steep continental slope (up to 18%), the major morphological characteristic of the Ligurian Sea continental margins consists in the presence of numerous submarine canyons running for most of them perpendicular to the coastlines (Figure 2.9). Most of these canyons are linked to rivers and are more or less perpendicular to the continental slope; most of them are superposed to previous tectonic lineaments generated during the alpine and/or rifting evolution of the area. Off Provence an east-west directed and Hercynian inherited fault zone controls the wide Stoechades canyon, while off central Liguria, a large and still uplifting continental block controls the margin structure and the canyons distribution; two features are particularly remarkable: off Nice, the Var and Paillon rivers canyon system, related submarine cone and sedimentary ridge and off Genoa, the complex coalescing canyons that can be followed from the continental shelf to the deep basin on almost 80 km.

The Ligurian margins canyons network results from three successive tectonic/sedimentary episodes:

– most of them were created as aerial valleys, likely superposed to tectonics lineaments, during the rifting stage (35–20 Ma) of the Ligurian domain creation. These valleys were progressively submerged during the deep basin formation as a consequence of the combined effects of tectonics, thermal and sedimentary loading subsidence;

– near the end of the Messinian salinity crisis, a rapid sea level drop (up to –1,500 m) due to the partial desiccation of the Mediterranean basins, leaded to aerial exposure of large parts of the continental margins and consequently to their strong erosion. Most of the submarine canyons were thus exposed, strongly eroded and acted as aerial valleys through which huge quantities of clastites were transported to be deposited at the foot of the continental slope in the bordering deep basin (see Briand [BRI 08] for complete discussion);

– finally, at the end of the Messinian episode, when the connection between the Mediterranean Sea and the Atlantic was re-established, in Zanclean times (5.2–3.6 Ma), the canyons/valleys were re-submerged (the local sea level was about 80 m higher than in present time), and partly fed by pelagic to hemipelagic sediments and then by gravity-flow deposits truncated by erosive episodes (related to sea level fluctuations) between upper Pliocene to Holocene. The Riviera-Ligurian, eastern Provence and Corsican margin segments show a comparable pattern of submarine canyons cross-cutting narrow and poorly sedimented continental slopes, except in the north-eastern domain of the Ligurian basin where the sediment supply has been more abundant.

2.5. Sedimentary cover and sedimentary processes

2.5.1. *Evolution of the sedimentary cover*

Initiated some 35 Ma ago, the continental borders of the Ligurian Sea have since been areas of various periods of sedimentation and erosional phases. The deep Ligurian basin, definitively created as such only since the last 15 Ma, has itself been progressively fed by a huge pile of sediments whose thickness may exceed 7–8 km.

Along the margins, most of the synrift sedimentation consists of terrigenous deposits at first derived from the southern parting continental blocks (Corsica, northern Sardinia, Peloritani-Calabria, Kabylia), then chiefly from the erosion of the two tectonically active bordering northern Alps and Apennines domains. These clastics were trapped in a series of developing half-grabens progressively invaded by marine waters and related shallow marine sedimentation (Figures 2.7 and 2.8). By middle Miocene (around 20 Ma), the wedges of intermixed clastics and marine sediments were already deposited on the various block-faulted slope segments while hemipelagic to fine clastic sedimentation started to cover, and morphologically erase, the magmatic reliefs emplaced in the opening deep basin. Similar sedimentation, mixing terrigenous and marine deposits depending of the surrounding tectonic evolution, was operative until Messinian times (–7.2 Ma), the period during which the Mediterranean environmental conditions were temporarily but drastically modified. After an episode of increasing seawater salinity likely driven by oceanic circulation restrictions, huge brines started to develop within the deep basins leading, later on, to the deposition of thick (several hundred meters to 1 km) stacked salt layers. Near the end of the Messinian crisis (around –5.35 Ma), a sudden and complete closure of the hydrologic exchanges between the Mediterranean Sea and the Atlantic Ocean leaded to a climax of seawater evaporation and to a general lowering of the sea level of the Mediterranean Sea (estimated up to –1,500 m with respect to the present level). This resulted in large aerial exposures of previously submerged slopes and to large-scale erosional processes (see [MAS 19]). Huge flux of clastics were transported towards the foot of the continental slope by the newly emerged sub-marine canyons and deposited as cones of clastics, which can be well identified on seismic data and locally observed in outcrops during deep dives.

In summary, across the Ligurian continental slope, and up to the deep basin (Figure 2.10), the results of the Messinian crisis are now successively recorded by an erosional surface (up to approximately −1,500 m water depth), thick coarse clastic wedge on the lower slope and finally a sequence of evaporite layers reflecting the three main events of the Messinian episode.

At the transition between the uppermost Messinian and the lowermost Pliocene, −5.32 Ma, a new sudden event occurred as a consequence of an abrupt Gibraltar straight opening. The Atlantic seawater refilled the Mediterranean Sea, potentially in only few years (7–8 years according to some models). This event leaded to major modifications of the sedimentary and depositional conditions, which were suddenly jumping from shallow water to deep water marine environments, as well as demonstrated by scientific deep-sea drilling data. In the deep basin, this is attested by the deposition of coccolith-rich oozes and marls directly overlying evaporites; on the Ligurian margin, the so-called Zanclean (lower Pliocene) crisis is recorded by a rapid sea level rise, which leads to the new submersion of slope canyons and to the creation of rias (= submerged aerial valleys); there the sedimentary consequences are two folds: − (a) most of the clastics, produced by the erosion of the nearby mountain chains (Alps, Apennines), are trapped in these submerged valleys or at river mouths (estuaries) as terrigenous deltaic bodies known as “Gilbert” deltas; − (b) these products are thus not anymore deposited on the continental slopes, which are, temporarily, chiefly areas of hemipelagic to pelagic sediments. The continental shelf remains an area of non-deposition even though local prograding sedimentary wedges are constructed (e.g. off Savona-Genoa or off north-eastern Tuscany). Since upper Pliocene, throughout Pleistocene and during the Holocene, the recent sedimentary cover – mainly made of clastics, provided by the erosion of the two bordering chains (and mixed to a small component of hemipelagic sediments) – is submitted to spectacular sedimentary reworking processes including channelized turbidite systems, slope instabilities and sedimentary mass transport mechanisms.

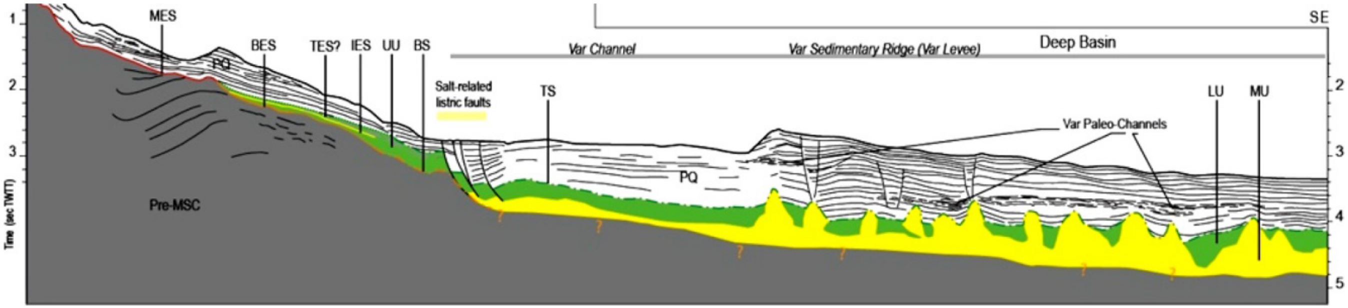

Figure 2.10. *Geological cross-section (based on seismic reflection profiles) of the northern Ligurian continental margin, between Nice and the abyssal plain, showing the lower and upper Messinian (yellow and green, Pliocene and Quaternary sedimentary cover (white) [HAS 14], modified from Lofi* et al. *[LOF 11]). For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

2.5.2. *Prevailing sedimentary mechanisms*

The Ligurian Sea has recorded – and still records – in its sediment cover the results of sedimentary mechanisms known in the World Ocean, such as pelagic to hemipelagic sedimentation (decantation of fine particles from biologic, aerial and detrital origins). Among these mechanisms, three are however prevailing, particularly along the northern borders of the basin: slope failures, gravity flows (including debris flows, turbidity currents and hyperpycnal flows) and deep sedimentary constructions. A classical case study of sedimentary construction is illustrated at the level of the submarine Var/Paillon valley system (Figure 2.11).

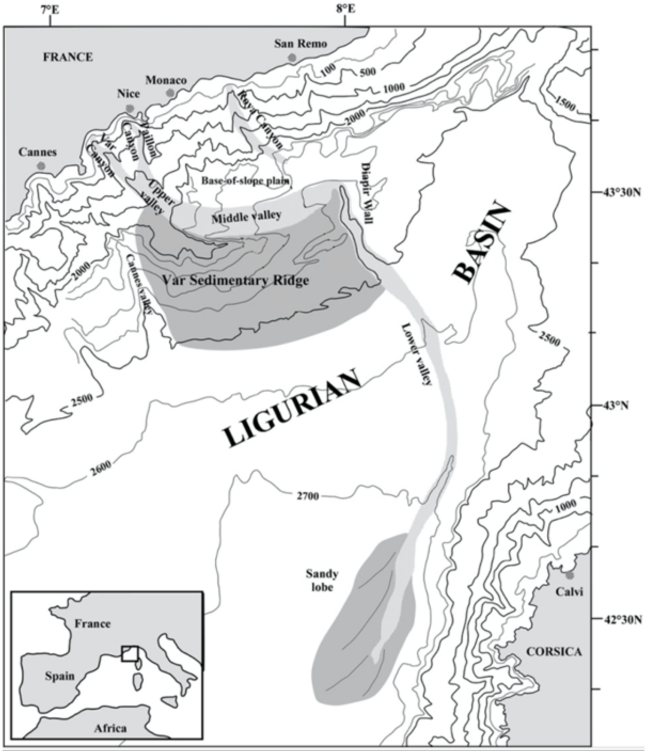

Figure 2.11. *The Var/Paillon system includes two submarine canyons (Var and Paillon canyons), a submarine fan, and a long (up to 50 km) sedimentary ridge (Var sedimentary ridge); fine turbidites are channelized through the Var submarine valley until the north-western Corsica margin where they are finally deposited in a distal fan (sandy lobes) [JOR 11]. (Picture from [MIG 06]). For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

The Var Sedimentary Ridge results from the activity of various types of gravity flows and repeated overflows of fine-grained particles. The morphology of the Var Sedimentary Ridge, which can be followed up to the abyssal plain, is moreover controlled by two independent parameters: the Coriolis force, which tends to deviate gravity flows towards West, and salt diapirs (issued from the underlying Messinian salt deposits), whose merging reliefs control the path of transported particles across the abyssal plain. Both sandy and muddy gravity-flow deposits originating from the Var/Paillon system can be detected up to western Corsica where they have constructed a distal lobe.

Gravity flows represent one of the most efficient particle-transport mechanisms along the Ligurian continental slopes. Turbidity-current activity is, however, depending of the amount of sediments delivered by aerial erosion on the margin; for example, most of the terrigenous produced in Corsica are transported towards east as a consequence of the dissymmetry of Corsica (globally tilted eastwards). Gravity flows are particularly active on the northern Ligurian Sea (Figure 2.12), along which three necessary conditions are present: (a) abundant terrigenous supply (erosion of still uplifting reliefs), (b) slope gradient and slope instabilities (inherited from the geological evolution and from seismo-tectonic reactivation) and (c) available pathways (the numerous submarine canyons cross-cutting the continental slope).

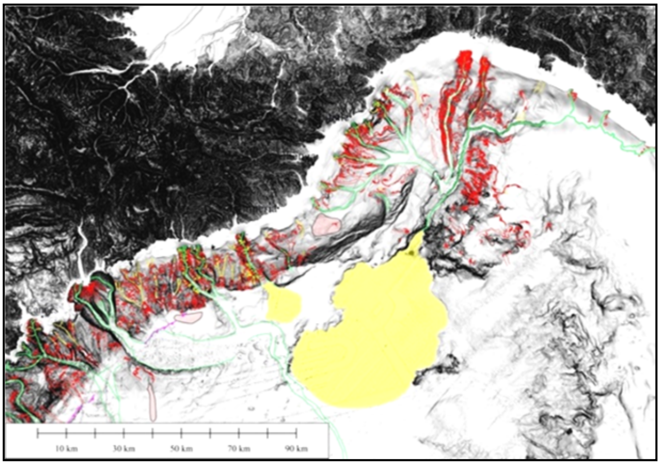

Figure 2.12. *Morphology of the northern Ligurian basin and continental margins [MIG 16] depicting the numerous submarine canyons, which crosscut the continental slope. The most important are off Nice (Var and Paillon canyons), off Ventimiglia (Roya canyon) and the almost 80 km long Genoa canyon system. For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

Finally, detailed bathymetric data (Figure 2.13) indicate that slope instabilities are obviously one of the major sedimentary mechanisms active along the whole Ligurian continental margin [HAS 14, KEL 16, MIG 11].

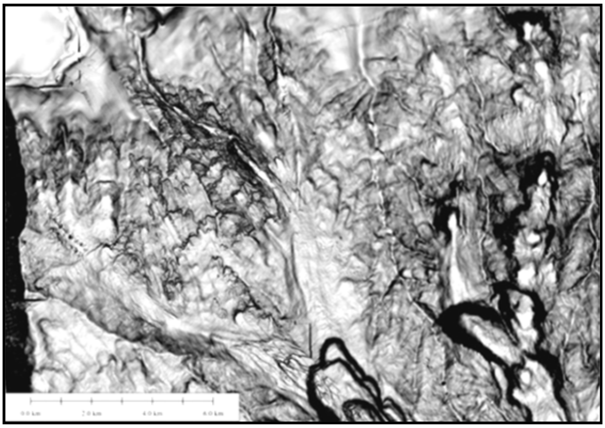

Figure 2.13. *Morphology of a small area of the lower continental slope southeast of Nice (Migeon, unpublished); this map (constructed at a 2M DTM) has been obtained using an automatic underwater vehicle (AUV); it illustrates the presence of numerous gullies acting as pathways for turbidites and the abundance of sedimentary scars (at all scales) indicating that the cover is quasi permanently remobilized by collapses*

High-definition mapping conducted along the French Riviera, and particularly off Nice, has revealed the presence of numerous sedimentary scars at all scales [KEL 16], from several kilometers to a few tens of meters (Figure 2.14). These features stress that the poorly consolidated, and unstable, sedimentary cover, resting moreover on steep slopes, is permanently remobilized by mass-wasting events in response to various mechanisms such as regional seismicity, sediment overloading and fluid circulation within the sediment. This results in the initiation of high-frequency debris flows and turbidity currents leading to sediment redistribution at the foot of the margin (mass-transport deposits) and even potentially to tsunamis such as the well-documented tsunami event, which has occurred off Nice in October 1979.

This brief review of the main sedimentary mechanisms, whose effects are imprinting the Ligurian continental slope, clearly demonstrates that on this area – already cross-cutted by canyon-driven turbidites, the sedimentary cover – is particularly unstable and almost permanently remobilized by sedimentary collapses.

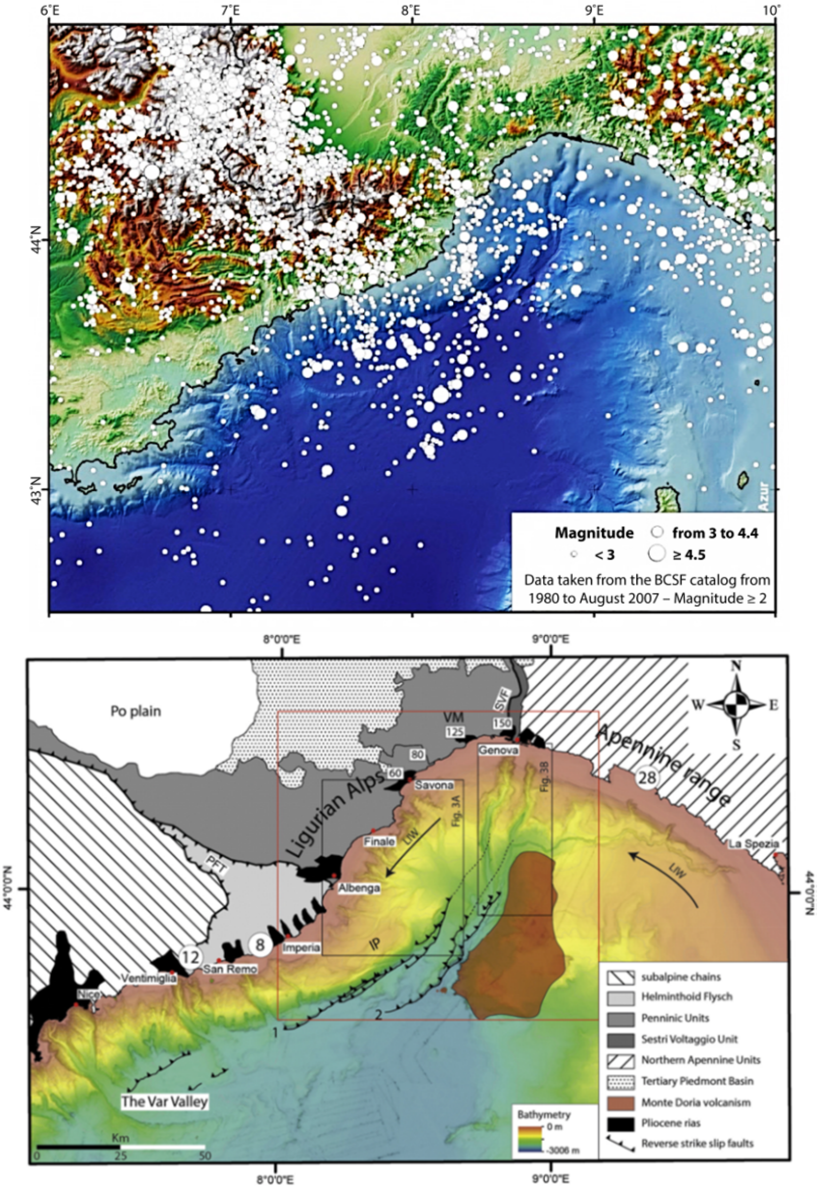

Figure 2.14. *(a) Instrumental seismicity (1980–2007) within the Ligurian Sea and Southern Alps domains. (b) Active fault zones evidenced at the foot of the Ligurian slope (after Soulet* et al. *[SOU 16]); these faults are interpreted as generated by a series of compressive events occurring in response to the still ongoing convergence between Europe and Africa. For color versions of the figures, see www.iste.co.uk/migon/mediterranean1.zip*

The steepness of the slope, inherited from its tectonic origin, is obviously one of the reasons to be taken in account to explain the presence of numerous sedimentary scars imaged on bathymetric data. We, however, also should keep in mind that the western Mediterranean Sea has been created, as young and small oceanic space, between two moving mega-plates – Europe and Africa. As such, this space is nowadays submitted to the effects of the still active general convergence between the two plates. Within the Ligurian Sea, and particularly along its northern margin, this is attested by a moderate but significant seismic activity as shown in Figure 2.14a.

Even though parts of the seismic events may be explained by the still tectonically-driven uplift of the nearby Alps and Apennines, it is suspected that a large number of the seisms recorded in the basin and on its margins are the consequence of the general convergence between the two plates generating new and large-scale fault zones at the foot of the Ligurian continental slope (Figure 2.14b). Therefore, we may anticipate that, in a geologically near-future (5–10 Ma), the Ligurian Sea will disappear, and that parts of its oceanic substratum and of its surrounding margins will be incorporated in a new collision chain to be built between Corsica/Sardinia and southern France.

The various seismically active faults, detected at the foot of the Ligurian margin (Figure 2.14b), may forecast such probable geodynamic scenario and are likely already driving parts of the sedimentary collapses occurring along the continental slopes.

2.6. A few concluding remarks

In this chapter, we have attempted to provide to a non-specialist scientific reader a synthesis of the origin of the Ligurian Sea and of the main geological mechanisms that have accompanied the formation of this basin. The Ligurian Sea can be regarded as a seawater “swimming pool” where various oceanographic (hydrological, climatic, chemical, geochemical, biological, etc.) processes discussed in this book are altogether operating and interfering.

Definitively created some 15 Ma ago, as the north-eastern corner of the western Mediterranean Sea, the deep Ligurian basin, and its continental borders, have since been only submitted to loading subsidence, due to the progressive deposition of thick sedimentary layers resting on its young, cooling and subsiding oceanic-type substratum. Tectonics has originally strongly controlled the structures of its continental margins, particularly within the northern areas where recent tectonics is starting to reactivate some former lineaments and may, in a near future, modify the overall margin morphology.

Three main geological/sedimentary characteristics of the Ligurian Sea should be emphasized, since they are obviously directly impacting several of its oceanographic parameters and characteristics:

– the steepness of the continental slopes that obviously exert a direct control on the oceanic deep and surface circulation, and may locally favor upwelling processes and thus nutrients and plankton abundance and repartitions;

– the presence of numerous submarine canyons that are directly conducting large parts of the terrigenous supply, including various nutrients and contaminants from aerial origin, to the deep sea; these particles are then made available to quickly enter into the chain food. Moreover, the canyons favor important erosion and reworking of the sediments deposited on the continental slope;

– the strong instability of the sedimentary cover. Owing to the almost permanent particles remobilization they induce, slope sedimentary collapses should also have a direct impact on benthic fauna stabilization and repartition.

As we already pointed out the Ligurian basin bordering, very narrow, shelves and quite abrupt continental slopes are submitted to significant natural geological mechanisms (freshwater fluxes, seism, sedimentary instabilities, local tsunamis), as well as to significant human activities. One may thus question on which types of complementary studies may be necessary to better understand the impacts of these events on the present-time geological, and consequently environmental, evolutions of the Ligurian basin and of its continental margin. In our opinion, it is now necessary to develop, or increase, existing *in situ* measurements and systems allowing monitoring, in real time, processes such as seismic activities and/or slope sediments mobilization, as well as *in situ* pore water circulations [ROD 15]. It is only when such automatic monitoring tools will be operational that we will be able to better understand the effects of natural geological mechanisms on the variability of the environmental conditions operating in the area.

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3

Physical Oceanography of the Ligurian Sea

3.1. Introduction

"A Sea made to human scale", as remarkably defined by Ramon Margalef in his introduction to the western Mediterranean, "keeping the inhabitants of its shore together, as neighbours" [MAR 85]. Indeed, because they were shorter, safer and easier than inland navigational ways of communication, developed early in the classic historical era. Important commercial, naval routes connecting the Greek peninsula or Rome to western harbors exploited the first knowledge of the surface circulation, for example as shown in the classic geographic encyclopedia of Strabone (about 20 BC). Furthermore, the first treaty of oceanography [MAR 25] reported the seminal descriptions of water properties and motions, as observed along the coasts between Romagna and Provence. However, the interest of modern, physical oceanographers in the Mediterranean was a late development because – compared to other oceanic basins, the apparent homogeneity of its water masses, the continental origin of the forcing, the absence of tides, were seen to infer a slow horizontal basin-scale circulation, mostly regulated by straits [AST 99]. However, the discovery of winter deep water convection in the northwestern Mediterranean, a mechanism that supplies a vertical basin-scale circulation, unknown anywhere else in the

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Chapter written by Louis PRIEUR, Fabrizio D'ORTENZIO, Vincent TAILLANDIER and Pierre TESTOR.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

world's oceans, progressively renewed the attention of the scientific community. In particular, the Ligurian Sea has been revealed as a key basin where the Mediterranean waters form, mix and spread according to this mechanism.

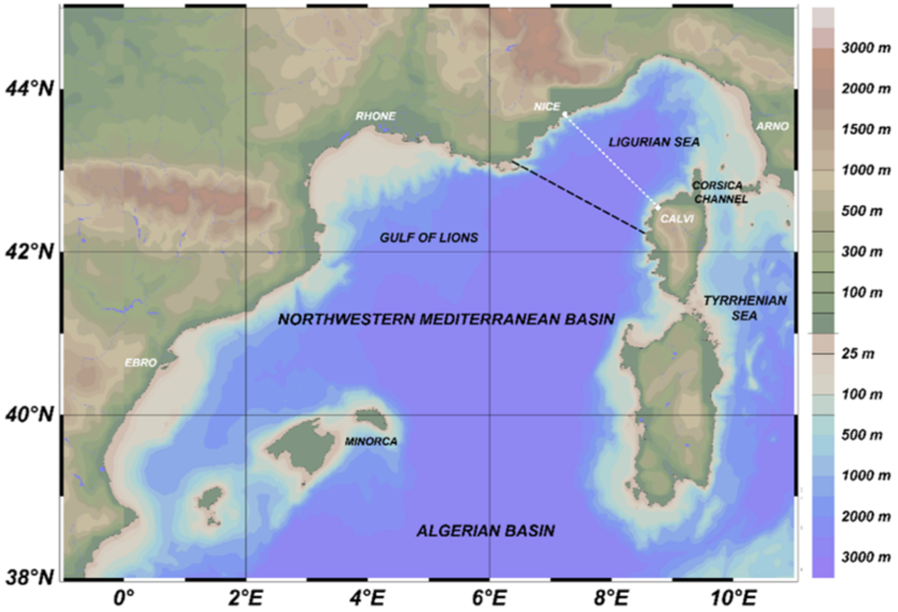
It should be kept in mind that the Mediterranean Sea can be characterized as a concentration basin. Within the Mediterranean Sea, evaporation dominates the total hydric budget; freshwater balance is negative and thus surface waters are transformed into saltier and colder water masses [BET 79, HOP 99, ROB 01]. The Ligurian Sea is one of the main actors in this transformation process. The modification of its surface waters can be intense and powerful during winter, inducing a tremendous alteration in the density of the water. Consequently, becoming denser, modified waters suddenly lose their buoyancy, rapidly sinking to depth. Therefore, the mechanism of dense water convection has been addressed in close link with horizontal circulation patterns and water mass properties, thanks to the availability of the longest series of open ocean observations.

The main objective of this chapter is to review state-of-the-art of physical oceanography in the Ligurian Sea. In some way, chronological descriptions are considered as stages of our comprehension of the Ligurian Sea. In the 1960s and 1970s, the large-scale embedding circulation was fixed and the main water masses were identified and described. In the 1980s and 1990s, this picture became progressively more complex with the discovery of the Ligurian front and its instabilities, which opened the first questions on the mechanisms that drive the large-scale circulation patterns. Finally, in recent years, the extremely long time series established in the Ligurian Sea provided an exceptional occasion to infer on the decadal evolution of the basin, opening still more questions on the response of oceans to climate change.

3.2. Circulation patterns from large scale to frontal dynamics

The Ligurian Sea is a deep basin (2600 m maximum depth), bordered by a steep continental shelf (except for the most eastern coast), connected with the Tyrrhenian Sea by the narrow Corsica channel (430 m deep, 42 km wide), and widely opened along its southwestern boundary (Figure 3.1, top panel, black line). Coastal borders are, for the most part, mountainous (see Chapter 2), which trigger atmospheric cyclogenesis around the Alpine arc and channel the major wind regimes, heading either southwest or northeast along the coastline ([LIO 06] and references therein). The climate is generally arid, precipitation is relatively scarce and concentrated in autumn, and insulation is among the highest in the Northern Hemisphere ([DRO 14] and references therein). The basin receives runoffs drained from the Alps; the Arno river provides the most important discharge volumes [AST 94].

On the basis of early surveys made in the 1950s and 1960s, the first picture of the circulation over the northwestern Mediterranean is proposed (Figure 3.1, bottom panel). The recurrently observed large-scale cyclonic circulation was identified from the density contrast of surface waters and considered as a permanent feature of the whole basin [GOS 68].



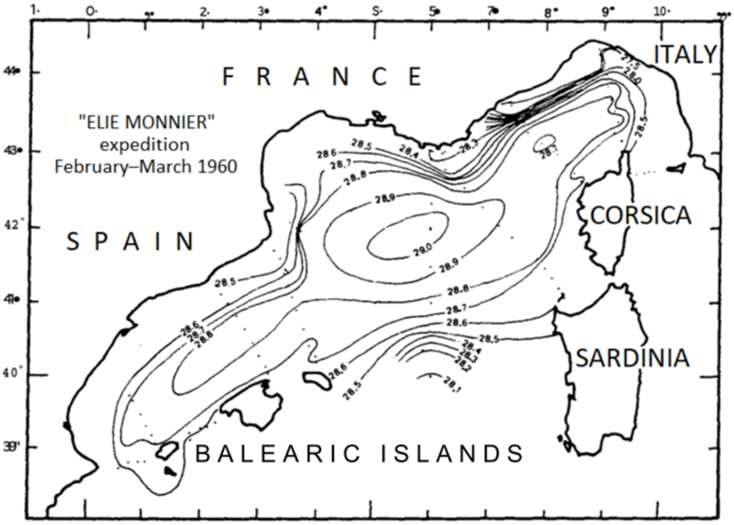


Figure 3.1. *The Ligurian Sea. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

COMMENTS ON FIGURE 3.1.– *Top panel: geographical situation of the Ligurian Sea at the eastern part of the northwestern Mediterranean Sea. Color scale represents bathymetry (for the ocean) and orography (for the land); white line: section Nice-Calvi; black line: indicative southwestern open boundary with the Gulf of Lion. Bottom panel (reproduced from Béthoux and Prieur [BET 83]): distribution of surface density excess (kg/m^3) observed during the cruise "Elie Monnier" in winter 1960; seven transects were collected (points on the map), documenting the cyclonic pattern of the surface circulation flowing southwestwards along the continental coast and northeastwards between Balearic Islands and Corsica.*

The internal structure underlying the large-scale pattern is composed of well-defined water masses arranged as a permanent doming (Figure 3.3). Characterized by a salinity maximum, Levantine intermediate water (LIW, see Box 3.1) flows in the layer 300–700 m. Originating in the eastern Mediterranean, LIW is overlapped by winter cold water (WCW), characterized by a temperature minimum in the layer 100–200 m, and deep water (DW, lately also called western Mediterranean deep water), which occupies the underneath layer down to the sea floor. In the temperature–salinity diagram (Figure 3.3, right panel), LIW appears saltier offshore Corsica than offshore Nice and in the Corsica channel, the salinity minimum is found in the center of the section. On the contrary, surface waters are saltier in the center than at the edges of the section (with salinity less than 38).

The horizontal circulation in the Ligurian Sea (or Ligurian Current) has a cyclonic aspect and is dominated by a geostrophic flow parallel to the coasts and entering from the northwest of Corsica. This flow goes around the high densities of the central zone which form a dome and exits towards the southwest along the Provençal coast. Observations actually show that the dome aspect results from a permanent density front between the flow zone and the central zone. This front has a depth thickness of more than 200 m throughout the seasons; the across-front horizontal density gradient is strong so that a 25 km-wide geostrophic jet flows along the front. This structure is robust as it balances the two dominant terms of the geostrophic equations but is also subject to several alterations under the effect of different forcings, which will be examined below.

The surface density front is found on average plumbing the 2000 m isobaths. The current is maximum (oscillating between 30 and 50 cm/s) at about 10 km from the front, and is generally much weaker near the coast which is about 30–40 km away from the front. Water transport (arrows) is about 1 Sv northwest of Corsica, but it is augmented by a seasonal flow (0–0.5 Sv) coming from the Tyrrhenian through the Corsican channel. It currently fluctuates between 0.8 and 1.5 Sv off the coast of Nice. The part of the Ligurian Sea off the front is called the central zone (CZ) and has horizontally homogeneous temperature and salinity characteristics (isopycnals being horizontal). This CZ is not circular but has an oblong shape, aligned on a SW–NE axis. Its surface area depends on the position of the surface front with respect to the coasts. The flow area itself is called the frontal zone (FZ), and the part between the FZ and the coast is called the peripheral zone (PZ). The PZ, when it exists, is only traversed by transient flows that may be in the opposite direction to the Ligurian Current.

The water masses encountered in the Ligurian Sea are the same as in the entire western Mediterranean. The surface water (SW) is low in salt and warm except in winter (which is classically called MAW (Modified Atlantic Water) and originates from Gibraltar via the Algerian basin). The winter cold water (WCW) is found at the bottom of the Ligurian Current (250–300 m) in summer and at the surface in winter. The LIW (Levantine Intermediate Water) originates in the eastern Mediterranean, passing through the Sicilian Strait in the western Mediterranean, and moves up to the Ligurian Sea via the west of Corsica. The LIW, warm and salty, is more pronounced under the Ligurian Current, but is also present to a lesser extent in the central zone. The LIW in the Ligurian Sea generally follows a cyclonic route under the geostrophic surface jet, at a depth of 400–500 m in the PZ and a velocity of about 4.5 cm/s. The LIW is also found in the CZ, but with characteristics less pronounced than at the periphery, and at depths near 200–300 m in general.

The above description corresponds to a "large scale" vision of the circulation. However, due to different types of forcing, flows are disrupted. Water exchanges between areas that are favored by these disturbances would be unlikely under the conditions of undisturbed geostrophic equilibrium.

At a mid-scale (10–50 km), the geostrophic jet undulates under the effects of surface fluxes (heat, evaporation, wind), and tends to form meanders that gradually deepen (especially in autumn and winter) and trigger baroclinic instability (zoom BI [GAS 78]). This instability tends to restore a new geostrophic equilibrium by transporting the surface water near the front into the depths (in the CZ–FZ), under the current and in the trough of the meander, while the crest of the meander sees water coming in from the depth to the surface. In winter, this mechanism suddenly supplies the surface layer of the core zone with salt and heat (from the FZ LIW), which can then become denser through exchanges with the atmosphere, and possibly form deep water in the ZC (zoom WC).

Like any dynamic instability, this BI tends to restore a geostrophic equilibrium, but it takes about 5–10 days to develop. Another type of instability is found in frontal areas that can restore equilibrium more quickly: the symmetric instability (zoom SC [THO 13]) triggers secondary circulations in an almost vertical plane. This instability does not occur naturally in a geostrophic flow. It can be triggered by the effect of even a moderate wind on a jet flow, resulting in a strong and local Ekman buoyancy flux, which destabilizes the surface layer at the front level. The visible effect on temperature, salinity and all variables (O_2, Chla, etc.) is that the frontal zone is subjected to a strong downward convergence (several meters per day) compensated by upwelling in the lightweight part of the flow, and often by another upwelling at the dense edge of the front. Identifying these processes requires sampling strategies with a kilometric resolution and the equivalent mesh size in the models, as the ascending and descending high vertical velocities are temporarily localized only in the frontal area. Water exchanges between the FZ and the CZ are at a sub-mesoscale, i.e. 1–10 km horizontally and 0–100 m vertically.

Other small-scale physical processes have been observed, in particular at the level of the LIW thermohaline front (zoom THF). This front, observed from variations in temperature, salinity, O_2 and nutrients, is located at the boundary between two water masses having about the same density. Thin layers of interleaving layers then develop between these two water masses, which can persist. The term “stirring” is then used because waters do not mix much at these small scales [LEV 18].

To complete the picture, the center of the Ligurian Sea is sometimes crossed by sub-coherent vortices (zoom SCV) of about 30 km in diameter [BOS 17]. These are small vortices that rotate quickly and are very thick (several hundred meters) and enclose a mass of water isolated from the outside. These eddies can travel long distances and can be formed during deep convections in the northwestern Mediterranean or on the edges of geostrophic flows [BOS 15, DAM 17].

Conclusion

All these meso- and sub-mesoscale processes participate in the long-term exchanging of T, S and O_2, etc., between the PZ, FZ and CZ, in the direction of horizontal and/or isopycnal gradients. Thus, during their route around the CZ and despite the role of the front as a barrier that sustains the geostrophic flow permanence, the waters of the Ligurian currents lose heat and salt to the central zone where advection is weak.

Box 3.1. *Circulation in the Ligurian Sea (see Figure 3.2)*

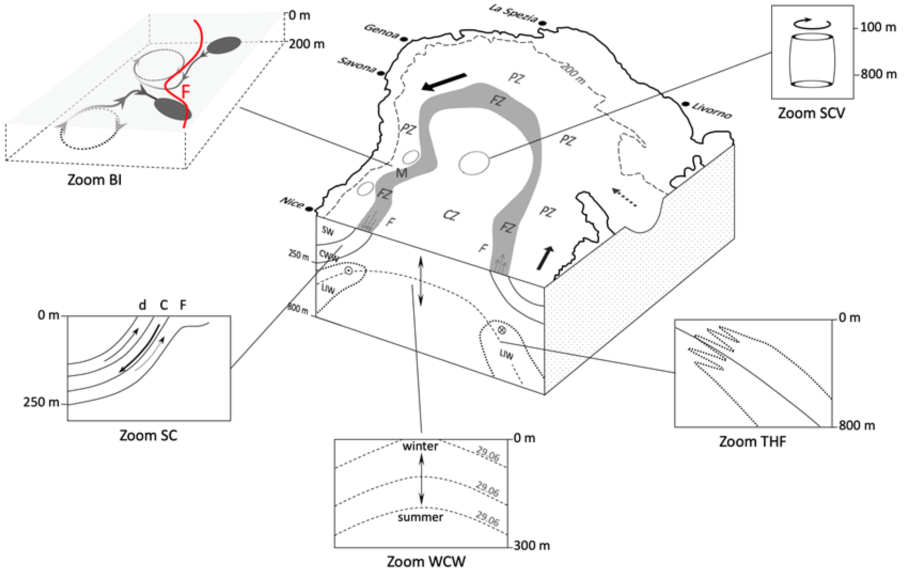


Figure 3.2. *Schematic 3D representation of the Ligurian Sea circulation. Continuous and dotted lines represent density and salinity contours respectively. CZ: central zone; FZ: frontal zone; PZ: peripheral zone; SW: surface water; DW: deep water; WCW: winter cold water; LIW: Levantine intermediate water; F: front; M: meandering; d: divergence (upwelling); C: convergence (downwelling); BI: baroclinic icirculation; SC: secondary instability; THF: thermohaline front; SCV: sub-coherent vortex; WC: winter convection. This figure was built with the help of Antoine Sciandra*

The evidence of isopycnal doming, in association with strong heat fluxes and wind forcing during winter, has inferred the first mechanisms of DW formation. Dedicated cruises in the late 1960s determined that dense waters are formed in the Gulf of Lion [MED 70] and, although less regularly, in the Ligurian Sea [AST 72]. In both regions, surface waters with density greater than 29.05 are recurrently observed during winter. Surface density greater than 29.09, frequently observed in the Gulf of Lion, is also sporadically observed in the Ligurian Sea [GOS 67, GOS 68], supporting the evidence that DW can also be formed in the Ligurian Sea [PRI 83].

The doming structure was primarily interpreted as a response to cyclonic atmospheric perturbations that trigger upwards vertical velocity at the center of the basin [SAI 62, SAI 63]. However, the interplay between the doming aspect and the large-scale circulation was reconsidered later on the basis of targeted surveys conducted during the 1980s and 1990s.

Indeed, the first high-resolution observations at the edges of the cyclonic circulation revealed the presence of a density front that separates the coastal area from offshore ([SOU 90], Figure 3.4, top panel). Moreover, the front delineated a vein of current heading southwest along the continental coast. It should be noted that the velocity maximum was observed 10–20 nautical miles offshore French coasts (Figure 3.4, bottom panel).

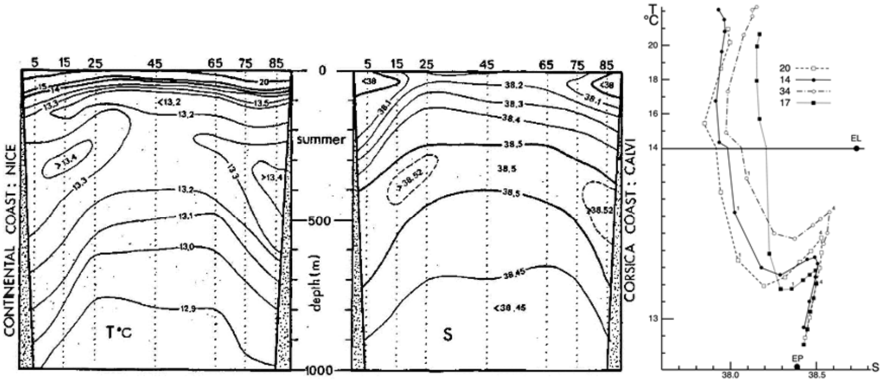


Figure 3.3. *Summertime potential temperature (left panel) and salinity (central panel) in the first 1000 m along the section Nice-Calvi (indicated in Figure 3.1)*

COMMENTS ON FIGURE 3.3.– *The distance from the continental coast is indicated in the upper x-axis. Right panel: temperature–salinity diagrams offshore Nice (box 14), offshore Calvi (box 20), at the center of the section (box 17) and at the Corsica Channel (box 34). Climatological views from the statistical study of Nyffeler* et al. *[NYF 80], which compiled hydrological data during 1950–1973 and a division of the Ligurian Sea in 34 boxes (reproduced from Béthoux and Prieur [BET 83]).*

Geostrophic approximation

In the geostrophic balance, the flow is horizontal and perpendicular to the horizontal gradient of the density field. In this approximation, the flow can be derived using the thermal wind equations [CUS 11] that associate the vertical shear of the current with the horizontal gradient of density:

$$\partial v/\partial z = -(g/\rho_0 f)\, \partial\rho/\partial x \; ; \partial u/\partial z = (g/\rho_0 f)\, \partial\rho/\partial y$$

where (u,v) are the horizontal components of the current and ρ is the density field, in orthogonal coordinates (x, y, z), g is the standard gravity, ρ_0 is a reference density and f is the Coriolis parameter. If there are null current and horizontal isopycn at a reference depth, the geostrophic current (m/s) and the geostrophic transport (Sverdrup:

1 Sv = 10^6 m^3/s) can be computed by integrating these equations from the reference depth to the surface. The adjustment of the flow with the underlying density field is established over a characteristic horizontal length scale, commonly defined as the internal radius of deformation (see, for example, [CUS 11, GIL 82, PON 83]).

The mixed layer depth and residual buoyancy

The depth of the mixed layer can be inferred by the buoyancy content of the surface layer. Considering a level of reference h (specified at 300 or 650 m in Figure 3.8), the buoyancy content from the surface to h can be derived from the profile of density excess as:

$$C(h) = \int_0^h [\rho(h) - \rho(z)]dz \ (units\colon kg/m^2)$$

This quantity indicates the strength of stratification for the water column h. If the residual buoyancy is null for the level of reference h, the upper layer from h to the surface is completely mixed.

Computation of trends

The series of the successive maxima and the series of successive minima are extracted from the original time series. The filtered time series is established at each time by the middle point between the two min–max series. This filter can be iterated as many times as necessary to compute the trend of a noisy time series (Ibanez, personal communication).

Box 3.2. *Geostrophic approximation*

The vein of current appeared as a frontal jet of limited extension (about 30 km wide) fully developed from inshore up to the density front; its vertical structure extended over a thick upper layer with velocities as high as 43 cm/s at surface and of 25 cm/s at 170 m depth.

The current system that shapes the cyclonic circulation of the Ligurian Sea does not follow the coast but is located offshore the shelf break, suggesting an alternative mechanism to explain the doming characteristic of the density field. The doming structure can be sketched by a continuous flow surrounding the central area, in geostrophic balance with offshore isopycnal slopes [BET 83, NYF 80, PRI 83]. Refer to Box 3.2 for the definitions of geostrophy.

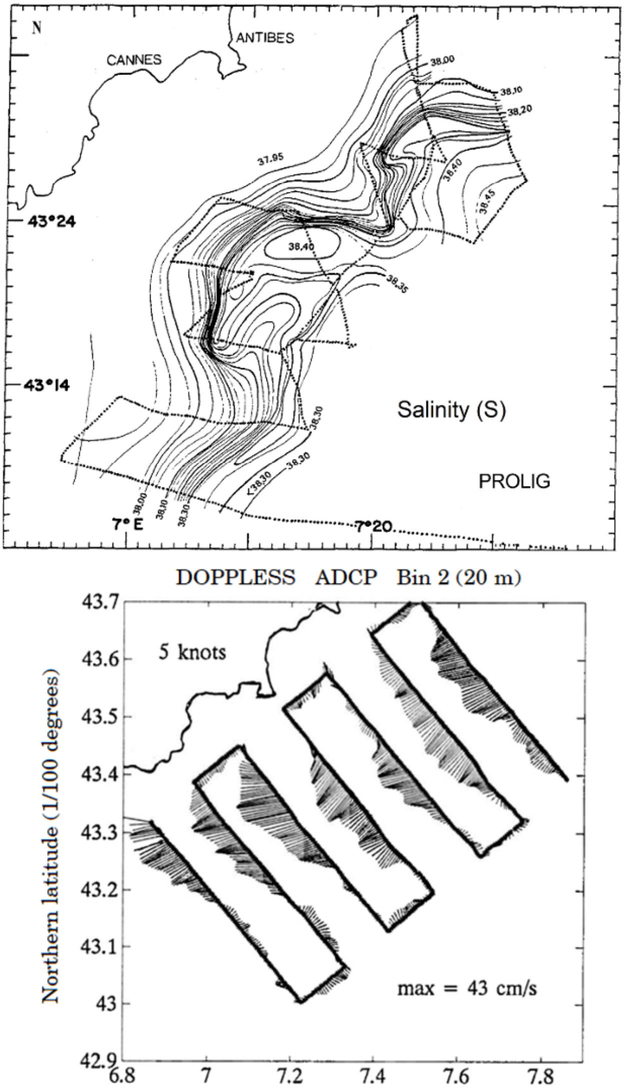
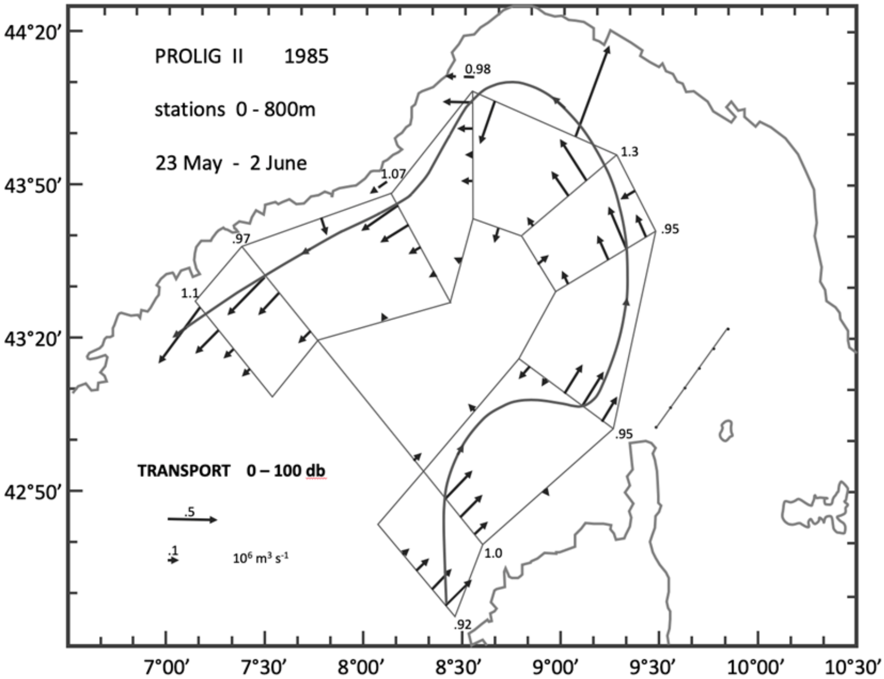


Figure 3.4. *PROLIG cruise*

COMMENTS ON FIGURE 3.4.– *Top panel (reproduced from Sournia* et al. *[SOU 90]): interpolated map of surface salinity obtained during the PROLIG cruise and characterizing the density front offshore Nice on March 20–21, 1980. The ship pathway is indicated by dotted lines; isohalines are drawn every 0.025 from 37.95 to 38.45. Bottom panel (original figure): ocean current at 20 m depth offshore Nice on May 10–11, 1992, obtained during the DOPPLESS cruise. An acoustic Doppler current profiler was towed at a speed of 5 knots.*

The hypothesis was further confirmed by the PROLIG-II cruise (Figure 3.5). In the observed mapping of the circulation over the whole Ligurian Sea, the geostrophic transport of the surrounding flow remains constant, varying from 0.92 Sv up to 1.10 Sv in the upper 200 m. The section Nice-Calvi also reveals variations of the LIW characteristics along the section. Potential temperature and salinity were found to be larger offshore Calvi than offshore Nice (by 0.15°C and 0.05 psu respectively); they were also larger and deeper than in the central area (by 0.20°C and 0.07 psu respectively). The vein of LIW flows at 4–5 cm/s underneath the geostrophic jet, around the central area. LIW core properties are altered along its course as a result of exchanges triggered by isopycnal mixing or episodic baroclinic instability [CRE 87]; these cross-shore exchange processes also favor the spreading of LIW in the central area. As additional evidence, in the layer 0–300 m, the slopes of some representative isopycns (Figure 3.5) are larger offshore Nice than offshore Calvi, indicating a stronger surface geostrophic current along the continental coast than that along Corsica.



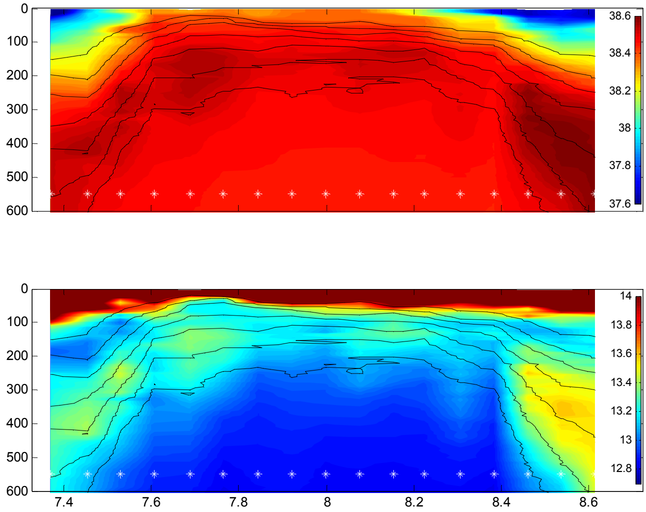


Figure 3.5. *PROLIG-II cruise. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

COMMENTS ON FIGURE 3.5.– *Top panel: map of the geostrophic flow in the upper layer (0–200 m) obtained during the PROLIG-II cruise on May 23–June 2, 1985. Transports (defined in the Box 3.2) are derived between pairs of stations, with reference at 800 dbar. For every section of six stations, the total transport (in Sv) is reported at the extremity of the section. The core of the flow is sketched by a curve passing by maximum transports. Bottom panels: salinity and potential temperature along the section Nice-Calvi during the same cruise (17 stations, about 10 km spacing). Isopycnal levels of 28.85, 28.95, 29, 29.04, 29.065, 29.08 and 29.09 are indicated by black lines.*

This synoptic view of the Ligurian Sea provided by PROLIG-II was complemented with original observations (with the YOYO cruise in May 1989) that focused on the transition from the coast to the central area offshore Nice. A refined description of the underlying dynamics across the density front was obtained with high-resolution sampling of the density field (one cast every 2 km). This survey confirms that the geostrophic flow is confined between the coast and the central area, which is generally located at the connection of the shelf with the abyssal plain. Consequently, a cross-shore delineation of the frontal structure in three zones is proposed, differentiating surface salinities as well as WCW and LIW properties: coastal ZP (no density gradient and no geostrophic current), frontal ZF (density gradient and current) and central ZC (no gradient and no current, see Figure 3.6, all panels). The existence of the delineation has been further intensively used, notably to interpret biological and biogeochemical observations in ecosystemic studies (e.g. [BOU 87, NIE 08, STE 08]).

This delineation of the frontal structure provides a consistent framework to characterize cross-shore exchanges of heat and salt that modulate water mass properties in the central area (detailed in the next section). In the surface layer, the salinity gradient remains confined in the extension of the frontal zone.

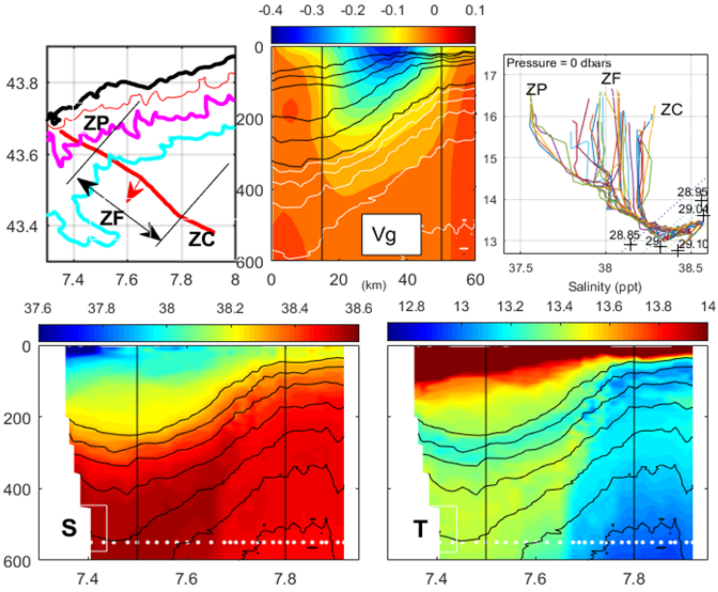


Figure 3.6. *YOYO cruise. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

COMMENTS ON FIGURE 3.6.– *Upper left panel: location of the cross-shore section during the YOYO cruise with a collection of 34 casts obtained on May 8–9, 1989 (2 km spacing). Isobaths of 200 m (black line), 1000 m (purple line) and 2000 m (blue line) are indicated. Upper middle panel: section of geostrophic current as defined in Box 3.2 (cm/s, positive northeastwards) derived from the mass field with a reference at 600 dbar; superimposed isopycns 28.5–29.0 (incremented every 0.1, black lines) and 29.01–29.09 (incremented every 0.03, white lines). Upper right panel: temperature–salinity diagram for the 34 casts. Lower panels: sections of potential temperature (right) and salinity (left). Isopycns 28.85, 28.95, 29, 29.04, 29.065, 29.08 and 29.09 are indicated by black lines. The central zone (ZC), coastal zone (ZP) and frontal zone (ZF) are identified and described in each figure.*

As further documented through autumn cruises [AND 09], the surface layer in the central area receives fresh waters from the coast during cooling periods, when isopycnal slopes under the thermocline are weak. Just below the surface, the layer occupied by WCW spreads in the frontal zone down to the coastal zone between the isopycns 28.85 and 29 (Figure 3.6, lower right panel). WCW is generally formed in early winter, when the isopycn 28.85 outcrops at the surface, which almost exclusively occurs offshore [GAS 99, LAC 72]. In the layer below the interfacial isopycn 29, LIW appears saltier and warmer in the coastal and frontal zones than offshore. LIW salinity maximum follows the isopycn 29.065, along which LIW spreads inside the central zone from its core inside the frontal zone.

Before looking at long-term changes in water mass properties in the central area, in view of these processes of cross-shore exchange, the question of the persistence of the surrounding cyclonic circulation needs to be addressed. To do so, the intensity of the flow can be estimated across the frontal structure in the geostrophic approximation (defined in Box 3.2), which also accounts for the LIW core underneath the geostrophic jet. Again, the flow is concentrated in the frontal zone, and it remains weak on either side of the frontal zone. Seasonal variations of the transport have been computed and further analyzed since the 1980s (Figure 3.7). The transports have similar features during the two decadal periods and are comparable (as orders of magnitude) to the transports reported by Béthoux *et al.* [BET 82] from averaged data collected before 1980. The transport across the frontal zone endures seasonal variations in amplitude, from 0.8 Sv in summer to 1.6 Sv in autumn.

As shown by Astraldi and Gasparini [AST 92] and Vignudelli *et al.* [VIG 99], a constant part, originating from western Corsica, is augmented with a variable part entering through the Corsica channel in autumn and winter, which explains the maximum transport in this period. High scattering around the seasonal trends cannot be generated by interannual variability (which cannot be evaluated because of the length of the series), episodic events such as heavy rainfalls [BET 88] or underestimations when the two bounding stations are not outside of the flow. On the contrary, there is no seasonal trend in the transport of the LIW in the layer 200–650 m, which remains constant at about 0.3 Sv (Figure 3.7, left panel).

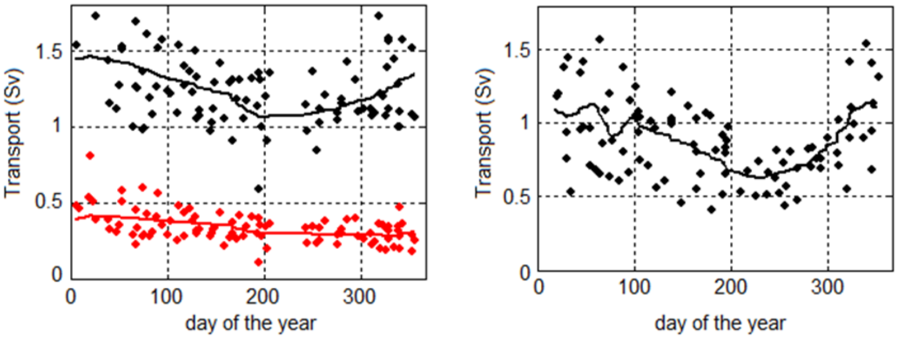


Figure 3.7. *Geostrophic transport across the frontal zone (in Sv). For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

COMMENTS ON FIGURE 3.7.– *Left panel: transport estimated for the period 1981–1996, as derived from 187 cross-shore sections for the layers 15–650 m (gray dots) and 200–650 m (red dots). One dot on January 18, 2002, at 2.3 Sv, is missing (out of scale). Right panel: transport estimated for the period 2003–2013, as derived from 100 cross-shore sections in the layer 15–400 m. Seasonal trends (lines) are obtained by two passes with the filter defined in Box 3.2. The two archives were collected monthly by the observation programs PROS-6 (1981–1996) and BOUSSOLE (2003–2013).*

Since 1999, direct current measurements of the upper layer (down to 150 m), regularly collected with a ship-mounted current profiler on the research vessel Tethys II (SAVED program[1]), have shown the permanence of the jet and its reduced extension (15–35 km wide).

This analysis confirmed that the cyclonic circulation of the Ligurian Sea is sketched by a permanent and continuous geostrophic jet. The jet delineates the central area and generates the doming aspect on most of the isopycnal levels, with respect to the scale of the internal deformation radius (defined in Box 3.2). The LIW core flows underneath the geostrophic jet and its course around the central area from Calvi to Nice lasts about 90 days. The previous results left open questions about the underlying mechanisms maintaining the jet, and consequently, the general circulation of the Ligurian Sea. Observations indicate that the horizontal density gradient, generating the jet, is confined inside the frontal zone. Inflows across lateral boundaries have then been quantified, either at the Corsica channel [AST 92] or by river runoffs [BET 88]. They both supply the coastal area with less dense waters

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[1] SAVED program: http://www.dt.insu.cnrs.fr/spip.php?article35.

and contribute to the relative confinement of the central area by generating, during winter, larger density increases in the central than in the coastal area [CRE 87]. They explain the seasonally variable part of the flow, observed during autumn and winter, as they reinforce the geostrophic transport at this period. The remaining steady transport observed in summer (0.6–0.8 Sv), when the other lateral runoffs are not significant, would thus be supplied by a stationary inflow along western Corsica.

3.3. Observation time series: sentinel of the Mediterranean Sea

In the previous section, we showed that the permanent cyclonic circulation over the Ligurian Sea is shaped by contrasts of water properties along a frontal structure, under the action of winter convection events in the central zone and seasonally variable lateral inflows in the coastal zone. The possible variations of this large-scale pattern can be monitored by the evolution of water mass properties in the central zone, under the caveat of horizontal exchanges of heat and salt across the frontal zone.

To address the question of possible variability, interannual trends of water mass properties have been recorded in the central area of the Ligurian Sea, thanks to long-term observation programs performed near the location (43°20’N, 7°55’E). They have been grouped as a unique archive of quality-controlled profiles that concatenates the PROS-6 program from September 1981 to January 2000 (780 casts down to 700 m), the DYFAMED program[2] [COP 18] from April 1994 to March 2018 (204 casts down to the sea bottom) and the BOUSSOLE program[3] from May 2003 to December 2013 (100 casts down to 400 m).

These 37 documented years have been grouped following the intensity of dense water formation, using two different indicators: the depth of mixed layer (estimated from residual buoyancy, see Box 3.2) and the surface density during winter (Figure 3.8, upper and middle panels). In addition, considering the role of the LIW in the deep convection, the depth layers of 300 and 600 m (i.e. the layer generally occupied by the LIW) are used to define the intensity of the dense water formation in the indicators used. “Strong” winter convection is defined when the mixed layer depth exceeds 650 m (i.e. the zero-residual buoyancy up to 650 m) or when the maximum

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[2] DYFAMED program: SEANOE 10.17882/43749.

[3] BOUSSOLE program: http://www.obs-vlfr.fr/Boussole/.

surface density is higher than 29.05. Eight years of "strong" convection are identified: each year between 1982 and 1986, then in 1988, 2006 and 2013. "Moderate" winter convection is defined when the mixed layer depth exceeds 300 m (i.e. zero residual buoyancy up to 300 m). In this case, six years of moderate convection are observed: 1994, 1999, 2000, 2005, 2008 and 2011. The other 23 years are characterized by "weak" convection, with a mixed layer depth always lower than 300 m. Water column analysis indicates that strong convection episodes occur when surface salinity is higher than 38.45, whereas "weak" convection episodes occur when surface salinities are lower than 38.40 (note that surface salinity of 38.20 indicates the invasion of coastal waters, see Figure 3.8, lower panel). The amplitude of the annual variations of residual buoyancy remains lower than 90 kg/m^2 for the years of "strong" winter convection. This is not the case for the years of weak convection as buoyancy might be cumulated from one year to the other.

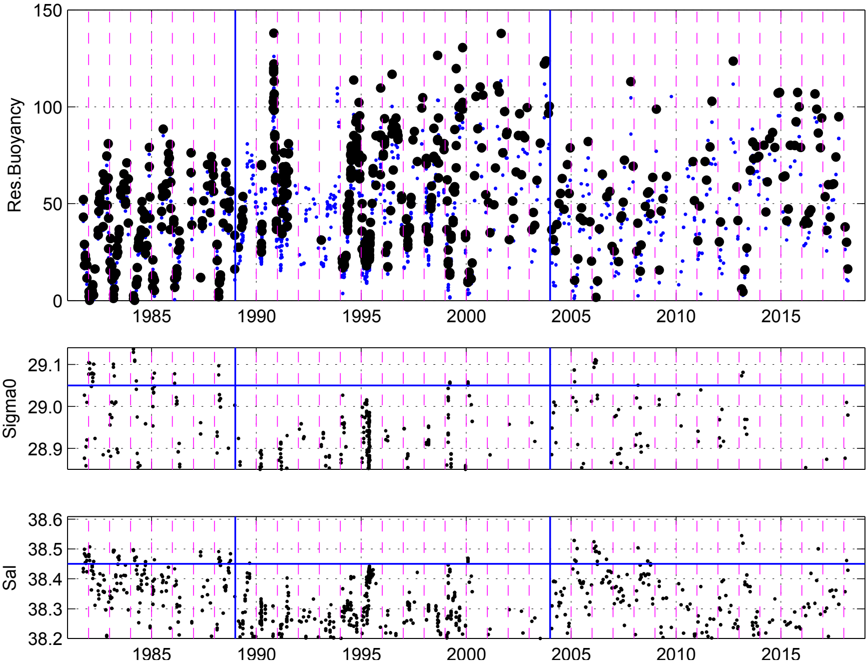

Figure 3.8. *Upper panel: residual buoyancy (see Box 3.2) in the first 650 m (black dots) and in the first 300 m (blue dots). Middle and lower panels: density and salinity in the layer 15–50 m. The period of weak convection 1989–2004 is indicated by vertical lines. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

To understand the interannual trends of the dense water formation, the changes in the WCW at surface are considered here as a good proxy of winter mixing (Figure 3.9). WCW, which is here identified by the isopycnal levels 28.85 and 29, is formed in winter, while the upper interface 28.85 outcrops, and it then remains in the first 100–200 m the rest of the year.

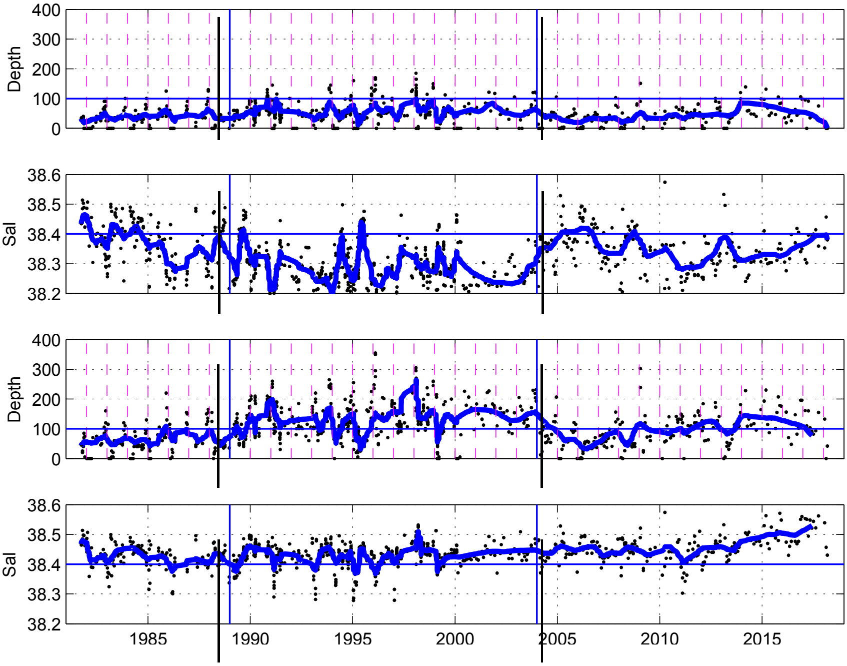

Figure 3.9. *Isopycnal depth and salinity for 28.85 (upper two panels) and 29 (lower two panels). Thick blue lines: multiannual trends are obtained by two passes with the filter defined in Box 3.2. The period of weak convection 1989–2004 is indicated by vertical lines. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

This mechanism is observed for most of the years, except 2014–2016. The salinity along the 28.85 isopycn is close to, or higher than, 38.40 during the years of "strong" and "moderate" convections, whereas salinity is lower than 38.40 during the years of "weak" convection. The lower interface of the WCW layer (i.e. the isopycn 29) outcrops only during the years of "moderate" and "strong" convection; it remains deeper than 100 m during the years of weak convection. However, salinity along this isopycn usually remains greater than 38.40. Note that during the two years before the strong convection event of 2006, the depths of the 28.85 and 29 isopycns progressively decrease and salinity progressively increases. After 2010, a trend of constant salinity increase is observed, which results in the WCW properties of 1980, unobserved until then.

Similarly, and perhaps still more, to understand trends in dense water formation, changes in LIW should be analyzed. The salinity maximum is used here as a proxy for the LIW (Figure 3.10). During the years of "strong" convection, salinity maximum is located at surface or in the first 100 m, with a corresponding density greater than 29.08. After the first years of strong convection, the depth of salinity maximum (or the LIW) rapidly increases to 300 m, reaching 500 m in 1999–2000. The depth of salinity maximum then progressively decreases until 2006, to reach the average depths of the 1980s; afterwards, it oscillates around 350 m.

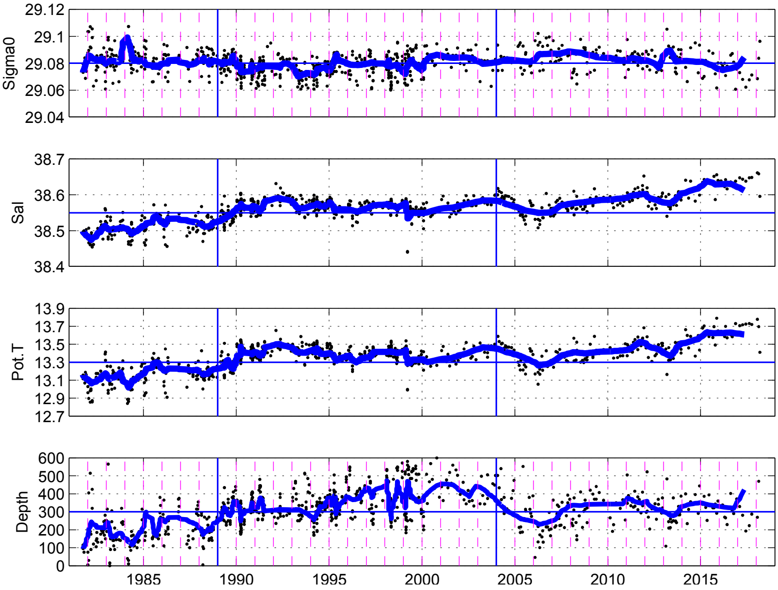

Figure 3.10. *Average values of density, salinity, potential temperature and depth inside a 50 m layer centered at the salinity maximum. Thick blue lines: multiannual trends are obtained by two passes with the filter defined in Box 3.2. The period of weak convection 1989–2004 is indicated by vertical blue lines. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

LIW is an exogenous water formed in the Levantine basin, which enters the Ligurian Sea by western Corsica. As reported in the previous section, the properties of the LIW core (underneath the geostrophic jet) change from

Calvi to Nice as they are transmitted through lateral processes into the central area, where they can accumulate or be transformed in DW by winter convection. It should be noted that during 1989–2004, in the absence of "strong" convection, the LIW layer cumulates salt and heat until the values of (38.60, 13.40), which have never been observed before. The properties observed in the 1980s are not reached anymore, even after the "strong" convection event of 2006. After 2007, water properties in the LIW layer regularly increase up to (13.70, 38.65), with constant density and depth.

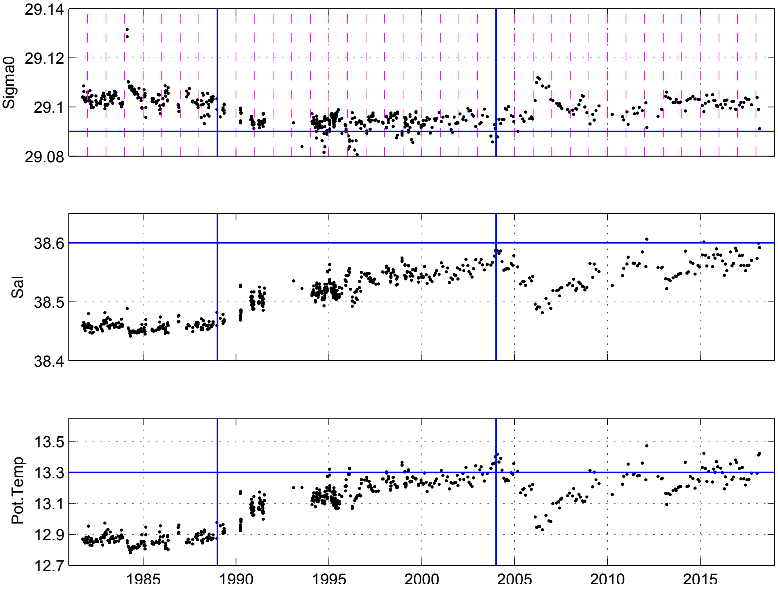

Figure 3.11. *Average values of density, salinity and potential temperature inside the layer 600–700 m. The period of weak convection 1989–2004 is indicated by vertical lines. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

The layer 600–700 m, underneath the salinity maximum, is the place of weak vertical gradients between LIW and DW (Figure 3.11). The corresponding water mass is homogeneous enough to reveal interannual trends similar to those reported around the salinity maximum (i.e. the LIW layer). Long-term series analysis indicates that the densities inside the 600–700 m layer are close to 29.09 during the years of weak convection, whereas, for the other years, density are closer to 29.11 (i.e. the density of DW). The difference could be ascribed to the fact that the part of LIW in this layer has increased, this lighter water injection thus decreasing density values with respect to the 1980s. This shift marks a trend for the LIW layer to thicken, which is consistent with the deepening of the salinity maximum and the stability of the LIW properties during the years of weak convection reported earlier. It could then be argued that LIW disappears from the 600–700 m layer during 2004–2006. Accordingly, temperature and salinity in the 600–700 m layer over the same period (2004–2006) come back to DW values (38.50, 12.90). They rapidly increase in the next four years, returning to the values observed before 2004. Nowadays, density is similar to the 1980s, although temperature and salinity are larger by 0.32°C and 0.10 psu. The persistent increase of water mass properties in this layer reveals the accumulation of LIW in the central area. Moreover, the trend since 2008 indicates that LIW has become saltier, warmer and thicker than in the beginning of the 1980s.

Evolution of the DW is analyzed by considering water mass properties in the layers 1800, 2000 and 2300 m (Figure 3.12). As noted by Marty and Chiaverini [MAR 10] or Schroeder *et al.* [SCH 10], a main event was observed in 2006: when winter convection reached the sea bottom at 2,365 m, salinity increased by 0.035 psu and temperature by 0.1°C. These represented important and abrupt variations compared to the average annual increase along the time series, by 0.005 psu for salinity and 0.022°C for temperature. After 2006, the values slightly decreased until 2010 and then stayed stable.

Considering DW properties in 1960 (38.41, 12.68), the general trend over 58 years was established at 1.1×10^{-3} psu/year and 3.6×10^{-3}°C/year (which is very close to the results obtained by Béthoux and Gentili [BET 96] over 18 years; see Figure 3.12, straight dashed lines). In this perspective, the brutal change in water properties during winter 2006 might be considered temporary as the trends before 2006 seemed to be retrieved after 2012.

Such a long-term, regular increase can be explained by the fact that a post-convection deep water always results from the mixing of WCW, LIW and the previous DW. Its salinity should increase with time in the same way as LIW salinity is increasing and thickening and the WCW layer is becoming thinner. Note that, apart from the years of the intense winter convection, the DW properties continue to experience changes as the deep reservoir of the Ligurian Sea is also fueled by DW formed in the Gulf of Lion [BOS 17, DAM 17, SEN 17].

The synthetic picture emerging from the analysis of these interannual trends indicates that the central area of the Ligurian Sea is mostly isolated from coastal contributions, because of the peripheral circulation, identified now by a geostrophic jet of the upper layer in the first 300 m.

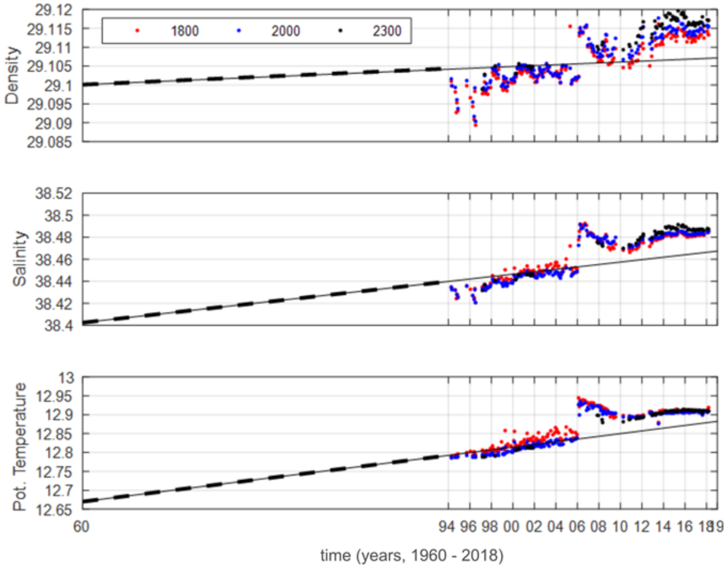

Figure 3.12. *Density, salinity and potential temperature at 1800 m (red dots), 2000 m (blue dots) and 2300 m (black dots). The trends reported by Béthoux and Gentili [BET 96], 3.6×10^{-3}°C/year, 1.1×10^{-3} psu/year, are indicated by the straight lines. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

However, the coastal–offshore exchanges can occur in the surface and the intermediate layers, when triggered by temporary dynamical instabilities of the geostrophic jet that develop in the frontal zone. Due to these exchanges, the central area increases in stratification with buoyancy intakes which, cumulated during a whole year, are not systematically mixed with DW during the following winter because of their intensity, with respect to winter buoyancy loss. During the years of moderate or weak winter convection, there is no mixing of surface and intermediate water masses with DW. There is thus an accumulation of buoyancy from the last intense convection episode until a new one occurs. Less salty waters accumulate in the surface layer, and the layer occupied by LIW thickens. As a result, increasingly stronger atmospheric fluxes during autumn and winter are necessary to reset the stratifying trend in the central area.

These mechanisms of exchange and accumulation, internal to the Ligurian Sea occur also in the Gulf of Lion, supplying the dense water reservoir that is siphoned off Gibraltar, together with dense waters formed during winter convection events. Considering the isopycn 29.04 as the top interface of the dense water reservoir, as its depth in the Algerian basin is about 300 m shallower than the sill of Gibraltar at 350 m depth, even moderate convection events can contribute to the Mediterranean outflow. The seasonal course of its depth is indicated through a large scattering of observations (Figure 3.13). It appears that this isopycn seldom outcrops, on average one winter every five years. Moreover, the depth variation of 70 m over one year (from 135 m in winter up to 207 m in autumn) agrees with previous estimates [BET 88]. This result supports the observed stability of the flow surrounding the Ligurian Sea, specially the steady inflow along western Corsica, as observed during the last decades.

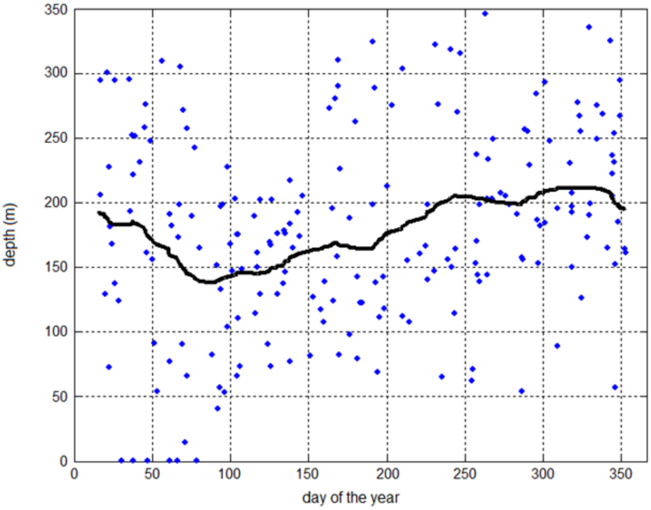

Figure 3.13. *Seasonal evolution of the depth of isopycn 29.04 as determined using the 204 observations (blue dots) at DYFAMED between 1994 and 2018. Seasonal trend (black line) is obtained after three passes of the filter defined in Box 3.2. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

As mentioned in the introduction of this chapter, the thermohaline circulation in the western Mediterranean is regulated by exchanges with the Atlantic Ocean at the strait of Gibraltar and by a deficit of fresh water, due to evaporation. The Atlantic inflow is about 20 times larger than the water loss towards the atmosphere; it is compensated by the Mediterranean outflow from the reservoir of dense water masses (higher than 29 kg/m^3 [BRY 09, GAS 85, MIN 91]). The outflow is estimated in the range of 0.7–1.0 Sv; thus, the closure of the Mediterranean annual water budget requires the same volume of dense waters to be formed from the surface layer. Considering that the dense waters required to balance the basin water budget are formed in the northwestern Mediterranean (including in the Ligurian Sea), and that the most important flow of the area is observed along western Corsica (generating then the geostrophic jet), it could be argued that the thermohaline engine (relatively stable along the years) is also responsible for the persistency of the jet observed in the Ligurian Sea. There is no observation of a permanent current under 300 m between the Gulf of Lion and the Algerian basin; only the densest waters flow around Menorca from spring to autumn, depleting the reservoir of the northwestern Mediterranean Sea (the seasonal trend of the isopycn 29.04 is presented in Figure 3.13). This depletion should be equilibrated in the surface layer through the inflow along western Corsica, which contributes to maintaining the cyclonic circulation of the Ligurian Sea, as explained by Béthoux *et al.* [BET 88].

3.4. Discussion and conclusion

An increase in temperature and salinity has been systematically observed in every water mass from surface to deep layers. The origin of the trends could be explained by the waters entering in to the Ligurian Sea along western Corsica, which appear to show the same changes as documented by historical ship observations [GOF 95, GOS 68, GRO 73, GRO 75] and more recently by profiling floats and gliders [BOS 15]. Very recently, during the DEWEX surveys [TES 18], the atypical increase in the water properties upstream of the Ligurian Sea has been decisive for the realism in modeling DW formation in the Gulf of Lion in 2013 [EST 16].

The long-term observation time series in the Ligurian Sea showed that the salinity increase started at the end of the 1980s, with the period of weak winter convection, and concomitantly with the Eastern Mediterranean Transient (EMT, [ROE 96]). The EMT, which consequently increased the salinity of LIW, has often been proposed as a precursor to the abrupt increase of DW properties that occurred in the winters of 2005 and 2006 in the Ligurian Sea [SCH 10]. The mechanism of accumulation of salt and heat during the 1990s and early 2000s, due to the lack of strong winter convection, can be considered as an alternative scenario to explain this abrupt increase [MAR 10]. Nevertheless, this catastrophic hydrological event of 2006 in the Ligurian Sea marked the DW properties of the whole western Mediterranean, a sharp increase in density with respect to the 1980s. This anomaly is superimposed over the warmer and saltier trends that DW experiences while not significantly affecting its density, due to compensation effects.

We have summarized the characteristics and changes of the water masses flowing inside the Ligurian Sea as they have been observed for more than 40 years, from seasonal to interannual timescales, and at intra-seasonal scales along their main pathway surrounding the central area (see Box 3.1). The analysis of this long-term time series relies on the existence of a permanent density front that isolates the central area from freshwater inflows in the coastal area, originating from continental runoffs or coming from the Algerian and Tyrrhenian Seas. This frontal structure sporadically allows water exchanges between the coastal and central areas. Recent advances provided by autonomous observing platforms, such as profiling floats and gliders, have revealed that exchanges across the front occur at sub-mesoscale scales and water transport are completed by small coherent eddies [BOS 15, BOS 16, BOS 17, DAM 17]. These are newly identified routes at the sub-mesoscale for LIW and WCW.

In the 1970s, baroclinic instability was the main mechanism evoked to explain these exchanges [GAS 78]. It turns out that other types of instabilities could act among a frontal jet, occurring more frequently and more rapidly, increasing stratification and re-adjusting the flow in geostrophic equilibrium [HAI 98, THO 13]. On the contrary, heat and buoyancy fluxes with atmosphere can trigger cross-shore exchanges by changing the depth of the mixed layer [DAS 14], activating secondary circulations [GIO 06, NIE 08] and structuring the marine ecosystems [LEV 18].

Thanks to relatively easy accessibility, the Ligurian Sea, its central area and its peripheral jet, appear to be an invaluable area to observe the climatic changes of the Mediterranean water masses as they circulate through the sea. However, it is even more important to monitor the unfortunately less accessible Gulf of Lion where recurrent winter DW formation occurs and feeds the downstream thermohaline cell. Since this mechanism remains active over decadal scales and trends to slightly increase the density of DW, the western Mediterranean circulation patterns will not change under the caveat that evaporation loss towards the atmosphere is maintained over the basin.

3.5. References

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4

The Carbonate System in the Ligurian Sea

4.1. Introduction

In little more than 200 years, human activities have released about 660 billion tons of carbon (Pg C) to the atmosphere [LEQ 18], which has major consequences on climate, ecosystems and people [IPC 14]. The oceans have absorbed and still absorb about a quarter of anthropogenic CO_2 emissions [LEQ 18], limiting the increase in atmospheric carbon dioxide (CO_2), but increasing ocean acidity [GAT 11]. The study of the oceanic carbonate system is therefore linked to two important environmental issues: (1) ocean CO_2 uptake and (2) ocean acidification and its impact on organisms, ecosystems and ecosystem services [GAT 15].

CO_2 uptake is difficult to measure due to variability induced by physical and biological processes. Methods to estimate the penetration of anthropogenic CO_2 in the ocean interior exist, but they are derived empirically and subject to scientific debate [SAB 10]. Moreover, it has recently been recognized that changes in the ocean circulation drive significant variability in carbon uptake [DEV 17]. Long-term observations of carbonate system variables (dissolved inorganic carbon, C_T, total alkalinity, A_T, CO_2 partial pressure, pCO_2, and pH, see Box 4.1) in the ocean remain challenging but highly needed in order to understand how the ocean is changing and how these changes relate to climate variability and predict future changes in the global carbon cycle.

Chapter written by Laurent COPPOLA, Jacqueline BOUTIN, Jean-Pierre GATTUSO, Dominique LEFEVRE and Nicolas METZL.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

Studies on the oceanic carbonate system have been mostly performed in the framework of international programs (JGOFS, WOCE, GO-SHIP) that coordinate oceanographic cruises to collect samples through the water column and perform accurate measurements of carbonate parameters (mostly C_T and A_T). Trends and variability in these ocean variables, including pH (e.g. [BAT 14]), have been quantified and compared with corresponding changes in atmospheric CO_2 through dedicated long-term efforts to maintain ocean time-series stations initiated through the JGOFS program (e.g. HOT, BATS, ESTOC, DYFAMED and others; WMO, 2014). These programs have generated high-quality databases of carbonate chemistry variables (e.g. GLODAP v2 [OLS 16]) that provide long-trend estimates of the oceanic carbon content based on A_T and C_T inventories. In addition to this ocean interior programs, continuous shipboard surface pCO_2 measurements on research and opportunity vessels, buoys or moorings are feeding the SOCAT database [BAK 16], which now allows annual estimates of ocean carbon uptake introduced in global carbon budgets [LEQ 18].

A recent study highlighted an “overaccumulation” of anthropogenic carbon in some oceanic regions and particularly in the Mediterranean Sea [LEE 11, PAL 15, SCH 10, TOU 11]. The study of the Mediterranean carbonate system is unique because of the intrinsic characteristics of this basin: warm waters and high total alkalinity (> 2500 µmol.kg^{-1}) associated with a permanent and rapid thermohaline circulation loop (residence time around 100 years; [MIL 05]). Several studies have characterized the Mediterranean carbonate system from samples collected along the zonal transect at the basin scale (e.g. [ALV 14]) and have shown that the Mediterranean exports dissolved inorganic carbon to the Atlantic Ocean with a net flux of 38 Tg C yr^{-1} [SCH 10]. Due to marked evaporation, A_T and S are higher in the Mediterranean Sea compared to the Atlantic water entering into the Mediterranean Sea [JIA 14]. On average, A_T in the Mediterranean Sea is 10% higher than that in the global ocean [PAL 15]. The relationship between S and A_T is partly controlled by inputs from rivers and the Black Sea, which are generally high in A_T [COP 93, SCH 07]. Due to its important role in carbon sequestration and ecological sensitivity to anthropogenic change with economic consequences [LAC 16], the Mediterranean Sea could provide insight into global trends [LEJ 10].

CRUISE & PLATFORMS	**START TIME**	**END TIME**	**DATA**	**DATASET DOI**
ANTARES	06/18/2010	10/16/2016	502	10.18142/233
CASCADE	03/02/2011	03/02/2011	10	10.17600/11010020
POINT B	01/09/2007	12/22/2015	1660	10.5194/os-13-411-2017
DEWEX	02/19/2013	04/14/2013	68	10.17600/13020010
MOOSE-GE	05/25/2010	05/26/2016	380	10.18142/235
DYFAMED	02/06/1998	12/10/2016	1809	10.17882/43749
DYFAMED (CARIOCA sensor)	1995–1997; 2013–2015		31600	10.17882/56709
W1M3A (PRO-CO_2 sensor)	2015	2017	15950	-
SOCAT (database)	1998	2016	53527	10.5194/essd-8-383-2016

Table 4.1. *List of cruises with A_T and C_T sampling in the Ligurian Sea from 1998 to 2016. Surface CO_2 data provided by fixed observatories (autonomous sensors) and by the surface ocean observation database (SOCAT) are also listed*

In this chapter, we mainly focus on seasonal cycles and long-term trends of the ocean carbonate system based on a synthesis of data collected in the Ligurian Sea from 1998 to 2016. It includes seawater sampling for A_T and C_T measurements and pCO_2 and pH calculated using the CO2SYS program [PIE 06] with the recommended constants of Mehrbach *et al.* [MEH 73], refitted by Dickson and Millero [DIC 87] and Dickson [DIC 90]. These samples were collected during oceanographic cruises (CASCADE, DEWEX, MOOSE-GE) and regular monitoring operations (weekly for SOMLIT-Point B and monthly for DYFAMED and ANTARES; see Table 4.1). We also use high-frequency pCO_2 data measured from the CARIOCA sensor at the DYFAMED/BOUSSOLE site [HOO 01, MER 18] and from the CO_2-PRO sensor at the W1M3A buoy [BOZ 13, CAN 15]. In addition, pCO_2 data available in the SOCAT database version 6 [BAK 16] are used to compare the long-term trends of pCO_2 and pH deduced from A_T and C_T data.

Any two of the four CO_2 variables (total carbon C_T, pCO_2, pH and total alkalinity A_T) can be used to determine the CO_2 system:

$C_T \equiv [CO_{2(aq)}] + [H_2CO_3] + [HCO_3^-] + [CO_3^{-2}]$

At seawater pH, we can simplify to: $C_T \equiv [HCO_3^-] + [CO_3^{-2}]$

C_T is also known as dissolved inorganic carbon (DIC)

A_T represents the ability of seawater to resist pH change upon addition of acid:

$A_T \equiv 2[CO_3^{-2}] + [HCO_3^-] + [H_2BO_3^-] + 2[HBO_3^{-2}] + 3[BO_3^{-3}] + [OH^-] +$ [organic/inorganic H^+ acceptors] - $[H^+]$

Acidity is a measure of H^+ concentration; the freer the H^+ ions, the lower the solution's pH and the greater the acidity ($pH = -\log[H^+]$)

The pH of seawater only varies between about 7.5 and 8.4

Carbon dioxide reacts with water to form carbonic acid: $CO_2 + H_2O \leftrightarrow H_2CO_3$

Carbonic acid then almost instantly dissociates in the seawater, releasing H^+ ions and bicarbonate molecules: $H_2CO_3 \leftrightarrow H^+ + HCO_3^-$

Bicarbonate ions also dissociate, releasing additional hydrogen ions and forming carbonate ions: $H^+ + HCO_3^- \leftrightarrow 2\,H^+ + CO_3^{2-}$

Box 4.1. *Carbonate system chemical reactions*

Except for the DYFAMED site in 1998–2000 [COP 02], all A_T and C_T water samples collected in 2004–2016 were shipped back to LOCEAN (Paris) where they were stored at 4 °C and analyzed within three months of collection by *Service National d'Analyse des Paramètres Océaniques du* CO_2 ($SNAPCO_2$ at Sorbonne University in Paris, France). C_T and A_T are measured via potentiometric titration following the methods described by Edmond [EDM 70] and Doe [DOE 94]. Accuracy of C_T and A_T was between 1.5 and 3 µmol kg^{-1}, depending on the sequence of measurements in 2004–2017. Repeatability of replicate samples conducted at SOMLIT-Point B in 2007–2015 was better than 3 µmol kg^{-1} for both C_T and A_T [KAP 17]. During C_T and A_T sampling, CTD casts (Seabird SBE25 for SOMLIT and SBE911 for open ocean studies) were performed to collect temperature (T) and salinity (S) profiles, which were used to estimate pCO_2 and pH. Nutrient samples were also collected systematically during the regular cruises during CTD casts by using Niskin bottles mounted on a rosette. In general, most samples were collected from the surface to the bottom depth in the open ocean zone and at two depths (near the surface and 50 m) in the coastal area (SOMLIT-Point B).

4.2. Distribution of the carbonate system in the Ligurian Sea

In the Ligurian Sea, episodes of dense water formation and deep mixing occur in winter. They are related to the deep convection process in the Gulf of Lion, which occurs every winter with higher intensity than in the Ligurian Sea [BOS 17, HOU 16]. The Ligurian Sea is also characterized by atmospheric inputs (see Chapter 5), rich in nutrients, influencing phytoplankton production and the export of organic matter to the mesopelagic zone [MAR 02].

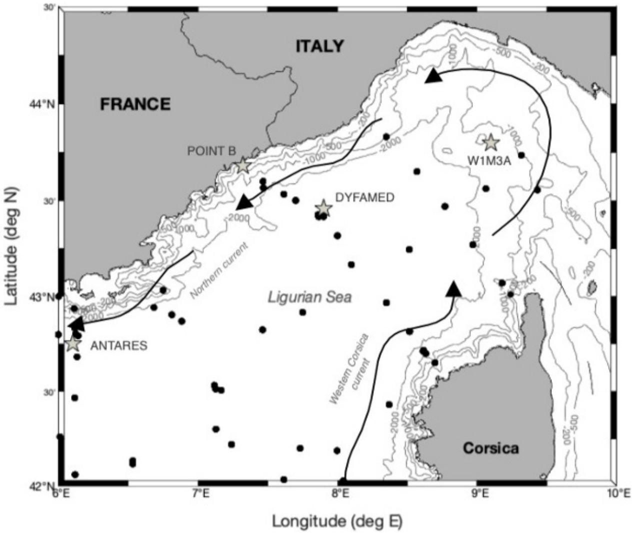

Figure 4.1. *The Ligurian Sea is located in the northern part of the western Mediterranean basin. It is located in the pathway of the Levantine Intermediate Water (LIW), which follows two main surface currents (the Western Corsican Current (WCC) and the Northern Current (NC), black arrows) that form a front between coastal and offshore waters (see Chapter 3). The sampling stations from 1998 to 2016 are indicated by black dots. The gray stars represent the time series of fixed observatories (DYFAMED, ANTARES, POINT B and W1M3A)*

Water column monthly climatology of potential T (theta) and practical S distributions in the Ligurian Sea are plotted in Figure 4.2. They include all samples collected during time series monitoring and regular cruises from 1998 to 2016 (Table 4.1). Results are consistent with those described by Marty *et al.* [MAR 02] and in Coppola *et al.* [COP 18] at the DYFAMED site: the modified Atlantic water (MAW) in the first 200 m with strong T–S seasonal variability, the Levantine intermediate water (LIW) more saline than in the rest of the Northwestern basin (200–800 m) with a core around 350 m (maximum of theta and salinity) and the western Mediterranean deep water (WMDW) warmer and more saline for the last decade due to intense vertical mixing during some winters and the deep-water spreading. These episodes of deep convection are now well-documented [HOU 16, SCH 08, SCH 17].

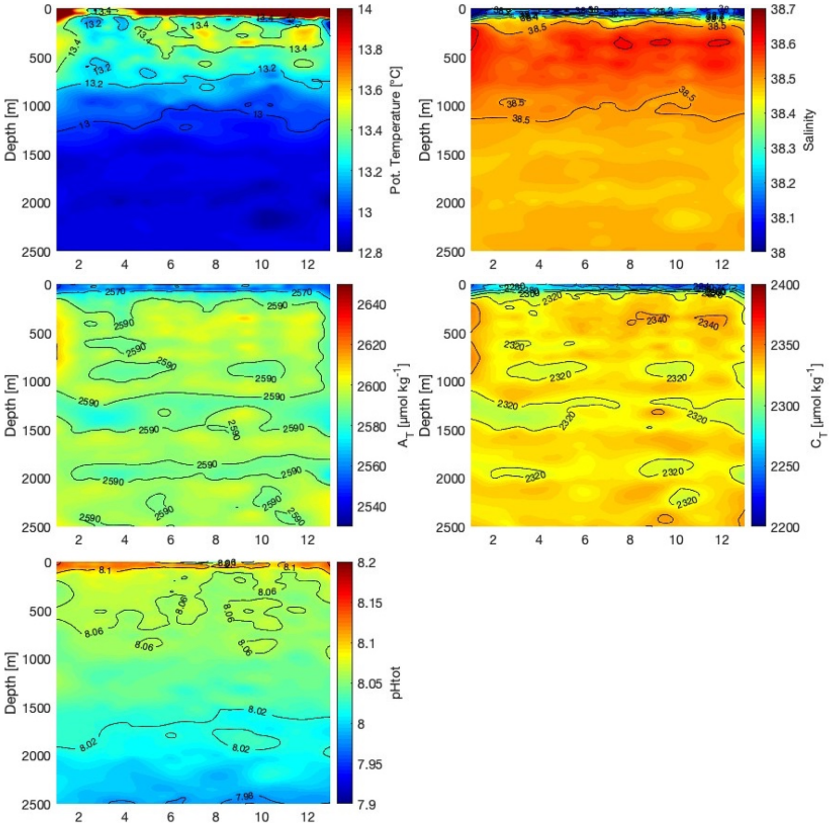

Figure 4.2. *Water column monthly climatology of potential T, S and carbonate variables (A_T, C_T and pH at the total scale) in the Ligurian Sea derived from cruises conducted from 1998 to 2016 (all stations shown in Figure 4.1). In the Ligurian Sea, the average C_T concentration ranges from 2200 in the surface to 2350 µmol kg^{-1} in deep waters). Total alkalinity follows the same pattern with depth and ranges from 2500 to 2600 µmol kg^{-1}. pH (total scale) is higher in the upper 100 m (8.15) and decreases progressively with depth (< 8 in deep waters). Based on all datasets in 1998–2016 (about 1200 samples in deep waters), the mean C_T and A_T below 300 m are respectively 2328 ± 9 and 2593 ± 7 µmol kg^{-1}. In the next section, we will also explore whether changes can be detected in deep layers. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

They considerably modified the deep-water structure to form a stratification of deep-water column where successive new deep waters overlapped, depending on the convection intensity and the newly formed deep-water volume. In the Ligurian Sea, wind forcing and heat loss flux are less important than in the Gulf of Lion, but deeper vertical mixing can occur in February/March, allowing ventilation of part of the LIW (Figure 4.2). When the mixed layer is very shallow, the LIW is reinforced (warmer and denser) and the minimum dissolved oxygen concentration becomes lower [COP 18].

In addition to the effect of T on CO_2 solubility, the distribution of C_T in the water column is driven by the antagonistic effects of (1) the biological carbon pump that increases the vertical gradient of C_T (lowering C_T at the surface and increasing it in the ocean interior) and (2) the exchange of CO_2 at the air–sea interface.

4.3. The seasonal cycle in surface water

The seasonal cycle of the carbonate system and ancillary variables in the surface water is shown in Figure 4.3. The monthly variability of T and S at the DYFAMED site was already reported by Marty and Chiavérini [MAR 10] and Coppola *et al.* [COP 18]. At the coastal SOMLIT-Point B site, seasonality was described by Kapsenberg *et al.* [KAP 17]. For the Ligurian Sea sub-basin (all cruises listed in Table 4.1), the same seasonal trend can be observed: a maximum sea surface temperature (SST) from July to September and a minimum SST in March when evaporation and heat loss prevail.

The seasonal variability of the surface S is more complex. S ranges from 37.2 to 38.6 with higher variability in the coastal zone. The haline content in the surface is highly variable and driven by evaporation and precipitation in the open ocean, while groundwater discharges could affect the surface S in the coastal zone [BEJ 17]. During the re-stratification period in offshore, the newly formed deep waters will mix with the Atlantic waters and the LIW that will reinvest the mixed patch, a phenomenon that seems to be more pronounced in the Ligurian Sea, probably because the mixed patch is higher in salinity. This is due to shallower vertical mixing and a more saline LIW, which is close to the sources in the basin: the Corsica Channel and southern Sardinia [BOS 15].

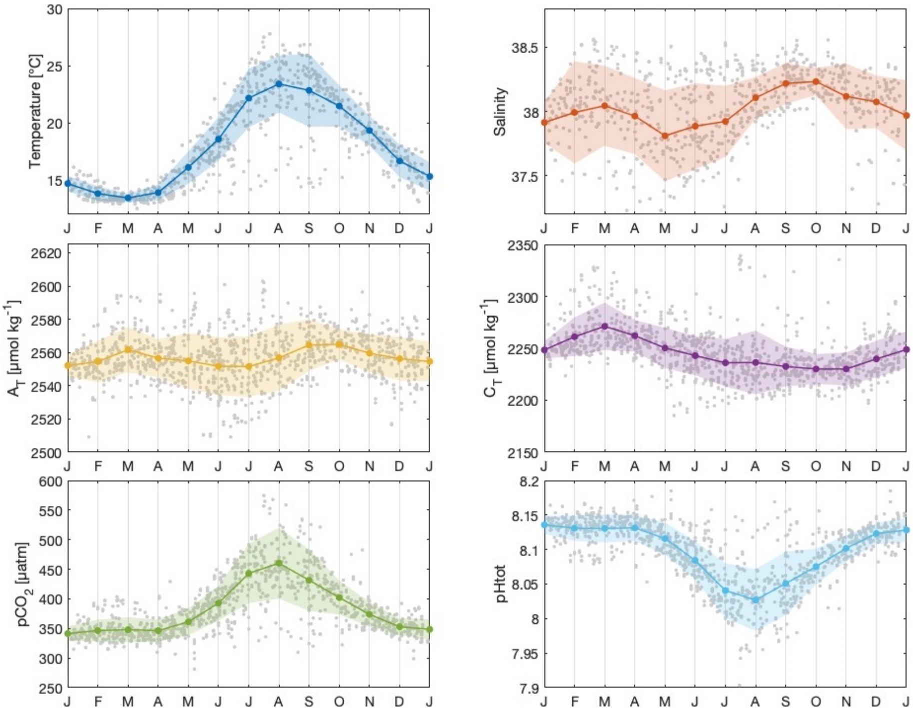

Figure 4.3. *Surface (0–20 m) seasonal variability of T, S, A_T, C_T, pCO_2 and pH (total scale) derived from 1998 to 2016 with monthly sampling (gray dots). The colored dots represent the mean values and the colored area the standard deviation of the respective values. The main processes underlying observed variations are evaporation, heat loss, precipitation, ground water discharge, mixing of different water masses and interactions between parameters themselves (see, for example, Figure 4.4). For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

The seasonal A_T cycle generally mimics that of S, with highest values in March and September. In surface waters, the A_T variability is controlled by freshwater addition, the effect of evaporation and S that contributes to more than 80% [MIL 98]. In the Mediterranean Sea, several studies have shown that the relationship between A_T and S is linear [COP 02, COP 93, HAS 15, JIA 14, RIV 10, SCH 07]. The same linear relationship has been observed between A_T and S with higher A_T associated with the presence of LIW (highest S values; Figure 4.4). In the coastal zone, the relationship is more complex and variable from year to year [KAP 17]. Since S is high in the Mediterranean Sea (concentration basin), total alkalinity is also high: values range from 2500 to 2600 μmol kg^{-1} (annual average 2557 ± 15 μmol kg^{-1} in surface waters in the Ligurian Sea). Low values (2500 μmol kg^{-1}) are observed only in the coastal site (Point B). Offshore, the lowest values are mainly due to calcium carbonate sedimentation ($CaCO_3$) and Atlantic water inflows.

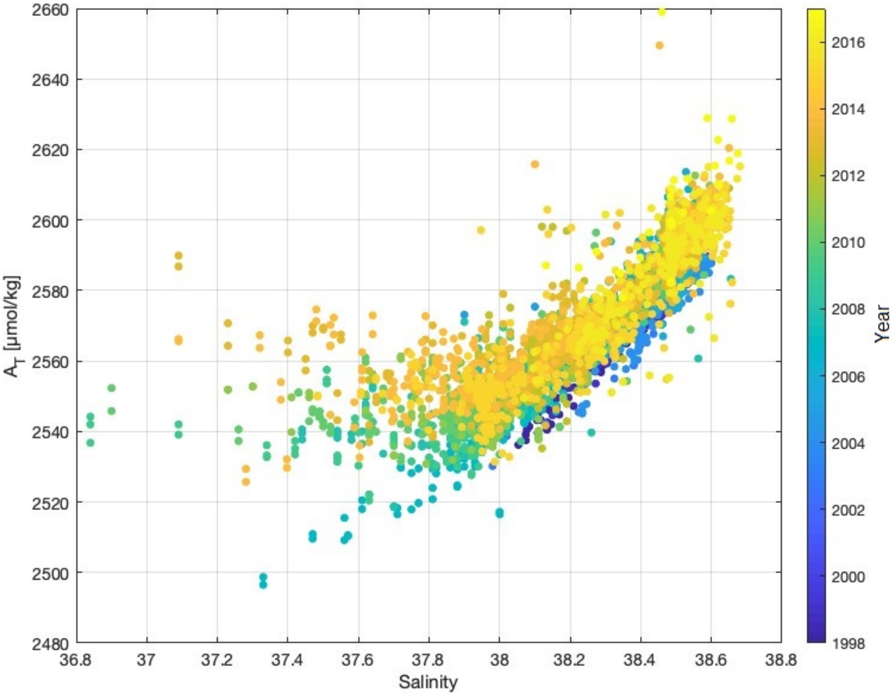

Figure 4.4. *Relationship between A_T and S for the entire water column (0–2400 m) in the Ligurian Sea (see the map in Figure 4.1). The different values of A_T and S are attributable to the different water masses composing the water column and to long-term variations (the color indicates the range of year: 1998–2016). For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

In the Ligurian Sea, C_T concentrations in surface waters range between 2200 and 2320 μmol kg^{-1}. As opposed to A_T, the seasonal cycle of C_T is pronounced and mirrors the SST cycle: C_T is maximum in March, followed by a sharp decline until July and a gradual decrease until November after which it increases again. The seasonal cycle, here represented from all data available in the Ligurian Sea, is a robust feature at the local scale, as seen at both Point B [KAP 17] and DYFAMED sites [COP 02, HAG 16].

The seasonal pattern of pCO_2 is also pronounced and mainly controlled by SST and C_T. It is higher during the stratification and warm period in summer and lower during "cold" winter. For the Ligurian Sea, pCO_2 values range from 300 to 550 µatm, as already reported for the DYFAMED site [COP 02, COP 04, HOO 01, MER 18] and Point B [KAP 17]. This is also the range of pCO_2 values observed in 1998–2016 in this region from various platforms and included in the SOCAT database [BAK 16]. The pCO_2 is highly dependent on the T variability: A T increase of +12°C from winter to summer would lead to the increase of pCO_2 by 200 µatm.

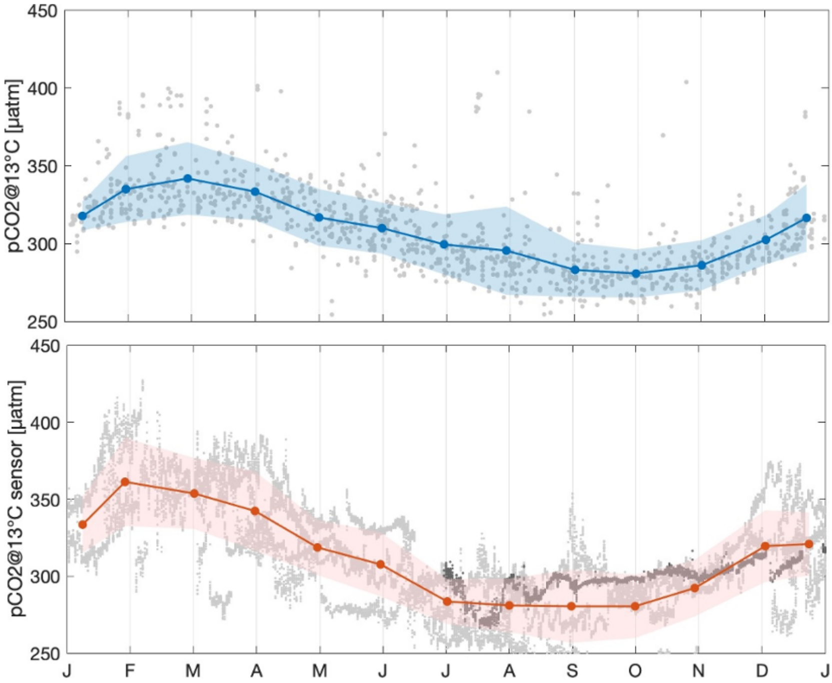

Figure 4.5. *Top: seasonal variations of pCO_2@13C in the surface (0–20 m) derived from the discrete measurement of C_T and A_T (gray dots) in the Ligurian Sea (see map in Figure 4.1). Bottom: seasonal variations of pCO_2@13C derived from hourly surface measurements of pCO_2 with the CARIOCA sensor at the DYFAMED/BOUSSOLE (gray light) and from the CO_2-PRO sensor in W1M3A sites (dark gray). Discrete and semi-continuous estimations exhibit similar seasonal variations ranging from 250 to 400 µatm and follow the C_T seasonal cycle (Figure 4.3). Although there are uncertainties associated with pCO_2 calculations based on C_T/A_T pairs, the pCO_2 and pCO_2@13C seasonal cycles presented in Figures 4.3 and 4.5 confirm the overall quality of C_T/A_T data that are used to detect long-term trends. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

To separate this effect, pCO_2 is normalized to constant T (here 13°C for winter, hereafter named pCO_2@13C) using the method described by Takahashi *et al.* [TAK 93] (Figure 4.5). pCO_2@13C increases when the mixed layer deepens in winter (C_T maximum). When primary production increases in March/April, the productive layer is mostly between 0 and 40 m and pCO_2@13C, like C_T, decreases [COP 02].

Finally, SST and C_T strongly influence the seasonal signal of pH [HAG 16, YAO 16]. In the Ligurian Sea, the surface pH at the total scale ranges between 8 and 8.15 (Figure 4.3). It is highest in winter when the vertical mixing of the surface water with cold and C_T-enriched deeper water is predominant and the exchanges of CO_2 with the atmosphere are important. Surface pH is still high in March/April when primary production increases as a result of the displacement of the carbonate equilibrium related to CO_2 consumption [COP 02]. Finally, surface pH is lowest in summer during the warm stratification period.

4.4. Long-term changes in the carbonate system and acidification

Long-term trends of the carbonate system in the surface, intermediate and deep waters provide crucial information on climate and anthropogenic impacts and allow identification of some anomalies. These observations are essential to explain the processes that govern these trends in the Mediterranean Sea [TOU 09, YAO 16]: warming, increase in atmospheric CO_2, ocean dynamics and changes in biological communities.

In this chapter, trends have been estimated using monthly or annual data measured at different depths: surface (0–20 m), intermediate (300–800 m) and deep (>2,000 m). Even though climate change impacts are usually detectable after 30 years (e.g. [MCK 11]), we establish here, for the first time, trend values for the carbonate system in the Ligurian Sea based on 18-year time series.

4.4.1. *Surface trends*

At the surface (0–20 m), both C_T and A_T exhibit a positive trend: 0.59 ± 0.34 µmol kg^{-1} yr^{-1} for C_T and 0.50 ± 0.21 µmol kg^{-1} yr^{-1} for A_T (Figure 4.6). pCO_2 and pH (total scale) show respectively an increase of

3.3 ± 0.7 µatm yr^{-1} and a decrease of −0.003 ± 0.001 unit yr^{-1} from 1998 to 2016. This is consistent with the coastal observations performed at Point B [KAP 17]. It can therefore be concluded that, at the basin scale, the different series (Point B, Dyfamed, Antares) lead to the same result: pCO_2 increases, leading to a decline in pH.

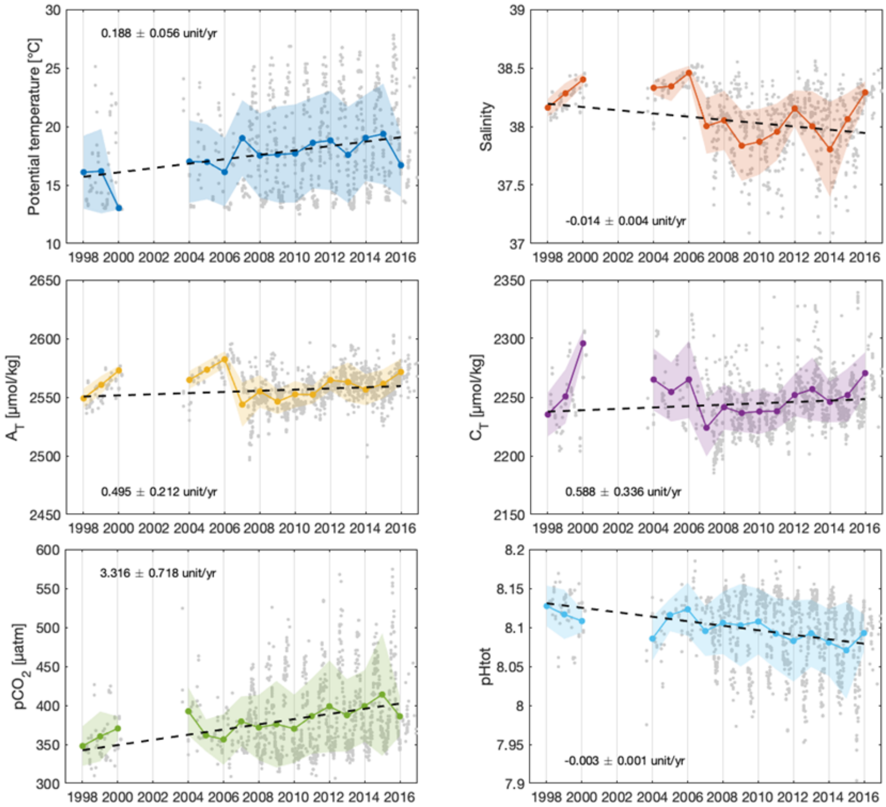

Figure 4.6. *Despite the data scatter, long-term trends of potential T, S, A_T, C_T, pCO_2 and pH (total scale) are visible in the surface waters (0–20 m) from 1998 to 2016. The colored dots represent the mean values and the colored area the standard deviation of the respective values. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

The pCO_2 trend derived here from monthly discrete measurements of C_T and A_T is consistent with the trend estimated by Merlivat *et al*. [MER 18] using the pCO_2 sensor deployed during two different periods (1995–1997 and 2013–2015). Based on CARIOCA hourly measurements, an annual increase of C_T, +1.40 ± 0.15 µmol kg^{-1} yr^{-1}, increase of pCO_2, 2.30 ± 0.23 µatm yr^{-1} and a decrease of pH −0.0022 ± 0.0002 are computed. In addition, the fugacity of CO_2 (fCO_2) from the surface water measured during all cruises in the Ligurian Sea [BAK 16] provides a fCO_2 trend of +3.73 ± 0.05 µatm yr^{-1} for 1998–2016 (Figure 4.7), although we note that no data were available in SOCAT during 2001–2009 (in surface pCO_2 and fCO_2 are similar).

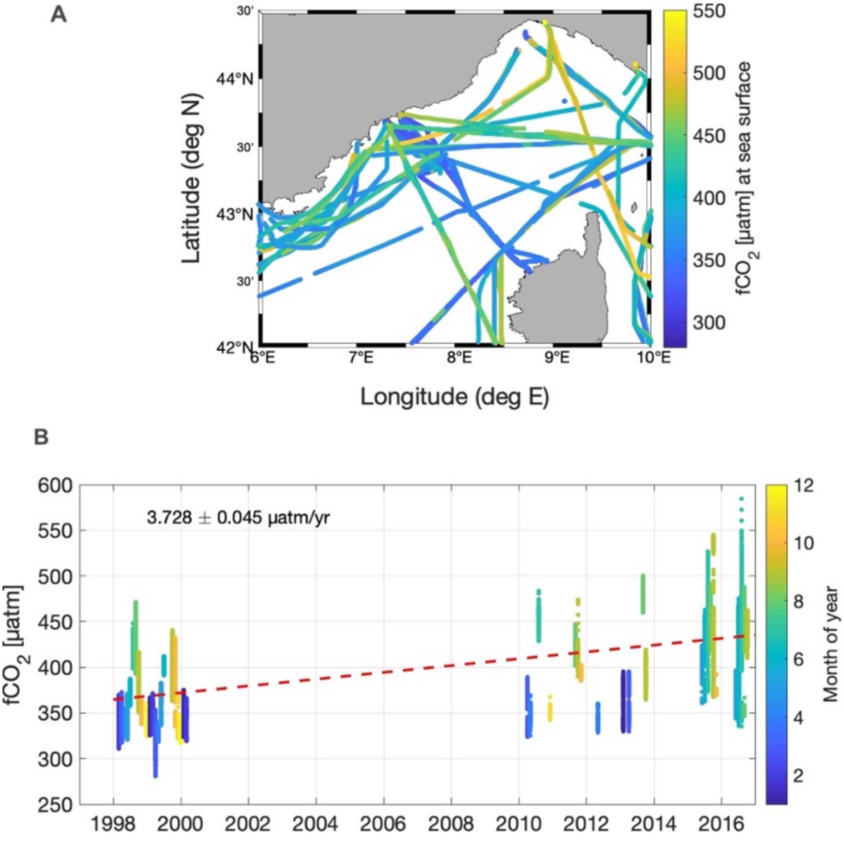

Figure 4.7. *A) Location of fCO_2 observations in the Ligurian Sea from the SOCAT-v6 database [BAK 16]. Color code is fCO_2 at sea surface (µatm). B) SOCAT fCO_2 data for the period 1998–2016 in the Ligurian Sea (color code is the month). The red line is the trend of 3.73 ± 0.05 µatm yr^{-1} derived from all seasons. Despite the lack of data from 2001 to 2009, the averaged trend seems to be significant when the series of the different seasons are merged. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

The estimated increase in pCO_2 of +2.3 to +3 µatm yr^{-1} are higher than that in the atmosphere (about 2 ppm yr^{-1} as recorded at station Lampedusa; [DLU 18]), suggesting that the CO_2 sink is decreasing. Most of this signal is due to both C_T increase and warming observed in recent years (Figure 4.6), but opposed to the unexpected positive trend in A_T.

Using surface pCO_2 observations available in the Ligurian Sea region (42.5°N–44.5°N, 6°E–10°E) in SOCAT version 6 [BAK 16] and assuming an A_T/S relationship based on the Ligurian Sea dataset (Figure 4.4), we calculate a pH trend of − 0.0026 units yr^{-1} for the period 1998–2016, close to the CARIOCA sensor result (−0.0022 ± 0.0002) and close to the pH trend (−0.003 ± 0.001 units yr^{-1}) evaluated from C_T and A_T (Figure 4.6). The difference in pH trend between these three estimates may be linked to the changes in A_T that are disregarded when A_T is derived from S. Therefore, the pH trend also depends on A_T in this region, although the origin of the observed positive A_T trend is not yet explained [KAP 17]. However, all results based on different observations indicate a clear decrease in pH in the Ligurian Sea in the last two decades. These results reinforce the acidification issue already reported in the Mediterranean Sea [WMO 14].

4.4.2. *Interior trends*

Recent changes observed in the characteristics of LIW and WMDW becoming warmer and saltier in the northwestern basin modified the biogeochemical distributions in the water column in the Ligurian Sea [COP 18, PAS 15] and probably the trends in carbonate variables.

In the layer 300–800 m, we used observations from DYFAMED, ANTARES, DEWEX and MOOSE-GE cruises. At this depth, no seasonal signal is observed (Figure 4.2). Total alkalinity and carbon show a positive trend with a more sustained increase for C_T and A_T than in the surface (respectively + 1.18 ± 0.09 and + 0.80 ± 0.08 µmol kg^{-1} yr^{-1}; Figure 4.8). pCO_2 shows an increase around 1.16 ± 0.18 µatm yr^{-1}, less important than in the surface, which results in a lower decrease in pH (−0.001 unit yr^{-1}). Although the C_T increase is significant with depth, the difference in pCO_2 and pH trends in the surface, and the deeper layer is likely to be linked to the warming up of surface waters.

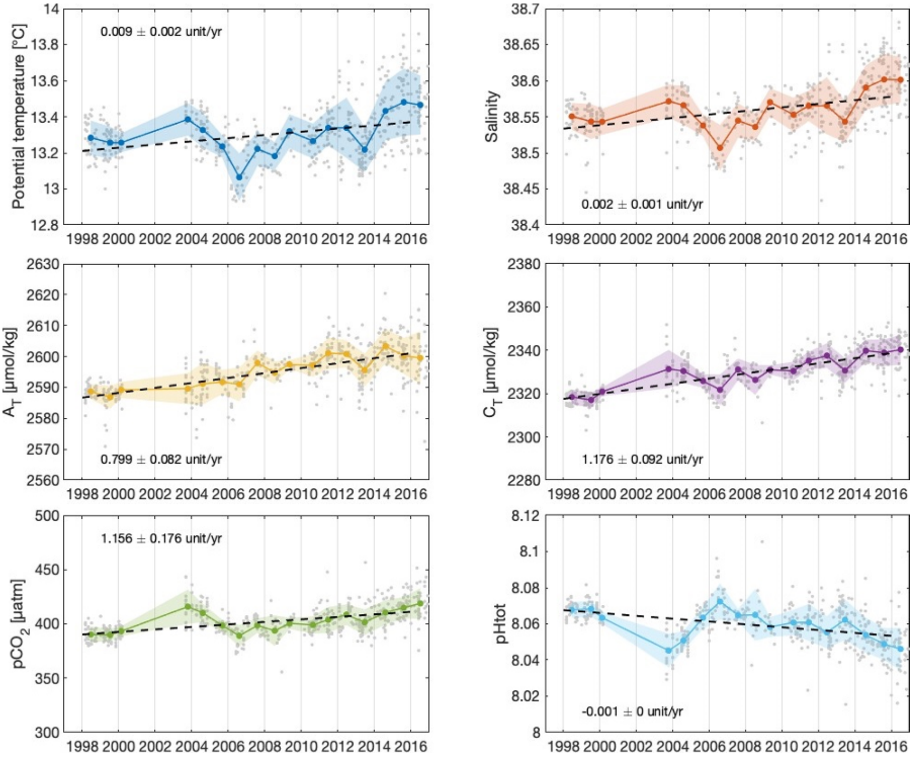

Figure 4.8. *Long-term trend in the intermediate waters (300–800 m) of potential T, S, A_T, C_T, pCO_2 and pH (total scale) from 1998 to 2016. The colored dots represent the mean values and the colored area the standard deviation of the respective values. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

In deep waters, below 2000 m, A_T, C_T, pCO_2 and pH (total scale) show the same trend as in the 300–800 m layer, with slightly higher values for pCO_2 and pH (1.27 ± 0.30 µatm yr^{-1} and −0.002 unit yr^{-1} respectively; Figure 4.9). The trends in deep waters have also been impacted by the 2005/2006 anomaly, where an abrupt vertical mixing in the Ligurian Sea led to warmer, more saline and more oxygenated newly-formed deep water that had invaded the western basin [MAR 10, SCH 08, SMI 08]. This rapid change is clearly visible on the potential T and S trend (Temperature and salinity − Figure 4.9) and has already been discussed in many papers [HOU 16, MAR 10, SCH 08, SMI 08, ZUN 12].

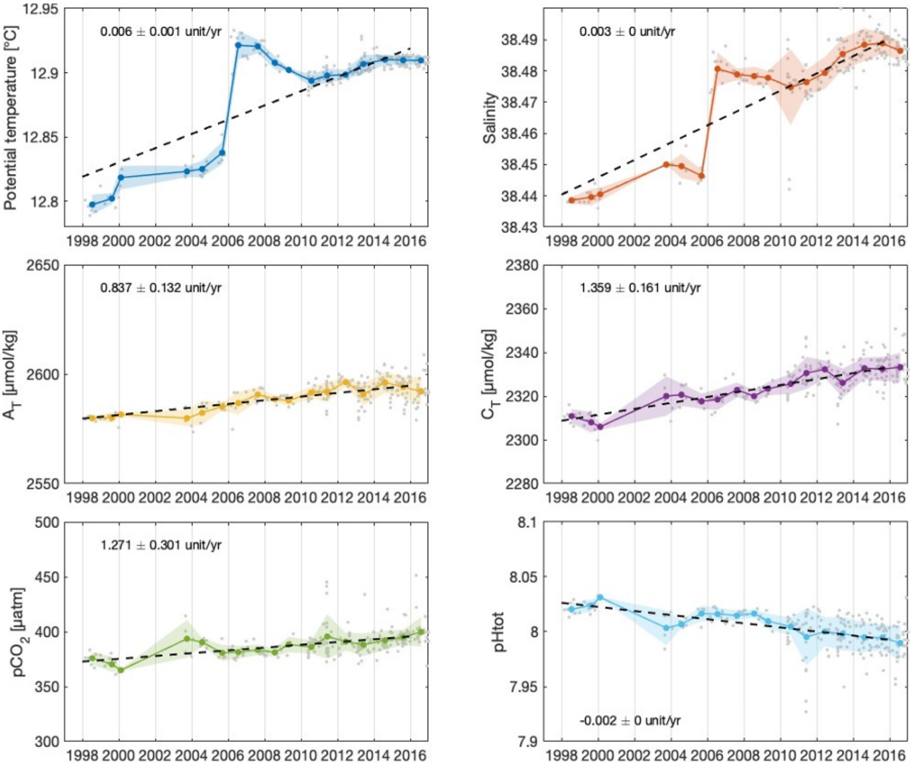

Figure 4.9. *Long-term trend in the deep waters (below 2000 m) of potential T, S, A_T, C_T, pCO_2 and pH (total scale) from 1998 to 2016. The colored dots represent the mean values and the colored area the standard deviation of the respective values. Note the anomaly observed in 2005/2006 only for T and S, discussed in the text. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

The abrupt pH increase observed in 2005–2006 in the layer 300–800 m (Figure 4.8) coincides with an increase in S, potential T, total carbon and alkalinity [TOU 09, TOU 11]. This event could be related to the modification of the main deep-water formation site in the eastern Mediterranean basin. Indeed, in the late 1980s to the early 1990s, nearly 20% of the eastern basin bottom waters were replaced by very dense waters initially formed in the Aegean Sea instead of the original deep-water formation site in the Adriatic Sea (see Chapter 3). This phenomenon, known as the Eastern Mediterranean Transient (EMT), has disrupted the distribution of the main water masses [ROE 07]. One of the consequences for the waters of the Ligurian Sea, is that an older water mass, and therefore poorer in oxygen (reinforcement of the oxygen minimum layer) and richer in anthropogenic carbon, has probably been introduced at intermediate depths.

Another hypothesis to explain this anomaly would be the absence and/or low intensity of convection processes for several years, which led to a warmer, saltier and more oxygen-depleted LIW. The outbreak of intense convection in 2005 in the Gulf of Lion and in 2006 in the Ligurian Sea, due to successive cold winters, led to a massive supply of warmer and saltier water from the surface to the bottom. In 2005, this would have occurred through a deep-water dispersion mechanism, following the very intense bottom reaching the convection event in the central Gulf of Lion (called Western Mediterranean Transient, WMT) and in 2006 by intense vertical mixing in the Ligurian Sea, which led to a very rapid increase of T, S and O_2 [COP 18].

4.5. Changes in the carbonate system in the Ligurian Sea in the Mediterranean Sea and global contexts

A model simulation of anthropogenic carbon storage and acidification indicates that the surface water acidification rate in the Mediterranean Sea has increased since 1800 (estimation of delta pH of −0.08 unit; [PAL 15]). In the Ligurian Sea, *in situ* dataset from 1998 to 2016 presented here provides the same delta pH range (−0.08 to −0.05 units in the surface and deep waters respectively). For this period, Merlivat *et al.* [MER 18] compute a change of −0.040 ± 0.004 for surface waters. From basic marine carbonate chemistry, it is well-known that, as atmospheric CO_2 increases, surface-ocean pCO_2 increases, reducing seawater pH. Deep waters of the Mediterranean Sea exhibit changes in pH, which are higher than typical global ocean deep waters due to faster ventilation times. Furthermore, typical Mediterranean Sea anomalies, such as EMT and WMT signals, have severely disrupted the distribution of water masses. As the Mediterranean Sea is warmer and more alkaline than other offshore areas, this could potentially represent a larger and faster decrease in pH and then higher acidification impacts.

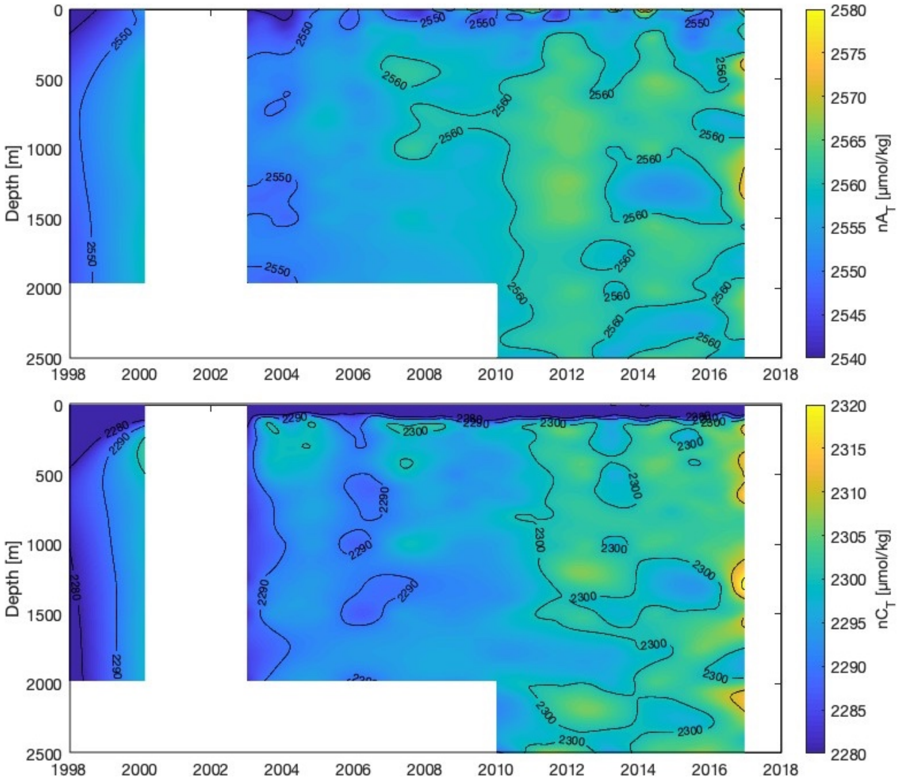

Figure 4.10. *Time series of normalized A_T (nA_T) and normalized C_T (nC_T) in the Ligurian Sea from 1998 to 2016 (all data shown in Figure 4.1 are merged). The increase of these parameters visible after 2010 from 300 to 2500 m could result from the anthropogenic impact and water mass characteristic modifications. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

To observe the change in the water column, we estimate a normalized A_T (nA_T) and C_T (nC_T) adapted for the Mediterranean Sea ($nX = X * 38/S$, where X corresponds to C_T and A_T values). In Figure 4.10, variability of nA_T and nC_T shows an accumulation of CO_2 and A_T after 2010 from 300 to 2,500 m. This could be a signal of the anthropogenic impact, and also due to a modification of intermediate and deep-water mass characteristics. After the WMT, local intense deep convection occurred in the Ligurian Sea in 2010, 2012 and 2013. These events were short and accompanied by a new deep-water spreading recently formed in the Gulf of Lion [COP 18]. They produced a large input of salinity and heat fluxes from the surface to deep waters. It is possible that this supply induces a large transport of CO_2

from the surface to the intermediate and deep waters in addition to the rapid increase of salinity that stratified the deep-water column.

These observations highlight that the Ligurian Sea is a key region to observe changes in carbonate chemistry, and it highlights the importance of maintaining long-term time series of the oceanic carbonate system in relation to their hydrological and biogeochemical properties. This is particularly true in a very dynamic oceanic region such as the Mediterranean Sea, in terms of water mass changes and the ventilation process.

4.6. Conclusion

This synthesis shows the consistency of different analyses carried out through different oceanographic cruises and time-series stations located in the Ligurian Sea that now help to detect and understand long-term trends of A_T, C_T, pCO_2 and pH in this region. It is also a unique database to validate biogeochemical simulations to better understand the future role of Mediterranean Sea for both CO_2 uptake and acidification issues in the context of global changes. The observations conducted since 1995 in the Ligurian Sea show a clear increase in pCO_2 and associated decrease in pH over 18 years. This is observed in the surface from direct pCO_2 measurements, as well as in the water column (from A_T, C_T observations). The seasonality of the carbonates system is now well-observed in both coastal and open-ocean waters, and long-term trends start to be detected. However, the synthesis presented here also highlights significant interannual variability as observed in 2004–2007 at depth. In this context, autonomous sensors for pCO_2, pH, oxygen and nutrients – not only in the surface but also in the water column (e.g. moorings, Argo floats), and included in the integrated observing system should improve our vision of ocean carbon variables that become mandatory to constrain ocean acidification projections and the role of the Mediterranean Sea in the fate of the carbon pump and marine ecosystems.

4.7. Acknowledgments

We thank Liliane Merlivat, Catherine Goyet, Franck Touratier, Laure Mousseau, Roberto Bozzano, Sara Pensieri and Thibaut Wagener for their participation to this chapter. Service SNAPO-CO2, supported by CNRS/INSU and OSU Ecce Terra, is acknowledged for analyzing C_T and A_T

at LOCEAN since 2004. Thanks are due to the Service d'Observation Rade de Villefranche (SO-Rade) of the Observatoire Océanologique and the Service d'Observation en Milieu Littoral (SOMLIT/CNRS-INSU) for their kind permission to use the Point B data. The authors are also grateful to the MOOSE observation national network (funded by CNRS-INSU and Research Infrastructure ILICO) which sustain the DYFAMED and ANTARES time series and ship-based hydrographic sections in the northwestern Mediterranean Sea (MOOSE-GE). The Surface Ocean CO2 Atlas (SOCAT) is an international effort, endorsed by the International Ocean Carbon Coordination Project (IOCCP), the Surface Ocean Lower Atmosphere Study (SOLAS) and the Integrated Marine Biosphere Research (IMBeR) program, to deliver a uniformly quality-controlled surface ocean CO2 database. The many researchers and funding agencies responsible for the collection of data and quality control are thanked for their contributions to SOCAT.

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5

Emission Sources, Fluxes and Spatiotemporal Distribution of Nutritive Resources

5.1. Introduction

One of the most critical issues in oceanographic and climatic sciences is phytoplankton dynamics: on this depend both the sequestration of excess atmospheric CO_2 through photosynthesis and the proper functioning of marine food systems through plankton productivity. Biological productivity itself depends, to a very large extent, on the availability of nutrients. Hence, there is the need to fully understand the spatiotemporal variability of nutrient concentrations in the surface ocean, together with the physical, chemical and biological parameters that constrain this variability.

The Mediterranean Sea (Med) is considered one of the least productive seas in the world [BET 98]. Nutrient concentrations exhibit a decreasing gradient from west to east [MOU 12] that is commonly viewed as a consequence of the peculiar, so-called "anti-estuarine" Med circulation described in the Chapter 3: low amounts of nutrients enter the Med in surface via the Gibraltar Strait, much of which is consumed along the way to the eastern basin, and then exported to deep layers. On the way back to Gibraltar, the remaining nutrients are mostly exported to the Atlantic Ocean, which results in a significant loss of nutritive resources, presumably

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Chapter written by Christophe MIGON, Orens PASQUERON DE FOMMERVAULT and Fayçal KESSOURI.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

compensated by external inputs [BET 98]. Owing to the short residence time of its deep waters, its reduced size and intense, evolving fluxes of matter from its densely populated shores, the Med is very sensitive and reactive to climatic and environmental changes. Therefore, it is often considered a model of the Global Ocean, where many processes are exacerbated (e.g. [BET 99]). Indeed, paleoclimatic studies have already shown that the physical dynamics of the Med can drastically change as a result of climate change affecting intense exchanges with the atmosphere, and this can have major biogeochemical consequences as a result of disruptions in the dense water formation process that affects the availability of nutrients [BET 93].

What is our current knowledge on nutrients in the Med? Climatic and meteorological changes have most likely affected the physical ocean pump, and the supply of nutrients through external inputs has undergone significant changes over the past two decades. Together with the development in several riparian countries of environmental study agencies likely to provide regional information, a number of programs have generated much new data in recent years. In addition, data acquisition has evolved considerably. In this context, the time series acquired in the Ligurian Sea (LS) at the DYFAMED sampling station constitute an exceptional source of information that may be generalized to a certain extent to the Global Ocean. In particular, nutrient concentrations have been monitored for approximately 30 years.

5.2. What is required for biological development?

According to the photosynthesis reaction [5.1], marine phytoplankton development requires light and nutrients:

$$106CO_2 + 16HNO_3 + H_3PO_4 + 122H_2O \overset{h\nu}{\Leftrightarrow} (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138O_2 \qquad [5.1]$$

Owing to weak cloud coverage in the whole Med, light is never, or exceptionally delineated in time and space, a limiting factor [LAV 13].

Nutrients can be divided into two groups, macronutrients, i.e. nitrogen (N), phosphorus (P) and silicon (Si), and micronutrients, which include a variety of bioactive metals, generally occurring at trace concentrations (e.g. iron, copper, nickel). Organic ligands, mostly produced by marine plankton, determine to a large extent the trace metal speciation by stabilizing some redox forms of metals that are (or are not) necessary to phytoplankton. However, owing to the reduced dimensions of the Mediterranean basin, and to intense and varying land-based emission sources of metals, the control of plankton growth by metals is very unlikely. Heimbürger *et al.* [HEI 11] showed that most bioactive metals in the LS exhibit surface-enriched dissolved concentration profiles under stratified oligotrophic conditions (May–November). For example, this applies to cobalt, iron or zinc. Since these metals are found in excess in surface waters, their abundance exceeds the ability of plankton to assimilate them and remove them from surface waters. In other words, they cannot control phytoplankton growth. Some other metals such as nickel exhibit surface-depleted dissolved concentration profiles, and some others (e.g. copper) are found at the boundary between surface-enriched and surface-depleted distribution profiles. However, the surface-depleted pattern of given metal does not mean this metal controls primary production (PP; Box 5.1), and, actually, metals are probably not the limiting parameter of PP, as a general rule in the western Med. Indeed, the whole Med is a Low-Nutrient Low-Chlorophyll (LNLC) province, contrary to High-Nutrient Low-Chlorophyll (HNLC) oceanic regions that are much more distant from land-based emission sources (e.g. the Tropical Pacific Ocean), and where trace metals often control PP, while (macro)nutrients are not fully consumed.

Primary production (PP) is the amount of organic matter produced in the photic layer (gC m^{-3} d^{-1}, or gC m^{-2} d^{-1}, or gC m^{-3} yr^{-1}). Gross PP is the total amount of organic matter produced from inorganic compounds by autotrophic organisms via photosynthesis. Net PP (NPP) is the gross PP minus the loss of C by autotrophic respiration, which is the respiration of the primary producers themselves. Organic matter mineralized in the upper ocean by the activity of bacteria and zooplankton feeds “regenerated production” (RP) in a closed circuit. The RP is maintained by the nutrients directly recycled in the photic layer. Fecal pellets, molts, dead plankton, etc., i.e. particulate organic carbon (POC) and dissolved organic carbon (DOC) are exported from the surface to the deep ocean. They represent the exported production (EP). But almost all the EP is step by step re-oxidized in CO_2 and nutrients during its vertical transfer. The remaining fraction reflects the actual sequestration of atmospheric CO_2. At steady state, this downward vertical flux is balanced by an ascending vertical flux: the nutrients formed in the intermediate and deep ocean re-feed the surface ocean to close the loop by contributing to the PP. The PP resulting from the assimilation of deep nutrients brought to the surface is the new production (NP). While the RP corresponds to PP based on recycled nutrients and, therefore, does not yield any increase of plankton biomass, the NP corresponds to a new external input (i.e. from the atmosphere or land) of oxidized nutrients and yields an increase in biomass. The RP can be estimated by the assimilation of ammonium, which is the first step of the oxidation of organic N, thus the form that requires the least energy to be assimilated. In contrast, NPP can be estimated by the assimilation of nitrate and N_2. Ammonium is also brought to surface waters by non-marine external sources such as the atmospheric deposition, and theoretically yields an increase of biomass (and, thus, contributes to NPP). Nevertheless, these external loads are generally very low in the open Med, and the uptake of ammonium does provide a reliable estimation of the RP. Estimations of particulate NPP at the DYFAMED station (from 1993 to 1999) ranged between 100 and 300 mg C m^{-2} d^{-1} from August to January, and 1.8 g C m^{-2} d^{-1} in March/April, with annual NPP values between 86 and 232 g C m^{-2} yr^{-1} [MAR 02a].

The above refers to the production of POC. However, autotrophic organisms can excrete DOC, especially in conditions of low availability of nutrients. Although still poorly studied, dissolved PP might be of crucial importance in a context of global change: the more the ecosystem evolves towards P-limitation, the greater is phytoplanktonic exudation rate, i.e. greater is the contribution of dissolved PP to total PP [MOR 02, OBE 95]. This excretion seems to occur via a passive diffusion process, although López-Sandoval *et al.* [LOP 11] suggested that the DOC thus released might be a mechanism to compensate for the imbalance between strong solar radiation and nutrient depletion (as excreted DOM sustains bacterial consumption). To our knowledge, no quantitative study of dissolved PP has been carried out in the Ligurian area. However, estimations of dissolved PP along an east-to-west longitudinal transect in the Med ranged between 50 and 130 mg C m^{-2} d^{-1} during the oligotrophic period, with an increasing trend in production rates (dissolved and particulate) from East to West [LOP 11]. For comparative purposes, particulate PP was also measured during this transect, and it ranged between 95 and 210 mg C m^{-2} d^{-1}. The ratio of dissolved PP to particulate PP was 37%.

Ultimately, it should be pointed out that, until recently, the assimilation of dissolved CO_2 was viewed as the almost exclusive result of the photosynthetic activity of phytoplankton, which, in other words, means that the activity of non-autotrophic organisms (e.g. heterotrophs or chemiotrophs) is considered negligible. However, recent studies carried out in non-Mediterranean provinces (e.g. [BAL 19]) suggest that the fixation of CO_2 by non-autotrophic organisms ("dark CO_2 fixation") may be quite significant, peaking up to 22% of total PP [BAL 19]. Therefore, this assimilation process should be taken into account in global oceanic PP estimates, as it releases significant amounts of newly synthetized, bioavailable carbon.

Box 5.1. *Primary production*

In addition to macronutrients, many species of phytoplankton (from picophytoplankton to diatoms) also need B-vitamins (mostly vitamin B_{12}, an organometallic compound containing cobalt). Field studies and incubation experiments have both shown that the availability of B-vitamins is likely to enhance phytoplankton biomass [GOB 07, KOC 11, SAN 06], suggesting an actual role of vitamin B_{12} in PP. In coastal northwestern Med waters, Fiala has observed diatom blooms concomitantly to high concentrations of vitamin B_{12} [FIA 82]. However, the same author points out that the presence of the vitamin together with algae perhaps resulted from its excretion by algae themselves. Furthermore, Berland *et al.* [BER 78] previously stated from measurements on northwestern coastal waters that vitamins probably play a minor role in algal production. Regardless of the real importance of this vitamin in phytoplankton growth, Bonnet *et al.* [BON 13] showed that the concentrations of vitamin B_{12} in the western Med were significantly higher than those measured in the Pacific and Atlantic oceans, making unlikely any control of algal growth. Therefore, the following will only deal with macronutrients, hereinafter simply named "nutrients", of which availability in time and space supposedly determines plankton dynamics.

The chemical forms of inorganic N usually found in seawater are ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-). Ammonium is the most reduced form, and nitrate is the most oxidized, thus the most abundant. In seawater, N is absorbed and reduced by algae according to the reaction:

$$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+ \rightarrow N_{org} \qquad [5.2]$$

Hence the rarity in seawater of ammonium, the easiest form to fix in terms of energy. Some organic forms of N occur, but their potential assimilation by marine microorganisms is still poorly known, except, maybe, urea, which is known as a potential alternative N source for micro-organisms (e.g. [LOU 09]).

The chemical form of inorganic P is orthophosphate (PO_4^{3-}). A variety of organic forms of P exist in seawater, among which some spontaneously hydrolyze in PO_4^{3-}, some can be hydrolyzed under the effect of solar radiance, and some cannot be hydrolyzed. The bioavailability of organic P is a complex question (see section 5.6.3).

Silicon occurs in seawater as silicic acid ($Si(OH)_4$), which releases orthosilicate ion SiO_4^{4-}. Some marine organisms (e.g. diatoms, silicoflagellates, radiolarians) extract Si from ambient seawater to synthesize hard parts in biogenic opal (i.e. amorphous hydrated silica $SiO_2.nH_2O$). It is noteworthy that the other phytoplanktonic species do not need Si.

5.3. Sources of nutrients

5.3.1. *External sources*

5.3.1.1. *Riverine input*

As already presented in Chapter 3, the LS is surrounded by the permanent geostrophic Ligurian frontal jet flow that results from the cyclonic circulation of the Northern Current [MIL 99]. This results in a front (approximately 30 km width, >250 m depth) that generally shelters the central LS from lateral riverine loads by a strong horizontal density gradient [NIE 08], as confirmed by acoustic Doppler current profiler (ADCP) measurements [AND 00]. In addition, riverine inputs are poor in the LS. Therefore, despite episodic, infrequent intrusions of waters from the Northern Current in winter [MIL 99], the central LS is believed minimally affected by the riverine discharge, as well as any other lateral inputs. In addition, the behavior of nutrients brought by rivers (precipitation in the mixing zone, or conservation, or dissolution) is still largely unknown, and it may significantly vary from a river to another, as well as from low water to swelling. However, several works report the trapping of particulate nutrients in estuaries at increasing salinity and pH by particle flocculation, aggregation of dissolved/colloidal complexes with iron, and/or adsorption onto sedimenting inorganic particles (e.g. [SLA 11]). This particularly holds true for the case of PO_4^{3-} ions, owing to their capacity to adsorb onto suspended particles, notably clay particles, iron and aluminum hydroxides [KRO 91]. This adsorption capacity increases at pH values ranging between 5 and 8 [GOL 95a] and at seawater concentrations of Ca^{2+} and Mg^{2+} [GOL 95b]. In addition to the burial of P in shelf sediments, microbial denitrification (see Box 5.2) also leads to the removal of bioavailable N [ASM 17].

Denitrification: in anoxic waters, NO_3^- may act as an oxidizing agent with organic matter:

$$5\ CH_2O + 4\ NO_3^- + 4\ H^+ \rightarrow 5\ CO_2 + 2\ N_2 + 7\ H_2O$$

(*CH_2O is a mean hydrocarbonated organic substrate*)

This is denitrification, which occurs by steps:

$$NO_3^- \rightarrow NO_2^- \rightarrow N_2O \rightarrow N_2$$

Denitrification is the inverse reaction of diazotrophy (see section 5.3.1.3).

Box 5.2. *Denitrification*

Data on the magnitude of the denitrification process and on P burial in the western Med are very scarce. Nevertheless, it is probable that, among the external sources of nutrients to offshore waters, the riverine input is of minor-to-negligible importance in the LS. Therefore, it is likely that the external forcing that affects the central LS is essentially the atmospheric deposition.

5.3.1.2. *Submarine groundwater discharge*

Submarine groundwater discharge as a source of bioavailable nutrients to coastal waters is still largely ignored. This mixture of continental fresh water and seawater is a potential source of various chemicals, including nutrients. Although studies on this emission source are very scarce for the Med, the recent study of Rodellas *et al.* [ROD 15] allowed a better evaluation of the possible impact of submarine groundwater discharge: it represents an annual flux of 30–500 10^9 m^3 for the whole Med, i.e. a water discharge more significant than the total riverine input. The same authors have observed that submarine groundwater exhibits very high dissolved inorganic nitrogen (DIN) to dissolved inorganic phosphorus (DIP) ratios (between 80:1 and 430:1), which potentially impacts the relative abundances of nutrients (see section 5.6.2). These ratios might result from the more rapid removal of DIN from groundwater [SLO 04]. However, similarly to the riverine input, the actual impact of submarine groundwater-derived nutrients is questionable, especially since biological activity close to the discharge areas is likely to consume/remove nutrients. Regardless of the actual impact of submarine groundwater on offshore Ligurian waters, there is a strong need to better explore this almost unknown source of nutrients.

5.3.1.3. *Atmospheric deposition*

A peculiarity of the whole Med is its reduced dimensions (2.51 10^6 km^2, i.e. less than 1% of the world oceanic surface). Open waters are never further than 300 km off the coasts. The impact of atmospheric deposition is thus believed to be very significant. This suggests a strong impact of continental inputs on pelagic zones. Therefore, the even smaller LS (surface area: 5.3 10^4 km^2) is only affected by medium-range transport of atmospheric matter, suggesting that the chemical composition of its atmospheric aerosol is relatively homogeneous, as shown for the case of trace metals by Sandroni and Migon [SAN 97]. In addition, Med shores are densely populated, and subject to important touristic, industrial and agricultural activities. As a result, land-based and coastal emission sources are intense and varied. The northern shores are basically characterized by anthropogenic influences, while the southern ones globally exhibit natural mineral features. Finally, the Med meteorology is characterized by a succession of dry and wet seasons, including extreme events (occurrence of extreme rain events, Saharan dust storms), which has a great impact on the physico-chemical fate of atmospheric matter in the water column (see section 5.3.1.3.2).

The supposed importance of atmospheric inputs in the Med has led to many studies, both theoretical and experimental, on the possible fertilization of surface waters under oligotrophic conditions by atmospheric inputs. Many of them were dedicated to the LS (e.g. [BAR 05, MIG 89, MIG 99, RID 02]). However, the reality of atmospherically driven fertilization of the surface ocean is sometimes a subject of debate. On the basis of satellite observations, Volpe *et al.* [VOL 09] suggested that dust fertilization does not play a significant role in the sustainment of phytoplankton dynamics in the Med.

5.3.1.3.1. Emission sources

a) Continental lithogenic input/Saharan dust input

Owing to the direction of Earth's rotation, trade winds blow from the east, and Saharan dust loads usually move above the Atlantic Ocean, from Sahara to the American continent. However, the Med is relatively frequently affected by the deposition of Saharan mineral dust. The LS is often described as overall affected by a homogeneous European urban-dominated background material upon which episodic Saharan dust events are superimposed (e.g. [CHE 97, GUE 99]). Such pulsed events generally occur in spring and summer [MOU 97], although significant episodes may be observed at any other period of the year (e.g. an exceptional event occurred in the LS in February 2004 [BON 06]). Saharan dust is rich in iron, Si, N and P, although P is mostly found under the form of apatite, or hydroxyapatite, which is very insoluble. Interestingly, Ndour *et al.* [NDO 08] showed that, in the presence of light and titanium oxide TiO_2, mineral dust can yield a decrease of the nitrogen dioxide (NO_2) concentration in the troposphere and provide nitrate, according to the reaction:

$$NO_2 \xrightarrow[TiO_2]{h\nu} NO_{3^-} + HNO_2 \qquad [5.3]$$

While some authors predict an increase of the frequency of Saharan events in northwestern Med regions (e.g. [ROG 04]), Heimbürger *et al.* [HEI 10] suggested from monitoring between 1986 and 2008 that the occurrence of extreme events (e.g. in 2004, when a single event represented up to 99% of the annual iron deposition [BON 06]) should be ascribed to the natural variability of pulsed Saharan inputs.

b) Anthropogenic input

The atmosphere is a source of many N species that result from human activities. For example, nitric acid (HNO_3) is a significant component of rain acidity. Ammonia (NH_3), nitric oxide (NO) and nitrous oxide (N_2O) are emitted or formed by various processes in the atmosphere from atmospheric N_2. In addition to their mere deposition onto sea surface, these gaseous species can also generate particulate N, via gas-particle reactions. For example, HNO_3 may either deposit onto sea surface or generate ammonium nitrate NH_4NO_3:

$$NH_3\ (g) + HNO_3\ (g) \rightarrow NH_4NO_3\ (s) \qquad [5.4]$$

There are many sources of anthropogenic P. Among them, urban incinerators might be significant sources of P, in particular when they retrieve refuse from waste plants [MIG 01]. There are many species of non-reactive P, including polyphosphates of anthropogenic origin detergent powders – this source being in steep decline due to antipollution policies –, fertilizing agents, wastewaters, etc. This is very important because these compounds are likely to hydrolyze (see section 5.6.3). Hydrolysis leads to the release of reactive PO_4^{3-}, usable for organisms [KAR 97]. Time series at the ALOHA station, in the north Pacific (22°75'N, 158°W), have shown that the pool [reactive P + non-reactive P potentially available for microorganisms] was higher by a factor of 1.4–2.8 than the pool of dissolved reactive P [BJO 03]; Suzumura and Ingall [SUZ 04] showed that the dissolved organic fraction can represent up to 70–98% of total P in the oligotrophic surface waters of the Pacific Ocean. The organic fraction of nutrients basically increases with their anthropogenic character [COR 03]. Therefore, the occurrence of non-reactive forms of P and, to a lesser extent, N, is very important insofar as the anthropogenic pressure is currently increasing, and external inputs of nutrients, in particular atmospheric inputs, may carry significant loads of organic N and P derived from human activities.

Silicon has virtually no anthropogenic source.

In the LS, anthropogenic inputs generally originate from the north and the northeast, and prevail in winter (mostly in March, in agreement with advective transport of polluted air masses; [DUN 04]), and in September–October, when the autumnal equinox points to the moving of the polar front to the southward, yielding the arrival of polluted air masses from northern and northeastern regions of Europe [BAR 04]. Bartoli *et al.* [BAR 05] studied rain events at the coastal time-series sampling station of Cap Ferrat (southeastern France) from 1986 to 2003. They observed that the highest depositional fluxes of dissolved inorganic nutrients were associated with anthropogenic wet events.

c) Other sources

Volcanic emissions can be mentioned, but the LS is practically unaffected by the volcanic plumes emitted by Mount Etna, the closest active volcano [MAR 84]. Fires are also a significant source of nutrient, particularly P. In addition to the release of P from biomass burning, fires lay soils bare, and thus favor the remobilization of mineral phosphate [SUN 10]. Richon *et al.* [RIC 18] suggested from daily modeled fields of phosphate deposition that biomass combustion may bring more phosphate to the Med than mineral dust deposition.

The debate on uncertainties on the estimation of atmospheric wet and dry depositions is not closed (e.g. [IM 13]). However, the most important gap in our present knowledge on marine nutritive resources is probably the estimation of gaseous depositional fluxes. Data are very scarce overall, and maybe non-existent for the northwestern Med.

5.3.1.3.2. Bioavailability of atmospheric matter

The physico-chemical form of elements strongly determines their behavior and fate in the water column. The phase in which a given element enters the surface layer (i.e. dissolved vs. particular) determines its involvement in marine biogeochemical cycles. Particular phases can be partially assimilated, e.g. via enzymatic processes or via zooplanktonic grazing [MOO 84]. Nevertheless, it is commonly admitted that the solubility of atmospheric matter is a very acceptable proxy for its bioavailability. The dissolution of atmospherically transported elements in seawater is mainly driven by the nature of their source: mineral material is generally characterized by high loads of particles mainly composed of poorly soluble matter (e.g. Al, Si, Fe, carbonates, apatite) exhibiting a regular pattern within three-dimensional crystalline networks of which dissolution is complex and strongly driven by low pH values (for the case of their incorporation in rainwater). On the contrary, anthropogenic material is generally composed of low loads of non-silicated minerals (sulfates, nitrates, soots and condensed organic matter), limestones or evaporites, which exhibit an amorphous structure, and which are, therefore, very soluble whatever the pH of rain [SED 07]. In addition, there is a correlation between the origin of aerosols and their size. Crustal particles are generally significantly coarser than anthropogenic particles. Size itself has an influence on solubility because it determines the exchange surface with the aqueous phase, and it has been shown that the insoluble fraction increases with the size of particles. There is a negative correlation between pH and solubility. Interestingly, the relative alkalinity of Saharan dust inputs (rainwater: pH ranging between 5.5 and 7; Box 5.3) yields the “alkalinization” of anthropogenic material in the atmosphere, which is crucial for their bioavailability. Regarding nutrients, this effect yields a less good solubility of atmospheric material (which is believed more or less counterbalanced by the amount of nutrients brought by a Saharan event). Light also has an impact on the solubility of atmospheric loads [HAN 04]. Photochemistry, pH variation and physical settling of aerosol that reduces the average size of the residual aerosol and makes it potentially more vulnerable to the other chemical processes all contribute to the modification of nutrient solubility from dust.

The neutral value of pH (7 from chemical viewpoint) is 5.6 for a “natural rainwater”, which corresponds to the equilibrium of atmospheric CO_2 dissolved in pure water.

Neutrality corresponds to the equilibrium of pure water with CO_2:

$$CO_{2(g)} = CO_{2(diss)}$$

$$H_2O + CO_{2(diss)} = HCO_3^- + H^+$$

The sum of the two above reactions gives

$$H_2O + CO_{2(g)} = HCO_3^- + H^+$$

This results in a natural pH equal to 5.6.

Box 5.3. *Equilibria of pH in the atmosphere*

5.3.1.4. *Diazotrophy*

Earth’s atmosphere is composed of approximately 75% N_2 in mass, apart from water vapor. This inexhaustible reservoir of N is *a priori* inaccessible to marine micro-organisms, considering the very high stability of the molecule N_2. However, some organisms (prokaryotic microbes called diazotrophs) are capable of fixing N_2 by enzymatic means, according to the equation [5.5]:

$$2\ N_2 + 4\ H^+ + 3\ CH_2O + 3\ H_2O \rightarrow 4\ NH_4^+ + 3\ CO_2 \qquad [5.5]$$

This biological fixation of atmospheric molecular N (diazotrophy) depends on the availability of molybdenum, iron and P. The roles of P and iron in the limitation of N_2 fixation has been evidenced in some oceanic areas (e.g. [KAR 02]). However, in the LS, no relationship has been found up to now between the availability of these elements and the occurrence of diazotrophy [SAN 07].

The nature of diazotrophs is very diverse: large cyanobacteria (>10 µm) such as *Trichodesmium*, small cyanobacteria (<10 µm) such as *Crocosphaera*, free picodiazotrophs, or cyanobacterial symbionts of dinoflagellates or diatoms [VIL 91].

In the Med, nutrient budget and isotope fractionation studies (e.g. [BET 86, SAC 99]) have suggested a relatively high contribution of diazotrophy to NP. However, field measurements revealed significantly lower N_2 fixation rates (typically < 0.5 nmol N L^{-1} d^{-1}; e.g. [BON 11, SAN 07]). Owing to the activity of heterotrophic bacteria that live on organic matter, diazotrophy might be significant in aphotic layers. Benavides *et al.* [BEN 16] observed across the whole Med N_2 fixation rates ranging from 0.13 to 0.43 nmol N L^{-1} d^{-1} at the deep chlorophyll maximum and from undetectable (<0.031 nmol N L^{-1} d^{-1}) to 0.07 nmol N L^{-1} d^{-1} in waters below. The fixation of N_2 was indeed correlated with the presence of labile organic matter. At the DYFAMED station, daily integrated values of N_2 fixation ranged from 22 to 100 µmol N m^{-2} d^{-1}, with a maximum of 245 µmol N m^{-2} d^{-1} in August [SAN 07]. The contribution of diazotrophy to NP ranged from 2 to 55%.

5.3.2. *Inputs from deep layers*

5.3.2.1. *Dense water formation*

This key process, extensively described in Chapter 3, occurs every year in the Gulf of Lion, and, to a lesser extent, in the LS [LAV 13]. Basically, surface water moderates the action of the troposphere, and only some marine regions, characterized by strong external forcings (chiefly, winter temperature and occurrence of dry and cold winds), can trigger the diving of surface waters, and, thus, generate the vertical mixing of the upper water column. This results in the upwelling of oxidized nutrients accumulated in dark deep layers to the photic layer. Until a certain extent, the deeper is the mixed layer depth (MLD), the more efficient is the refueling of surface waters by nutrients. However, Heimbürger *et al.* [HEI 13] suggested that a succession of ML deepenings, even though of lesser magnitude, is sometimes more efficient.

5.3.2.2. *Interannual variability of the deepening of the mixed layer*

The MLD appears to play a key role in controlling nutrient availability in surface, although a direct, quantitative relationship between MLD and nutrient concentrations is difficult to establish due to undersampling. For this reason, Heimbürger *et al.* [HEI 13] used the Symphonie model [HER 08, MAR 08] to compare the interannual variability of the MLD with that of the exported fluxes of particulate matter at the DYFAMED time-series station.

In agreement with the prominent role of external conditions, MLD exhibits a marked interannual variability, e.g. from < 100 m depth (1989, 2007) to > 2000 m depth (2003, 2005, 2006). Basically, strong winter convection events were observed in 1996, 1997, 2004, 2005 and 2007 [HEI 13]. Despite some uncertainties, notably the occurrence of marine currents likely to bias export flux measurements, or the occurrence of nutrient-rich atmospheric inputs likely to fertilize surface waters, the causal relationship between MLD and nutrient concentrations in surface (and, therefore, the magnitude of exported fluxes) clearly appears. In addition, Marty and Chiaverini [MAR 10] pointed out a slight increase of micro- and nanophytoplankton concentrations at DYFAMED, presumably related to concomitant increase of vertical mixing intensity, i.e. to climatic/meteorological variability. Such observations highlight the importance of the process of dense water formation for the productivity of the LS, and the need to monitor its evolution.

5.3.3. *Budgets*

In summary, nutrients may originate from allochthonous and/or autochthonous sources. The first are mainly abiotic (vertical mixing, lateral advection, diffusion, wind events that break the autumnal stratification, groundwater and riverine discharges, atmospheric input), whereas the second are mainly biotic (excretion and mineralization) sources. Diazotrophy may be viewed as abiotic and biotic. However, all nutrient sources do not have the same importance. Table 5.1 compares various fluxes of inorganic nutrients to the photic layer in the LS: atmospheric inputs, winter mixing, diffusion and diazotrophy for the case of N.

Data from the DYFAMED and Cap Ferrat time-series stations allow another comparison of the same nutrient sources in the LS. Atmospheric fluxes of bioavailable dissolved inorganic N (DIN), i.e. roughly, nitrate + ammonium, and dissolved inorganic P (DIP), i.e. PO_4^{3-}, were measured in 2010, 2011 and 2013 at Cap Ferrat. Mean wet and dry DIN fluxes were 35 and 19 mmol m^{-2} $year^{-1}$, respectively. Mean wet and dry DIP fluxes were 0.11 and 0.64 mmol m^{-2} yr^{-1}, respectively (Table 5.2; data from Pasqueron de Fommervault *et al.* [PAS 15b]).

	Atmospheric inputs	**Winter mixing (*)**	**Diazotrophy [SAN 07]**	**Diffusion [MOU 02]**
DIN [mmol $m^{-2} yr^{-1}$]	54.4 ± 16	$2.2\ 10^3 \pm 2.2\ 10^3$	28.1	6.2
DIP [mmol $m^{-2} yr^{-1}$]	0.75 ± 0.3	90.9 ± 97.6	–	0.3
NP_N [gC $m^{-2} yr^{-1}$]	4.3 ± 1.2	174 ± 174	2.2	0.5
NP_P [gC $m^{-2} yr^{-1}$]	0.9 ± 0.4	116 ± 124	–	0.4

Table 5.1. *Comparison of annual mean fluxes of DIN and DIP to the surface layer considering different sources (mixing, diffusion, atmospheric inputs and N_2 fixation). New production (NP) values are converted in gC by using the standard molar ratios (ΔP/ΔN/ΔC = 1/16/106). NP_N and NP_P mean total new productions triggered by N and P, respectively. (*) Computed from median profiles of nutrient concentrations [PAS 15a] and modeled MLD values (Symphonie model) at the DYFAMED site. The reported values indicate the mean nutrient supply to the photic layer and associated standard deviations (winters 2010/2011, 2011/2012 and 2012/2013)*

	DIN				**DIP**		
	AI	**WM**	**Diazo**	**Diff**	**AI**	**WM**	**Diff**
2010	1.4	97.5	0.9	0.2	0.6	99.2	0.2
2011	2.7	95.1	1.8	0.4	0.8	98.7	0.5
2013	23.8	65.0	9.1	2.1	9.2	87.5	3.3

Table 5.2. *Relative importance of annual fluxes of DIN and DIP to the surface layer considering different sources (mixing, diffusion, atmospheric inputs and N2 fixation), all expressed in percentage of the total nutrient input. AI = atmospheric inputs, WM = winter mixing, Diazo = diazotrophy, Diff = diffusion*

5.4. Seasonal patterns

Nutrient concentrations in the LS exhibit typical seasonal patterns in relation to physical and biological processes. Their temporal variability can be described according to a three-step scenario [MIG 02]:

– in the winter, when the temperature of the surface layer water falls below that of the deep waters, mixing is induced and inorganic (oxidized) nutrients accumulated in deep layers are brought to the photic layer. Due to this strong vertical motion, phytoplankton often cannot increase, but sunniness in the LS then allows phytoplankton blooms to occur as early as in late February;

– during the bloom period, biological activity is the driving force of the downward transfer of large biogenic particulate material;

– when the water column stratifies, the photic layer becomes nutrient-depleted, and the MLD is at its shallowest level. Nutrient concentrations are very low, or under the detection limits, in particular PO_4^{3-} (see section 5.6). Throughout the entire oligotrophic period (summer and autumn), PP is minimal, and export fluxes are minimal as well. From November, approximately, due to autumnal meteorological conditions, episodic break downs of the water column stratification may occur, yielding minor blooms. At the end of the year, the ML deepens again in response of external forcings, and the seasonal cycle starts again. The seasonal pattern of nutrient concentrations resulting from the above at DYFAMED is illustrated by the composite year shown in Figure 5.1 for the case of phosphate.

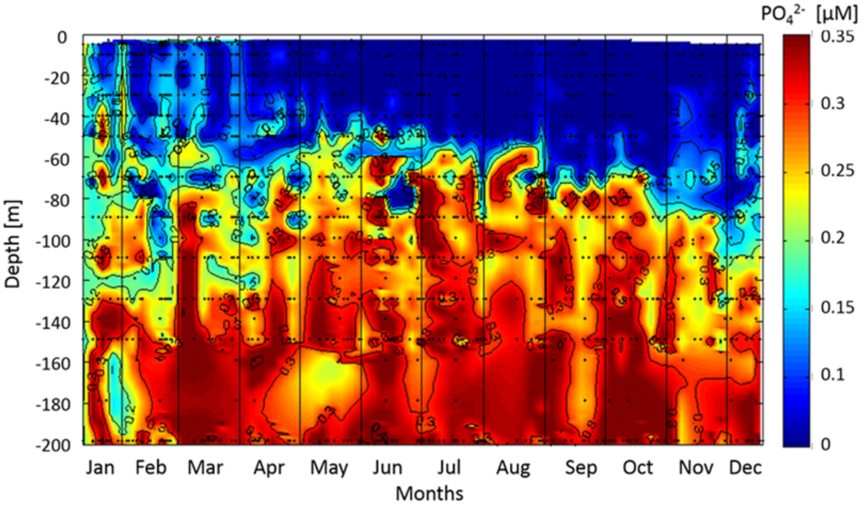

Figure 5.1. *Composite year for phosphate concentrations, drawn over a period of 20 years (1991–2011), within the 0–200 m layer at DYFAMED (after Pasqueron de Fommervault et al. [PAS 15a]). The heterogeneity of concentrations along the water column in January and February seems to contradict the homogenization that results from dense water formation, but it is just due to the fact that winter convection episodes do not occur at the time every year. The same explains the presence of some "holes", for example in June approximately −80 m. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

However, the variability of vertical export fluxes cannot be always ascribed to the availability of nutrients. At the end of the spring bloom, nutritive resources become scarce, and changes in phytoplankton populations (e.g. the clumping of diatoms) may significantly affect the intensity of the vertical export flux [WAN 89]. Indeed, high fluxes have been observed soon after the bloom at DYFAMED [STE 02], together with a change in dominant phytoplankton groups, as revealed by pigment data [MAR 02b]. Furthermore, the transition from phytoplankton bloom to zooplankton bloom, or changes in zooplankton communities, yields significant variations in downward fluxes, in particular with the occurrence of fecal pellets that act as efficient carriers for biogenic material [FOW 91] or the occurrence of, for example, salp blooms [MOR 88].

5.5. Spatial distribution

Using chlorophyll-a satellite observations, D'Ortenzio and Ribera d'Alcalà [DOR 09] proposed to characterize the Med in terms of "bioregions" (see Chapter 6). At the climatological scale, the LS is overall a "bloom" area, i.e. characterized by a spring bloom, typical of temperate seas. Lavigne *et al.* [LAV 13] demonstrated that the winter MLD controls this cycle in the LS by triggering important supplies of nutrients to the surface layer. Mayot *et al.* [MAY 16] reappraised the approach of the "bioregions" with the specific aim of accounting for interannual variability. Their analysis confirmed the recurrent blooming nature of the bioregion, and also highlighted the episodic occurrence of an "anomalous" trophic regime, characterized by a strong spring bloom. This regime temporally coincides with recorded events of exceptionally deep winter convection in the area. Exceptionally, an "intermittent" regime associated with a weak spring bloom was also observed. However, and despite a strong interannual variability in the magnitude of the peak, the NW Med, including the LS, is the only Med area where a spring bloom is recorded every year. At the beginning of winter, when the surface layer acquires a sufficient density, deep convection starts, and nutrients raise to the photic layer. Deep concentrations of nutrients can be found in surface, peaking up to 8 mmol N m^{-3} and 0.35 mmol P m^{-3}, with averages of 2.68 ± 0.97 µM (NO_3^-) and 0.12 ± 0.09 µM (PO_4^{3-}) in the 0–50 m surface layer in January at DYFAMED [PAS 15a]. At the end of the winter season, as soon as the deep vertical mixing is reduced, nutrients trapped inside the northern Gyre in the photic layer (about 0–60 m depth) are consumed very quickly by phytoplankton

[KES 18]. It is the so-called spring bloom. Transitions between different seasons may promote changes in stoichiometry (see section 5.6.2) driven by both physical and biological interactions. After the bloom, the nutriclines re-form. Nutriclines separate upper nutrient-depleted waters from lower nutrient-richer waters. They are characterized by steep vertical gradients of nutrient concentration, due to relatively high deep concentrations. In practice, they are determined by the first depth where the concentration exceeds a certain threshold, i.e. 1 mmol m^{-3} for N. In late summer, nutricline depths at DYFAMED have been located at 50 ± 8 m (nitracline) and 69 ± 12 m (phosphacline) [VAN 09]. The shallowness and steepness of nutriclines in the LS explain to a large extent why a spring bloom is recurrently observed there. Indeed, in this region, the MLD far exceeds the depths of nutriclines [PAS 15c]. A well-known feature of the Med is the west-to-east gradient of increasing deepening of nutriclines [PUJ 11]. As a result, nutriclines are relatively shallow in the LS, when compared to the rest of the Med. The discrepancy between nitra- and phosphacline is much lower than in the eastern Med, which agrees with the decreasing west-to-east gradient of nutritive resources. The relative locations of the two nutriclines, as well as their slopes, reflect the intensity of oligotrophy and the chemical limitation of PP (see section 5.6).

The cyclonic northern Gyre is surrounded by strong density fronts. At its boundaries, a very strong horizontal gradient can be observed in surface, and nutriclines show steep slopes at the density fronts. Fronts have strong vertical velocities along isopycnals, allowing more efficient injection of nutrients towards the surface layer. Several studies have shown strong diversities and increased biomass of plankton species at Ligurian fronts associated with intensified vertical injection of nutrients from deep water masses all over the year [MOL 05].

5.6. Chemical limitation of primary production

5.6.1. *The Redfield model*

The Redfield model [RED 34] is based on the idea that organisms maintain a constant chemical composition relative to the variations in their environment, which is usually called "stoichiometric homeostasis" (originally, only nitrate and phosphate were concerned by this concept, then the model was extended to all biogenic elements in aquatic systems). There is a concentration ratio fairly constant in seawater between nitrate and phosphate concentrations: both are taken up by plankton in ambient proportions and go back to solution when organisms die. Thus, biological activity modifies the titration of seawater in the proportions.

$$\Delta P/\Delta N/\Delta C = 1/16/106 \qquad [5.6]$$

according to the photosynthesis reaction (see equation [5.1]).

Of course, the chemical composition of biotic and abiotic compartments can widely vary with environmental conditions and growth rates of organisms, and it must be kept in mind that the Redfield model is only a proxy. In addition, the quantitative interpretation of molar ratios is sometimes difficult. However, qualitatively (e.g. interpretation of its seasonal variations), this model is of great use. Klausmeier *et al.* [KLA 04] modeled the optimal strategies of organisms according to the different ecological and environmental conditions. These authors inferred that exponential growth (i.e. large availability of resources) favors low N:P molar ratios, while the competitive acquisition of resources favors high N:P molar ratios.

5.6.2. *Peculiarity of N:P molar ratios in the Ligurian area*

A striking specificity of the Med is the anomalous value of nutrient molar ratios (about 22 in the western Med, up to 24 in the very oligotrophic eastern Med, against 16 in oceans; [BET 02]), compared to those of other oceanic regions. Owing to the predominance of NO_3^- and PO_4^{3-} over other inorganic forms of N (apart from the specific case of N_2) and P, respectively, N:P ratios can be assimilated to $NO_3^-:PO_4^{3-}$ ratios. In the LS (data from DYFAMED), ratios are constant in deep and intermediate layers, with minor scattering of the data, and median N:P values are about 20 [PAS 15a]. During the period of dense water formation, N:P ratio vertical profiles are almost rectilinear along the water column. N:P values exhibit an increasing scattering from sea bottom to surface waters about 20:1, which results in a typical T-shaped point cloud. The ratio remains relatively constant during the productive period until the peak of the bloom, when the decrease in nutrient stock leads to decreasing uptake, so that excretion reaches its maximum. Due to slower regeneration of bioavailable P relative to N, this results in a decrease in the N:P ratio. As soon as the stratification of the water column is initiated, the ratio evolves towards higher values, meaning increasing depletion of the photic layer, i.e. increasing oligotrophy. In surface, the ratio may then be as high as 60 or even more. In autumn, oligotrophy goes on, and reaches its maximum, yielding the highest observed N:P values (up to approximately 70; [PAS 15a]). In winter, the intense replenishment of surface waters resulting from winter convection lowers the year-end ratio, and the loop is closed.

The convective nutrient ratio is expected to reflect the nutrient ratio at depth, which is clearly non-Redfield in the Ligurian area. When the MLD is deeper than approximately 200 m, convective nutrient inputs exhibit N:P ratios about 21–22, close to the deep value, and ratios increase when the MLD is shallow (< 200 m). This suggests that the depth reached by the MLD influences the nutrient stoichiometry. It also mirrors a shallower nitracline relative to phosphacline, and, therefore, DIN convective inputs are higher than DIP ones for shallow MLD. However, the Ligurian N:P ratio is high compared with the typical Redfield value of 16. Several authors have pointed out that the Redfield model may not be relevant in semi-enclosed marine areas such as the Med (e.g. [WAN 12]), where external inputs may have a strong impact on nutrient stoichiometry. In the LS, high N:P values may be explained by several causes:

– the influence of external sources of nutrients is strong. In particular, atmospheric fluxes are generally N-enriched, relative to P [BAR 05]. The same applies to riverine and submarine groundwater discharges: respectively, N:P molar ratios range between 40 and 140 [LUD 09], and between 80 and 430 [ROD 15], mainly because DIP is rapidly removed from groundwater [SLO 04]. However, the actual impact of riverine inputs on offshore nutrient stoichiometry is believed minor, and that of groundwater discharges is not documented enough;

– the occurrence of diazotrophy, regardless of the significance of this process, allows access to an inexhaustible reservoir of N;

– bacterial denitrification removes bioavailable N. Unfortunately, our knowledge on the occurrence and magnitude of this process is very poorly known. However, Krom *et al.* [KRO 04] reported no significant denitrification rates in the water column in the eastern Med;

– the residence time of western Med deep waters might be too short (22 ± 4 years; [ROE 13]) to allow the complete remineralization of the pool of semi-labile organic matter into bioavailable DIP.

Regardless of their respective contribution, all these causes converge on the reinforcement of P-limitation of phytoplankton and heterotrophic bacteria.

5.6.3. *Model of P-limitation*

The anomalously high N:P ratio suggests that phytoplankton and heterotrophic bacteria in the LS are limited by the availability of PO_4^{3-}. Very clearly, PP is controlled by P in oligotrophic conditions (e.g. [THI 98], as everywhere in the Med). In winter, nutrients may not limit phytoplankton productivity because both NO_3^- and PO_4^{3-} are abundant in the photic layer as a result of convective inputs. In blooming conditions, the analysis of DYFAMED time-series from 1991 to 2011 suggests that NO_3^- and PO_4^{3-} may play a similar role through an alternation of periods of N-depletion relative to P, and periods of P-depletion relative to N [PAS 15a]. In this sense, DYFAMED findings shake up the paradigm according to which NO_3^- regulates phytoplankton dynamics in blooming conditions (e.g. [MAR 02b]), or even a combination of N and P does, with PO_4^{3-} stimulation of NO_3^- consumption, as observed in the Tropical Atlantic Ocean by Raimbault and Pujo-Pay [RAI 93]. Apart from this debate on P or N-limitation, one cannot discard the possible episodic control of diatom production by Si during the early bloom period, as suggested by Marty *et al.* [MAR 02b], although the probable evolutions of Si:P molar ratios (see section 5.7) render this hypothesis rather unlikely.

One can thus reasonably assume that P, under its reactive form PO_4^{3-}, controls biological production most of the time, and particularly in conditions of nutrient depletion. The assimilation of PO_4^{3-} by bacteria and phytoplankton is rapid, and it is only possible in the presence of several ions (in particular K^+), and of micronutrients (vitamins, Co, Fe, etc.), which never limit plankton growth in the LS (see section 5.2). However, in the case of ultra-oligotrophy, i.e. when PO_4^{3-} concentrations are close to zero, what strategy do micro-organisms develop? There are many organic forms of P in seawater, as well as a variety of polyphosphates. Organic P and polyphosphates are generated by human activities, or come from living organisms. Polyphosphates are mineral compounds produced by the polycondensation of PO_4^{3-}, and characterized by the repetition of the structural pattern PO_3M. They complex a variety of cations such as Ca^{2+}, Mg^{2+}, Fe^{2+} and Mn^{2+}. They are generally spontaneously decomposed (hydrolyzed) by water (e.g. polyphosphates formerly used in washing powders, such as sodium tri-polyphosphate $Na_5P_3O_{10}$). Organic forms of P are also numerous, and they essentially come from living organisms. DNA, TPA, phospholipids and proteins contain phosphates under the form of phosphate esters. These compounds are more or less stable and degrade under the action of acids, bases or enzymes and release PO_4^{3-} ions in water. These species are generally viewed as non-reactive, because they require more energy to be assimilated. However, they can be fixed and their role might be crucial because they represent the only available nutritive resource when the stock of inorganic is exhausted, according to two possibilities:

– many of these species are likely to hydrolyze, either spontaneously in ambient seawater, or under the action of UV, or under by enzymatic means. This hydrolysis leads to the release of reactive orthophosphate;

– algae and heterotrophic bacteria are capable of ectoenzymatic activity (e.g. alkaline phosphatase) that enables us to take up mineral phosphate after hydrolysis of dissolved organic P (DOP), which comes mainly from bacterial excretion. The more depleted in PO_4^{3-} is the medium, the more important is the activity of alkaline phosphatase. At the DYFAMED station, in September, heterotrophic bacteria shift from a P-limitation to a labile carbon-limitation, at depths where PO_4^{3-} is always under the detection limits, and which corresponds to a turnover time of the alkaline phosphatase of approximately 100 h [VAN 02]. In case of PO_4^{3-} and DOP depletion, some algal species can act as phagocytes of bacteria to use their P. In addition, some organic forms of P (e.g. phosphonates, characterized by the functional group RPO_3^{2-}, known to be present in oligotrophic waters) can act as chelating agents, and, thus, have an indirect role in the bioavailability of nutritive substances [NOW 00], or they can be hydrolyzed prior to be utilized by biota [DYH 06].

In conditions of low (or very low) availability (e.g. the LS during the oligotrophic period), PO_4^{3-} is assimilated by small organisms, which have a strong affinity for it (the smaller is a cell, higher is its surface–volume ratio, allowing a better output in nutrient absorption). In that case, the trophic web is mainly of microbial type, i.e. it is characterized by the competition between small algae and heterotrophic bacteria. Hence, a clear dominance of picoplanktonic populations is observed in oligotrophic environments. In conditions of better availability (e.g. spring bloom in the LS), PO_4^{3-} is assimilated by larger organisms, which have a less strong affinity for PO_4^{3-}. Trophic chains are more extended (there is more PO_4^{3-} to share). Therefore, in a model of trophic chain controlled by P, the excretion of dissolved organic carbon (DOC) may be higher than what bacteria are able to consume (if we assume that their growth is controlled by the availability of P). This yields an accumulation of DOC in surface waters and, then, its export to depths, as observed at DYFAMED [AVR 02]. In case of higher availability of PO_4^{3-}, more extended trophic chains yield an export of C to deep layers by the sedimentation of particles, i.e. export of POC [THI 97]. This model suggests that the shift from oligotrophy to eutrophy finds expression in a shift from a system characterized by DOC export to a system characterized by particulate organic carbon (POC) export.

5.7. Decadal trends and possible consequences for regional productivity

External inputs of nutrients shift under the pressure of climate change and anthropogenic inputs (e.g. the ban on polyphosphates in detergents, or the upgrade of waste water treatment plants), and according to the frequency and intensity of rain events [BAR 05]. Changes in nutrient concentrations may also result from water mass changes. The increase in the frequency and the magnitude of convection events between 2003 and 2006, presumably due to a significant warming and salinification of the water column (see Chapter 4), has yielded a noticeable increase in nutrient concentration. The analysis of DYFAMED time-series over the period 1991–2011 by Pasqueron de Fommervault *et al.* [PAS 15a] is, to our knowledge, the only recent one existing in the LS. This work has documented statistically significant trends:

– slowing down of nitrate concentration increase by a factor of two;

– reversal of the trend for phosphate concentration;

– silicate concentration: stable. Silicon has virtually no anthropogenic source. The damming of Aswan (169 10^9 m^3 water) and the damming on the Danube River have yielded the decrease of inputs of $Si(OH)_4$ in the eastern Med, which has supposedly impacted nutrient budgets in the western Med, including the LS. However, after Slattery and Phillips [SLA 11], the impact of dams is overestimated downstream river mouths.

DYFAMED time-series have also shown that the N:P ratio increased in deep water (below 800 m, where the variability of nutrient concentrations is the smallest) by 4.2% over 20 years, against an increase in Si:P by 3.2% during the same period, while Si:N did not evolve significantly (Figure 5.2).

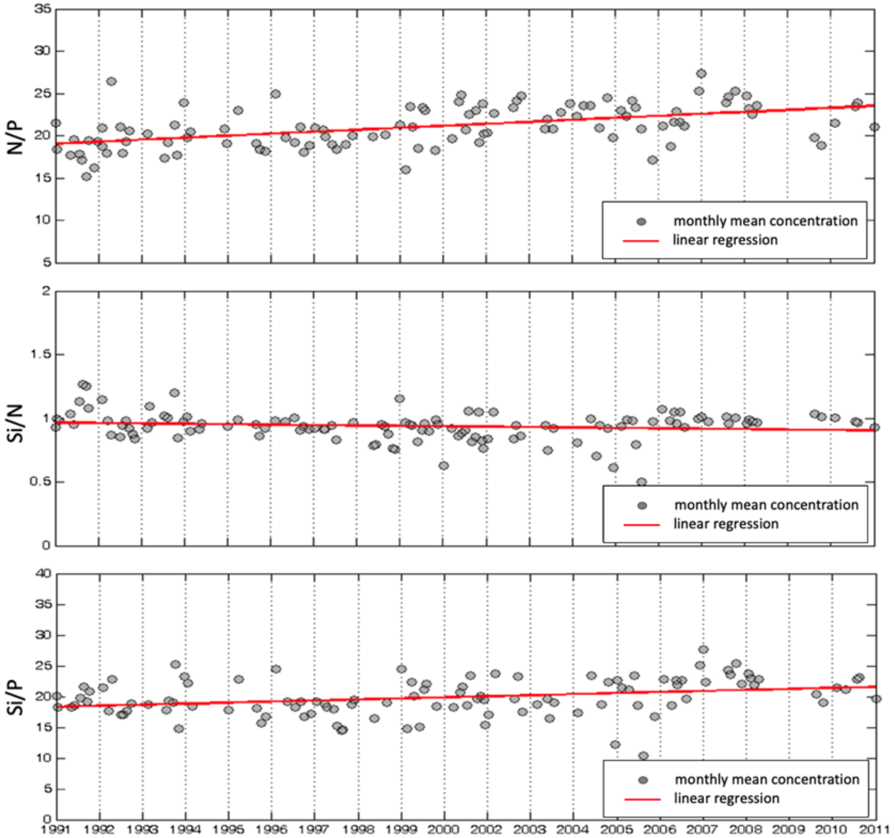

Figure 5.2. *Temporal changes in N:P (+4.2 in 20 years), N:Si (no significant trend) and Si:P (+3.2 in 20 years) molar ratios at DYFAMED averaged over the 800–2000 m-depth layer, from 1991 to 2011. For a color version of this figure, www.iste.co.uk/migon/mediterranean1.zip*

This suggests a current increase of N:P and, to a lesser extent, an increase of Si:P, i.e. an increase of P-limitation throughout the year. This implies an increasing proportion of heterotrophic bacterial production. The trends observed at DYFAMED might mirror a current increase of oligotrophy in the LS. This shift is also reflected by an increasing discrepancy between molar ratios observed and the Redfield model. Evolving external inputs are probably an important cause of the increasing oligotrophy of the LS, apart from accidental events (e.g. in 2003–2006). These findings are in agreement with the hypothesis of increasing oligotrophy and stratification of the Global Ocean (e.g. [BEH 06]).

5.8. Concluding remarks

Through regular transdisciplinary decadal-scale monitoring, the study of the LS, which is particularly subject to climatic, meteorological and environmental changes, has led to major advances in our understanding of offshore marine ecosystems. Our knowledge of nutritive resources remains very incomplete; however, several areas of research require further investigation. Among these, the following future research avenues should be particularly highlighted:

– some emission sources remain very poorly known. Gaseous deposition is almost undocumented. Failure to take this incoming flow into account could lead us to an erroneous picture of nutrient stocks and dynamics. Moreover, groundwater discharge requires future investigations, and the estimation of net riverine fluxes suffers from gaps due to poor knowledge of biogeochemical processes occurring in mixing zones;

– undersampling does not currently allow us to precisely assess the spatiotemporal variability of nutrient concentrations. The development of sensors dedicated to nutrients will allow acquisition of data at very high frequency by using autonomous platforms. This will probably change our view of nutrient dynamics and their relationship to physics and biology.

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6

Primary Production in the Ligurian Sea

6.1. Annual cycle of phytoplankton biomass, production and community structure in the Ligurian Sea

6.1.1. *Regional context of the area*

The availability of earth-orbiting satellite sensors, coupled with past *in situ* observations, allowed the concept of oceanic “biogeochemical provinces” to be refined by oceanographers at the end of the 20th Century [LON 98, PLA 91, REY 19]. In the original division of the global ocean into provinces, Longhurst considered the Mediterranean Sea as a single, subtropical oceanographic province, without any spatial subdivisions, but regional oceanographic and ecological characteristics were described [LON 98].

For the western Mediterranean Sea region, Morel and André [MOR 91a] performed the first spatiotemporal description of phytoplankton biomass and production from ocean-color satellite data, with images from the coastal zone color scanner (CZCS), experiment sensor and a spectral light–photosynthesis model ([MOR 91a], see Box 6.1). This description, which included the Ligurian Sea, depicted several major seasonal features: the very low chlorophyll-*a* concentration in winter, the phytoplankton spring and fall blooms, and the low chlorophyll-*a* concentration in summer [MOR 91a]. These characteristics of phytoplankton dynamics in the Ligurian Sea had been first described in the 1960s from transects across the area and related to some physical–biogeochemical processes

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Chapter written by Nicolas MAYOT, Paul NIVAL and Marina LEVY.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

[GOS 61, GOS 63]. The MEDIPROD experiments in the 1960s–1970s (mostly MEDIPROD I, II and III; [JAC 73]) and more recently the DeWEX experiment in 2012, allowed further *in situ* understanding and quantification of the plankton dynamics and biogeochemical budgets for the Northwest Mediterranean over an annual cycle [CON 18].

Phytoplankton primary production (in gC m^{-2}) can be estimated with empirical or semi-analytical models applied to satellite observations (see the reviews from Babin *et al.* [BAB 15] and Behrenfeld and Falkowski [BEH 97]). The model developed by Morel [MOR 91b] is a "wavelength-resolved model" and corresponds to a light photosynthesis model applied to satellite observations. This type of model evaluates the daily primary production at each depth between the surface and the depth of the productive layer (e.g. 200 m), over the duration of the day and within the spectral limits of the photosynthetic domain (400 and 700 nm). The model, for a day and at a certain depth (z), can be described as follows:

$$\mathrm{PP(z)} = \mathrm{P^B_{max}} \times \mathrm{Chla(z)} \int_{t=0}^{24\,h} \int_{\lambda=400}^{700\,nm} f\big(E(\mathrm{z},t,\lambda), a^*_{ph}\big)\, d\lambda\, dt$$

where Chla (mg m^{-3}) is the chlorophyll-a concentration measured by satellite, $\mathrm{P^B_{max}}$ (gC $[\mathrm{mgChla}]^{-1}$ h^{-1}) is the chlorophyll-normalized maximum rate of carbon fixation at saturating irradiance, E (mol photons m^{-2} s^{-1}) is the irradiance and a^*_{ph} (m^2 mg Chla^{-1}) is the chlorophyll-specific phytoplankton absorption coefficient. The function (f) within the integral describes the photosynthesis versus irradiance curve, which could be used to express the relationship between a^*_{ph} and the photosynthetically available radiation (i.e. E(λ) integrated between 400 and 700 nm). Therefore, this type of model explicitly includes optical and photosynthetic processes, and can be adapted to different oceanic regions.

Box 6.1. *Estimation of phytoplankton primary production using satellite observations*

As a brief overview, in winter, deep convection processes reduce the residence time of phytoplankton cells in the surface layer, resulting in very low pigment levels in the central Northwest Mediterranean, in a region known as the "blue hole" [BAR 03]. The phytoplankton spring bloom could be considered as the "reverse figure of the winter pattern" [MOR 91a], with the phytoplankton able to consume the nutrients upwelled in winter as soon as the water column is more stable. In fact, the phytoplankton bloom development in this area is similar to the one described by Sverdrup [SVE 53], with the bloom onset occurring when the turbulent mixing in the upper ocean weakens [LAV 13, MAY 17a]. The low chlorophyll-*a* concentration in summer in the upper surface layer is due to the absence of nutrients in this layer. During this season, phytoplankton cells develop around the euphotic depth and close to the nutricline (nitra- or phosphacline, [JAC 73]), forming a subsurface chlorophyll maximum (SCM, Figure 6.1). In the Ligurian Sea, light availability and nutrient concentrations are relatively high at the SCM depth, therefore, the SCM is also a subsurface biomass maximum (SBM, [BAR 19]). In early summer, the SBM is intense and located above the euphotic depth, while later in the season, the SBM deepens below the euphotic depth and tends to be less pronounced before shallowing in fall [BAR 19]. The seasonal depth distribution of the SBM is primarily driven by the light availability [BAR 19, MIG 14]. Finally, Morel and André [MOR 91a] and Mayot *et al.* [MAY 17a] suggested that the observed fall bloom was the result of a deepening of the mixed layer depth that spreads the top layer of the SBM and injects some nutrients into the surface layer.

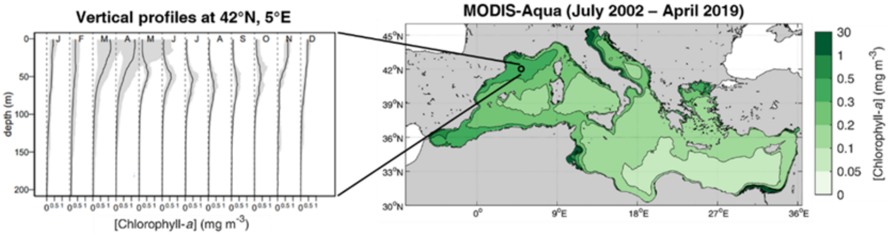

Figure 6.1. *Spatial distribution (climatologies) of chlorophyll-a concentration. (Left) Monthly vertical profiles (black line: median value; grey zone: 10–90 percentile range) observed in the water column at the location 42°N, 5°E (modified from Lavigne et al. [LAV 15]). (Right) Surface chlorophyll-a concentration from the satellite sensor MODIS-Aqua (from NASA Ocean Biology Processing Group). For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

Recurrent estimations of annual primary production cycles in the euphotic layer of the central Ligurian Sea were obtained at the DYFAMED sampling station [MAR 02a]. The seasonal cycle of primary production followed phytoplankton biomass, with estimates of depth-integrated (0–100 m) daily primary production, rate varying between approximately 0.1 gC m^{-2} d^{-1} in winter and approximately 2 gC m^{-2} d^{-1} in summer. The estimates, of annual primary production derived from the temporal integration of the daily estimates varied between 86 and 232 gC m^{-2} yr^{-1} [MAR 02a]. These *in situ* estimates are similar to the more recent values obtained from light–photosynthesis models applied to satellite ocean-color data (78–204 gC m^{-2} yr^{-1}) [BOS 04, OLI 11, UIT 12].

These general ecological characteristics, associated with the Northwest Mediterranean area, are different from the rest of the Mediterranean basin. For example, Antoine *et al.* [ANT 95] used the same approach as Morel and André [MOR 91a] to demonstrate that phytoplankton biomass and production were two times higher in the Northwest Mediterranean area than in the Levantine Sea, confirmed later by other investigators [BOS 04, UIT 12]. D'Ortenzio and Ribera d'Alcalà [DOR 09] suggested that the dynamics of the open-ocean area of the Ligurian Sea were similar to the "mid-latitude nutrient-limited spring production peak" regime defined by Longhurst [LON 95]. Several studies confirmed the recurrent presence of this typical regime in the Ligurian Sea (e.g. [MAY 16]). Other biogeochemical (e.g. species distribution) and physical (e.g. hydrology and surface currents) characteristics are also well defined and homogeneous in this large area [AYA 18], which supports the idea that the Ligurian Sea, and more generally the Northwest Mediterranean area, is a key region in the Mediterranean Sea.

6.1.2. *The diversity of phytoplankton species: the base of community ecology*

Quantification of phytoplankton biomass and diversity was originally done by identifying and counting phytoplankton cells in samples collected with plankton nets or bottles. The total volume of phytoplankton cells was used as a proxy for the total phytoplankton biomass. In the early 20th Century, several researchers described and discussed the seasonal variation of phytoplankton species in various parts of the Ligurian Sea: Alexander Nathansohn, Jules Pavillard and Francis Bernard, from samples collected around Monaco; Guy Léger from samples collected offshore in the Ligurian Sea; and Achille Forti, Michael Bernhard and Leopoldo Rampi focused on the Italian coast. The next sections provide an overview, instead of an exhaustive assessment, about the micro-, nano- and picophytoplankton species, described in these early studies.

6.1.2.1. *Micro-phytoplankton (20–200 μm)*

Diatoms and dinoflagellates, well differentiated by their morphology and ecology, are the two taxonomic groups that dominate this size class. Diatoms have a rigid siliceous skeleton (frustule). Most diatom species bloom in waters with high nutrient concentrations, although some are able to develop in more oligotrophic conditions. A substantial spring bloom of diatom cells generally induces the formation and sedimentation of large marine snow aggregates. Dinoflagellates, with or without a rigid outer cell covering (or theca), can be autotrophs, as well as mixotrophs or heterotrophs. Dinoflagellate cells always have two flagella but can display very different shapes, from round to long armed. Some species are well known for producing toxins and inducing harmful algal blooms. Nevertheless, as diatoms, dinoflagellates are tracers of changes in the microplankton community.

During winter, the presence of the diatom species *Thalassiothrix frauenfeldii* (now *Thalassionema frauenfeldii*) was noted in the first half of the 20th Century [FOR 22, PAV 37, RAM 38] and was later confirmed, in 1998 and 1999, with observations from the Bay of Villefranche [GOM 03]. In spring, *Nitzschia seriata* was the common diatom species observed in the Ligurian Sea, both in coastal (e.g. Bay of Napoli, La Spezia, San Remo; [BER 67, NAT 09, RAM 38]) and offshore locations [LEG 64, LEG 72]. Later, in the 1970s, an important springtime presence of the diatom genus *Nitzschia* in the Bay of Villefranche was reported [RAS 79]. Claustre *et al.* specifically studied a spring bloom of *Nitzschia seriata* in 1986 and suggested different physiological states of the cells that composed this bloom [CLA 89]. The absence of *Nitzschia seriata* in spring was also noted and reported several times (e.g. around Monaco, [PAV 37]). In summer, although there was a low abundance of diatoms observed in the phytoplankton community, diatoms of the genera *Rhizosolenia* and *Leptocylindrus* were detected [PAV 37, RAM 38]. Another common diatom genus observed, mostly in fall, was *Chaetoceros* [PAV 37, RAM 38], also confirmed by Rassoulzadegan [RAS 79].

Dinoflagellate species collected by a plankton net are as diverse as diatom species. Halim [HAL 60] made an inventory of 198 dinoflagellate species, including the description of seven new species, from samples collected in the Bay of Villefranche. Some species presented strong seasonal variations due to changes in environmental factors [HAL 60]. Tunin-Ley *et al.* [TUN 07], in a careful study of the genus *Ceratium* in coastal waters (Bay of Villefranche), showed that over a year, the dinoflagellate population was dominated by *C. furca* (in spring) and *C. fusus* (in winter). Some species displayed a seasonal cycle that might be linked to water temperature, such as *C. candelabrum* mostly observed in winter. Tunin-Ley *et al.* [TUN 07] also suggested that seasonal variations of dinoflagellates in the microphytoplankton community were related to competition with diatoms for nutrients and through predation by salps and copepods.

Rampi also observed tychoplanktonic organisms (benthic organisms dispersed through the water column via a disturbance to their habitat, e.g. suspension induced by waves), such as the diatom genus *Licmophora* [RAM 38]. Recently, the tychoplanktonic and harmful dinoflagellate species *Ostreopsis ovata* received more attention in coastal areas of the Ligurian Sea. This dinoflagellate, continuously monitored in Ligurian Sea coastal waters, grows in a mucilaginous layer on macroalgae and can be dispersed in the surface layer from waves. During an *Ostreopsis* bloom, the observed concentration can reach 10^6 cells L^{-1} and the cells can be transported via aerosols into the atmosphere. Cohu and Lemée [COH 12] showed that the presence of this dinoflagellate in summer depends on temperature (>20 °C) and light. Meroni *et al.* [MER 18] also showed that the dynamics of *Ostreopsis* depends on biotic and abiotic parameters, which explains the presence of this species in urban shores and sheltered bays. This species produces a metabolite similar to “palytoxine” (the most powerful toxin produced by marine species) called “ovatoxine”, which might be present among the pelagic and benthic communities, potentially causing human diseases.

6.1.2.2. *Nano-phytoplankton (2–20 μm)*

In the early 20th Century, observations of phytoplankton cells among the nanophytoplankton were difficult with a standard microscope, and only few characteristics (e.g. flagella) allowed their identification to some taxon levels. However, coccolithophore species were easily identified with their coccoliths (disc-like plates) that surround their cells and form a coccosphere (calcareous skeletons).

Bernard, with observations from two coastal sampling sites (around Banyuls and Monaco), suggested that the volume of the nanoplankton was at a maximum from the end of spring to the end of summer [BER 38]. Then, he gave an early quantitative estimation of the number of coccolithophore species present in the Ligurian Sea [BER 39]. A total of 44 species were recorded and the dominant species were *Oolithotus fragilis* and *Emiliania huxleyi* (under the names *Coccolithus fragilis* and *Pontosphaere huxleyi*, respectively). Some species were found in deep waters and supposed to be heterotrophs. Bernard emphasized that these species could appear under different shapes over their life cycle [BER 39]. In the eastern part of the Ligurian Sea, around La Spezia (Italy), coccolithophores were also observed to be a major part of the phytoplankton community [BER 67].

Most of these studies were done with samples collected in coastal waters. Léger was one of the first to carry out a survey offshore [LEG 72]. He estimated the abundance of coccolithophores at different seasons in the central part of Ligurian Sea. From his observations, coccolithophores increased in winter and did not produce a bloom. He showed that silicoflagellata, with an annual maximum concentration in winter (to 5.5 10^3 cells L^{-1}) in coastal waters [NIV 65], could also be an important nanoplankton component in offshore water.

The summer season was investigated during a transect off Villefranche [JAC 76]. Although the diatom and dinoflagellate abundances were the same in coastal and offshore waters, the nanoplankton component was dominant offshore, especially *Chrysochromulina* (0.5 106 cells L^{-1}), one coccolithophore species and *Dictyocha fibula* (5000 cells L^{-1}).

6.1.2.3. *Pico-phytoplankton (0.2–2 µm)*

Sieburth *et al.* [SIE 78] and Waterbury *et al.* [WAT 79] revealed the existence of phytoplankton cells smaller than nanophytolankton cells, passing through 2 µm pore size filters. The cyanobacteria (i.e. photosynthetic bacteria) *Synechococcus* [WAT 86] and *Prochlorococcus* [CHI 92] are the most common picophytoplankton organisms. Vaulot *et al.* [VAU 90] documented the presence of *Prochlorococcus* in the Mediterranean Sea. Their specific photosynthetic pigment, the phycobilin pigment, has an intense fluorescence quantum yield in the orange region of the visible spectrum which is detectable by flow cytometry, and thus can be used to identify the presence of picophytoplankton organisms in a sample. Aside from cyanobacteria, several other picophytoplankton groups have been discovered in other taxonomic groups (i.e. in Chlorophyta: Chlorophyceae and Prasinophyceae; Prymnesiophyceae and Pelagophyceae) with different cell structures and flagella types [LEE 18].

6.1.3. *Phytoplankton community structure*

The development of chlorophyll-*a* concentration measurement techniques allowed a more rapid approximation of the phytoplankton biomass. Nowadays, high-performance liquid chromatography (HPLC) technology is widely used to identify and quantify the concentration of several photosynthetic pigments from a sample. The concentrations of phytoplankton pigments in a sample can be used to detect the presence of different photosynthetic autotrophs by using a diagnostic pigment approach (see Box 6.2 and Table 6.1).

In addition to chlorophyll-a, the dominant photosynthetic pigment, a phytoplankton cell could contain accessory pigments. The pigments associated with chlorophyll-a have different functions, for example, photoprotection or to extend the light absorption spectrum. Several accessory pigments exist of different classes (e.g. carotenoids, phycobiliproteins and chlorophylls), and could be specific to a phytoplankton group [BID 90, JEF 74]. Therefore, to study the structure of the phytoplankton community in a sampled area, one can estimate the concentration of accessory pigments and relate this information to the presence of specific phytoplankton taxa.

To this end, Claustre [CLA 94] proposed an approach to detect and quantify the presence of seven phytoplankton groups (i.e. diatoms, dinoflagellates, nanoflagellates, green flagellates, cryptophytes, cyanobacteria and prochlorophytes) based on the concentration of nine accessory pigments, named diagnostic pigments (or biomarker pigments), determined by HPLC analysis. Vidussi *et al.* [VID 01] proposed the possibility of using the typical cell size of the organisms within each taxon to assign taxon to three different phytoplankton size classes: picophytoplankton (< 2 µm), nanophytoplankton (2–20 µm) and microphytoplankton (> 20 µm). This size description of the phytoplankton community is convenient for the study of ocean biogeochemical processes (e.g. phytoplankton photophysiology and biological carbon export [GUI 09, UIT 08]). Therefore, Uitz *et al.* [UIT 06] refined the approach of Claustre [CLA 94] with the three size specific groupings as proposed by Vidussi *et al.* [VID 01].

Box 6.2. *Community structure with HPLC*

In the Ligurian Sea, the diagnostic pigment approach allowed the description of seasonal succession of phytoplankton groups, in relation to the total phytoplankton biomass and production, and the hydrological environment. This description has been made in coastal locations (e.g. in the Bay of Villefranche) and offshore (e.g. the DYFAMED-BOUSSOLE sampling site).

Taxonomic groups	**Diagnostic Pigments**	**Typical Size Classes proposed by Vidussi *et al.* (2001)**	**Genera and species cited in this chapter**
Considered in the diagnostic pigment approach of Claustre [CLA 94], Vidussi et al. [VID 01] and Uitz et al. [UIT 06]			
Diatoms	Fucoxanthin	microphytoplankton (> 20 µm)	*Thalassionema, Nitzschia seriata, Rhizosolenia, Leptocylindrus, Chaetoceros, Minidiscus, Licmophora*
Dinoflagellates	Peridinin		*Ceratium, Ostreopsis*
Haptophyta (Prymnesiophyceae)	19'-Hexanoyloxyfucoxanthin 19'-Butanoyloxyfucoxanthin	nanophytoplankton (> 2–20 µm)	*Oolithotus fragilis, Emiliania huxleyi* *Chrysochromulina*
Cryptophyta (Cryptophyceae)	Alloxanthin		
Chlorophyta (Chlorophyceae, Prasinophyceae)	Total chlorophyll-b	picophytoplankton (< 2 µm)	
Cyanobacteria	Zeaxanthin		*Synechococcus, Prochlorococcus*
Not considered in the diagnostic pigment approach of Claustre [CLA 94], Vidussi et al. [VID 01] and Uitz et al. [UIT 06]			
Silicoflagellata	19'-Hexanoyloxyfucoxanthin 19'-butanoyloxyfucoxanthin	microphytoplankton (> 20 µm)	*Dictyocha fibula*
Pelagophyceae	19'-Butanoyloxyfucoxanthin Fucoxanthin	picophytoplankton (< 2 µm)	

Table 6.1. *Phytoplankton taxonomic groups targeted by the diagnostic pigment approach presented in the Box 6.2, as well as the phytoplankton genera, species and other taxonomic groups mentioned in this chapter*

On average over the annual cycle, the phytoplankton biomass and production in the euphotic zone of the Ligurian Sea is mostly dominated by nanoflagellates (mainly haptophyta), both in coastal [BUS 95] and open-ocean areas [MAR 02b], see Figure 6.2. However, this annual nanophytoplankton domination is challenged in spring. Specifically, the diatom biomass can exceed the nanoflagellate biomass during the phytoplankton spring bloom [MAR 02b]. This classical view of a spring bloom dominated by diatoms has not been observed every year [BUS 95, MAR 02b, VID 00]. Bustillos-Guzman *et al.* [BUS 95] suggested year-to-year variability in the spring nutrient concentrations and light conditions may explain these observations. Recently, it was proposed that the winter water column mixing influences the spring nitrate to silicate ratio in the surface layer [SEV 17]. Ultimately, a lower (higher) quantity of diatoms in the phytoplankton community can induce a decrease (increase) in the springtime primary production of organic carbon [MAY 17b] (Figure 6.2).

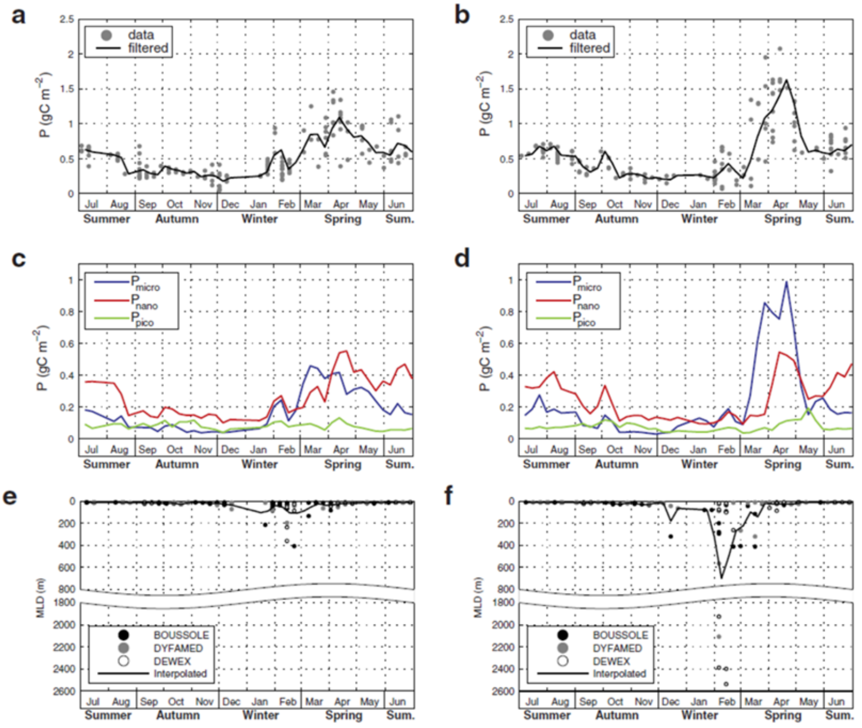

Figure 6.2. *Climatological annual cycles of total (top) and class-specific (middle) phytoplankton primary production in the euphotic layer, and of the mixed layer depth (bottom), in the Northwest Mediterranean region (modified from Mayot* et al. *[MAY 17b]). During years with a shallow (a, c and e) or deep (b, c and f) winter water column mixing. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

After the spring bloom, and when the water column starts to be strongly stratified, the annual biomass peak of nanoflagellates occurs [BUS 95]. Vidussi *et al.* [VID 00] particularly focused on this transition period and reported this switch in the phytoplankton community from diatoms to haptophyta and an increasing contribution of picophytoplankton groups, mostly cyanobacteria. In general, *Synechococcus* is dominant in the surface layer, while haptophyta and *Prochlorococcus* are located around the SCM [MAR 02b, VID 00]. This vertical distinction was explained by the ability of cyanobacteria to grow under high solar radiation and use regenerated forms of nitrogen [MAR 02b, VID 00]. Overall, the picophytoplankton biomass can overcome the nanophytoplankton biomass in the near surface layer [KHE 14] without dominating integrated phytoplankton biomass over the euphotic zone [MAR 02b, MAY 17b] (Figure 6.2).

During mixing of the water column in winter, the phytoplankton community seems to be mostly dominated by nanophytoplankton groups [MAR 02b, MAY 17b]. However, the diagnostic pigment approach used in these studies relies on the collection of water samples at sea, which is rarely done in harsh winter conditions. Consequently, it is important to develop methods to study the phytoplankton community structure from autonomous platforms (e.g. remote sensing, autonomous underwater vehicles). Studies based on ocean-color [NAV 17, UIT 12] and *in situ* bio-optical data (e.g. from a mooring; [ORG 13]) have already proven the success of these methods, and confirmed the general view of seasonal succession of phytoplankton groups in the Ligurian Sea but with higher spatiotemporal resolution.

However, these approaches prevent, for now, a description of the phytoplankton community at low taxonomic levels, which can be achieved with single cell observations. The introduction of imaging flow cytometers (measuring different parameters of particles: spectral, fluorescent and morphological) offers a way to identify several categories of living particles (e.g. viruses, bacteria, phytoplankton) and their biomasses. Seagoing and autonomous flow cytometers allow the study of short timescale events or processes concerning pico-, nano- and micro-phytoplankton groups. For example, several studies based on single cell imagery systems conducted in the Bay of Villefranche emphasized the importance of pico-eukaryotes, silicoflagellata and nanophytoplankton groups in the first stage of the spring phytoplankton bloom [PED 17, ROM 15, THY 14]. These phytoplankton groups might have a faster response to the favorable spring bloom conditions compared to the large diatoms and dinoflagellates, due to bottom-up processes [ROM 15, THY 14] and zooplankton grazing pressure [ROM 15]. In the open ocean of the Northwest Mediterranean region, a single cell study also emphasized the possibility to observe recurrent spring blooms of a nanoplanktonic diatom species in this area (*Minidiscus*; [LEB 18]).

6.2. From the influence of small spatiotemporal features to the interannual and long-term variability

Associated with the large scale and general (climatological) annual cycle of phytoplankton dynamics, small spatiotemporal processes occur and may play a lead role at local scales. For example, during the MEDIPROD experiment cruises, a sharp boundary between offshore green waters and coastal blue waters was discovered. This boundary is due to the highly dynamic geostrophic frontal jet flow associated with the Ligurian coastal Current (i.e. northern branch, [BET 83], see also Chapter 3). Phytoplankton biomass, as well as the abundances of meso- and macro-zooplankton, can be more important in this frontal structure [BOU 87, GOR 00]. The front is characterized by a strong horizontal density gradient and substantial meandering activity [BET 83, PIT 14]. Moreover, geostrophic vertical motions in this frontal structure (convergence and divergence processes) can induce an upwelling of deep-water masses, rich in nutrients, and a downwelling of surface waters containing phytoplankton cells (e.g. [BOU 87]). In fact, several glider surveys detected frontal submesoscale processes that can transport phytoplankton biomass down to 120 m [NIE 08].

Wind and precipitation events can significantly influence vertical water column stability and nutrient concentrations. At some coastal locations and in the spring, nutrients introduced into surface waters by rain events can favor the development of nanophytoplankton groups [KLE 97]. Such local processes can ultimately affect, for example, phytoplankton bloom development [PED 17, ROM 15, THY 14]. Offshore, the occurrence of short-term and intense wind-driven vertical mixing episodes of the water column may stop or delay the typical spring bloom development [MAR 02b, MAY 17a], and be crucial in the amount of organic carbon exported at depth [BER 12, KES 18, ULS 16]. Later in the year, at the transition from the spring bloom to the summer oligotrophic phase, illustrated by the establishment of the SBM, wind events may cause a shoaling of the nutricline and increase nutrient concentrations in the surface layer, as well as primary production [AND 00]. Diatoms can rapidly respond to these short-term summer events, but, ultimately, it is the smaller phytoplankton size classes that are mainly associated with these brief enhancements of the primary production [BUS 95, VID 00].

Physical (sub)mesoscale eddy features are also recurrent in the Ligurian Sea and can influence the phytoplankton dynamics. Mesoscale cyclonic eddies generated by a recirculation of coastal currents in summer in the Ligurian Sea can generate a horizontal distinction in the distribution of picophytoplankton species in the surface layer [MAR 18]. In spring, eddies that form at the border of the deep convection patch may play a key role in water column stratification and in the phytoplankton spring bloom [LÉV 98b, LÉV 99]. Furthermore, eddies generated in the mixed patch of convected waters (i.e. sub-mesoscale coherent vortices) can persist for an extended period and affect the phytoplankton distribution in summer [BOS 17]. It is still necessary to evaluate the contribution of these small-scale physical features on the larger, sub-basin, description of the phytoplankton dynamics, not only by new field experiments, but also by improving hydrodynamics/biochemistry coupled models (see section 6.3).

Finally, in contrast to these small spatiotemporal variabilities, significant questions remain about the long-term trend of phytoplankton dynamics in the Ligurian Sea, and more generally at the scale of the Northwest Mediterranean basin [THE 11]. As already mentioned in previous sections, interannual variability in the springtime phytoplankton biomass [LAV 13, MAY 16, VOL 12], community structure [MAR 02a, SAN 71, SEV 14] and production [EST 96, MAR 02a, MAY 17b] occur in the Northwest Mediterranean region. In the open-ocean sector, the principal cause of the interannual variability in the springtime primary production may be the influence of the winter mixing on nutrient availability (concentration and stoichiometry) and zooplankton grazing pressure [MAY 17a, SEV 17]. Although a phytoplankton spring bloom that deviates from the norm has a limited consequence on the annual phytoplankton production (about 6%; [MAY 17b]), the food web structure in Ligurian Sea, as well as the export of particulate organic carbon to depth in this area, might be impacted [LEG 91, RAM 16]. This underlines the importance of predicting the general trends in the Ligurian (e.g. more subtropical or temperate regimes) in the next century, principally in response to the ongoing climate changes [MAR 15].

From nine years of observations (1991–1999), Marty *et al.* [MAR 02b] suggested a general increase in the phytoplankton biomass in the open-ocean area of the Ligurian Sea, driven by an increase in the annual average proportion of pico- and nanophytoplankton in the phytoplankton community. Similar conclusions were derived at coastal locations [PED 17]. When using multiannual, satellite-derived surface chlorophyll-a concentration, the interannual variability in the observed seasonal cycle (i.e. year-to-year change in spring bloom intensity) is the most important feature [MAY 16, SAL 19] with a potential increase in the annual phytoplankton biomass [SAL 19]. Modeling studies of the Northwest Mediterranean region provide insights into future changes that could face the Ligurian Sea. Some studies suggest an increase in water column stratification [ADL 15, SOM 18] that could change the availability of silicon, influencing diatom development and potentially leading to a general reduction of springtime phytoplankton production [HER 13]. However, the physical circulation models are very sensitive to the Atlantic forcing used at the boundary conditions [ADL 15]. In addition, some recent modeling simulations seem to indicate that mesoscale activities [MAC 18] and changes in external nutrient inputs (Atlantic, atmospheric and riverine sources; [LAZ 12, RIC 19]) have crucial roles in the projection of future changes in primary production in the Northwest Mediterranean basin.

6.3. Modeling the impact of the physics on phytoplankton growth and distribution

The biogeochemistry of the Ligurian Sea shares important characteristics with other temperate regions of the ocean, such as the North Atlantic. Modeling studies of this complex system has paved the way for the understanding of the coupling between the physics of the ocean and the response of the biogeochemistry in environments that are prone to strong seasonal variations of the surface mixed layer and to strong mesoscale dynamics.

Unlike the rest of the Mediterranean basin that is predominantly oligotrophic, the productive Ligurian Sea is a typical temperate system, characterized by an increase in phytoplankton biomass that starts in the fall, often interrupted in winter and a stronger, more intense bloom in spring that ends in summer [DOR 14, HOU 16, MAY 16].

It is now fairly well established that the seasonal variations of the mixed layer are a main driver of the seasonal variations in phytoplankton biomass, although there remain some uncertainties regarding the ability of phytoplankton to grow in deep mixed layer and regarding the control that grazing may exert on the onset and decay of the phytoplankton bloom [BEH 18]. The deep-winter convection in the Northwestern Mediterranean plays a key role in setting the bloom [MAY 16]. It ensures the seasonal replenishment of the euphotic layer with nutrients, which are progressively being consumed between winter and summer. One-dimensional modeling studies of the phytoplankton phenology in the Ligurian Sea have suggested that the onset of seasonal stratification over the deep-convection area, which is tightly linked to the time at which the net heat flux received by the ocean from the atmosphere becomes positive, drives the onset of the surface bloom [LÉV 98a, LÉV 98b]. This has been confirmed recently, thanks to the development of new technologies that have enabled continuous measurements in the field [MAY 17a].

This classical seasonal scenario is, however, strongly modulated by temporal and spatial signals of smaller scale. For instance, high frequency atmospheric events (from one to a few days), such as wind bursts, are sufficient to destroy the stratification and temporarily interrupt the bloom. Similarly, periods of mild weather in winter allow for short periods of stratification that are associated with more elevated phytoplankton biomass at the sea surface [LÉV 98a, MAY 17a].

In addition, mesoscale dynamics have also been shown to strongly modulate the phytoplankton phenology. The first ocean color images over the Ligurian Sea in the early 1980s have revealed phytoplankton heterogeneity at scales similar to mesoscale eddies over this area, during winter and spring [MOR 91a], suggesting a strong impact by mesoscale dynamics. The region is indeed the location of intense mesoscale activity, which originates primarily from the baroclinic instability of the current surrounding the deep-convection area. One of the first biogeochemical modeling studies conducted at mesoscale resolution aimed at understanding the physical processes involved in this physical control [LÉV 00, LÉV 98b, LÉV 99]. The model, although highly idealized, was able to reproduce the spatial heterogeneity in the onset of the bloom, which started from the border of the convective area before amplifying in its core. Interestingly, the onset of the bloom around the convective area occurred a few weeks in advance of seasonal stratification. This was due to the restratifying action of mesoscale eddies that acted to flatten the isopycnals around the convective area, preventing vertical mixing and enabling an early bloom there. A decade later, this process was very elegantly confirmed by *in situ* observations in the North Atlantic [MAH 12]. Another impact of the mesoscale and sub-mesoscale dynamics is through the associated frontal vertical velocities, which constitute an efficient pathway to supply nutrients to the euphotic layer. Model results suggest that this process constitutes a year-long source of new nutrients to the euphotic layer that adds up to the one-off winter supply associated with deep convection in the summer season, and enables the duration of the bloom to be extended [LÉV 00]. These small-scale phenomena likely play an important role in the strong year-to-year variability in the timing and amplitude of the bloom [MAY 16], which cannot be explained by variations in mixed layer depth alone [LAV 13].

Since these early modeling studies in the 1990s, more complex biogeochemical and dynamical models of the Mediterranean Sea have been developed [RIC 18] and have enabled us to tackle the richness of the biogeochemical processes in this small but extremely representative region of the world's ocean. Further development of such models – as increased knowledge of important biogeochemical processes becomes available – through dedicated field and lab studies, combined with increased computer capacities – in order to better resolve small-scale physical processes – will allow us to better project the future changes that the Ligurian Sea ecosystems are facing in response to climate change.

6.4. References

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7

Pelagic Viruses, Bacteria and Archaea

In the following, a short synthesis of concepts in marine microbial ecology will be provided. For more detailed information (and further literature), please consult the different editions of Microbial Ecology of the Oceans [GAS 18] Gasol J.M., Kirchman D.L., Microbial Ecology of the Oceans, 3rd Edition, Wiley-Blackwell, 2018, [KIR 00] Kirchman D.L., Microbial ecology of the oceans. First Edition, John Wiley & Sons, 2000, [KIR 08] Kirchman D.L., Microbial Ecology of the Oceans, Second Edition, John Wiley & Sons, Inc., 2008.

7.1. Background

The Ligurian Sea is vertically divided into three main depth zones (Figure 7.1). The epipelagic or sunlight zone extends from the water surface down to a depth of 200 m. This upper layer is influenced by light and is especially productive because the primary producers (algae and cyanobacteria) produce biomass through photosynthesis. This primary production is the major foundation of life in the oceans. Below the epipelagic zone, there is the mesopelagic or twilight zone, extending down to approximately 1,000 m. This zone of the ocean is the sandwich layer between euphotic surface waters and the deep ocean and acts as hub between them. The physical, chemical and biological processes in this layer strongly influence the marine carbon cycle. Below this layer, the bathypelagic zone extends from 1,000 to 4,000 meters below the surface. The meso- and

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Chapter written by Markus WEINBAUER and Branko VELIMIROV.

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

especially the bathypelagic zone (both together also known as the "dark ocean") are characterized by high pressure.

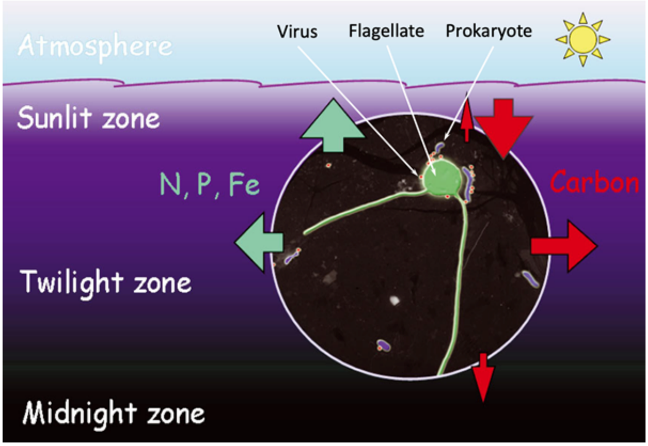

Figure 7.1. *Crucial role of the microbial loop (blue: prokaryotes; red: viruses; green: flagellate) for nutrient regeneration and carbon processing in the twilight zone. Redrawn from Weinbauer* et al. *[WEI 13]. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip*

7.1.1. *Microbial food webs*

It is now well-established that micro-organisms play a crucial role in microbial food webs and biogeochemical cycles [AZA 83, POM 74]. The classical concept of the grazing food chain composed of phytoplankton and herbivorous and carnivorous zooplankton has been extended by several concepts concerning micro-organisms.

Dissolved organic matter (DOM) is, for example, released or "exuded" from phytoplankton or produced by during feeding of zooplankton. Bacteria and archaea (together called prokaryotes) are the main users of DOM, and are consumed by flagellates and ciliates, which are eaten in turn by meso- and macrozooplankton. Thus, bacterial assimilation and subsequent grazing on bacteria return carbon that would otherwise be lost, back to the food web. Such grazing also results in a remineralization of organic matter. These pathways are referred to as the microbial loop. Viral lysis is another important source of prokaryotic mortality. Viral lysis does not only kill cells and releases new viral particle, but also converts cells into DOM (the cell content) and particulate organic matter (POM, cell wall fragments). These lysis products are taken up by prokaryotes thus generating a viral loop or viral shunt [WIL 99], which stimulates prokaryotic production and respiration [FUH 99]. Hence, viral lysis catalyzes nutrient cycling and "lubricates" the microbial food web [SUT 07] (Figure 7.2).

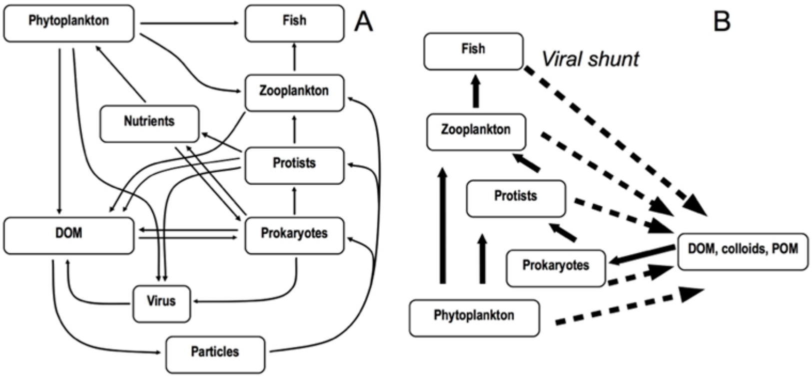

Figure 7.2. *Idealized food webs. A) Simplified planktonic food web with grazing food web (phytoplankton – zooplankton), microbial loop (DOM – bacteria – protists) and B) viral shunt*

7.1.2. *Microbe-mediated ecosystem functions and biogeochemical cycles*

The carbon pool in the form of DOM is approximately as large as the carbon pool in atmospheric CO_2 and in all global biota. Thus, the fate of dissolved organic carbon (DOC) and particulate organic carbon (POC) is an important factor influencing climate. One of the most significant functions of bacteria in the ocean is the transformation of DOC partly into biomass and hence into POC which is utilizable again in the food web and is partly sequestered into CO_2 by respiration.

At the microscale level, the microbial community is operationally structured (by filtration) into free and particle attached micro-organisms. Attached micro-organisms are embedded in a nutrient-rich organic matrix, and prokaryotic abundances and activities on particles can be one or two order of magnitude higher than in surrounding waters [SIM 02]. Organic aggregates (marine snow) and the plume of sinking (or rising) particles are considered to be hot spots of biogeochemical transformations mediated by micro-organisms [AZA 01, AZA 98]. The fate of most of the organic carbon generated by primary production in the upper ocean is remineralization to CO_2. A small fraction of the fixed carbon is not mineralized but stored for millennia as refractory DOM (see Volume 2, Chapter 1 of this book series). Recently, the microbial carbon pump has been proposed as a conceptual framework to address this important, multifaceted biogeochemical problem [JIA 10].

7.2. Study sites

The study site Point B is a permanent coastal station (Point B: 43°51'10''N, 07°19'00''E; bottom depth: > 90 m) at the entrance of the Bay of Villefranche and is influenced by the cyclonic Liguro-Provençal Current running from east to west along the French Riviera [NIV 76]. Under prevailing conditions, this current enters the Bay, which results in continuous water renewal. There is no noteworthy shelf in this steeply descending bay. Water stratification begins typically in March is strongest in summer and starts to erode in fall. During the onset of the stabilization of the water column in spring, a phytoplankton bloom develops; during the erosion of the stratification in fall, phytoplankton blooms have been observed as well [BUS 95]. The study site is considered as an oligotrophic coastal system [SHE 92].

The study site Point C (43°51'00"N, 07°19'00"E) is located right off the entrance of the Bay of Villefranche (France, NW Mediterranean Sea) where the water depth is >300 m. Another investigation site was located 200–300 m off the research station STARES0 in the Gulf of Calvi (42°35'N, 8°45'E) (Corsica). A dense *Posidonia oceanica* bed characterizes the shallow benthos of the gulf.

Another important study site in the Ligurian Sea is the JGOFS (Joint Global Ocean Flux Studies) site DYFAMED (Dynamique des Flux Atmosphériques en Mediterranée) (43°12'50''N, 07°15'20''E) where the water depth is approximately 2,400 m.

7.3. Diel variability of micro-organisms

Planktonic microbial communities often appear stable over periods of days and thus tight links are assumed to exist between different functional groups (i.e. producers and consumers). At Point B and DYFAMED diel, variations of prokaryotic and viral parameters were observed [BET 02, GHI 07]. At DYFAMED, the activity of attached bacteria was characterized by pronounced diel variations in the upper mixed water column with higher activities at night. This activity was due to bacteria attached to organic aggregates. These diel variations in activities were concomitant to changes in bacterial community structure, mainly in the upper layer. Most of the attached phylotypes were also free-living phylotypes, suggesting that attached bacteria probably originate from the colonization of newly-formed particles by free-living bacteria in the upper layer [GHI 07].

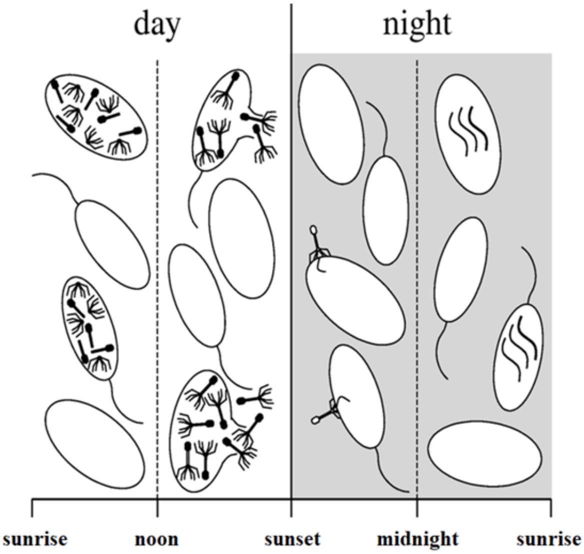

Figure 7.3. *Idealized diel cycle of viral infection and lysis of bacteria. Viruses infect bacteria during the night and start propagating (reproducing first DNA strands and then start assembling, i.e. packing DNA into virus protein capsids). Around late noon (when bacterial production starts to rise as by product of rising phytoplankton production), virus assembly culminates and results in the lysis of cells and the release of newly formed viruses*

Diel variations in substrate availability (largely due to variations in phytoplankton production) can lead to pronounced diel patterns in prokaryotic activity in the euphotic zone. To test the relationship between prokaryotic production and viral infection, three sites were investigated by following distinct water masses in the North Sea. Prokaryotic production was approximately 1.5- to 5-fold higher during the day than at night. The viral lysis of bacteria occurred in the afternoon, and infection during early night (Figure 7.3). Moreover, lysis and viral production took place during high prokaryotic activity; this could be a strategy to increase the number of newly produced viruses [WIN 04]. It is reasonable to assume that such diel cycles also exist in the Ligurian Sea.

7.4. Seasonal variability of micro-organisms

Based on a stratification index, three types of periods differing with respect to water column stability were identified (as also previously shown for Point B [BUS 95]: 1) a summer stratified period, 2) mixed period and 3) semi-mixed period (for spring and fall–winter conditions). The fall–winter semi-mixed periods are very short. The spring bloom typically starts with the establishment of water stratification.

In temperate marine ecosystems, the spring phytoplankton bloom is often a period during which changes in microbial activity are prominent. This was also the case at Point B as prokaryotic production and respiration showed maxima following the gross primary production and chlorophyll a (Chl a) maximum. Interestingly, elevated Chl a concentrations were also observed in fall together with an elevated prokaryotic abundance and respiration. Such fall Chl a maxima are not only known for the Ligurian Sea [BUS 95] but also from other Mediterranean bays. Moreover, differences between hydrologically defined periods support the idea that phytoplankton blooms fuel PP, for example by the release of organic matter or the formation of detritus. In this sense, typical seasonal variability was detected.

Low prokaryotic production rates occurred in autumn and winter, i.e. during the mixing period, whereas the highest activity occurred after the spring phytoplankton bloom and in early summer. Overall, prokaryotic production rates were significantly higher during the stratified and semi-stratified than during the mixed period. Prokaryotic production represented between approximately 1% and 70% of gross primary production, and reached the highest values during the spring blooms (up to 37–70%).

Seasonal changes of bacterial community composition (BCC) were observed at Point B. Several periods grouped together such winter community and phytoplankton spring blooms. Another cluster was related with the *Synechococcus* sp. bloom period of late spring, as well as with summer samples. The changes in phylotypes during blooms have been observed before. It has to be noted, however, that BCC does not always change along with prokaryotic activity during phytoplankton blooms. Nevertheless, a stability of bacterial communities in the sense of annually re-occurring phylotypes has been demonstrated. In the Gulf of Calvi, the number of Denaturing gradient gel electrophoresis (DGGE) phylotypes varied only little between summer and winter, although prokaryotic abundance varied by an order of magnitude and prokaryotic production by almost two orders of magnitude [HAL 00, VEL 92].

Some chemical and most biological parameters showed a strong seasonal variability at Point C [WEI 13], thus confirming the emerging view that this mesopelagic water layer is more dynamic than previously thought. Community respiration was likely influenced by seasonal changes as indicated by its indirect relationship with water density. The high community respiration rates confirm that the twilight zone plays a critical role as a hub between surface and deep water. Statistical analyses indicate that water stratification, dissolved organic carbon, and transparent exopolymeric particles (TEP) are controlling factors of bacterial community composition, whereas the archaeal community is likely controlled by other (unknown) mechanisms.

Prokaryotic abundance in the epi-, meso-, and bathypelagic at DYFAMED varied on a seasonal scale [GHI 07, WIN 09b]. In addition, prokaryotic diversity as assessed by DGGE and randomly amplified polymorphic DNA (RAPD) fingerprints showed a strong seasonal variability [WIN 09a, WIN 10]. Single-strand conformation polymorphism (SSCP) revealed that free-living and attached prokaryotes clustered separately; in addition, within these prokaryotic groups, there was a clear distinction between spring and summer communities [GHI 07].

At Point B, viral abundance peaked typically approximately one month after the spring bloom and simultaneously with a peak in prokaryotic abundance. The virus to prokaryote ratio ranged typically from 4 to 55. Viral abundance was positively related to prokaryotic abundance.

In addition, a negative relationship existed between the frequency of infected cells (FIC) and the frequency of lysogenic cells (FLC was detected at Point B). Such a negative relationship was also documented before from a survey at DYFAMED and oxic and anoxic seawater [WEI 03]. This could indicate that environments exist, where one of the two viral life styles prevail. FIC was related to viral abundance and prokaryotic abundance and production, whereas FLC was negatively related to prokaryotic abundance and production. The interpretation of that is that lysogeny is a survival strategy at low host abundance and activity, whereas high host abundance and activity seems to favor the lytic lifecycle.

At DYFAMED, viral abundance varied on a seasonal scale. A strong seasonal variability was also shown by RAPD fingerprints. Overall, the seasonal variability of viral and prokaryotic parameters at DYFAMED is driven by the seasonal mixing of the water column [WIN 09a, WIN 09b, WIN 10].

7.5. Variability of micro-organisms: sunlight versus dark ocean

DGGE community profiles and sequence analyses of DGGE bands and a literature comparison suggest some specificity of the mesopelagic zone (Point C) regarding bacterial and archaeal community composition, thus further confirming the peculiarity of this water layer [WEI 13].

At DYFAMED, prokaryotic abundance decreased with depth by approximately an order of magnitude [TAM 02, WIN 09b]. Prokaryotic production decreased by at least an order of magnitude with depth [TAM 02, WEI 03]. The potential assimilation rates of extracellular polymeric substances (EPS) in the epipelagic decreased slightly with depth, whereas glucose assimilation rates decreased by more than two orders of magnitude. The percentages of bacteria assimilating glucose decreased with depth by two fold for EPS. In contrast, the contribution by *Euryarchaea* to EPS consumption increases with depth by six fold. In the bathypelagic, about 50% of active cells consuming glucose are *Euryarchaea*. This hints at potential differences in the roles of bacteria and archaea in the deep-sea biogeochemical cycles, and shed light on the importance of deep-sea *Euryarchaea* in the degradation of dissolved organic matter. Furthermore – as at Point C [WEI 13] – the correlations with parameters differed between bacteria and archaea, thus supporting the idea that their roles might deviate in the dark ocean [BOU 11]. Aminopeptidase and phosphatase activity were higher in the epipelagic than in the dark ocean [TAM 02].

In bathypelagic waters at DYFAMED, prokaryotic-induced exoenzymatic activity is affected by pressure conditions. Generally, aminopeptidase and phosphatase rates measured in samples maintained under *in situ* pressure conditions were 2.3 times higher than those measured in their decompressed counterparts [TAM 02]. This shows that there are adaptations of prokaryotes to high pressure (barophilic prokaryotes).

The relative abundance of *Crenarchaea* and *Euryarchaea* in the epipelagic zone increased as stratification decreased. As in other environments, the proportion of *Crenarchaea* was highest in mesopelagic waters. Based on detection frequencies calculated for each depth layer, specific bacterial and archaeal phylotypes could be detected indifferent depth layers [WIN 09a]. The sequence analysis of RAPD-PCR bands showed that the majority of sequences from the microbial fraction were related to *Alphaproteobacteria*, *Cyanobacteria*, *Gammaproteobacteria*, *Firmicutes* and *Eukaryota*. In other environments, most of the sequences from the virus fraction (>90%) do not yield hits as in the nr database of GenBank. The links between changes in the microbial and viral community were strongest in the bathypelagic zone. This suggests a strong co-development of virus and host communities in deep waters. The data also indicate that virus communities in the bathypelagic zone can exhibit substantial temporal dynamics [WIN 10]. An SSCP analysis revealed distinct communities for 0–40 m, 60–150 m and 200–1,000 m [GHI 08].

Deep vertical mixing at DYFAMED represents the beginning of a seasonal succession. The effects of this succession were detectable throughout the water column and did lead to distinct prokaryotic and viral communities in different depth layers during the stratified period [WIN 09a, WIN 09b, WIN 10]. In addition, nitrate, phosphate, salinity and temperature were strong predictors for the depth variability of bacterial communities [GHI 08] and these parameters are linked to deep vertical mixing.

The seasonal variability of prokaryotic abundance and viral abundance and their subpopulations as well as apparent prokaryotic and viral richness, and community composition were comparable between the different depth layers. This suggests that the dark ocean shows a dynamic comparable to that of the surface ocean [WIN 09a, WIN 09b, WIN 10].

7.6. Effect of episodic events on micro-organisms: upwelling and aerosols

Other potential sources of changes can occur on a different time scale and at less predictable frequencies such as wind-driven upwelling, forest fires and deposition of aerosols. Data of forcing factors for prokaryotic and viral abundance, activity and diversity are summarized in Tables 7.1 and 7.2.

Forcing factor	Environment	Effect
Sahara dust	Point B in situ	+PA, +PP, +PGE
	Point B exp.	+VA, +PA, +PP, +CR
Volcano ash	Point B exp.	+VA, +BA, +PP, +CR
Black carbon-rich aerosols	Point B exp.	+/VA, -FIC, -VP, +PA, +PP, +CR
Turbulence	Point B exp.	PP
Global warming (GW)	Point C exp.	+PA, +PR
Ocean acidification (OA)	Point C exp.	-PR
GW+OA	Point C exp.	+/-PR

Table 7.1. *Forcing factors for viral and prokaryotic biomass and activity. +, stimulation; -, repression; +/-, unclear effect. PA, prokaryotic abundance; PP, prokaryotic respiration; PGE, prokaryotic growth efficiency; CR, community respiration; VA, viral abundance; FIC, fraction of infected cells*

7.6.1. *Upwelling*

Meteorological, temperature and salinity data suggest that in July 2003, deep water entered the Bay of Villefranche due to an upwelling event driven by a storm [BON 10]. Such events have been documented before [NIV 75, NIV 76]. Since deeper water is characterized by low viral and prokaryotic abundance [WIN 09b], the low values of these parameters after the storm are likely due to upwelling of deep water. In addition, bacterial community structure in 30 m clustered together with pre-bloom and bloom communities.

7.6.2. *Sahara dust aerosols*

Sahara dust deposition events are frequently recorded in the NW Mediterranean; they typically occur as dry deposition [RID 02]. Rain and Sahara dust can contain phosphorus and organic carbon, and this can stimulate prokaryotic production [MIG 99, PUL 08, RID 02].

In February 2004, a strong Sahara dust wet deposition event occurred, which was associated with a cold front and even reached central Europe (EUMETSAT data base; http://www.eumetsat.int/Home/index.htm). Rain occurred between February 20 and February 24. Aerosol deposition of Fe and Ca was approximately seven and three fold higher than in the previous week, while wet deposition of phosphate and nitrate was five and six fold higher compared to the values usually recorded at that time of the year. In addition, particle load measured a few days after the event was almost two fold higher than the month before. In addition, nitrate and phosphate concentrations were higher than in the week before.

Forcing factor	**Environment**	**Cluster bacteria**	**Cluster archaea**	**Stimulated phylotypes**	**Repressed phylotypes**
Sahara dust	Point B exp.	yes	na	*Polaribacter, Roseobacter, Ruegeria, Antarctobacter, Tenacibaculum*	*Lexinella, Sulfonomonas, Thalassobius*
Volcano ash	Point B exp.	yes	na	*Glaciecola*	
Black carbon-rich aerosols	Point B exp.	yes	na	*Glaciecola*	
Turbulence	Point B exp.	yes	na	*Oceanospirillum, Rhodobacter*	*Roseobacter*
Global warming (GW)	Point C exp.	yes	yes		

Ocean acidification (OA)	Point C exp.	yes	yes		
GW+OA	Point C exp.	yes	yes	*Polaribacter*	

Table 7.2. *Forcing factors for prokaryotic diversity. na, not analyzed*

On February 25, Sahara dust had reached 30 m as indicated by particle profiles. At this depth, the prokaryotic production was 2.1- to 2.3-fold higher than in shallower water [BON 10]. The depth-integrated value of prokaryotic production at this sampling date was 2.9-fold higher than on January 20, 2004 and 2.7-fold higher than on February 19, 2003. The Sahara dust event was associated with high viral abundance, particularly, at 20 m. In addition, we could only detect elevated phosphate but not elevated DOC values after the end of the wet deposition event. Pulido-Villena *et al.* [PUL 08] calculated phosphate and DOC input from deposition data and data measured *in situ* in the NW Mediterranean Sea (45 km off the Bay of Villefranche) and estimated that during a dry deposition event in June 2006, 0.01 µM phosphate and 2.6 µM DOC were added to the mixed water column. Such an import of DOC is likely too small to be detectable against the background values (approximately 60 µM in January and February 2004).

For prokaryotic respiration, no consistent effects were found following the Sahara dust deposition event. However, after the Sahara dust event, prokaryotic growth efficiency (PGE) ranged from 0.02 to 0.24 (average: 0.10) across the water column with the highest value in 30 m, whereas before the event, PGE ranged from 0.004 to 0.02. The adsorption of organic matter to the dust particles along with colonization of particles by bacteria and subsequent use of organic material could have caused the change in prokaryotic activity.

After the Saharan dust deposition event, particular changes were observed in the dominance pattern from the DGGE profiles. At 30 m, richness showed a strong increase, whereas it was rather stable at all other depths and richness was higher than for the pre-deposition event sampling. In addition, bacterial community composition was different after the deposition event, indicating that Sahara dust deposition can influence bacterial diversity. The adsorption of organic matter to the dust particles along with colonization of particles by bacteria and subsequent use of organic material could have caused the change in richness (e.g. by increasing the number of niches).

Experimental studies with dust collected during the wet deposition event in February 2004 showed that the dust stimulates prokaryotic production. This is probably due to the high organic matter content of the dust particles or due to adsorption of DOC from the water column [LEK 10], since it is well known that prokaryotic production is elevated on particles. There is also evidence from experimental studies that bacterial community composition changes due to dust deposition [LEK 10, ROM 11]. In addition, viral abundance was stimulated in this experiment.

7.6.3. *Volcano ash aerosols*

Volcano ash deposition is now considered as an important source of inorganic bioavailable iron that can relieve Fe-limitation in the ocean. As volcano ash also releases PO_4, volcano ash deposition could also affect nutrient dynamics and bloom development in a P-limited system such as the Ligurian Sea and the Mediterranean Sea in general. Ash was collected from the Eyjafjallajökull eruption in 2010. This material was also deposited into the Mediterranean Sea. In a 54 hour experiment with Point B water, it was shown that the development of a phytoplankton bloom was not enhanced or even repressed by ash additions of 2 and 20 mg l^{-1}, whereas higher ash concentrations (200 mg l^{-1}) induced a phytoplankton bloom as indicated by elevated Chl a levels. Concurrently, net community production (NCP) and gross primary production (GPP) were enhanced at T24h at the highest ash additions. The metabolic balance was roughly neutral at low or no ash additions, but shifted towards phototrophy at the highest ash additions. The data on inorganic nutrient development and release estimates from ash material assays suggest relieving of P-limitation concomitant with nitrate and silicate use from ash. The concentration of TEP increased with increasing ash levels. The abundances of the heterotrophic compartment (bacteria, viruses and ciliates) also indicated dose–dependent responses. The data suggest that heterotrophs won the competition for inorganic nutrients at ash levels of 2 and 20 mg l^{-1}, whereas phytoplankton won at levels of 200 mg l^{-1}. Preliminary data suggest that enhanced TEP formation and attachment of bacteria to particles caused changes in activity. Overall, our experiments point to a strong potential of volcano ash deposition as forcing factor for nutrient dynamics and the activity of microbial plankton in a P-limited system.

At the end of the experiment, a phylotype appeared in all ASH-200 replicates (*Rhodobacteraceae*, 99% similarity). For attached bacteria, there was an immediate significant difference between treatments at T0h. In ASH-20 and ASH-200, an *Alteromonas*/*Glaciecola*-related phylotype appeared and in ASH-20, the *Vibrio pomeroyi* phylotype appeared, whereas only in the control, ASH-2 and ASH-20 *Rhodobacteriaceae* was present. At Tfinal, *Haliscomenobacter* (*Bacteriodetes*) was present in the control, *Alteromonas*/*Glaciecola* ASH-2 in ASH-20 and ASH-200 and *Synechococcus* in ASH-200. Interestingly, the *Glaciecola* phylotype (identical sequence) was also found in treatments with BC aerosols where experiments were performed with Point B water but in a different year (see section 7.6.4).

7.6.4. *Black carbon-rich aerosols*

Black carbon (BC, soot) has anthropogenic and non-anthropogenic origins. While BC can contribute significantly to dissolved and particulate organic carbon pools in marine systems, data are still sparse for the water column. Due to the association of BC aerosols with organic acids, the deposition of BC aerosols at the surface of the ocean can decrease the pH in seawater and thus represents a non-pCO_2-based source of ocean acidification. Data from experiments with reference material and BC aerosols suggest that BC strongly absorbs organic carbon and micro-organisms [CAT 10]. This “active charcoal” effect has several consequences. BC traps dissolved organic matter and this increases the size of organic particles. On the one hand, this could increase export of organic matter into the interior of the ocean and, on the other hand, this could increase the oxidation of organic matter in surface water; the net-outcome remains unknown. The observed increased prokaryotic production after BC addition could be due to the accumulation of organic matter by adsorption to BC (thus creating hot spots of biogeochemical transformation), direct use of BC and/or reduction of prokaryotic mortality by BC-mediated reduction of viral lysis [MAL 15]. UV exposure, a feature that can be expected when BC is released into the atmosphere before deposition into water occurs, makes BC more bioavailable. BC also changes bacterial community composition. DGGE results suggested that BC has the potential to favor phylotypes related to *Glaciecola* sp. Finally, there is evidence that BC and atmospheric brown clouds (ABCs) will overall enhance global warming and the frequency of forest fires and dust storms, and will contribute to ocean acidification. Thus, strong indirect effects on micro-organisms can be expected. Overall, there is evidence that BC is (at least regionally) a strong forcing factor for the microbial food web and microbe-mediated biogeochemical cycles. Due to the prospected increase of BC emission in the years to come, the role of BC for microbe-mediated processes should become even more prominent [WEI 12].

During an *in situ* study, compared to 2002 and 2004, the summer period of 2003 (July–August) was characterized by a higher frequency of forest fires in the west of the sampling area. The main wind direction during the forest fire period was westerly and the deposition of fly ash into the Bay of Villefranche could be observed on one occasion. The number of forest fires was 25–50% higher in 2003 than in 2002 or 2004. Moreover, the forest fires destroyed 20–100 times more forest area, and large fires (>1 km_2 destruction) were seven times more frequent in 2003 than in 2002 and 2004 [BON 10]. During this period, NO_3 and PO_4 concentration and prokaryotic production and growth efficiency were higher than during the period before or afterwards. This increase of prokaryotic activity is likely due to input of PO4 by ash deposition.

7.6.5. *Conclusions*

It has been argued that monthly sampling is sufficient to detect seasonal changes in bacterial community composition. Seasonality with reoccurring patterns has also been found in our study (section 7.4). However, it has also been argued that episodic events can occur at shorter time scales. Such events are documented for the Ligurian Sea. All these events were followed by changes in biomass/activity or changes in richness. Although firm cause–effect relationships cannot be established by descriptive studies, the data indicate that short-term events create disturbances in productivity and diversity. According to the intermediate disturbance hypothesis, this could contribute to sustaining bacterial diversity in the Ligurian Sea [MOT 13].

In conclusion, our data suggest that irregular short-term events can significantly modify the seasonal variability of bacterial richness and ecosystem processes. This could 1) cause interannual variability, 2) mask relationships between parameters such as richness and production, and 3) sustain richness by providing intermediate disturbances.

7.7. Effect of turbulence on micro-organisms

Prokaryotes and viruses are too small to be affected directly by turbulence. However, they can be influenced indirectly, e.g. when turbulence influences photosynthetic extracellular release or the formation of organic aggregates. At Point B, turbulence stimulated prokaryotic production and increased prokaryotic cell length; turbulence also caused the formation of organic micro-aggregates with attached prokaryotes. Thus, turbulence likely influenced prokaryotes indirectly by affecting micro-aggregate formation and nutrient availability. Turbulence had only a small influence on the number of bacterial and archaeal bands as detected by 16S rRNA DGGE. However, considering presence versus absence of specific bands and their intensities, turbulence had a strong effect on community composition. Not only a negative effect of viruses was detected, but also that some bands increased in intensity in the presence of active viruses, for example one of three phylotypes affiliated with the *Rhodobacteriaceae*. Turbulence influenced negatively a phylotype affiliated with *Roseobacter* (in terms of band intensity), whereas the relative band intensity of a *Rhodobacter* increased in the turbulence treatments, and a phylotype related to *Oceanospirillum* was detectable (by DGGE) only in the turbulence treatment. Thus, turbulence likely plays a significant and previously neglected role in shaping prokaryotic diversity, aggregation and production [MAL 09].

7.8. Effect of global warming and ocean acidification on micro-organisms

In the Ligurian Sea, the effects of ocean acidification and the additional effect of elevated temperature on microbial communities were assessed for mesopelagic communities (300 m water depth) from Point C in short-term (3–5 days) experiments. A gradient of pCO_2 levels (five experiments) ranging from pre-industrial levels to levels higher than those projected for the end of the century was used to test the effect of ocean acidification on biomass accumulation and prokaryotic respiration. In addition, two temperature levels were applied: current and elevated (+ 3°C). Triplicate experiments were also done (at 13°C) using two pCO_2 levels: ambient (approximately 400 µatm) and at elevated pCO_2 (approximately 1,000 µatm; predicted end of century scenario). In some experiments, statistically significant effects of elevated pCO_2 were found for nutrient concentrations, TEP, microbial abundance and prokaryotic respiration. However, these effects were not consistent across experiments. No consistent additive or subtractive effects of elevated pCO_2 levels and temperature were found. These results suggest a context-dependent response whereby the metabolic and/or compositional differences of the community can influence the response to climate-related stressors.

The potential effect of climate change (global warming and ocean acidification) on microbial communities on mesopelagic communities was also studied in long-term (two months) experiments at Point C. Elevated temperature (by 3°C) had either a neutral or a stimulating effect on prokaryotic abundance and respiration, whereas elevated pCO_2 levels (corresponding to end of century predictions) had a neutral or negative effect on prokaryotic respiration. Effects of both potential stressors on prokaryotic respiration were rather antagonistic than synergistic. The data suggest that global warming could short circuit the biological pump by enhanced organic matter oxidation, whereas ocean acidification would likely prime it; the effect of both stressors could be a dampening of the effect of climate change. Analyses of bacterial and archaeal community composition as assessed by 16S rRNA DGGE suggest strong shifts by elevated temperature and (for bacteria) by elevated pCO_2 plus elevated temperature. No specific phylotype were associated with treatment effects, except for the absence of a *Polaribacter* related phylotypes in the treatment with elevated temperature plus elevated pCO_2. However, phylotypes belonging *Flavobacterium*/*Cytophaga*/*Bacteroides* clusters were more often affected by the various treatments than *Alphaproteobacteria*, *Gammaproteobacteria* or *Actinobacteria*, thus suggesting a potential influence of elevated temperature and pCO_2 on bacteria often associated with organic particles. In addition, archaea were affected by the treatments and the effect was strongest in treatments with both stressors.

7.9. Effect of P-limitation on micro-organisms

The Bay of Villefranche is typically P-limited in summer [DOL 95, TAN 04, THI 97, THI 98]. It has been suggested that P limitation of prokaryotes was relieved in summer 2003 due to input of fly ashes originating from strong forest fires [BON 10]. It has also been shown that P addition stimulates viral growth and roseophage genomics indicates P limitation. Thus, one could expect that relieving P limitation and stimulating prokaryotes production would also increase viral production. Indeed, the addition of P enhanced prokaryotic growth and viral production at Point B. The concentrations of total dissolved nitrogen increased linearly with decreasing viral abundance, prokaryotic production and PGE across treatments. Our data suggest that microbial growth can also be P-limited in winter and that viral lysis products can be readily used by prokaryotes depending on nutrient availability [MOT 15].

The Bay of Villefranche is typically P-limited in summer. However, in 2003, phosphate concentrations were higher during the summer period than in late spring and early fall 2003. In parallel, the frequency of forest fires was high during summer 2003 and might have supplied nutrients, since it is well known that fly ash from forest fires contains inorganic nutrients (e.g. phosphorus). As in other studies [THI 97], an increase in DOC concentration was detected following the spring bloom event in 2003. However, this accumulation phase of DOC ended earlier in 2003 than in previous years, i.e. before the seasonal erosion of the thermocline due to storms (winter mixing), although the strong forest fires should have supplied additional organic carbon in this year (e.g. in the form of black carbon) to the system. The phosphorus input by forest fires could have relieved the P-limitation and stimulated prokaryotic production. In addition, it is possible that not only phosphate, but also some organic P has been imported by atmospheric deposition originating from forest fires and used by heterotrophic bacteria. The consequence of the atmospheric input could have been the oxidation of the accumulated DOC by relieving the competition for phosphate between bacterio- and phytoplankton [THI 97, THI 98]. Therefore, it is possible that less carbon was exported due to winter mixing in this year.

7.10. Effect of viral lysis and flagellate grazing on prokaryotic diversity and growth

Viral lysis and grazing by flagellates are the main factors causing mortality of prokaryotes, and thus shaping diversity and activity of prokaryotes [PER 05a, PER 05b, WEI 04a, WEI 04b]. At Point B, viral lysis influenced bacterial community composition and diversity as assessed by DGGE and TRFLP. For example, a phylotype related to *Roseobacter* was negatively affected by viruses [MAL 09, MOT 13]. Bacterial community composition and diversity as assessed by DGGE were also influenced by grazing. *Polaribacter* assessed by catalyzed reporter deposition fluorescence *in situ* hybridization (CARD-FISH) showed defense against grazing, while *Roseobacter* was highly susceptible to grazing. This supports the hypotheses that grazing influenced bacterial community composition.

At Point B, experiments were performed with and without viruses. The phylotype composition showed strong differences between the two treatments [MOT 13].

At Point B, viral lysis increased cell size and negatively affects the formation of aggregates [MAL 09]. It is possible that the formation of aggregates was only delayed as shown for algal marine snow in the Northern Adriatic [PED 93]. *Synechococcus* at Point B and in the Gulf of Mexico needs the presence of viruses for its growth. This is probably due to lysis products of heterotrophic bacteria which are essential for the growth of *Synechococcus* [WEI 11].

At Point B, prokaryote respiration was stimulated by viruses (up to 113%), whereas prokaryotic production and PGE were reduced (up to 51%). This suggest that viruses enhance the role of bacteria as oxidizers of organic matter, hence as producers of CO_2, and remineralizers of CO_2, N, P and Fe. Prokaryotic growth efficiency depended on the fraction of prokaryotes production destroyed by viruses (shunting efficiency). Including data from the western North Pacific and the Southern Ocean, it was shown that prokaryotic growth efficiency is negatively correlated with shunting efficiency. Predictions from a carbon flow model are consistent with the above results showing that decreased prokaryotic growth efficiency can be largely explained by viral-induced conversion of prokaryotes biomass to dissolved organic carbon. Thus, viruses exert the major influence on patterns in carbon fluxes mediated by bacteria in marine pelagic environments [MOT 09].

It is well-known that grazing by flagellates reduces prokaryotes abundance and growth at Point B. In contrast to a current model of the effects of grazing, the cell size distribution was unimodal and not bimodal. However, significant shifts towards larger cell size classes were observed.

This finding is in accordance with the idea that increasing the cell length is a prokaryote strategy to reduce susceptibility to grazing by small flagellates. Only weak evidence was found for the complementary strategy of reducing cell size. Increasing the cell size is likely a prokaryote defense strategy against grazing by small flagellates in marine systems.

7.11. Nanobacteria, ultramicrobacteria and starvation forms

Although the existence of 0.2 µm filterable bacteria has been known since the early 1980's, they are not taken into account when modeling microbial food webs, due to an overall lack of information concerning this specific size class. Diversity studied typically use 0.2 µm pore size filters to collect bacteria. Hence, these bacteria lack in diversity studies. According to physiological studies on starvation forms and investigations on small prokaryote cells in marine ecosystems, a 0.2 µm filtrate may consist of different phenotypes: starvation forms of typical marine bacteria, ultramicrobacteria or prokaryotes cells, even larger than 0.2 µm, but flexible enough to pass the nominal filter pore size. In a study from the Bay of Calvi, three filtered seawater fractions revealed different DGGE patterns of dominant bands for the 0.2 µm filterable and the total bacterial populations within the samples. In addition, the 0.2 µm filterable bacterial compartment exhibited obvious differences in band patterns for winter and summer samples, which were not observed for the total bacterial fraction. According to the current knowledge concerning the status of 0.2 µm filterable bacteria, DGGE patterns indicate that most of the fragments representing 0.2 µm filterable bacteria were rather starvation forms of marine bacteria than ultramicrobacteria. The phylogenetic affiliation of the 0.2 µm filterable bacteria clustered mainly with known, typical marine isolates of both *Gammaproteobacteria*, *Alphaproteobacteria* and the *Cytophaga-Flavobacterium-Bacteroidetes* branch [HAL 00]. In addition, such small cells could be obtained in the laboratory during starvation experiments, indicating that bacteria that survive periods of nutrient deprivation manifest a decrease of cell size. It could be shown that despite conceptual shortcomings and problems with definitions of what is meant by "small", starvation forms and ultramicrobacteria are clearly distinguishable according to physiological characteristics [VEL 01].

7.12. Microbial diversity hypothesis

A general model of species diversity predicts that the latter is maximized when productivity and disturbance are balanced.

Based on this model, it was hypothesized that the response of bacterial diversity to the ratio of viral to bacterial production (viral production/prokaryotic production) would be dome-shaped. In order to test this hypothesis, data were obtained on changes in bacterial communities (16S rRNA gene TRFLP) along a wide viral production/prokaryotic production gradient (more than two orders of magnitude), using seawater incubations from Point B surface waters, i.e. control and treatments with additions of phosphate, viruses or both. Statistically robust dome-shaped response patterns of bacterial diversity to viral production/prokaryotic production were observed, with significantly high bacterial diversity at intermediate viral production/prokaryotic production. This was consistent with the model-based hypothesis, indicating that bacterial production and viral-induced mortality interactively affect bacterial diversity in seawater [MOT 13].

7.13. Horizontal gene transfer

Weinbauer and Rassoulzadegan estimated 1013 transductants per year in the Mediterranean basin [WEI 04b]. These estimates suggest (in the absence of hard data) that transduction could be a significant and overlooked mechanism in marine microbial ecology.

The most surprising results, however, were reported for auxotrophic *E. coli* cells, to which amino acid prototrophy could be transferred by marine phages (from the Bay of Calvi) at the extremely high rates of up to 2.6×10^{-3} per virus [CHI 00, CHI 97]. This transfer of DNA from marine phages to a non-marine enterobacterium could result from broad-host-range transduction. Although it is often assumed that phages do not trespass the genus barrier, this concept has been questioned. It has been argued that narrow host ranges are an isolation artifact, and it has been shown that host range can vary greatly between marine phages. A large variability of host ranges has also reported for cyanophages.

Experiments where the amino acid deficient strain *E. coli* AB1157 was exposed to a particle fraction harvested from a marine oligotrophic environment (Bay of Calvi), ranging in diameter size between 100 and

130 nm indicated evidence for horizontal gene transfer resulting in revertant cells with restoration of all genetic deficiencies. All revertant strains were able to produce particles of comparable size that were again infectious, appearing at the beginning of the stationary phase. Ultrastructural investigation showed a structural resemblance with membrane vesicles; however, PFGE indicated that the DNA content of some of the particles was 370 kbp, much higher than that of the so far known previously described membrane vesicles providing evidence of a new mechanism for horizontal gene transfer [CHI 11, VEL 11]. DNA extracted from outer membrane vesicles (OMVs) were affiliated to known Alphaproteobacteria, and Gammaproteobacteria, i.e. *Ahrensia kielensis* and *Pseudoalteromonas marina*, respectively. This DNA was larger than 30 kbp with all sequences in single copy and identified as prokaryotic sequences. Inserted viral sequences were not found [VEL 18]. Transmission electron microscopical inspection of OMVs of *A. kielensis* and *P. marina* showed two types of vesicles: bi-layered OMVs with a diameter between 30 and 250 nm and double bi-layered OMVs ranging between 80 and 200 nm. Bi-layered OMVs are characterized by either the presence of a large electron-dense substance or electron translucent. Double bi-layered OMVs contained an electron-dense substance in the core region surrounded by the second bilayer [HAG 14].

Overall, these data suggest that horizontal gene transfer (mediated by viruses and OMV) could have a strong effect on the metabolic versatility and diversity of prokaryotes.

7.14. Acknowledgments

The captain and the crew of the Saggita II and Thethys II are acknowledged for their help with sampling. This chapter is strongly based on the work of Martin Agis, Osana Bonilla-Findji, Clémence Coetsier, Aurélie Dufour, Jinwen Liu, Andrea Malits, Chiaki Motegi and Christian Winter.

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Acronyms

AIRWIN: Air Water Interface. A research project within the European FP5 program and launched in 2001. The aim of the project was to investigate the structure of biological communities living and growing in the sea-surface microlayer, and their role in the transport and cycling of natural organic matter.

BATS: Bermuda Atlantic Time-series Study (http://bats.bios.edu).

BCA: Black Carbon Aerosol (soot).

BOUSSOLE: *BOUée pour l'acquiSition d'une Série Optique à Long termE* (http://www.obs-vlfr.fr/Boussole/html/home/home.php).

CARD-FISH: CAtalyzed Reported Deposition Fluorescence *In Situ* Hybridization, a single-cell based method to detect specific bacterial groups.

CARIOCA: NKE sensor to measure the partial pressure of dissolved CO_2 in seawater in order to quantify air/ocean exchanges.

CNEXO: *Centre National pour l'Exploitation des Océans.*

CNR: *Consiglio Nazionale delle Ricerche.*

CNRS: *Centre National de la Recherche Scientifique.*

The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, First Edition.
Edited by Christophe Migon, Paul Nival and Antoine Sciandra.

CO2SYS: carbonate system calculator using discrete measurements of any two of the other carbonate system parameters (total alkalinity, pH or dissolved inorganic carbon).

DEWEX: DEep Water formation EXperiment was a project carried out over a full annual cycle from June 2012 to September 2013 to better characterize and understand dense water formation phenomena in the northwestern Mediterranean.

DGGE: Denaturing Gradient Gel Electrophoresis usually of PCR-amplified 16S rDNA fragments separated in polyacrylamide gels with linear chemical gradients ranging from 25 to 55% denaturants that are then compared; a genetic fingerprint to profile unknown bacterial communities.

DYFAMED: *DYnamique des Flux Atmosphériques en MEDiterranée* (https://www.seanoe.org/data/00326/43749/).

ECOMARGE: *ECOsystèmes des MARGEs continentales*. ECOMARGE was a French research project initiated in 1983–1984. One of its main goals was the qualitative and quantitative study of particle flux and energy transfer across continental margins.

EROS-2000: European River Ocean System-2000. An interdisciplinary long-term research project on biogeochemical processes in the European coastal environment, which was launched in 1988 in the framework of the European Communities' Environmental R&D Programme.

ESTOC: European Station for Time-series in the Ocean Canary islands (http://siboy.plocan.eu/ESTOC).

EURATOM (or EAEC): European Atomic Energy Community.

GLODAPv2: GLobal Ocean Data Analysis Project version 2 dataset.

GO-SHIP: Global Ocean Ship-based Hydrographic Investigations Program (http://www.go-ship.org).

HOT: Hawaii Ocean Time-Series (http://hahana.soest.hawaii.edu/hot/).

IAEA: International Atomic Energy Agency.

JGOFS: Joint Global Ocean Flux Study.

LOCEAN: *Laboratoire d'Océanographie et du Climat: Expérimentations et Approches Numériques*.

MedFlux: a collaborative research project between scientists from the U.S. and Europe, which was started in 2002 and was mainly funded by the U.S. National Science Foundation. The fieldwork took place in the Ligurian Sea at the DYFAMED long-term site. The goal of the project was to develop a seamless description of carbon fluxes and associated mineral ballast fluxes throughout the water column.

MOOSE-GE: Mediterranean Ocean Observing System for the Environment – Grande Échelle. Annual cruise carried out every summer since 2010 in the north-western Mediterranean basin and supported by the MOOSE program. The objectives of the cruise are to maintain deep moorings and to monitor the physical, chemical and biological properties of water masses from surface to bottom.

PFGE: Pulsed Field Gel Electrophoresis, a method to size-specifically separate DNA fragments (e.g. viruses with different genome size).

PGE: Prokaryotic Growth Efficiency.

RAPD: Randomly Amplified Polymorphic DNA, i.e. random amplification of genomic DNA.

RAPD-PCR: RAPD Polymerase Chain Amplification (DNA amplification).

SOCAT: Surface Ocean CO_2 ATlas (https://www.socat.info).

SOMLIT: *Service d'Observation en Milieu LITtoral* (http://somlit.epoc.u-bordeaux1.fr/).

SSCP: Single Strand Conformational Polymorphism, usually of PCR-amplified 16S rDNA fragment separated in polyacrylamide gels; a genetic fingerprint to profile unknown bacterial communities.

TRFLP: Terminal Restriction Fragment, Length Polymorphism, of PCR-amplified 16S rDNA fragments on polyacrylamide gels or sequencers; a genetic fingerprint to profile unknown bacterial communities.

W1M3A: Fixed-Point Open Ocean Observatory in the Ligurian Sea (http://www.w1m3a.cnr.it/).

WMO: World Meteorological Office (https://public.wmo.int/).

WOCE: World Ocean Circulation Experiment (https://www.nodc.noaa.gov/).

WoRMS: World Register of Marine Species (http://www.marinespecies.org/).

Glossary

Absorbance: a measure of the attenuation of light when passing through a material.

Accessory pigments: pigments found in photosynthetic organisms that have a different molecular structure from chlorophyll-a, and absorb light of wavelengths not absorbed by chlorophyll-a.

Accretion: areas on mid-oceanic ridges on which new basaltic layers are progressively emplaced during ocean opening.

Adsorption: this should not be confused with absorption. It is a surface phenomenon by which atoms, ions or molecules from a liquid or gaseous phase are fixed onto a solid surface. It involves several types of processes such as low-energy van der Waals bonding, covalent or ionic chemical bonding. Desorption is the reverse of adsorption.

Alkaline phosphatase: an enzyme whose catalytic function is optimal at alkaline pH. In the field of oceanography, it hydrolyzes organic forms of phosphorus to phosphate, thus allowing their assimilation by autotrophic organisms.

Alkalinization: the process of making alkaline.

Alkylated compounds: alkylation refers to the transfer of an alkyl group (i.e. an alkane missing one hydrogen) from one molecule to another. Alkylated compounds result from this transfer.

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Amorphous structure: this refers to any non-crystalline solid structure. Atoms and molecules are not organized into a well-structured lattice pattern, which makes such structures soluble, basically, and of which solubility is not dependent on pH.

Ancillary variables: all core variables used in oceanography to describe the marine environment and useful here for CO_2 study (e.g. T, S, O_2, nutrients, Chl-a).

Anomaly: a value that is different from its general long trend (annual or decadal).

Apatite: a group of phosphate minerals that includes hydroxylapatite, fluorapatite and chlorapatite. Its generic formula is $Ca_5(PO_4)_3(F, Cl, OH)$. In general, apatite is very insoluble.

Archaea: one of the three domains of life (beside Bacteria and Eukarya).

Aromaticity degree: the measure of stability of a molecule, this is linked to the number of aromatic rings.

Atmospheric aerosol: an aerosol is a suspension of fine solid or liquid particles in a gaseous environment (e.g. mist, airborne dust, haze). Several types of aerosols (mineral, biogenic, anthropogenic) occur in the atmosphere. They play a key role in Earth’s climate.

Atmospheric deposition: this term gathers the dry deposition (gravitational deposition of airborne particles and gases) and the wet deposition (rainfall).

Autotrophy: a mode of nutrition that characterizes the organisms that produce their own food using light, water, carbon dioxide or other chemical components. Autotrophs serve as primary producers in food webs, for example, plants.

Auxotrophic: auxotroph organisms are unable to synthesize specific organic compounds required for their growth and rely on other organisms that produce and secrete such compounds.

Baroclinic instability: this 3D instability occurs when a surface-intensified geostrophic flow is meandering. It tends to restore a new geostrophic equilibrium by transporting surface water, under the current and in the trough of the meander, while the crest of the meander sees water coming from the depth to surface.

Bioactive metals: in oceanography, these are metals that are needed by organisms' growth (e.g. Fe, Cu, Co, Zn and many others).

Bioavailability: availability of something (chemicals, nutrients) for living organisms. Solubility is often viewed as a proxy of bioavailability.

Biogenic particles: particles produced by biological activity.

Biogeochemistry: a study of the cycle in which chemical elements and substances are transferred between earth scale living systems and the environment.

Biomagnification or **bioamplification:** this refers to the increasing concentration of any substance (here, contaminants) in the organs and tissues of an organism at higher and higher levels along a food chain.

Bioregions: this refers to marine areas of which boundaries are defined by geographical and ecological characteristics.

Bioturbation: this refers to the mixing, or any perturbation, of soils or sediments by living organisms (e.g. the burrowing of soils by earthworms).

Blastozoid: an individual produced by asexual reproduction (budding).

Bloom: fast and significant increase of algal populations.

Brines: highly salty and dense sea waters.

Buoyancy content: see definition in Chapter 3, Box 3.2 "The geostrophic approximation".

Carbonate system: this regroups chemical variables (total alkalinity, dissolved inorganic carbon, pH, pCO_2) that control the seawater pH, the regulation of the CO_2 content of the atmosphere via the biological pump, determine the ocean's influence on fossil fuel CO_2 uptake, and determine the extent of burial of $CaCO_3$ in marine sediments.

Chelating agents: dissolved organic compounds capable of binding a central metal ion or atom to form a coordination complex.

Chromophoric dissolved organic matter (CDOM): the fraction of DOM that absorbs light at UV and visible wavelengths.

Ciliates: a diverse monophyletic group of protists (unicellular eukaryotes) characterized by having cilia or ciliary structures used for swimming and feeding. Ciliates are distinguished cytologically by having two types of nuclei.

Clastites (or **clastic deposits**): surface formations resulting from the weathering of rocks and minerals by a set of mechanical, physico-chemical or biological processes. Clastic sediments and deposits are composed of fragments of older weathered or eroded minerals and rocks.

Cnidocyte: a stinging cell produced by the species of the phylum Cnidaria (Corals, medusae; siphonophores, sea anemones, hydroids) (formerly designed as nematocyte). The cnidocyte can send a kind of arrow attached to the cell with a line, which stings and maintains a prey.

Coccolith-rich oozes and **marls:** marine sediments made from calcareous skeletons of marine micro-organisms.

Colloblasts: sticking elements produced by ctenophore tentacles to secure their prey.

Continental margin: progressive crustal and morphological transition between continental and oceanic domains.

Convection (winter): natural convection occurs in winter when the atmospheric forcing cools sea surface, capping a layer of warm and salty layers.

Coprophagy: nutritional behavior describing organisms that cover at least part of their nutritional needs by feeding on their own excrements or those of other organisms.

Cyanophages: phages infecting cyanobacteria (former blue algae).

Cyclogenesis: the formation of atmospheric cyclonic depression.

Cyclonic circulation: the circulation is cyclonic when the stream horizontally curves anticlockwise in the North hemisphere. More precisely, the curl of velocity is oriented as the rotation axis of Earth when projected on the local vertical.

Decay (nuclear physics): the spontaneous conversion of a nuclide into another nuclide or into another energy state of the same nuclide by emitting radiation. For a collection of atoms, the number of decay events expected to occur within a given interval of time is proportional to the number of atoms present. This decay rate is characteristic for each radionuclide.

Deep convection: the main process of deep-water formation in the world's oceans. It occurs in specific regions of high heat loss to the atmosphere.

Demethylation: methylation is the bonding of a methyl group (CH_3-) to a substrate. Demethylation is the reverse reaction (removal of the methyl group).

Density field: three-dimensional pattern of density. Density increases with depth in the ocean except if local gravitational instability occurs temporarily.

Diagnostic pigment: a noticeable pigment whose detection in water samples indicates the presence of a phytoplankton community.

Diazotrophs: micro-organisms capable of assimilating molecular nitrogen (N_2) by enzymatic means. For these organisms, the reservoir of nitrogen is quasi-inexhaustible.

Dinoflagellates: a diverse monophyletic group of protists (unicellular eukaryotes) distinguished by the possession of two flagella typically arranged, one latitudinally and the other longitudinally, in grooves on the cell surface. Dinoflagellates are distinguished cytologically by a nucleus with condensed chromosomes. Dinoflagellates typically swim rotating about their longitudinal axis, thus spinning like a dynamo.

Dissolved organic carbon (DOC): by convention, a complex mixture of organic molecules that passes through a 0.2 µm filter.

Divalent Hg: the valence of a chemical element is the maximal number of covalent or ionic bonds it can form depending on its electronic configuration. Divalent mercury is Hg^{II} (oxidation state = 2).

***e* ratio:** the ratio between export production and total primary production as defined by Downs in his PhD dissertation (Downs, 1989).

Ecological niche: a volume in a virtual multifactorial space where growth, reproduction and survival of a species is optimal. Temperature–salinity is a simple two-factor virtual space familiar to oceanographers (T–S graph). It is easy to find the niche for summer species (high T and low S) and spring species (low T and high S).

Ecosystem services: benefits that humans derive from healthy ecosystems (e.g. fish stocks, O_2 production, biodiversity, pollination), some of them being potentially affected by global warming and acidification.

Ectoenzymatic activity: this reports on the activity of ectoenzymes (enzymes found at the surface of a cell or outside of it). The ratio between two ectoenzymatic activities characteristic of two different nutrients can be an indicator of inorganic nutrient imbalance.

Ectothermic species: fishes, amphibians, reptiles and invertebrates whose regulation of body temperature depends on external sources, such as sunlight or a heated rock surface.

Electronic Transport System: this refers to the transfer of electrons from electron donors to electron acceptors via redox reactions. Here, it is an indirect measurement of respiration.

Endemism: the ecological state of a species being unique (not found elsewhere) to a defined geographic location or habitat type.

Epipelagic: this refers to the marine surface layer in which light penetrates deep enough to allow photosynthesis. Generally, the epipelagic layer ranges from the surface to 200 m depth.

Equivalent spherical diameter: a measure classically used to evaluate the size of an irregularly shaped object. It represents the diameter of a sphere of equivalent volume.

Eukaryotes: organisms whose cells have a clearly defined nucleus.

Euphotic zone or **photic layer:** in a marine ecosystem, the euphotic zone is the layer closer to the surface that receives enough light for photosynthesis to occur. Its lower depth limit is generally defined by the 1% light level.

Eurythermic species: species that can tolerate a wide range of ambient temperatures.

Eutrophy: the trophic state resulting from excessive enrichment of surface waters with mineral nutrients. It is characterized by the overproduction of autotrophic organisms (algae and cyanobacteria in particular).

Evaporites: water-soluble minerals resulting from concentration and evaporation of aqueous solutions. Gypsum, carbonates or sand roses are evaporites.

Excreta: waste matter discharged from the body, especially feces and urine.

Exoskeleton: rigid or articulate envelope that supports and protects the soft tissues of certain animals, for example the hard chitinous cuticle of arthropods.

Exudates: dissolved organic molecules released by phytoplankton.

Exudation: the oozing of an organic liquid. In oceanography, it refers to the oozing of organic matter from phytoplankton.

***f* ratio:** the ratio of New Production to Total Production, i.e. production based on new nutrient upwelled in the euphotic zone to total production, sum of new and regenerated production. The last one is based on regenerated nutrients by biological activity (recycled by bacterial, excreted by animals).

Fallout (nuclear physics): deposition of radioactive material on the Earth from the atmosphere.

Femtoplankton: plankton organisms < 0.2 µm, in maximum dimension, exclusively viruses.

Fickian-like diffusion law: Fick's laws are used to determine the diffusion of matter. A Fick-like law can be used to obtain the diffusion coefficient.

Flocculation: it is the process by which colloids form flocs or flakes.

Flocs or **flocculent matter:** undefined aggregations of organic and inorganic matter that has a loosely clumped texture, a flocculant mass of fine particles and colloidal material.

Front: separation between two water masses different in density, salinity or temperature. At the front, the horizontal gradient of density is strong.

Fugacity (CO_2 gas): for real gas, fugacity is defined as the pressure of an ideal gas that would have the same temperature and pressure to have the same free energy.

Gabbros and **chiefly basalts:** volcanic rocks originating from the upper mantle and emplaced at the mid-oceanic ridge axis.

Gelatinous organisms: a collective term for invertebrates characterized by a body of soft gelatinous matter, generally largely transparent; a polyphyletic group including medusae, appendicularians, siphonophores, etc.

General circulation: in the ocean or in any basin, the general circulation corresponds to the pattern of the main flow.

Generation time: the time between two generations, for example, the time between cell divisions in prokaryotes and protists, or time between egg hatching and egg production in copepods.

Geostrophic balance: see definition in Chapter 3, Box 3.2 "The geostrophic approximation".

Geostrophic current/transport/jet: see definition in Chapter 3, Box 3.2 "The geostrophic approximation".

Gonozoid: an individual having gonads, male or female.

Graben structures: tectonic features derived from extensive constraints leading to either crustal or sedimentary foundering.

Gullies: small submarine valleys through which sediments are transiting.

Heterotrophy: mode of nutrition in which organisms get their energy by consuming other organisms (plants or animals), for example ingesting prey items. Heterotrophs are secondary and tertiary consumers in food webs.

HNLC marine provinces: oligotrophic regions (LC = low chlorophyll) where macronutrients (N, P, Si) are available (HN = high nutrient). Biological productivity in these areas is limited by the scarcity of micronutrients (trace metals), due to the remoteness of land-based emission sources of trace metals.

Holoplankton: organisms whose entire life cycles are completed in the plankton.

Humic-like substances: organic compounds that are important components of humus. They can also be produced by biological activity (phytoplankton and bacteria) in seawater.

Hydrolysis: a chemical and enzymatic reaction where a covalent bond is broken by a molecule of water. It results in the fragmentation of, for example, a polymer, and thus frees repeat units. It can occur either spontaneously or under the effect of solar radiation (UV).

Hydrophilic compounds: compounds with an affinity for water, and a tendency to dissolve in it. Such compounds are ionic.

Hydroxyapatite: see **apatite**.

Hydrozoan: species of the cnidarian group living on the bottom or in the water.

Hyperpycnal flows: interstratified and dense, sediment-rich water layers.

Instabilities: the ocean is almost in equilibrium. Instability occurs when one or several forces act to locally alter the equilibrium.

Internal radius of deformation: horizontal distance from which the effect of the Coriolis force prevails over that of the pressure gradient. Then the flow direction is perpendicular to, and not in the direction of, this gradient.

Isopycnal/interfacial isopycnal: a line or surface of the same density/the frontier between two water masses may be an isopycnal.

Jet: intense stream, relatively narrow and thick in the same direction.

Labile: in chemistry, this reports on the kinetic instability of a bond or a chemical compound.

Lateralization: left–right structural or functional differences between the left and right sides of the body or the brain.

Lithogenic: this reports on any material of mineral or sedimentary origin.

LNLC marine provinces: the opposite of HNLC ones (LN = low nutrient). They are characterized by low concentrations of macronutrients.

Macroplankton: plankton organisms ranging from 2 to 20 cm.

Marine snow: relatively large aggregates of organic matter, mineral particles, dead organisms, fecal pellets, all bounded by colloids that sediment slowly. They appear from a submarine at depth like snowflakes in a winter sky.

Meroplankton: organisms that are in the plankton for only part of their life cycle (typically a larval stage), and the rest commonly spent as a benthic organism or as a member of the nekton (the swimmers).

Mesopelagic: this relates to the pelagic zone between the euphotic and the aphotic (without light) zone, which is approximately between 200 m and 1000 m depth, also known as the twilight zone.

Mesoplankton: plankton organisms ranging from 200 to 20,000 µm in maximum dimension.

Mesotrophic: intermediate level of biological productivity between oligotrophy (i.e. low productivity) and eutrophy (i.e. excessive productivity).

Metal speciation: the determination of the chemical forms or species of a metal. This mainly refers to the oxidation state, and also physico-chemistry (dissolved or particulate, complexed by organic matter or not, etc.).

Metazoans: multicellular organisms.

Methylation: see **Demethylation**.

Micro-feeders: equivalent to microphagous.

Microphagous: a term referring to feeding on small prey (less than 200 µm).

Microplankton: plankton organisms ranging from 20 to 200 µm in maximum dimension.

Mixed layer: a layer where there is no change in density, temperature and salinity. A mixed layer can be without vertical velocity.

Mixing layer: the surface layer of the ocean where turbulent mixing is currently active.

Mixotrophy: a trophic mode that combines both autotrophy and heterotrophy, for example photosynthesis and ingestion of prey items.

Molt: a loss of feathers, hair or skin, especially as a regular feature of an animal's life cycle. In crustaceans, molting is the shedding of the exoskeleton, typically to let the organism grow.

Morphotypes: organisms sharing a particular, distinguishable morphology, which may or may not correspond with a species, strain or race.

Nanoplankton: plankton organisms ranging from 2 to 20 µm in maximum dimension.

Nekton: aquatic animals that are able to swim and move independently of the currents.

Neritic: a region of the oceans that extends from the low tide mark to the edge of the continental shelf.

Niche theory: based on the hypothesis that each species in a community has a specific domain of preference in a multivariable space (an ecological niche).

nr database: an online database of DNA sequences and their phylogenetic affiliation.

Nutricline: the depth zone where nutrient concentrations increase rapidly with depth. The transition layer between the nutrient-rich water at the surface and the nutrient-poor water below.

Nychthemeral migration: the nycthemeron is a day-long period. The two parts of the day relative to light drive the migration activity of some plankton animals. This migration, which is a vertical excursion from the depth to surface at sunset and a return trip at sunrise, is dependent on light intensity. Moon light and sun eclipses might influence this migration.

Oligotrich: this usually refers to planktonic ciliates without shells or a lorica (shell) with ciliature composed of bristles or trichia, arranged in an open or full circle surrounding the mouth; typically cone-shaped or spherical.

Oligotrophy: a trophic state characterized by low availability of nutritive resources and low biological productivity.

OMVs: outer membrane vesicles, which are produced via budding and which may contain DNA, RNA and enzymes. OMVs have diameters ranging from 40 to 200 nm and are expected to play a key role as vectors for horizontal gene transfer.

Ontogenic migration: this migration is driven by the physiology of the animal. Copepods at the end of their juvenile development migrate from the surface to a deep layer, usually at the end of summer, when food resources decline (e.g. *Calanus helgolandicus* in the Ligurian Sea).

Oocyte: a cell that develops in an ovule. The fertilized ovule becomes an egg.

Oozoid: an individual that has developed from an egg (e.g. salps).

Organic ligands: see **chelating agents**.

Organometallic compounds: chemical compounds that contain a covalent bound between a metal and a carbon atom within an organic group.

Oxygen minimum zone (OMZ): a zone where the concentration of dissolved oxygen in seawater is at its minimum.

Parapods: lateral expansion of each segment of worm's body used to crawl on the bottom or swim in the water, usually composed of long setae or paddle.

Partial pressure (CO_2 gas): this is defined as the product of CO_2 mole fraction and total pressure and this is expressed in µatm. In practice, the correction for the non-ideal nature of CO_2 gas is negligible (< 1 µatm) and CO_2 partial pressure is often treated identically to its fugacity.

Petrogenic hydrocarbons: hydrocarbon compounds associated with products derived from petroleum or petroleum sources.

Phages: bacterial viruses.

Philopatric: an organism that has the tendency to stay in, or habitually returns to, a particular area.

Phorozoid: an individual asexually produced by the oozoid of a doliolid species that has the role of collecting food to maintain the colony like an Old Nurse.

Phospholipids: lipids (i.e. a biomolecule that is soluble in nonpolar solvents) generally consisting of hydrophobic fatty acids and a phosphate group.

Photic layer: the marine surface layer whose solar illumination allows algal development.

Photobleaching: photochemical degradation of fluorophores leading to a decrease (or loss) of fluorescence.

Photoprotection: mechanisms to protect the photosynthetic apparatus of phytoplankton cells from damages caused by strong light intensity.

Photoreduction: reduction reaction induced by light.

Phylotype: typically, bacteria with the same or a very similar 16S rDNA sequence (often used as a proxy for bacterial species).

Physiographic characteristics: morphological characteristics of a domain (aerial or submarine).

Picoplankton: plankton organisms ranging from 0.2 to 2 µm in maximum dimension.

Pigment: phytoplankton cells contain pigments to absorb light energy in order to perform, for example, photosynthesis. Chlorophyll-a is the primary pigment used in photosynthesis.

Plankton: living organisms in the water column whose motility is insufficient to overcome currents and movements of water masses.

Pneumatophore: siphonophore polyp that produces and stores gas in such a way as to give buoyancy to the colony. Specially developed in the genus *Physalia*.

Polycondensation: a polymerization process that occurs by condensation, i.e. by steps (monomers give dimers, then trimers, etc.). Polycondensation is to be distinguished from chain-growth polymerization.

Polyp: an individual with a stomach cavity that is usually connected to the other individuals, in the colony. The mouth, surrounded by tentacles covered with cnidocysts and designed to catch prey, is also used to evacuate the undigested food.

Polyphosphates: salts or esters formed from the structural unit orthophosphate having linear or cyclic structures.

Potential temperature: the temperature of a water mass that has been adiabatically moved (i.e. without heat exchange with the environment) to a reference pressure.

Prokaryotes: single-celled organisms that have no distinct nucleus with a membrane.

Protists: a hyper-diverse group of unicellular eukaryotes.

Pyrolytic hydrocarbons: hydrocarbons generated by the thermal decomposition of organic compounds in the absence of oxygen, to avoid oxidation and combustion.

Radiolarians: protists, mostly marine and planktonic, amoeboid with skeletons of opaline silica.

Radionuclides: radioactive nuclides. Nuclides are atoms characterized by the composition of their nucleus (i.e. their number of protons and neutrons).

Reactive orthophosphate (PO_4^{3-}): the structural unit of phosphorus that is most easily assimilated by autotrophic organisms.

Recruitment: in biology, when a juvenile organism joins a population, whether by birth or immigration, usually at a stage whereby the organisms are settled and able to be detected by an observer. In the study of fisheries, recruitment refers to the number of fishes surviving to enter the fishery or to some life history stage such as settlement or maturity.

Remineralization: a conversion of organic matter into nutrients by bacteria.

Residence time: this measures the average time spent by a molecule of water in a reservoir. The residence time defined for steady-state systems is equal to the reservoir volume divided by the inflow or outflow rate.

Residual buoyancy: see definition in Chapter 3, Box 3.2 “The geostrophic approximation”.

Resilience: in ecology, resilience is the capacity of an ecosystem to respond to a perturbation or disturbance by withstanding damage and recovering quickly.

Revertant strains: bacterial strains that exhibit genetic features they obtained from other bacterial strains via horizontal gene transfer, as achieved by exposition to outer membrane vesicles.

Rias: submerged former aerial valleys.

Rifting: surface signature (series of grabens) of crustal processes leading to continental breaking.

Roseophage: bacterial virus infecting the genus *Roseobacter*.

Salt diapirs: ascending sedimentary deformations due to the presence of interstratified salt layers.

Scars: typical marine morphologies due to sedimentary instabilities and failures.

Sediment trap: a device for collecting sinking particles in the water column. The sinking material is caught at a recorded depth in a “funnel”-like tube of a known area and over a defined length of time.

Sentinel species: species that act as indicators of a danger to human life or of an ecosystem damage by providing advance warning of danger.

Septum (pl. septa): a membrane that separates two parts of a cell or an organ.

Seta (pl. setae): a kind of short hair or bristle.

Shear: vectorial difference of velocity between two depths or two locations (dimension: s^{-1}).

Somites: body segments of a copepod.

Stoichiometry: molar proportions of chemical compounds or elements in a chemical formula or in a chemical reaction. It is based on the law of conservation of mass.

Stolon: an expansion of the body built with different tissues of the animal (ectoderm, endoderm and/or mesoderm) on which buds appear, giving a new individual or are transported from a producing site. Stolon is also the plumbing or network of feeding tubes and nerves joining the different individuals in a colony of individuals.

Stratification of the water column: superimposition of water layers of different densities and properties (temperature, salinity, oxygenation) that prevents water mixing and homogenization. It mostly results from the action of heat and evaporation.

Subduction: progressive disappearance of an oceanic crust below either a continent or another domain of oceanic crust.

Subsidence: slow foundering of a crustal, or oceanic, domain and its sedimentary covers, as consequence of its progressive cooling.

Suspensivore (mode): an organism that feeds on suspended material.

Symbiont: an organism living in a state of symbiosis, i.e. with another organism.

Synrift units: sedimentary units deposited during rifting processes.

Taxon: taxonomic unit of any rank (species, genus, family, etc.).

Terrigenous fans: deep "fan-shaped" sedimentary units deposited along continental slopes.

Thermocline: physical barrier materializing a strong change of temperature with depth, generally in the upper layer.

Tintinnid: a ciliate of the order Choreotrichida and suborder Tintinnidia characterized by the possession of a lorica (shell) into which the ciliate can withdraw into.

Trace metals: metals found in very low concentrations (traces).

Transductants: bacterial cells into which new genetic material has been transduced, usually by a bacteriophage that experienced a faulty DNA-assembly by incorporating bacterial host DNA instead of viral DNA before its release during the lytic cycle (revertant strain).

Transparent exopolymeric particles (TEP): a class of organic aggregates (particles) with specific staining properties.

Turn-over time: a period of time necessary to change all the quantity of the variable considered.

Umbrella species: species useful for making conservation-related decisions, typically because protecting them indirectly protects the many other species living in the ecological community of their habitat.

Upwelling: wind-driven motion of dense, cold and nutrient-rich water masses towards the ocean surface. Owing to their high concentration in plankton, upwelled waters are characterized by high fishery production.

Ventilation: a process by which "young" surface waters, which have recently been in contact with the atmosphere, are injected into the ocean interior and exported away from their sources (for instance, supply of oxygen to deep water by downwelling or mixing processes).

Viral lysis: lysis of cells by viruses, resulting in the death of the cell, the release of newly formed viruses, cell content and cell debris.

Zooid: an individual. A general term to which (blast-, oo-, phoro-, gono-) is usually added, to indicate its origin or role.

List of Authors

Jacqueline BOUTIN
LOCEAN
CNRS
Paris
France

Laurent COPPOLA
IMEV
SU/CNRS
Villefranche-sur-Mer
France

Fabrizio D'ORTENZIO
LOV
SU/CNRS
Villefranche-sur-Mer
France

Jean-Pierre GATTUSO
LOV
SU/CNRS
Villefranche-sur-Mer
France

Virginie HASSOUN
GEOAZUR
Nice-Sophia Antipolis University
Valbonne
France

Fayçal KESSOURI
Southern California Coastal
Water Research Project
USA

Dominique LEFEVRE
MIO
Aix-Marseille University
France

Marina LEVY
LOCEAN
CNRS
Paris
France

Jean MASCLE
IMEV
SU/CNRS
Villefranche-sur-Mer
France

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Nicolas MAYOT
Bigelow Laboratory for Ocean Sciences
Boothbay
USA

Nicolas METZL
LOCEAN
CNRS
Paris
France

Sébastien MIGEON
GEOAZUR
Nice-Sophia Antipolis University
Valbonne
France

Christophe MIGON
LOV
SU/CNRS
Villefranche-sur-Mer
France

Paul NIVAL
LOV
SU/CNRS
Villefranche-sur-Mer
France

Orens PASQUERON DE FOMMERVAULT
ALSEAMAR
Meyreuil
France

Louis PRIEUR
LOV
SU/CNRS
Villefranche-sur-Mer
France

Antoine SCIANDRA
LOV
SU/CNRS
Villefranche-sur-Mer
France

Vincent TAILLANDIER
LOV
SU/CNRS
Villefranche-sur-Mer
France

Pierre TESTOR
LOCEAN
CNRS
Paris
France

Branko VELIMIROV
Medical University of Vienna
Austria

Markus WEINBAUER
LOV
SU/CNRS
Villefranche-sur-Mer
France

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