Universidade de Aveiro Departamento de Biologia
2018

FÁBIO EMANUEL LOPES DE MATOS

ANÁLISE DE REDES DA PAISAGEM SUBMARINA DE CANHÃO – IMPLICAÇÕES PARA O PLANEAMENTO E GESTÃO DA BIODIVERSIDADE

NETWORK ANALYSIS OF SUBMARINE CANYON SEASCAPE – IMPLICATIONS FOR PLANNING AND BIODIVERSITY MANAGEMENT

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia e Ecologia das Alterações Globais, realizada sob a orientação científica da Doutora Maria Marina Ribeiro Pais da Cunha, Professora Auxiliar do Departamento de Biologia da Universidade de Aveiro e co-orientação do Doutor Joan Baptista Claret Company, Investigador Sénior do Institut de Ciències del Mar de Barcelona, Espanha.

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“We are drowning in information, while starving for wisdom. The world henceforth will be run by synthesizers, people able to put together the right information at the right time, think critically about it, and make important choices wisely.”

E. Wilson, 1998, Consilience

“It is better to light one candle than to curse the darkness.”

Adage

o júri

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“There and back again.”

Four years have passed! Once more, I would like to thank Marina for the opportunities and support given on this adventure. For the good mood and the advice during this journey. I would like also to thank Batis, for his support and interest on this project. For his welcome to my visits to Barcelona and the valuable discussions.

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À Mariana, à Sofia e aos meus pais, um obrigado especial por terem partilhado o doutoramento comigo, apoiando-me sempre.

palavras-chave

Canhões submarinos, *Lophelia pertusa*, análise de redes, mapeamento de conhecimento, conservação, conectividade potential

resumo

Os canhões submarinos são estruturas geomorfológicas complexas localizadas nas margens continentais. São reconhecidos como zonas importantes de biodiversidade no mar profundo onde os níveis de produtividade biológica são de modo geral superiores às áreas adjacentes. Estes ecossistemas marinhos desempenham um papel fundamental na prestação de bens e serviços essenciais ao bem-estar humano. Não obstante, estes ecossistemas estão cada vez mais sujeitos a efeitos nefastos que advêm de ações diretas das atividades humanas, mas também, resultantes de alterações climáticas. O isolamento natural dos canhões submarinos em conjunto com estas mudanças, pode ter implicações para a conectividade das populações biológicas que os habitam, bem como para a manutenção da biodiversidade associada. Avaliar as causas e efeitos ecológicos de tais mudanças só será possível através de uma abordagem holística e interdisciplinar.

Partindo de uma base de dados bibliográfica abrangente de publicações dedicadas ao estudo de canhões submarinos, usei técnicas de *data mining* e de análise de redes para mapear o conhecimento reunido até agora. Foram identificados clusters de conhecimento, a evolução histórica da investigação em canhões submarinos, bem como, os tópicos emergentes e lacunas no conhecimento sobre estas estruturas. Os tópicos mais desenvolvidos dizem respeito a áreas associadas à "Geologia e Geofísica", "Processos Oceanográficos" e "Biologia e Ecologia". Por outro lado, temas como "Biogeoquímica" e modelação ecológica estão entre os menos explorados. Estudos referentes a impactos antropogénicos nestes ecossistemas e alterações induzidas por processos climáticos foram detetados apenas em publicação datadas da última década. A rede de tópicos gerada reflete uma interdisciplinaridade latente na investigação associada a canhões que se desenvolveu principalmente durante o século XXI, apoiada por colaborações internacionais da comunidade científica. No entanto, a investigação científica em canhões submarinos apresenta uma tendência clara direccionada para determinados temas e áreas geográficas. Tópicos específicos são abordados preferencialmente em determinados canhões, enquanto que um número muito pequeno destas estruturas concentra a maior parte dos trabalhos desenvolvidos. Este resultado juntamente com o número reduzido de estudos interdisciplinares, foi a mais importante limitação detetada que poderá dificultar a integração do conhecimento já reunido sobre estas estruturas, impedido uma compreensão mais abrangente dos padrões e processos associados aos canhões submarinos. Os resultados alcançados foram disponibilizados numa plataforma online aberta para exploração interativa e direcionada dos conteúdos.

resumo

No sentido de avaliar a importância dos canhões para a conservação e gestão da biodiversidade no mar profundo, foi definida como área de estudo o Mar Mediterrâneo e selecionada como espécie modelo, um coral de água fria: *Lophelia pertusa*. O Mar Mediterrâneo engloba vários sistemas de canhões submarinos enquanto que *L. pertusa* é uma espécie engenheira de ecossistemas que cria refúgio, áreas de berçário e habitat para uma panóplia de outras espécies, ocorrendo frequentemente em canhões. Uma vez que a distribuição de *L. pertusa* no Mar Mediterrâneo está provavelmente subestimada e que esta informação é fundamental para avaliar a relevância dos canhões na área de estudo, desenvolvi um modelo de nicho ecológico baseado em variáveis ambientais e uma abordagem conjunta de três algoritmos. Os resultados obtidos foram mapas de adequação ambiental, bem como, de avaliação da capacidade de previsão do modelo. Os resultados sugerem que no mar Mediterrâneo, esta espécie de coral encontra condições ambientais próximas dos seus limites fisiológicos. Apesar disso, áreas com condições favoráveis à ocorrência de *L. pertusa* foram detetadas em canhões submarinos, principalmente no Mediterrâneo Ocidental e Central. A par da qualidade dos habitats, a distribuição dos organismos, a dinâmica meta-populacional e a resiliência das populações a perturbações estão fortemente relacionadas com a conectividade dos ecossistemas. Neste contexto, simulei o transporte de larvas de *L. pertusa* no Mar Mediterrâneo usando um modelo biofísico para estimar o seu potencial de dispersão. Com os resultados do modelo e usando análises de rede, avaliei a disponibilidade de habitat com base em parâmetros como a qualidade, configuração espacial da paisagem marinha e variabilidade oceanográfica. Os resultados sugerem que a conectividade entre as eco-regiões do Mar Mediterrâneo é baixa e que a intensificação de eventos impulsionados por condições climáticas (por exemplo, *dense shelf water cascading*) pode agravar este cenário. No entanto, a potencial troca de larvas entre colónias dentro da mesma eco-região foi significativa, podendo favorecer a resiliência das populações a perturbações locais. Áreas de habitat com boa qualidade e com fluxo de larvas foram identificadas como prioritárias para a conservação de *L. pertusa*, com benefícios eventuais também para a fauna associada a este coral. Mais uma vez, áreas de habitat incluídas em canhões submarinos foram identificadas como as mais relevantes no Mar Mediterrâneo, devendo desempenhar um papel importante na conectividade de populações desta espécie. Contudo, estas áreas estão igualmente sujeitas de forma intensa a atividades humanas com efeitos prejudiciais nos ecossistemas, e que, aliadas aos efeitos das alterações climáticas, podem dificultar a implementação de medidas de conservação eficazes. Com a exceção de três áreas marinhas protegidas francesas no Golfo do Leão, o desenvolvimento de esforços de conservação no Mar Mediterrâneo que incluam áreas com canhões submarinos é ainda negligenciável.

Os resultados apresentados nesta tese fornecem evidências científicas que poderão apoiar medidas de conservação e gestão com vista à criação de redes de áreas marinhas protegidas no Mar Mediterrâneo. Neste sentido, proponho os canhões submarinos como áreas prioritárias para a conservação da biodiversidade de mar profundo na área de estudo.

keywords

Submarine canyons, *Lophelia pertusa*, network analyis, knowledge mapping, conservation, potential connectivity

abstract

Submarine canyons are complex and heterogeneous geomorphologic structures highly relevant for the biodiversity and productivity of continental margins. These marine ecosystems play a key role providing invaluable goods and services for human well-being but are also increasingly subjected to the effects of anthropogenic pressure and climate change. The natural isolation of canyons may act synergistically with these changes with implications for population connectivity and the maintenance of biodiversity. The understanding of the causes and ecological consequences of such changes requires holistic and interdisciplinary approaches.

I mapped the landscape of submarine canyon research based on a comprehensive bibliographic data set and using data mining techniques and network analysis. The existing knowledge clusters, historical trends, emergent topics and knowledge gaps in canyon research were identified and characterized. Topics such as “Geology & Geophysics”, “Oceanographic Processes” and “Biology & Ecology” were among the most studied while, for instance, “Biogeochemistry” and ecological modelling were among the less explored. Topics regarding anthropogenic impacts and climate-driven processes were only detected on publication of the last decade. The knowledge network reflects a latent interdisciplinarity in canyon research that developed mostly in the new millennium, supported by a well implemented and international collaboration network. The research efforts have been mainly directed towards only a few canyon systems and a thematic bias was identified, with specific topics addressed preferentially in particular canyons. This spatial and thematic bias, together with the paucity of truly inter-disciplinary studies, may be the most important limitation to the integrated knowledge and development of canyon research and hinders a global, more comprehensive understanding of canyon patterns and processes. The scientific landscape mapping and the complementary results are made available online as an open and interactive platform.

In order to assess the importance of submarine canyons for the conservation and management on the deep sea, a study area and a modelling species were selected: the Mediterranean Sea and *Lophelia pertusa*, a cold-water coral species. The Mediterranean Sea encompasses several submarine canyon systems and *L. pertusa* is an ecosystem engineering species that occurs frequently in these geomorphological features and provides refuge, nursery grounds and physical support for a remarkable diversity of other life forms.

abstract

Considering that the distribution of *L. pertusa* in the Mediterranean Sea is probably underestimated and that this information is crucial to assess the relevance of canyons in the Mediterranean seascape, I estimated the habitat suitability and draw uncertainty maps for this region based on environmental predictors and an ensemble approach of three machine-learning algorithms.

The results suggest that in the Mediterranean Sea*, L. pertusa* encounters environmental settings close to its physiological limits but, despite the highly variable quality of the seascape, submarine canyons were identified as high suitability areas, especially across the Western and Central Mediterranean margins. In addition to the environmental suitability, the ecosystem connectivity determines the species distribution, the metapopulation dynamics and population resilience. I simulated the transport of *L. pertusa* larvae in the Mediterranean Sea using a biophysical model to estimate their potential dispersal as well as a network analysis to evaluate the habitat availability based on parameters such as suitability, spatial configuration of the seascape and the oceanographic conditions variability. The results suggest that connectivity among Mediterranean ecoregions is weak and that the intensification of climate-driven events (e.g., dense shelf water cascading) may worsen this scenario. However, the potential exchange of larvae between colonies within the same ecoregion was significant, favoring population resilience to local disturbances. Habitat areas with high quality and larval flux were identified as a priority for the conservation of *L. pertusa*, and subsequently also for their associated fauna. Once again, I showed that habitat areas on submarine canyons may play an important role in the connectivity of *L. pertusa* Mediterranean populations. However, these habitat areas are subjected to intense anthropogenic pressures, which allied to the effects of climate change, may impose greater challenges to their conservation. Apart from three French marine protected areas in the Gulf of Lion, the development of conservation efforts considering submarine canyon in the Mediterranean Sea is negligible.

The knowledge produced in this thesis provides scientific evidence to support decision-making in conservation and planning of marine protected areas networks in the Mediterranean Sea and illustrates the relevance of submarine canyon for the management and conservation of deep-sea biodiversity.

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Section 1 - Introduction

1.1 - General background

Global alterations in the marine ecosystems induced by human activities and climate change are occurring faster and intensifying (Halpern et al. 2008; Sweetman et al. 2017; Danovaro 2018). The understanding of the causes and ecological consequences of such changes on a complex and dynamic environment as the marine domain requires holistic and interdisciplinary approaches.

Until recently the deep sea was a realm "out of sight, out of mind". Considered as one of the last frontiers on Earth for humankind, the deep sea started to be more intensively studied only during the last century (Glover et al. 2010; Danovaro et al. 2014). The deep-sea research endeavour became progressively more collaborative and multi-disciplinary involving areas such as geology, biology, oceanography, and engineering. However, despite the efforts made, the deep sea remains largely unexplored and its processes and patterns are not fully comprehended. Albeit the knowledge gaps, the scientific exploration brought to light a diversified seascape populated by a multitude of life forms and rich in natural resources (e.g., mineralogical, genetic, biotech facilitators; Ramirez-Llodra et al. 2011; Mengerink et al. 2014). The continental margins, in particular, encompass heterogeneous and highly complex ecosystems shaped by steep environmental gradients, that interact with different water masses and receive inputs both from land and the oceans' surface (Levin and Sibuet 2012). Submarine canyons are among the most distinctive ecosystems occurring at continental margins. The global compilation of bathymetric data, based on the interpretation of the Shuttle Radar Topography Mapping 30-arc second (approximately 1 km) database (Becker et al. 2009), mapped 9477 large canyons thalwegs (Figure 1.1.1) widespread over all ocean basins (Harris and Whiteway 2011; Harris et al. 2014). The natural isolation of canyons may act synergistically with the global changes observed in the deep sea, with implications to population connectivity and the maintenance of biodiversity. Multidisciplinary approaches such as ecological modelling and network analysis can help to synthesize the current knowledge on submarine canyons and produce a global vision of their connectivity, providing scientific evidence to support decision-making in marine spatial planning and conservation.

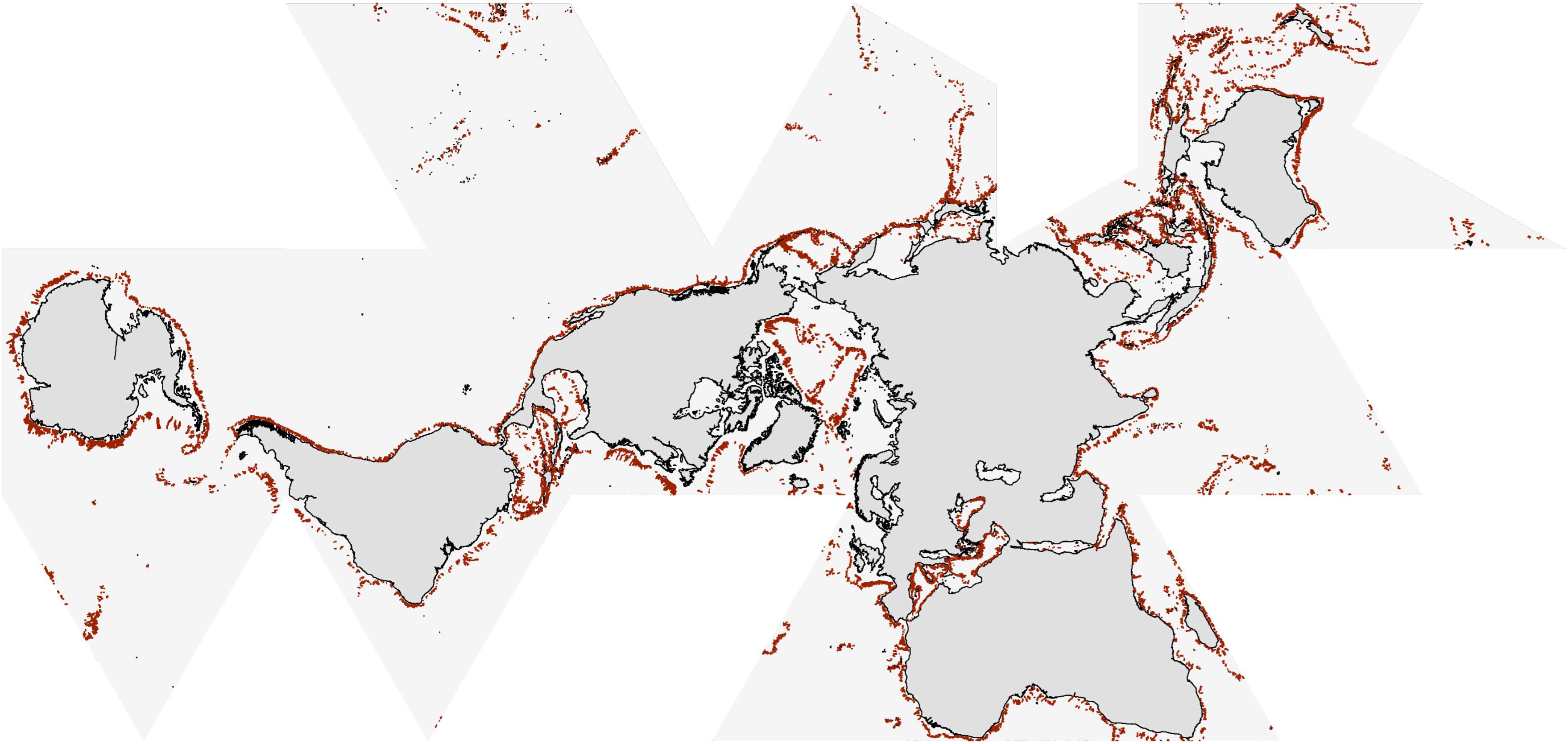


Figure 1.1.1 - Worldwide distribution of the largest submarines canyons identified in Harris et al. 2014, based on the Shuttle Radar Topography Mapping 30-arc second (Becker et al. 2009).

1.2 - Submarine canyons

Typically, submarine canyons are characterized as steep-sided, V-shaped valleys incising the continental shelves or starting at their edge (Amblas et al. 2018), Figure 1.2.1. Widely spread along the continental margins, canyons captured scientific attention because of their dynamism and recognized influence both on the surrounding environment and inhabiting faunal communities (Harris and Whiteway 2011; Levin and Sibuet 2012).

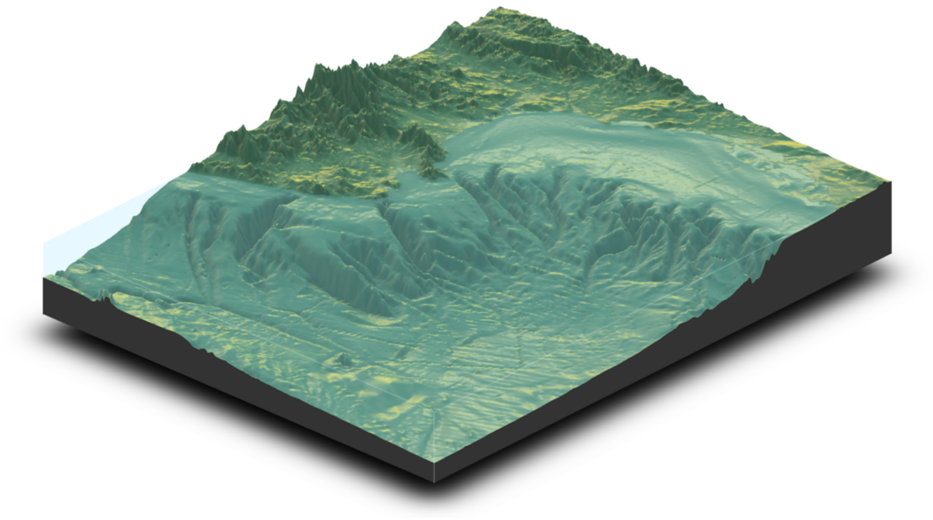


Figure 1.2.1 - Topography of submarine canyons along the Gulf of Lion and the Catalan continental margin (exaggerated vertical scale), in the Mediterranean Sea, one of the ocean regions with the highest concentration of canyons. Bathymetric data extracted from the EMODnet Digital Bathymetry (DTM; Ferrini et al. 2016).

The study of submarine canyons evolved along the 20th century, following the exploration of the geomorphological and geophysical characteristics of the seafloor and the improvement of remote sensing techniques (e.g., sidescan sonar, multibeam echo sounder; Amblas et al. 2018). Although the formation of submarine canyons is a process still not fully comprehended, it is hypothesised that these geomorphological features may result from the interplay of three major controlling factors: geodynamic setting and structural controls, depositional/erosive processes (e.g., storm-induced turbidity currents), and sea level changes (Puig et al. 2014; Ceramicola et al. 2015). The recent technological advances have reduced technical difficulties in canyon sampling and monitoring, allowing the development of various research fields. The implementation of cable observatories with multi-parametric sensors allowed a more profound investigation of the canyon environment regarding oceanography, geology, and chemistry and created the opportunities to integrate these scientific disciplines and explore submarine canyons more holistically (Matabos et al. 2014; Cabrera De Leo et al. 2018).

Canyon topography interacts strongly with currents and circulation patterns leading to one of the most obvious examples of influence of canyons on the surrounding environment (e.g., Ahumada-Sempoal et al. 2013). This influence extends then to the sediment dynamics and the transport of materials, with canyons acting as preferential conduits and connecting the continental slope to the deepest areas of the seafloor (Weaver et al. 2004; Canals et al. 2006). The synergies between the canyon topography, the hydrodynamic regimes and the enhanced transport of sediments and organic matter, have important consequences on the fauna inhabiting submarine canyons and downstream abyssal areas. The heterogenous environment along the canyon thalweg and flanks (e.g., topography, types of substrates, productivity) provides various and complex habitats (McClain and Barry 2010; Levin et al. 2010). Multiple biodiversity patterns were described along the canyon sections, or between canyons and the adjacent slopes (Cunha et al. 2011). Despite the important variations among taxonomic groups and geographical locations, higher biomasses of macro- and megafauna were frequently found in the submarine canyon habitats when compared to the adjacent or open slopes (Cúrdia et al. 2004; De Leo et al. 2010; Kavanaugh et al. 2015). Additionally, submarine canyons provide nursery areas (Fernandez-Arcaya et al. 2013) and natural refugia for numerous species (Yoklavich et al. 2000; Huvenne et al. 2011), including many of economic importance (Company et al. 2012). Their biological relevance highlights canyon ecosystems as key geomorphological features for marine spatial management and the conservation of deep-sea ecosystems (DFO Canada 2008; Commonwealth of Australia 2012).

The productivity of many submarine canyons and their proximity to densely populated areas, make these ecosystems particularly prone to the impacts of human activities (e.g., Lastras et al. 2016). Anthropogenic impacts on canyons are widely described: fishing pressure and gear impacts on the seafloor, cable laying, pipeline construction, waste dumping (e.g., Canals et al. 2006; Ramirez-Llodra et al. 2011; Ramirez-Llodra et al. 2013; Fabri et al. 2014). In addition to anthropogenic impacts, climate change may also affect canyon ecosystems with consequences that are difficult to predict: How will ocean warming and acidification impact the diversity, abundance, and distribution of canyon biological communities? How will climate-driven changes on water circulation influence the ecosystem connectivity?

Although submarine canyons are one of the most studied ecosystems in the deep sea, important knowledge gaps remain. Rising from this awareness, an international initiative aiming to facilitate the collaboration between the canyon scientific community was implemented in 2012. During the first

International Symposium on Submarine Canyons at Brest, France, the International Network for submarine Canyon Investigation and Scientific Exchange (INCISE, www.incisenet.org) was formed with the declared object of stimulating discussions across disciplines focused on submarine canyon research (Huvenne and Davies 2014). To tackle the most prominent research topics, different working groups were created focusing on the canyon processes in space and time, the role of scale and heterogeneity in community patterns, conservation and new ways to study these geomorphological features. Currently, most of the broad-scale environmental processes are better understood and well documented in the literature. However, the fine-scale effects of these processes on ecosystems functioning and patterns are still largely ignored requiring more integrative approaches in the future (Amaro et al. 2016; Fernandez-Arcaya et al. 2017).

1.3 - Ecosystem connectivity

Ecosystem connectivity is a fundamental process for the maintenance and conservation of biodiversity (Gaines et al. 2003; Cowen and Sponaugle 2009; Rayfield et al. 2011) and one of the less explored topics in submarine canyon research (Fernandez-Arcaya et al. 2017). Despite its intuitive appeal, the concept of connectivity is context-dependent and often inconsistently defined (Calabrese and Fagan 2004). In ecology, this process involves the transference of organisms, materials and energy which in turn determine the ecosystems structure, functioning and productivity. These ecological flows may be constrained by physical barriers, environmental conditions and organisms' biology and behaviour.

Initially described in the context of terrestrial ecosystems, the concept of connectivity evolved to face different research perspectives and operational needs (Kool et al. 2013). In this thesis three broad typologies of connectivity are distinguished: structural, functional and realized connectivity (Treml and Kool 2017). The structural connectivity, also known as "connectedness" (Opermanis et al. 2012), refers to the physical links between seascape elements. This type of connectivity facilitates the ecological flows and is crucial for the viability of metapopulations (Saura and Torne 2009); it incorporates information on the physical attributes of the seascape (e.g., habitat location, size and shape) and ignores the influence of the biological attributes such as the species dispersal capacity (Calabrese and Fagan 2004). On the other hand, in addition to seascape structure, functional connectivity includes species-level characteristics (e.g., environmental tolerance and life-history traits) and the organisms' response to the seascape patterns (e.g., larval behaviour, post-settlement mortality); it is characterized as "potential connectivity" and refers to population connectivity defined as the transference of individuals and genetic material among sub-populations of a species (Opermanis et al. 2012; Treml et al. 2015). Population connectivity may concern the population growth and vital rates that are mechanisms closely related to the relative contribution of net immigration to total recruitment (defined as *demographic connectivity*); or be assessed from the evolutionary point of view, by analysing the degree to which gene flow affects the processes within populations (defined as *genetic connectivity*). In both cases, the connections among subpopulations or habitat patches depend of the species responses to the structural topology of the habitats and physical environment (e.g., temperature, oceans currents; Treml and Kool 2017). Finally, the realized connectivity measures the effective connections between populations and is based on empirical approaches, such as direct observations on dispersal and recruitment, larval tracking and genetic data (Calabrese and Fagan 2004).

1.3.1 - Measuring marine connectivity

In the context of the complexity of canyon ecosystems and the increasing scientific evidence on their exposure to global changes and direct anthropogenic impacts, connectivity studies may be particularly relevant. In marine organisms, connectivity is frequently ensured by the dispersal of larvae or other propagules. However, quantifying larval supply, for instance, is particularly challenging in the deep sea due to sampling difficulties (Hilário et al. 2015). Moreover, ecosystem connectivity is scale-dependent in space and time (Moilanen and Hanski 2001), varying not only according to the processes involved (e.g., dispersal, migration) but also according to how species perceive and use the ecosystems (Kool et al. 2013). Different but complementary methodologies are currently being used to assess connectivity in marine ecosystems, covering different spatial and temporal scale ranges (Figure 1.3.1).

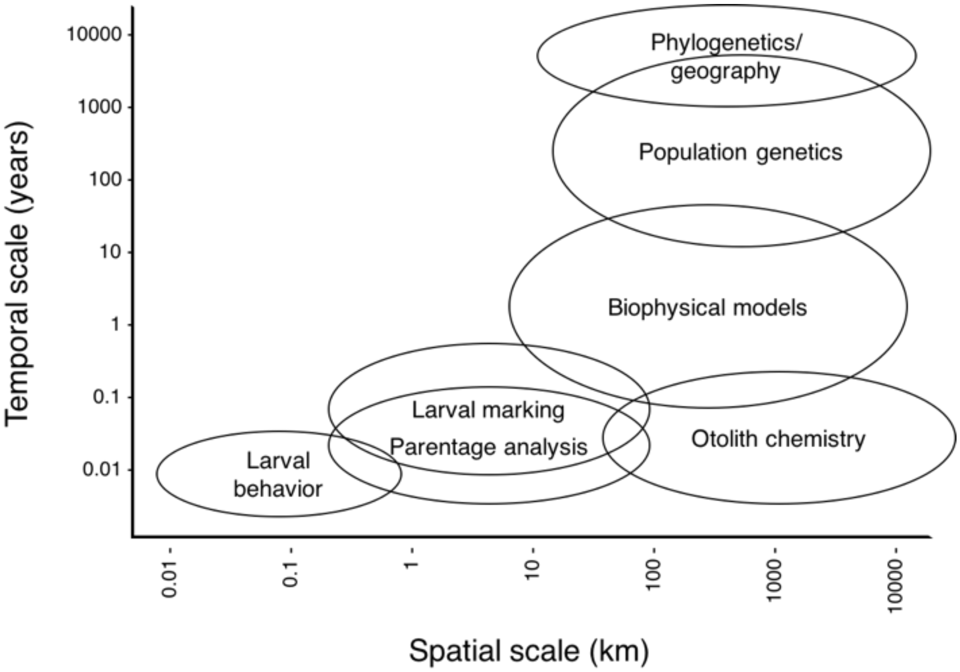


Figure 1.3.1 - The spatial and temporal scales covered by different approaches and techniques that can be used to provide information on ecosystem connectivity (from Jones et al. 2009).

The estimation of structural connectivity is focused on the properties and spatial arrangement of habitat patches (i.e., isolated, clustered distributed), and on the geographic distances or environmental differences among one another. Therefore, the structural connectivity represents the broad geographic pattern and assumes that connectivity mechanisms are largely driven by the spatial arrangement and physical attributes of habitat patches, overlooking the influences of biological factors (Treml and Kool 2017). The quantification of the structural connectivity of a seascape includes the physical influence of ocean currents (hydrodynamic connectivity *sensu* Pringle 2001) on the time it takes for passive particles to flow between habitat patches. This kind of assessment is usually achieved by modelling approaches based on Lagrangian (e.g., Ross et al. 2017a) and Eulerian frameworks (e.g., Treml et al. 2008) which cover, simultaneously, large temporal and spatial scales. The different typologies of connectivity are not necessarily mutually exclusive (Treml and Kool 2017). The inclusion of biological traits to a hydrodynamic connectivity model allows the estimation of potential connectivity of populations and habitat patches. This technique often requires the simplification of the mechanisms involved (e.g., dynamism of the oceanographic circulation) and assumptions on the species life traits (e.g., uniform larval supply; Treml et al. 2008) since most of this information is lacking, especially for deep sea species (Hilário et al. 2015). Functional connectivity is, therefore, a broad term that can range from very simplistic estimation of potential connectivity to complex models aiming to estimate the realized connectivity (Treml and Kool 2017). Molecular techniques, including genetic markers, have been successfully used to study the realized connectivity of marine species. These methods allow the analysis of population structure and gene flow, revealing the “ghost of dispersal past” (Benzie 1999) and broad phylogeographic patterns. Other techniques used for this purpose are based on environmental markers, including stable isotopes and elemental tracers, that provide indirect estimates of dispersal and allow to discriminate among larval sources (e.g., Carson et al. 2011). However, the applicability of these approaches is challenging owing to the small size of larvae and the vastness of the deep sea (Génio et al. 2015) and it is also limited for studies at regional and global scale since they are more time consuming and resource demanding than modelling techniques.

1.4 - Ecological modelling

The vastness of the oceans, the complex interactions of numerous environmental drives with organism responses and the increasing demand for scientific-based information by policy and decision-makers, has prompted the use of ecological modelling techniques (Schmolke et al. 2010), including in the deep sea (Levin and Sibuet 2012). Seascape ecology is a discipline that links oceanography and applied ecology through spatially explicit methodologies (Hidalgo et al. 2016), often using ecological modelling approaches. This research field has facilitated the exploration of ideas and theories in the marine environment, helping to grasp ecological patterns and predict the ecosystem response under different scenarios of global change. Ecological modelling consists in constructing and analysing ecological processes using numerical models. These models can be analytic or simulation-based and can be supported by purely biological information or by its combination with the physical proprieties of the environment in biophysical models (Jørgensen et al. 2009).

1.4.1 - Ecological niche modelling

Fundamental knowledge on species distribution is necessary to address societal challenges related to hazards, resources, and the environment (Sayre et al. 2017) yet that knowledge is frequently lacking, especially for deep-sea ecosystems. Ecological Niche Models (ENMs) have been developed to predict the environmental niche and geographic range of species based on correlations of known occurrences with environmental variables – correlative models (Peterson and Soberón 2012). In situations with a focus on predicting the geographic distribution of the species rather than understanding conditions that allow the persistence of its populations, correlative models are also referred as Species Distribution Models (Peterson and Soberón 2012). A second approach, known as mechanistic modelling, combines species functional traits (e.g., physiology, behaviour) and fitness components (e.g., survival, reproduction) with spatial data to map species distribution (Kearney and Porter 2009). A “hybrid” or “process-oriented” methodology can also be used for this purpose, coupling hypotheses on niche, dispersal and biotic interactions (Robinson et al. 2011).

Under the scope of this thesis, only the correlative approach was considered. For this method, the concept of ecological niche provides the central theoretical basis for describing species–environment relationship (Miller 2010). The ecological niche can be represented as a multidimensional object enclosing the set of environmental conditions that individuals of a species require to reproduce and survive (Hutchinson 1978). Three typologies of ecological niches are recognised: the fundamental, potential and realised. The fundamental niche considers the range of environmental conditions that a species is physiologically able to tolerate while the realised niche reflects the fundamental niche actually occupied as a result of biotic interactions (Miller 2010). The potential niche is an intermediate entity defined in strictly environmental dimensions (e.g., temperature, salinity), not accounting for the geographical space; it represents the fundamental conditions of the landscape that are suitable for the species distribution (Peterson et al. 2015).

ENMs show both advantages and disadvantages when compared to the mechanistic and hybrid approaches. The interpretation of correlation models will always be limited by the degree of interaction among abiotic and biotic factors, sometimes impossible to disentangle and explore. On the other hand, ENMs are more applicable and less data-demanding, albeit with limited use in pinpointing fine-grain and the individual-level tolerance limits (Peterson et al. 2015). A common source of uncertainty associated with ENM is the spatial and taxonomic data bias. Spatial bias in occurrence data commonly derives from sampling accessibility (e.g., closeness to the coast or shallower locations) and is particularly challenging to address in presence-only or presence-background data (Robinson et al. 2011). To minimize the negative effect of this issue on the accuracy of model estimations, various correction methods were developed (Phillips et al. 2009). Regarding environmental predictors, data quality issues derive from constraints related to their accuracy and coarse spatial-temporal resolution caused by patchy and remote observations. However, the implementation of ocean observing programs (e.g., http://www.goosocean.org/), and development of remote sensing technology and modelling techniques have resulted on progressive improvements in the mapping of physical and chemical parameters of the seascape with promising benefits for ecological modelling (Robinson et al. 2011; Sayre et al. 2017).

A wide range of ENMs algorithms are now available based on generalized regression and machine learning methods (Miller 2010). The appropriateness of each algorithm varies according to the type of presence data used (presence/absence data versus presence-only data; Valverde et al. 2008), and type of output wanted (probability versus suitability; Miller 2010). The panoply of studies comparing the different algorithms and assessing model accuracy have not identified a single algorithm that is consistently superior regardless of the species, study area or sample characteristic (Segurado and Araújo 2004). The variability observed among model predictions have prompted the use of ensemble modelling frameworks that combine the output of multiple models into a single estimation while allowing to assess the uncertainty and agreement levels between model outputs (Araújo and New 2007).

Model evaluation is a fundamental step in ENM and is typically achieved through dataset partitioning and cross-validation methods or more rarely, but preferably, with validation using an external and completely independent dataset (Guisan et al. 2006). Several accuracy metrics are available for the assessment of model prediction based on the dependence of data prevalence and on the threshold definition (Miller 2010).

1.4.2 - Biophysical modelling

For most marine species, population connectivity is determined largely by the transport of larvae and/or juveniles between suitable habitat patches (Treml et al. 2008). Hence, this process needs to be considered to ensure the proper management and conservation of species and ecosystems (Gaines et al. 2003). Biophysical modelling simulates a biological system using numerical formalizations of the physical properties of the environment. Biophysical models have been used for some decades on marine coastal ecosystems and surficial waters to explore and test ecological hypothesis on how biological and hydrodynamic processes affect larval dispersal and connectivity. However, on deep-sea ecosystems, only recently this approach began to be more feasible (e.g., Young et al. 2012; Fox et al. 2016; Ross et al. 2017a; Henry et al. 2018). This shortfall is due mainly to the many knowledge gaps regarding the biological traits of deep-sea species and the absence of oceanographic data with enough resolution to translate fine scale hydrodynamic processes (Hilário et al. 2015).

The spatially explicit nature of biophysical models allows to elucidate biogeographic patterns and support conservation measures. Their oceanographic component is based on numerical configurations that solve ocean circulations (advection and diffusion mechanisms) in a realistic way (van Sebille et al. 2018). The biological processes are then modelled integrating the spatial-temporal heterogeneity of the physical data from the oceanographic model (e.g., velocity fields, temperature and salinity values) together with the species life traits (e.g., spawning time and location, swimming behaviour, planktonic life duration – PLD; Ådlandsvik et al. 2009).

1.4.3 - Network analysis

Network analysis has emerged as a powerful approach to disentangle complexity within dynamic systems, by providing an efficient mean to visualise, analyse and interpret pairwise relationships between network objects (Pascual-Hortal and Saura 2006). A suite of tools was developed to explore and quantify the spatial and temporal patterns of such relationships (Jacoby and Freeman 2016). Many of these tools are based on the Graph Theory, a branch of mathematics, commonly used in numerous research fields (Ricotta et al. 2000) including science and technology studies (e.g., scientometrics (Tancoigne et al. 2014; Raimbault et al. 2016) and ecology (Jacoby and Freeman 2016).

In ecology, this approach has been used to quantify ecosystems connectivity, identify the role of habitat patches in the seascape and prioritizing areas for conservation (Kool et al. 2013; Engelhard et al. 2016; Treml and Kool 2017). A graph-based framework is less data-demanding than other methods (Treml et al. 2008; Urban et al. 2009) and combines spatially explicit habitat data with information on the dispersal capacity of species (Calabrese and Fagan 2004). A graph (Figure 1.4.1) is composed by a set of nodes, each representing the attributes of a habitat patch (e.g., area, habitat suitability) and by edges (links) drawn between a pair of connected nodes illustrating the degree of connectivity between them (Pascual-Hortal and Saura 2006). A network with nodes representing fixed geographic location and directed edges is called of spatial graph (Dale and Fortin 2010).

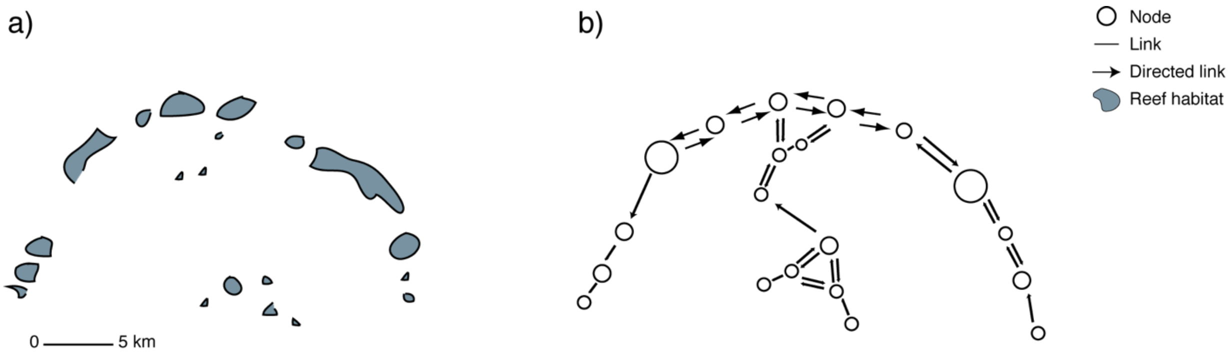


Figure 1.4.1 – a) Diagram of a coral reef ecosystem with individual reefs represented by grey patches. (b) Spatial graph representing the same ecosystem, where reefs are symbolized by nodes, and directed dispersal of individuals is represented by weighted edges (adapted from Saunders et al. 2016).

The edges of a graph network are drawn based on an adjacency matrix or an edge list that compiles the information related to each edge. In an adjacency matrix, each element in the matrix A_{ij} represents some form of interaction between source (*i*) and destinations (*j*) nodes. The matrix can be either symmetric or asymmetric ($A_{ij} \neq A_{ji}$) to represent non-directed or directed interactions between nodes (Jacoby and Freeman 2016). The edges can be described by the presence/absence of connections (binary) or may be weighted reflecting different degrees of connectivity between the nodes in the network (e.g., probability of connection, flux of individuals; Minor and Urban 2008). Different thresholds may be imposed to the edge weight to simplify the illustration of the network structure and improve its readability.

Network analysis based on a graph approach is by nature a multiscale methodology allowing to assess ecosystem connectivity by integrating simultaneously the estimates of connectivity at the patch- and landscape level (Urban and Keitt 2001). Moreover, in studies applied to marine ecology, graph-based analyses can consider the asymmetric characteristics of larval dispersal and the variability in connectedness inherent to currents directionality and variations (Treml et al. 2008).

Only few studies on the biophysics of marine larval dispersal addressed the importance of the spatial and temporal patterns of the potential larval transport to population dynamics (Treml et al. 2008). This caveat is even more accentuated in deep-sea ecosystem studies. Network analyses based on Graph Theory applied to studies of ecosystem connectivity benefit of several metrics developed. These metrics facilitate the identification and exploration of several proprieties of the network, contributing to understand relationships between structure and processes in biological systems (Dale and Fortin 2010; Jacoby and Freeman 2016).

1.5 - Conservation and management

Despite the remoteness of the deep sea, the effects of climate change (e.g., Orr et al. 2005; Lunden et al. 2014; Sato et al. 2017) and human activities (e.g., Clark et al. 2016; D'Onghia et al. 2017) are difficult to remain unnoticed. The changes observed in the water temperature, pH and levels of dissolved oxygen increase the vulnerability of the continental margin ecosystems to direct human impacts by reducing the resilience of the biological communities to physical or chemical damages (Levin and Sibuet 2012). The technological developments, besides advancing the scientific knowledge, also facilitated fishing and exploiting natural resources even deeper. This trend is favoured by the depletion of resources on land and continental shelves (Levin and Sibuet 2012) leading, for instance, to the deep-water drilling for oil and gas (Cordes et al. 2016b) cobalt-rich ferromanganese crusts at seamounts (Gollner et al. 2017), and fisheries moving deeper into offshore waters (Clark et al. 2016). The public awareness on the vulnerability of the deep-sea ecosystems and on the wider societal and economic benefits they provide has prompted a renewed interest in deep sea conservation (Glover et al. 2010; Ressurreição et al. 2011; Jobstvogt et al. 2014).

Submarine canyons have been proposed as priority areas for conservation on continental margins because of their biological, ecological and scientific importance (Davies et al. 2014). Nevertheless, the management and conservation of canyon ecosystems involve complex frameworks which depend upon their geographic location and different levels of the legislation regime (international, national, and regional; Fernandez-Arcaya et al. 2017). One of the most relevant conservation and management case studies related to submarine canyons is The Gully MPA (Canada, DFO Canada 2008), created in 2004 with distinct zones of protection based on different purposes: conservation, management and research. Despite some other examples (e.g., The Cassidagne Canyon in the Mediterranean Sea; Fabri et al. 2016), the effective protection of submarine canyons worldwide remains incipient. The area of canyons within exclusive economic zones and therefore under the jurisdiction of individual countries, was estimated in 91.9% of the total canyon area worldwide. However, only 13.6% of the 9477 large canyons benefit from some level of protection (with at least 10% of their area) and just 10.3% of all canyon have their total extent within an MPA (Fernandez-Arcaya et al. 2017).

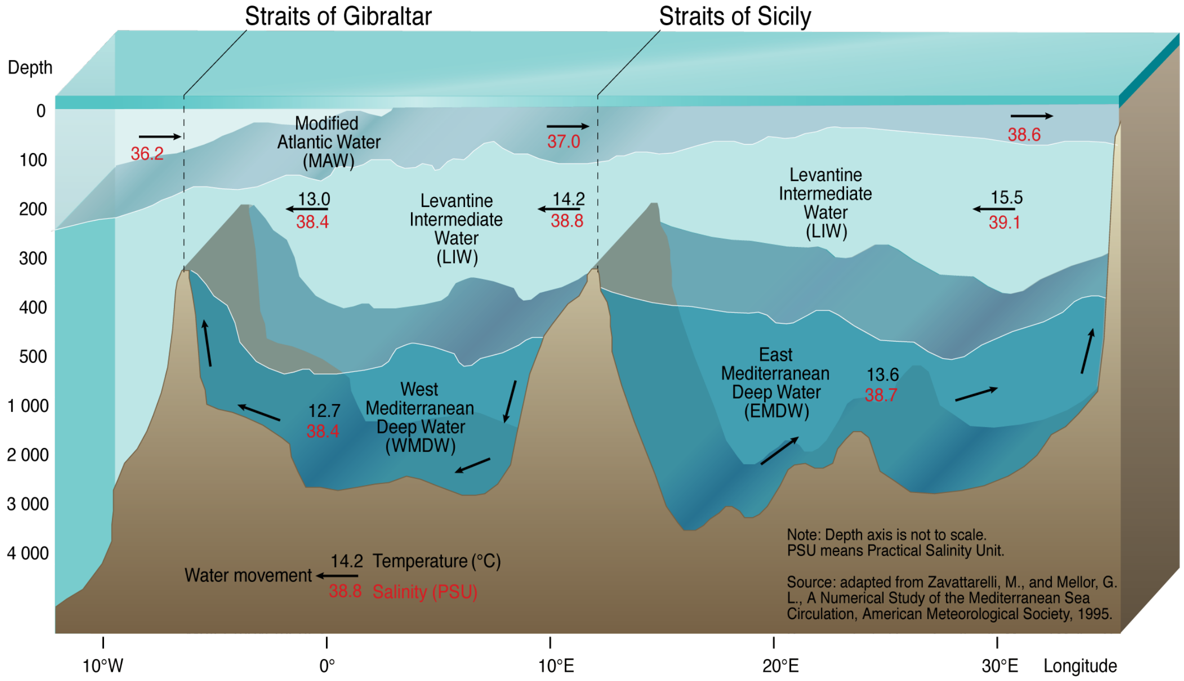
The increasing human pressure over the marine realm has led to consider the cost-benefit analyses in the ecosystem conservation planning and the adoption of a precautionary system that balances the use of marine resources with the maintenance of a productive and healthy marine environment (Barbier et al. 2014; Mengerink et al. 2014). Moreover, a straight collaboration not only among the scientific community but also with the managers, policy-makers and other stakeholders, is recommend and should be fostered (Mengerink et al. 2014).

1.6 - Study area – the Mediterranean Sea

The Mediterranean Sea is a semi-enclosed water body divided by the Strait of Sicily into the Western and Central-Eastern major basins (Robinson et al. 2001; Sardà et al. 2004). The Mediterranean Sea is connected to the Atlantic Ocean by the narrow Strait of Gibraltar and to the Black Sea in the eastern region through the Bosphorus Strait. The connection to the Atlantic Ocean exerts an important control on the Mediterranean water circulation (Amblas et al. 2004). The Western basin includes the Alboran

Sea, the Ligurian Sea and the Tyrrhenian Sea, while the Central-Eastern region comprises the Adriatic Sea, the Ionian Sea, the Levantine Sea and the Aegean Sea.

The water circulation in the study area is markedly influenced by topography, wind stress and the buoyancy flux resulting from the freshwater inputs and heat fluxes, and the complex hydrodynamics of the water masses (i.e., eddies, current meanders and bifurcations). The Mediterranean Sea comprises three main water masses (Zavatarielli and Mellor 1995): the Modified Atlantic Water (MAW), found in the surface layer; the Levantine Intermediate Water (LIW), formed in the Levantine basin and circulating at mid-depths from the Central-Eastern basin; and the Mediterranean Deep Water (MDW), formed in both the Western and Central-Eastern basins (Figure 1.6.1).



Note: Depth axis is not to scale.
PSU means Practical Salinity Unit.

Source: adapted from Zavattarelli, M., and Mellor, G. L., A Numerical Study of the Mediterranean Sea Circulation, American Meteorological Society, 1995.

Figure 1.6.1 - Vertical distribution of the Mediterranean Sea main water masses: the Modified Atlantic Water (MAW), Levantine Intermediate Water (LIW) and Mediterranean Deep Water (MDW). Mapped by GRID-Arendal and accessible at http://www.grida.no/resources/5885

The less dense water flowing from Atlantic Ocean into the Mediterranean Sea dominates the upper layers and is continuously modified by interactions with the atmosphere and the other water masses. The MAW flows eastwards along the North African slope (Figure 1.6.2), with a generally counter-clockwise circulation pattern, diverging then into two branches, one following North and the other entering the Central-Eastern Mediterranean basin through the Strait of Sicily (Schroeder et al. 2012).

The branch that follows North, circulates along the northern coast of Sicily running afterwards in a mostly cyclonic path along the Italian, French and the Catalan margins (Tanhua et al. 2013). From this main circulation pathway, a set of eddies develops and occasionally interacts with the central Western Mediterranean waters promoting their mixture within the basin (Sardà et al. 2004; Schroeder et al. 2012).

In the Central-Eastern Mediterranean basin, the general circulation is characterized by well-defined gyres (forced by topography and wind) which are linked by jets and follow multiple paths into the Levantine basin. The surface water running through the Central-Eastern Mediterranean convects latterly with the Levantine Intermediate Water at mid-depths, spreading then eastwards into the Levantine basin, and to westwards to the Ionian and northwards to the Adriatic Seas (Tanhua et al. 2013).

Mesoscale variability is generalized across the Mediterranean Sea resulting in changes of the water masses properties (e.g., temperature, salinity) and current patterns. This variability is more evident during exceptionally cold winters, when cold and dry air masses increase the evaporation levels and decrease the temperature of the MAW. This climate-driven phenomenon results in a dramatic increase in the water density inducing the occurrence of dense-shelf water cascading (DSWC) events and is responsible for the formation of the Mediterranean deep-water masses. This process has a decadal-base frequency and occurs in specific zones of the Mediterranean Sea (Figure 1.6.2), such as, the Gulf of Lion (Puig et al. 2013) and Otranto Strait (Robinson et al. 2001).

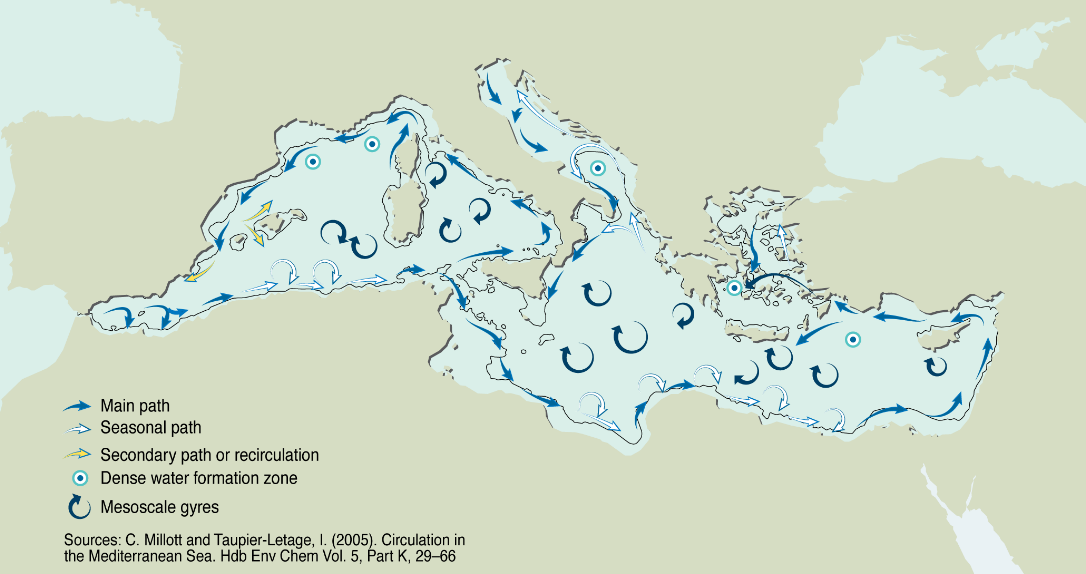


Figure 1.6.2 – Large-scale circulation in the Mediterranean Sea as described by Millot and Taupier-Letage (2005). The surface circulation is characterized by sub-basin-scale and mesoscale gyres interconnected and bounded by currents and jets with strong seasonal and inter-annual variability. Mapped by GRID-Arendal and accessible at http://www.grida.no/resources/5915

The Mediterranean Sea shows a diverse geomorphological seascape (Figure 1.6.3). The continental shelf is in general narrow and separated from the bathyal zone by steep continental slopes (Amblas et al. 2004; Harris et al. 2014) often incised by various submarine canyons. The Mediterranean submarine canyons, albeit among the smallest and shallower in the world, are the most closely spaced (Harris and Whiteway 2011). The drying up of the Mediterranean Sea during the late Miocene “Messinian Salinity Crisis” may have played an important role on the formation of canyon systems by promoting the erosion of the continental margins (Lofi et al. 2005; Rouchy and Caruso 2006). The incipient incisions produced were then further developed by submarine processes following the sea level rise in Mediterranean Sea. (Harris and Whiteway 2011). In the Western Mediterranean basin, in particularly, the occurrence of DSWC events may have also contributed for the erosion of submarine canyons through the cascading of erosive density currents (Canals et al. 2006; Harris and Whiteway 2011). The cataloguing of submarine canyons is largely dependent on the quality and resolution of the available seafloor data (Harris et al. 2014). For the European sector of the Mediterranean Sea the seafloor data compilation is quite advanced compared to the African sector. Its improvement will likely increase the number of canyons estimated so far (Ceramicola et al. 2015). The particular spatial arrangement of canyons in the Mediterranean Sea may have important implications to population connectivity and the maintenance of biodiversity, making this area an interesting deep-sea case study.

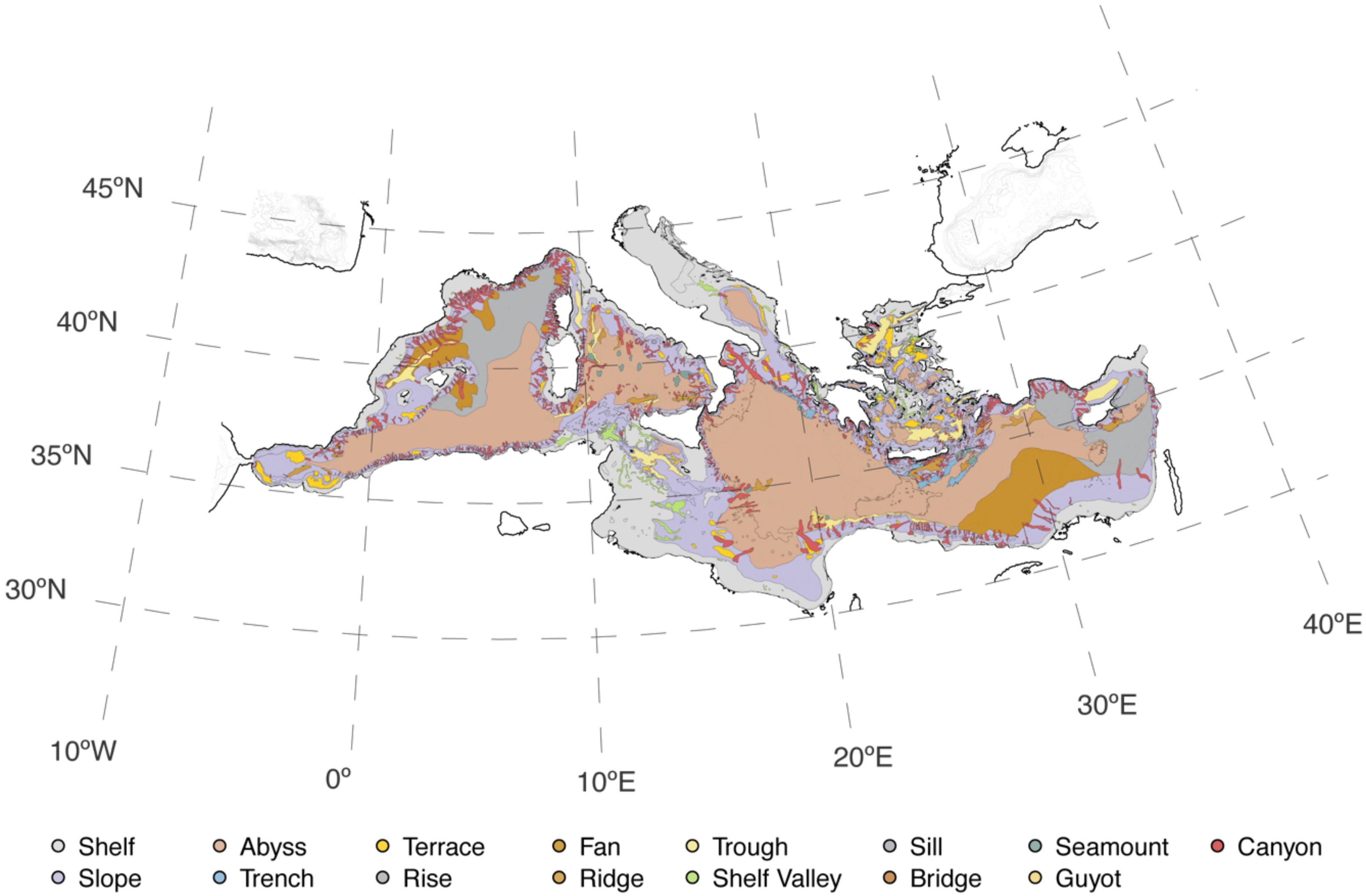


Figure 1.6.3 - Geomorphic features map of the Mediterranean according to Harris et al. (2014).

1.7 - Modelling species

Among the most iconic organisms found in submarine canyons are the Cold-water corals (CWC). These organisms are ecosystem engineers capable of depositing calcium carbonate and to build-up biogenic frameworks that provide habitat, refuges, feeding areas and nurseries for other species, even after the death of the coral (Roberts et al. 2006). These biogenic structures increase the habitat complexity and support highly diverse biological communities (Tursi et al. 2004; Rosso et al. 2010; D'Onghia et al. 2012). Hence, impacts on CWC and the physical structures they form would extend to the associated fauna (Cordes et al. 2016a). Because of CWC biological traits, namely, slow growth rates and low tolerance to disturbance, these organisms can be highly impacted by anthropogenic activities (Fabri et al. 2014) and for that reason were classified as Vulnerable Marine Ecosystems (VME; FAO 2009). In addition to impacts caused by direct human activities, the acidification and increasing temperature of ocean waters due to climate change may also significantly affect the survival of CWC (Georgian et al. 2016).

The Mediterranean Sea hosts populations of CWC mainly composed by colonial scleractinian species (Chimienti et al. 2018). Deep-water scleractinian corals occur mainly between 50 and 1000 m water depths (Roberts et al. 2006) and their occurrence, abundance and diversity is determined by seascape attributes such as substrate, temperature, salinity and water currents (Delibrias and Taviani 1984; Dullo et al. 2008; Brooke et al. 2013). Because of the heterogeneous topography, prevalence of hard substrate and enhanced productivity and hydrodynamics, submarine canyons are frequently referred as hotspots of CWC when compared to other areas (Orejas et al. 2009; De Leo et al. 2010). Among the CWC, *Lophelia pertusa* is one the most studied species in terms of biology and ecology (e.g., Le Goff-Vitry et al. 2004; Waller and Tyler 2005; Brooke and Young 2009; Larsson and Purser 2011; Larsson et al. 2014; Lunden et al. 2014; Strömberg and Larsson 2017). The life history of *L. pertusa* is characterized by a planktonic larval stage and a sessile adult existence, making this species an ideal model to study connectivity in the deep sea (e.g., Fox et al. 2016; Ross et al. 2017a). Moreover, *L. pertusa* is a habitat forming species and its conservation is crucial for other species using this habitat with resulting benefits for biodiversity management.

1.8 - Rationale and aims of the thesis

Submarine canyons are complex and heterogeneous geomorphologic structures highly relevant for the biodiversity and productivity of continental margins. These marine ecosystems play a key role providing invaluable goods and services for human well-being but are also increasingly subjected to the effects of anthropogenic pressure (Ramirez-Llodra et al. 2013) and climate change (Danovaro 2018). Knowledge on canyon ecosystems connectivity may contribute to assess the resilience of their biological communities, understand and anticipate their responses to global change, and define the appropriate scale of management and effective conservation strategies in order to preserve these benefits. As such, this thesis aims to contribute to increase the knowledge on these issues, by:

- Compiling and systematizing the available physical and biological information on submarine canyons
- Contributing to the knowledge of connectivity between canyons
- Addressing ecological, societal and management implications of the habitat loss or degradation in submarine canyons

Research synthesis is particularly important to facilitate the creation and exchange of knowledge (Fazey et al. 2013). The scientific research conducted on submarine canyon is extensively documented and the relevance of its compilation was recognized during the 2nd International Symposium on Submarine Canyons (Edinburgh, 2014). An integrative study of the literature content would help to characterize and identify knowledge gaps on the current canyon research landscape, facilitating the planning of future research agendas and optimizing the use of limited resources typical of deep-sea research. Under this assumption, I conducted a semantic analysis of the published literature on canyon research applying a network approach which I used as a starting point for this thesis. This work constitutes the first chapter of the Results section.

I used the Mediterranean Sea as a case study and *L. pertusa* as a modelling species to assess the relevance of submarine canyons for biodiversity conservation in the Mediterranean seascape. The Mediterranean Sea is populated by a considerable number of submarine canyons, closely spaced, and potentially highly susceptible to impacts of climate change and anthropogenic activities. *Lophelia pertusa* was selected as the model organism because of its prevalence in some Mediterranean canyons and its relatively well-known life-history traits and ecology. Moreover, the ecological relevance of *L. pertusa* as an ecosystem engineering species offers additional benefits in terms of conservation and management of the canyon biological communities. Notwithstanding, to achieve the second and third main objectives of this thesis, I used a multidisciplinary approach which required a certain degree of simplification considering the spatial-temporal scales involved and the current knowledge gaps.

In the marine environment, including the deep sea, the application of ENMs increased over the recent years mainly with the purpose of supporting conservation planning, evaluating the probable responses of species to climate change, and understanding processes that drive biogeographic patterns (e.g., Bentlage et al. 2013; Howell et al. 2016; Basher and Costello 2016; Pennino et al. 2016). The current distribution of *L. pertusa* in the Mediterranean Sea may be still underestimated since very few surveys targeting this species were conducted in comparison to other oceanic regions (Zibrowius 2003). This lack of knowledge is hindering the development of effective conservation measures aiming to protect this VME and associated fauna in the study area. The estimation of the Mediterranean seascape environmental suitability for *L. pertusa* constitutes the second chapter of the Results section.

Connectivity is an essential process for the biodiversity maintenance and population persistence, and therefore, mandatory for proposing science-based options for spatial planning and sustainable resource management (Luque et al. 2012). The spatial arrangement of Mediterranean canyons and the seascape suitability may play an important role on population connectivity and the maintenance of biodiversity. Studying this role at the basin scale is only possible by using modelling approaches (Van den Beld et al. 2017). In this context, I adopted a comprehensive and spatially explicit approach that considers metapopulation dynamics and the spatial heterogeneity of the Mediterranean seascape. I combined the seascape suitability described in the second chapter of this thesis with a biophysical model in order to estimate the potential connectivity of *L. pertusa* in the study area. I further analysed the outcomes of the biophysical model using a spatial graph-based approach to estimate the seascape connectivity and habitat availability of the species in the Mediterranean Sea. This information is essential for the management and conservation of this VME (e.g., design and implementation of marine protected areas networks). This work is presented in the third chapter of the Results section.

Finally, in the section 3 I highlight the main results of the thesis and discuss how the knowledge gathered on submarine canyon in the Mediterranean Sea will contribute with scientific evidence to support decision-making in the conservation and management of a VME and associated fauna in the study area.

Chapters 2.1, 2.2. and 2.3 of this thesis are presented as research articles and are in press, submitted and being prepared for submission, respectively.

- **F.L. Matos**, S.W. Ross, V.A.I. Huvenne, J.S. Davies, M.R. Cunha (in press). *Canyons pride and prejudice: Exploring the submarine canyon research landscape, a history of geographic and thematic bias*, Progress in Oceanography. https://doi.org/10.1016/j.pocean.2018.04.010
- **F.L. Matos**, J. B. Company, M.R. Cunha. *Mediterranean seascape suitability for Lophelia pertusa: challenging the physiological limits*. Submitted to the Scientific Reports (under review)
- **F.L. Matos**, J. Aguzzi, J. B. Company, M.R. Cunha. *Gone with the stream: connecting dots across the Mediterranean seascape of Lophelia pertusa*. Prepared for submission.

Section 2 - Results

2.1 - Canyons pride and prejudice: exploring the submarine canyon research landscape, a history of geographic and thematic bias

2.1.1 - Abstract

We mapped submarine canyon research using a scientometric approach to define and characterize its scientific landscape based on a comprehensive bibliographic dataset. The abundance of studies covering structural and functional aspects of submarine canyons allowed us to identify the existing knowledge clusters, historical trends, and emergent topics in canyon research. Our analysis documented a network of knowledge clusters of which four were particularly relevant: a strong cluster on “Geology & Geophysics”, well established since the beginnings of canyon research; a cluster on “Biology & Ecology” that gained strength primarily over the past two to three decades; a cluster on “Oceanographic Processes” which occupied a central position in the network and connected strongly to almost all the other clusters and especially to the fourth main cluster on “Modelling”. A smaller, but also well connected, cluster on “Biogeochemistry” related closely to “Biology & Ecology”, and three other small clusters (“Sedimentology”, “Sediments & Tidal Currents”, “Canyon Sampling”) bridged the main clusters. Finally, we identified three small, but specific satellite clusters (“Oil & Gas”, “Chemosynthetic Communities”, “Molecular & Symbionts”). The high-level structure of the knowledge network reflects a latent interdisciplinarity in canyon research. However, the evolution of the research lines over the past nine decades suggests that this pattern arose mostly in the new millennium. Emergent research topics in the last decade also reveal a concern regarding anthropogenic impacts and climate-driven processes. Our results also show a well implemented and international collaboration network, although research efforts have been mainly directed towards only a few canyon systems. A geographical and thematic bias also characterizes canyon research, with specific topics addressed preferentially in particular canyons by different leading research institutions. This spatial and thematic bias, together with the paucity of truly inter-disciplinary studies, may be the most important limitation to integrated knowledge and development in canyon research and hinders a global, more comprehensive understanding of canyon patterns and processes. The scientific landscape mapping and the complementary results are made available as an open and interactive platform that canyon stakeholders can use as a tool to identify knowledge gaps, to find key players in the global collaboration network and to facilitate planning of future research in submarine canyons.

Keywords: submarine canyons; research mapping; network analysis; textual analysis; knowledge clusters

2.1.2 - Introduction

The scientific literature provides a critical instrument for research dissemination and, thus, an important source of scientific and technological information (Huang et al. 2011; Kahane et al. 2015). Research mapping based on bibliographic data (e.g., abstracts, affiliations) offers an intuitive and structured framework to explore and describe research areas, detect knowledge gaps and cutting-edge topics, and identify key players in different scientific fields (Boyack et al. 2005; Oldham et al. 2012; Oldham et al. 2014b). A new methodology has been recently developed to reconstruct research dynamics over time (Chavalarias and Cointet 2013). Mapping and historic reconstruction techniques both provide important information that can help direct and enhance research coverage, by reducing duplication of efforts and promoting synergies (Boyack 2004; Oldham et al. 2014b).

Deep-sea scientific exploration has been hindered by costly and highly technology-dependent field work. To tackle these limitations requires strong institutional collaboration together with an extensive effort to seek research funding (Oldham et al. 2014a), as well as the adoption of multidisciplinary approaches integrated in well-designed strategies. Hence, future research agendas can benefit from detailed and visually explicit information on research trends and collaboration networks, particularly in stagnant or declining funding scenarios.

Submarine canyons are among the most iconic deep-sea ecosystems, with more than 9500 canyons catalogued worldwide along continental and island margins (Harris et al. 2014). The complexity of canyon systems and their influence on the surrounding environmental setting often requires scaling-up of proposed research to a regional level. Canyons influence water circulation (e.g., internal tides, currents), transport of sediments, nutrients and particulate matter (Liu et al. 2002; Allen and Durrieu de Madron 2009; Puig et al. 2014), as well as ecosystem functioning and services, including an important role in carbon storage (Masson et al. 2010). They often enhance regional biodiversity (Cunha et al. 2011) and biomass of various organisms (De Leo et al. 2010; Kavanaugh et al. 2015), including many economically exploited species (Yoklavich et al. 2000; Company et al. 2012). Moreover, canyons act as natural traps and conduits for litter and contaminants (Castro-Jimenez et al. 2013; Pham et al. 2014) and are often exposed to the impacts of various anthropogenic activities, such as fisheries (Puig et al. 2012; Paradis et al. 2017) and hydrocarbon exploration (Harris et al. 2007) that may operate synergistically with natural disturbance (Almeida et al. 2017). Overall there is a high spatial and temporal variability within and between canyons, both in terms of physical environment and biological communities, which emphasizes the complexity, diversity and uniqueness of these systems (e.g., Cunha et al. 2011). We are only beginning to understand the broad-scale physical and biological processes and patterns in submarine canyons, moving towards the integration of current fragmented knowledge in order to achieve a more comprehensive perspective on these important deep-sea features (Huvenne and Davies 2014; Amaro et al. 2016).

The large volume of publications and ready access to their digital formats facilitates the scientometric analysis of their content through textual retrieval techniques, such as text mining and natural language processing (NLP). These methods offer powerful tools to organize, classify, label and retrieve novel data patterns. Textual data processing requires multiple steps: assembling a collection of texts on a particular subject (corpus) for computational processing, formatting the corpus, and selecting analysis methods to detect relationships among data elements (e.g., clustering methods, graphs and network algorithms; Losiewicz et al. 2000). Co-word networks have been used for this purpose (e.g., Tancoigne et al. 2014; Ruiz-Martinez et al. 2015; Raimbault et al. 2016), combining the strengths of textual retrieval techniques with network analysis. Proximity measures that normalize the relationships and strengths in the network establish associations among nodes. Depending on the characteristics of nodes, the networks can be classified as homogeneous, if built from a single text field, or heterogeneous if built from distinct text fields (e.g., authors and affiliations; Barbier et al. 2012). Despite some criticism of co-word analysis related to interpretation issues and language ambiguity (Leydesdorff and Hellsten 2006), the structure of lexical co-occurrences allows the identification of relevant and directly interpretable commonalities between concepts, techniques, and research achievements (Rule et al. 2015; Raimbault et al. 2016). This approach has already produced important outcomes in different scientific fields contributing, for instance, to the development of research agendas (Tancoigne et al. 2014) and detecting the emergence of research lines (Raimbault et al. 2016).

This paper tackles some of the most pressing canyon research issues identified during past meetings of the International Network for submarine Canyon Investigation and Scientific Exchange (INCISE; Huvenne and Davies 2014), and provides evidence-based indicators to support planning of future research. We map the scientific landscape and overall trends of submarine canyons research based on the INCISE multidisciplinary literature database (Ross et al. 2017b). The analysis of the canyon research landscape addresses four specific objectives: (1) outlining the main knowledge clusters (and their relationships) in canyon research, (2) tracing canyon research evolution and detecting emergent research topics, (3) identifying the most well-studied submarine canyons and putative research biases, and (4) mapping the collaboration network of the canyons' scientific community.

2.1.3 - Material and Methods

The epistemic analyses (analyses relating to knowledge) of the canyon research landscape were performed using the digital platform CorTexT (http://www.cortext.net). This tool offers a set of scripts developed to support the processing and analysis of large text corpora using information retrieval, natural language processing, scientometric methods and network analysis (Tancoigne et al. 2014). Complementary analyses and data visualization processing were carried out using R (R Core Team 2016).

2.1.3.1 - Text corpus

The corpus was extracted from the INCISE database on the submarine canyon scientific literature (Ross et al. 2017b, last updated August 2016). The foundation of this database was established during the 2nd INCISE meeting (Edinburgh, 2014) by the INCISE Working Group 2 and resulted from the recognized need for a comprehensive compilation of studies conducted in submarine canyons. The database was built with documents extracted from the scientific databases Scopus, ScienceDirect, the Thomson Reuters Web of Science and Google Scholar using the queries *"submarine canyon*"* and *submarine canyon** in the fields title, abstract and keywords. The documents retrieved were then checked individually and the ones not related with canyon research were excluded. Finally, the scientists from the entire INCISE community contributed their own canyon databases and references.

The selection of references for this study depended upon abstract availability. A total of 1968 references fulfilled this requirement, varying in type and scope, covering the period from 1929 to 2016 (Figure 2.1.1). In addition to the abstract field, we populated the corpus with information regarding the research subject areas and categories, and author affiliations. The information on subject areas and category fields of the reference sources, retrieved from the SCImago Journal & Country Rank (SJR) classification, was available for 91.1% of the documents. The information on the author affiliations retrieved from Scopus was available for 79.1% of the documents.

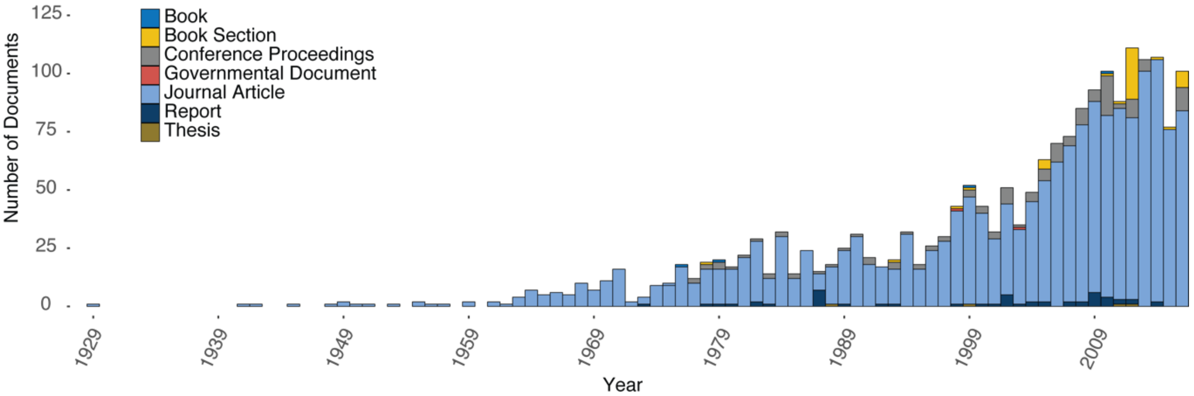


Figure 2.1.1 – Distribution of canyon related documents from 1929 to 2016, according to type. References composing the corpus were extracted from the INCISE canyons bibliographic database.

2.1.4 - Extraction and systematization of terms

We built a preliminary list of 4500 lexical units (single- and multiword terms) from the abstracts and considered this list sufficiently explicit and informative for the analyses. We extracted terms using NLP methods, a process based on collocations of terms and sensitive to lexical variations (e.g., singular and plural forms) producing single lexical entities by root word. Terms such as measurement units, geographic references, dubious expressions and canyon names (treated independently) were removed. We classified the terms in the resulting list by research topic and reduced language ambiguity by sorting and merging all synonyms. After this process, we indexed the terms retained back to the abstracts allowing their detection and subsequent use in the analyses.

2.1.5 - Mapping and network analyses

We built the networks using the most frequent entities (e.g., terms, canyon names, author affiliations) and their relationships. The links between entities were defined by a proximity measure based on the frequency of their co-occurrence. CorTexT divides proximity measures in two categories, direct (e.g., raw and chi-square) and indirect (e.g., distributional) depending on the transformation imposed on the data. The direct measures only consider co-occurrences between two elements not affecting the original statistics (for instance, the raw metric only considers the sum of all co-occurrences between two entities), while indirect measures ponder all co-occurrences in the network to determine a link between nodes (more information about these metrics available in: https://docs.cortext.net/metrics-definitions/). We applied the raw, distributional and chi-square metrics in order to construct collaboration networks (institutional affiliations and countries), homogenous networks (e.g., co-word mapping) and heterogeneous networks, respectively.

We estimated the *betweenness centrality* of terms which is a measure of centrality (Freeman 1978) based on shortest paths between terms in a network. This measure allows us to identify the nodes that have the highest relevance to the information spread over the network.

2.1.5.1 - Clustering

We determined the high-level structure (topical clustering) of the canyon research landscape using the Louvain community detection algorithm, which is capable of extracting cohesive groups from large networks (Blondel et al. 2008). We used a spatialization technique to optimize the arrangement of the nodes in a two-dimensional plot where spatial proximity represents the structural neighbourhood of the clusters (Raimbault et al. 2016). The size of the nodes reflects the frequency of the terms, and the thickness of the links and distance between nodes encodes the frequency of the terms' co-occurrence. Depending on the network size and the number of links, we imposed a filter threshold and, for visual simplicity and readability, retained only a specified number of the most relevant connections. The resulting knowledge clusters encompass related nodes coded by colour; the size of the circle drawn around each cluster is proportional to the number of documents containing the terms therein. Connections between nodes within a given cluster are stronger than connections between nodes of different clusters.

Every document entry in the corpus was matched against each cluster and labelled according to its content. This process allowed us to correlate the identified clusters with the most frequently-studied submarine canyons and with the research institutions through contingency matrices. These matrices were built considering the number of documents assigned to each variable and their correlation calculated against a null model assuming the independence of each distribution (Raimbault et al. 2016).

2.1.5.2 - Research dynamics

We used a bottom-up reconstruction of the epistemic dynamics based on the tracking of terms over time to capture the evolution of scientific fields in canyon research (Chavalarias and Cointet 2013). A river diagram illustrated the research dynamics following the methodology described in 2.1.5.1 using the top 100 terms. We divided the entire corpus (1929 - 2016) in 14 successive and regularly spaced time-slices of approximately 10 years each. Each time interval is partially overlapping with the previous one (four years) promoting a smoother flow of the existing research lines. We considered one decade as a reasonable time interval to capture research dynamics. Each period is composed of a group of vertical bars that correspond to distinct clusters in the network. This technique is sensitive to semantic changes (appearance and fading of terms), capturing the flow of concepts across time periods and recreating the dynamics of the research lines by the growth, forking, merging, or declining of thematic bars in a river plot. When relationships are detected between adjacent time periods, a stream flow connects the bars with a colour intensity reflecting the degree of connection (see Chavalarias and Cointet 2013; Rule et al. 2015).

2.1.6 - Results

Our analysis, namely the mapping of the research effort, the list of publications used, and the semantic and the collaboration networks, are available through an interactive online platform accessible at https://canyons-research-mapping.shinyapps.io/canyons-sci-landscape/ .

2.1.6.1 - Corpus overview

The number of documents composing the corpus was low and irregularly distributed during the first half of the 20th century, but began to grow during the 1960s, and maintained a constant level until the mid-1990s when it started to steadily increase, with a considerable rise since 2004 (Figure 2.1.1). Dominated by journal articles (88.5%), the corpus also includes conference proceedings, scientific reports, books, academic theses, governmental documents and maps. The information collected covers 814 clearly identified submarine canyon systems spread worldwide (Figure 2.1.2). In some documents, the studied canyons were not formally designated and were not recognizable in the figures of publications, therefore their locations could not be mapped.

Most of the documents (67.9%) used in our analysis correspond to single canyon studies. Nevertheless, from the 814 listed canyons, eleven canyons account for a disproportionate research effort (about 48%). These most frequently studied canyons, with more than 50 associated publications each, are located along the North American and European continental margins and off Taiwan island: Monterey, Baltimore, Hudson, Gully, Nazaré, Lacaze-Duthiers, Cap de Creus, Blanes, Gaoping (Kaoping), La Jolla and Alaminos (ordered by decreasing number of publications).

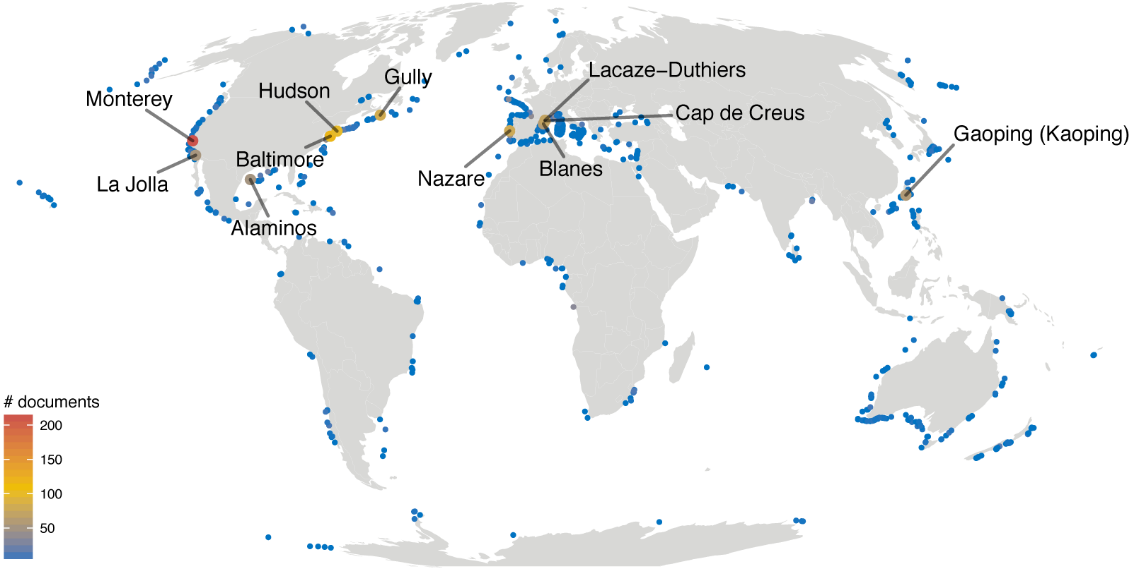


Figure 2.1.2 - Global distribution of the identified submarine canyons included in this study. The dots are coloured according to the associated research effort (total number of documents). The eleven canyons linked to at least 50 publications are identified.

We identified a total of 105 subject categories corresponding to 23 major subject areas according to SJR. We included approximately 70% of the references in at least one of the subject categories (e.g., Geology, Oceanography) of the subject area "Earth and Planetary Sciences", and ca. 34% in subject categories (e.g., Ecology, Evolution, Behavior and Systematics) of the subject area "Agricultural and Biological Sciences" (Figure 2.1.3). Less common, although relevant, are disciplines associated with the multidisciplinary area of "Environmental Science" or related to areas such as "Engineering" and "Energy" focused largely on underwater technology, geotechnical studies, drilling, hydrocarbon exploration and environmental hazards. These results suggest a strong research investment in the study of canyon environmental settings, also noticeable in the most frequent terms identified in the abstracts (Figure 2.1.4), which include "continental margin", "slope and shelf", "sea-level changes" and "fan systems".

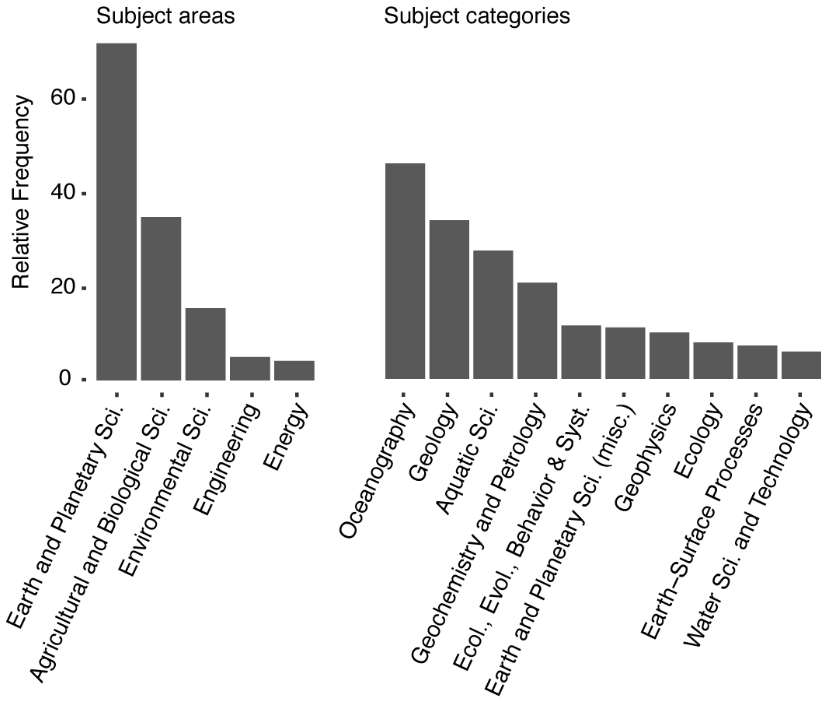


Figure 2.1.3 – The top 5 subject areas (left) and the 10 most frequent subject categories (right) in the full corpus according to the classification of the references' source in SCImago Journal & Country Rank (SJR). Sci. – Sciences; Ecol. – Ecology; Evol. – Evolution; Syst. – Systematics; Misc. – Miscellaneous.

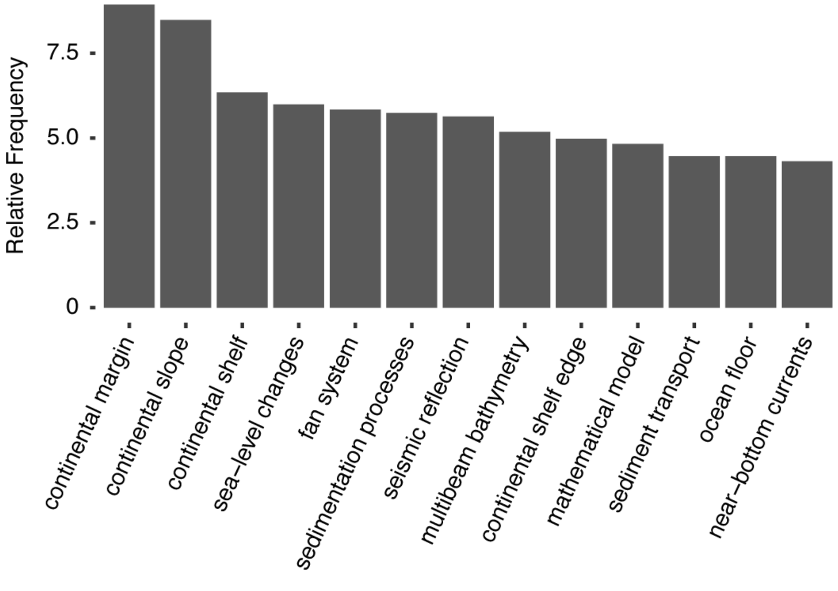


Figure 2.1.4 - The 15 most frequent terms occurring in the corpus.

2.1.6.2 - Canyon research snapshot and retrospective overview

The synonymization process resulted in a list of 1084 terms which were indexed back to the abstracts for analysis. These terms, which are associated with one or more subject categories, constitute a varied and complex semantic landscape. We interpreted the semantic network considering its global structure and the internal organization of the clusters, namely, the position, connections and distance between nodes (Figure 2.1.5).

Semantic co-word networks replicate the structure and relationships embedded in the corpus content. The labelling of clusters is based on their lexical content; however, since this is a static representation of the full corpus, it may not represent satisfactorily the whole context of the terms. This limitation may result in terms tagged under labels which would not usually be intuitive. An example is the inclusion of the term "marine sediments" under the category of "Biology & Ecology" (Figure 2.1.5) mainly due the large number of publications in the last two decades related with infaunal studies. However, when considering a different period, for instance, the documents of the first three decades (results not shown), the same term appeared associated with knowledge clusters such as "Geology" and "Sediment Dynamics". This shows that changes over time in the research topics associated to a given term are not retained by this static method. This limitation is overcome in the river diagram (Figure 2.1.6) which we used to interpret the evolution of our understanding on canyons and the way it induced the direction of research lines.

Mapping of the abstract contents exposed 11 lexical domains that can be linked to distinct topics representative of the current knowledge clusters on submarine canyons (Figure 2.1.5). The scientific fields detected confirm the trend already observed in the corpus overview (section 2.1.6.1), namely a research effort primarily directed to understanding the structural components of canyon systems. Despite the identification of distinct semantic units, the high-level structure of the network revealed an entangled connection pattern between knowledge clusters that reflects a latent interdisciplinarity in the canyon research spectrum. However, the evolution of the research lines suggests that this pattern has emerged only in recent years (Figure 2.1.6).

The global picture from the river diagram conveys an absence of a semantic chain crossing the full-time span of our analysis, suggesting a lack of research continuity at least in the earliest years (1929-1960). Moreover, before the 1980s, canyon research was considerably fragmented with few publications covering rather disparate topics, which is expressed in the diagram by a high number of bars in each time interval and very few connections between successive time intervals. This pattern changes after the 1980-90s, with topic groups starting to be more cohesive, interconnected and comprehensively addressed in the literature (larger height of the bars) reflecting the growing deep-sea scientific community and knowledge build up.

The largest knowledge cluster identified in the co-word network concerns the geological and geophysical characterization of canyons (“Geology & Geophysics”, Figure 2.1.5). This is also one of the earliest topics arising in the canyon research historical record that we compiled (Figure 2.1.6). This cluster is composed of terms related to the mostly geological survey and sampling of continental slopes and shelves (e.g., “seismic data”, “core samples”, “stratigraphic record”) and the search for relationships between the origin and evolution of submarine canyons with ocean eustasy (e.g., “sea-level changes”), tectonics (e.g., “tectonic activity”) and river systems (e.g., “river mouth”, “river inputs”). The role of these factors and of erosive processes (e.g., “mass-wasting processes”) on the canyons formation and evolution gave rise to new research lines dedicated to the study of “mass movements”, “turbidity flow”, “slope instability” and geo-hazards (e.g., “earthquakes”). In fact, these topics were recurrent along the history of canyon research in various branching systems of the river diagram (green, blue and yellow streams). Canyon research experienced an evident expansion between the 1960s and 1990s with the increasing effort on geophysical and geological surveys (e.g., the “Deep Sea Drilling Project”, Figure 2.1.6). These surveys deepened our understanding about the geological setting, geomorphology and sediment dynamics of canyons, highlighting the conduit effect of submarine canyons on materials transport and their deposition in fan systems.

Closely positioned and linked to the “Geology & Geophysics” cluster are three smaller clusters: “Sedimentology”, “Sediments & Tidal Currents” and “Oil & Gas” (Figure 2.1.5). The “Sedimentology” cluster is composed of terms related to sediment characteristics (e.g., “mineralogical composition”, “grain size”) and depositional structure (e.g., “physical stratification”, “depositional features”), while the “Sediments & Tidal Currents” cluster is more focused on processes related to sediment transport and erosion (e.g., “downslope transport”, “contour currents”, “turbidite activity). The third group addresses aspects related to hydrocarbon exploration (e.g., “3D seismic”, “Jurassic and Cretaceous periods”, “deltaic deposits”, “sedimentation basins”), essentially boosted during the 1960s and beginning of the 1990s by the investment in drilling programs and stratigraphic studies by academia, government agencies and private industry (stream system at the bottom of the river plot, Figure 2.1.6).

The second largest research cluster is “Biology & Ecology”. It covers a wide range of subjects including “trophic structure”, “community composition”, “spatial distribution” of emblematic organisms such as marine mammals (e.g., “whales”) and “cold-water corals”, but also commercially exploited species (e.g., “*Aristeus antennatus*”), their relationship with environmental factors, the effects of anthropogenic impacts (e.g., “fishing activities”, “marine litter”, “contaminants”) as well as other conservation issues (e.g., “marine protected areas”, identification and records of “Vulnerable Marine Ecosystems”). However, the research effort committed to these topics is traceable only in the last 30 years of the period covered by our analyses (Figure 2.1.6), with some of these topics only addressed in the most recent years. Examples are the relation of species distributions to the canyon versus adjacent environments (“Community Composition & Adjacent Areas” bar, encompassing the period 2007-2016, Figure 2.1.6), and the anthropogenic disturbance and conservation concerns (“ROV & fishing activities”, same interval, Figure 2.1.6). The technological developments and their growing application in oceanographic cruises, such as the use of remote operated vehicles (ROV) allowed recording and reporting of anthropogenic impacts in canyon ecosystems, namely, the documentation of fisheries, marine litter and contaminants impacts. Moreover, “ocean observatory systems” were also identified as one of the most important recent terms in canyon research associated with biological surveys.

Strongly connected and closely positioned to the “Biology & Ecology” cluster are two smaller clusters (Figure 2.1.5): one shaped by terms linked to “Canyon Sampling” (e.g., “canyon sites”) and studies of “foraminiferal assemblages” which includes references to the environmental setting (e.g., “pore-water”, “water-sediment interface”) and “climate change”, and the other, ”Biogeochemistry”, focused on the study of “organic matter”, “primary productivity”, “terrigenous inputs”, and references to studies on meiofaunal assemblages. Both clusters are less represented in the corpus and therefore their detection in the historical evolution of canyon research is difficult (Figure 2.1.6). More distant in the network are two very small satellite clusters of the “Biology & Ecology” and “Geology & Geophysics” main clusters, one regarding “Molecular & Symbionts” studies and the other linked to the occurrence of “Chemosynthetic Communities” in submarine canyons, both poorly represented in the literature until recently.

The next cluster, “Oceanographic Processes”, occupies a nearly central position in the network sharing several connections with the more peripheral clusters (Figure 2.1.5). This highlights oceanography as a core research topic in submarine canyon research. The terms composing this cluster are related to currents (e.g., current flow”, “near-bottom currents”), oceanographic phenomena (e.g., “dense shelf water cascading”), environmental seasonality (e.g., “winter season”), and particle transport (e.g., "sediment transport”, “suspended load”, “active conduit”, “lateral transport”). Although references to oceanographic processes are frequent in the corpus (Figure 2.1.5), they do not stand out throughout canyon research history until recently (Figure 2.1.6). The three time-intervals depicted in the dark cyan stream of the river diagram (between the bars “suspended sediment & marine storms” and “dense shelf water cascading & cascading events”) indicate a strong research investment in the study of environmentally complex, climate-driven oceanographic events, highlighting the emerging relevance of these topics in the last decades.

The complex biogeochemical interactions (e.g., “nutrient fluxes”) and the interaction between canyon topography and oceanography (e.g., “circulation patterns”, “flow interactions”) started to be explored mainly after the 1990s essentially by modelling approaches (both numerical and laboratorial). The last cluster detected was a “Modelling” hub, positioned in the upper part of the co-word network (Figure 2.1.5) and widely connected to several other clusters. It is composed of terms linked to ocean current patterns (e.g., “current system”, “circulation model”), tides (e.g., “internal tides”), waves and environmental variables. More recently, modelling approaches started to be used in biology studies, namely of species spatial distribution patterns (tracked in the river diagram for instance, in the “Whales & Mathematical Models” bar; Figure 2.1.6).

The 10 terms with the highest betweenness centrality are the top staple nodes in the canyon research landscape and have a determinant influence on the network structure and connectivity between knowledge clusters. These are: “active margin”, “adjacent slope”, “seismic reflection”, “sediment budget”, “sediment dispersal”, “burial efficiency”, “accretionary wedge”, “organic carbon”, “seasonal variation” and “flow dynamics.”. The terms “seismic reflection” and “accretionary wedge” shared connections only within the “Geology & Geophysics” cluster. The nodes “sediment dispersal” (Geology & Geophysics), “adjacent slope” (Biology & Ecology) and “seasonal variation” (Modelling) are connected to “Oceanographic Processes” highlighting, once more, the centrality of this knowledge cluster in canyon research. The connection between “Geology & Geophysics” and “Oceanographic Processes” is further reinforced by the node “sediment budget”. “Flow dynamics” established preferential connections between “Geology & Geophysics” and “Modelling”. The nodes “sediment dispersal” and “flow dynamics” from “Geology & Geophysics” and “sediment budget” from “Oceanography Processes” are also linked to the cluster “Sedimentology”, therefore reinforcing the connection between these two main clusters. The cluster “Biogeochemistry” links to “Geology & Geophysics” by the nodes “surficial sediments” and “active margin” and to “Biology & Ecology” by the nodes “organic carbon” and “adjacent slope” thus acting as a bridging topic between these two main knowledge clusters.

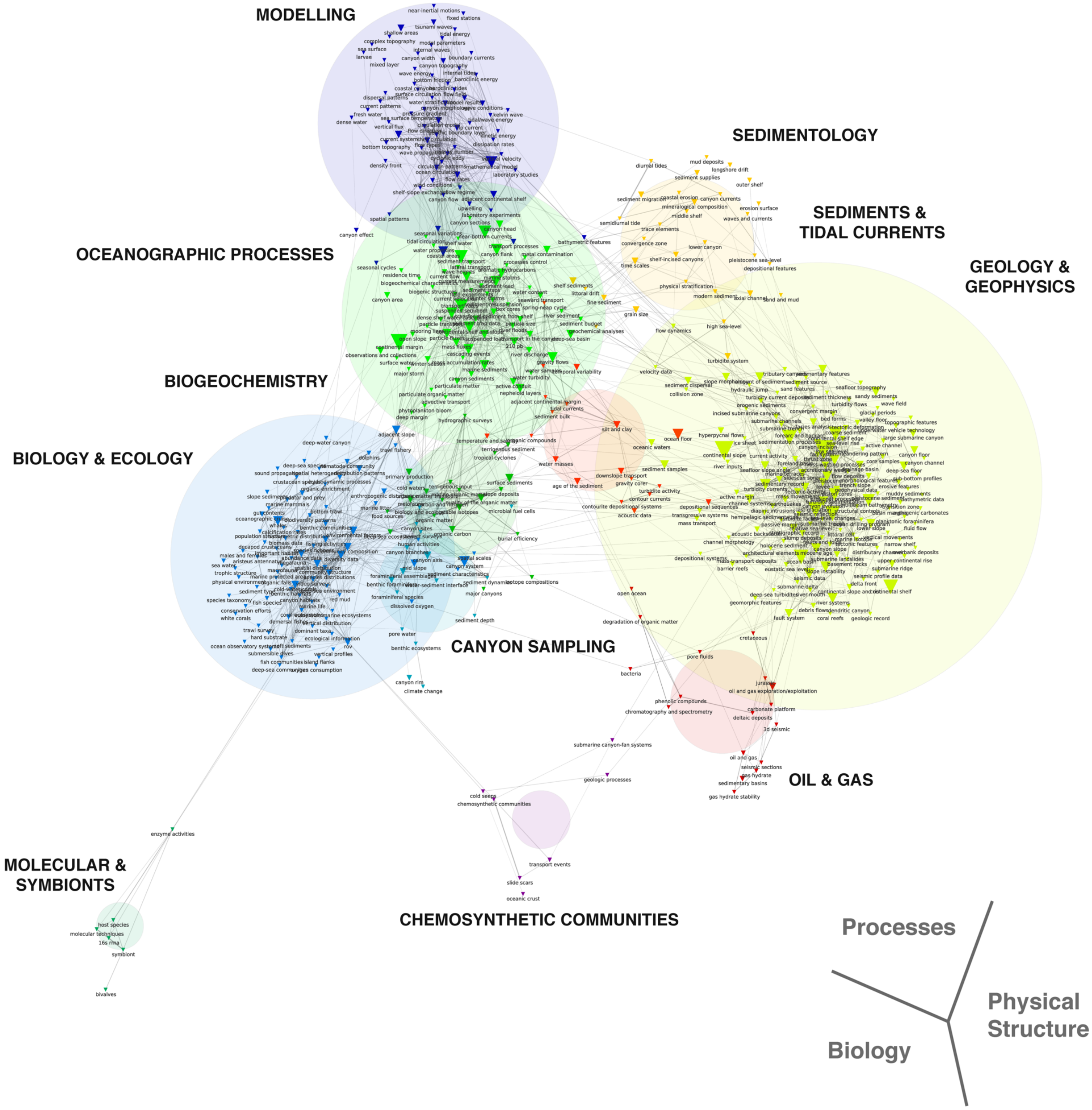


Figure 2.1.5 – Semantic network (measure: distributional, no filter applied to the edges) using the top 500 terms extracted from the abstracts. The 11 knowledge clusters are tagged according to their content and are globally divided in three categories (reading from the bottom-right, clockwise): canyons physical structure, biology and processes.

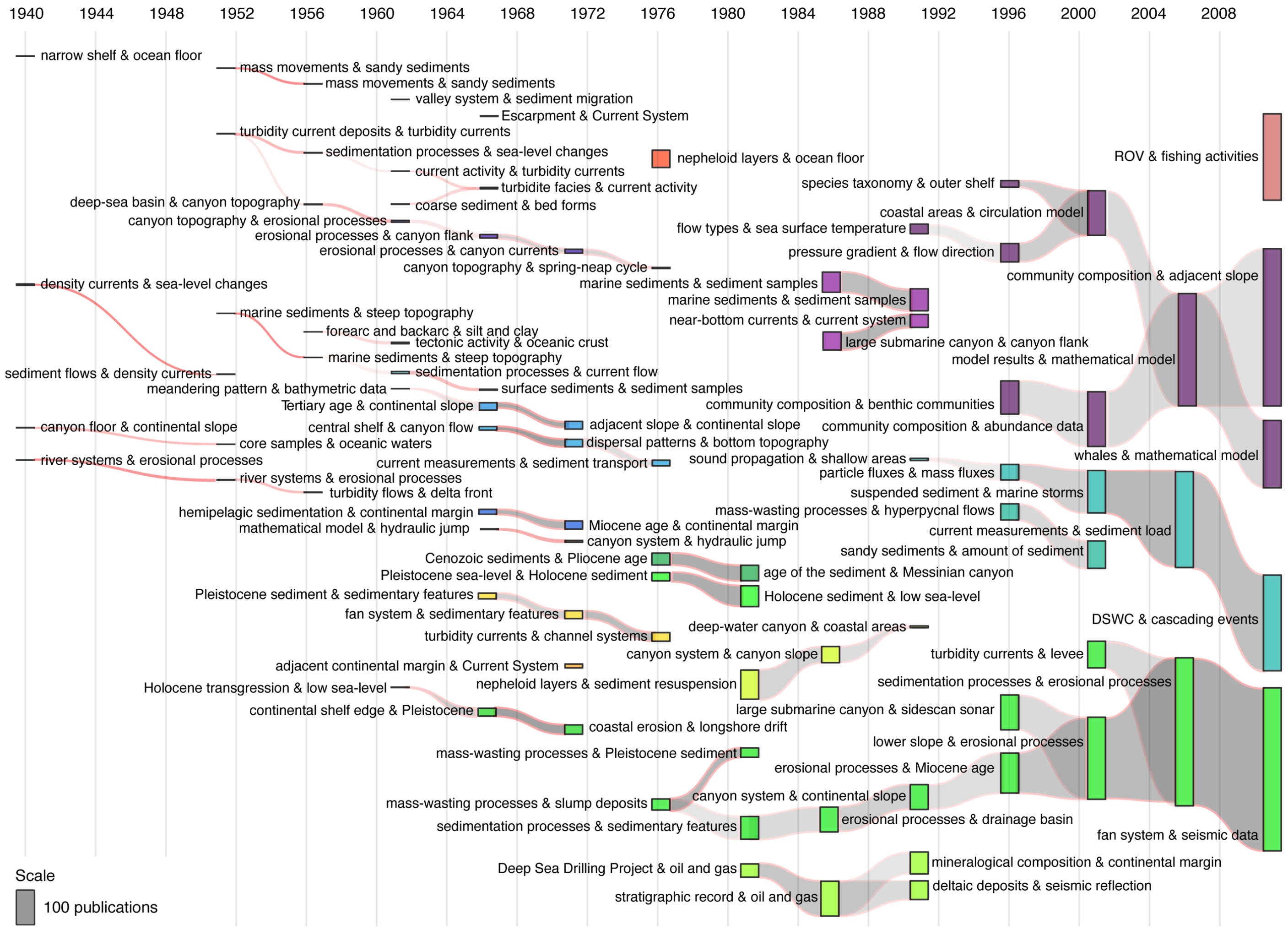


Figure 2.1.6 - River diagram illustrating canyon research dynamics over time (*x* axis) condensed in 14 time-snapshots of approximately 10 years each. Vertical bars represent the clusters detected in each time-period by the semantic network built with the 100 most frequent terms. Related clusters are connected between adjacent periods by a grey flow with a density reflecting the degree of connection. Vertical bars connected at any point in the timeframe share the same colour and are considered as part of the same system. Different tones of the same colour are indicative of clusters proximity. DSWC - Dense shelf water cascading.

2.1.6.3 - Geographic and thematic research bias in canyon research

2.1.6.3.1 - Research efforts in the most studied canyons

As previously mentioned (section 2.1.6.1) there is a strong imbalance in the observed number of publications in each canyon (11 canyons accounting for nearly half of the publication effort), which reflects a noticeable geographical bias in the allocation of research effort. Despite the considerable number of disciplinary fields explored in canyon research, there is some overlap in the explored subjects for the most frequently studied canyons (Figure 2.1.7). The biases in the studies are typically in favour of either the physical structure and environmental processes or the biological component, a trend also observed in the contingency matrix relating the knowledge clusters with each canyon (Figure 2.1.8).

In Figure 2.1.9 the geographical bias in canyon research is clearly depicted by the closer proximity of canyons from the same region, almost mirroring their geographical positions in a world map. The number of shared terms among the 11 canyons is rather low despite the multiple connection possibilities, which also reinforces the previous inference on thematic bias. The only exception, although affected by a geographical bias, was detected for the Mediterranean canyons, Cap de Creus and Lacaze-Duthiers. The work conducted so far in these two canyons was focused on shared research topics, predominantly related with “cold-water corals”, “dense shelf water cascading” and sedimentation processes. The geographically close Blanes Canyon, in turn, was studied mainly in terms of anthropogenic impacts (e.g., “fishing activities” and “marine litter”), “seasonal variations” and “fish communities”.

On the eastern margin of the Atlantic, the Nazaré Canyon is one of the most studied in terms of biodiversity patterns (e.g., “meiofauna”, “spatial distribution”, “organic matter” and “metal contamination”). On the opposite margin of the Atlantic, three canyons stand out with a high positive correlation to given knowledge clusters (Figure 2.1.8): the Alaminos and Baltimore canyons are very frequently associated with terms related to “Oil & Gas” exploration and exploitation, while studies conducted in The Gully canyon are focused on “Biology & Ecology”, particularly with studies on marine mammals (“whales” and “dolphins”) and conservation (“marine protected areas”; Figure 2.1.8 and 2.1.9). The last canyon from the list in this region, Hudson Canyon, was mostly studied regarding fish and crustacean communities and water circulation.

Two of the most emblematic submarine canyons in terms of scientific surveys, Monterey and La Jolla submarine canyons, are both located in the USA margin of the north-east Pacific. Monterey Canyon is linked to the study of “chemosynthetic communities”, underwater technologies (e.g., “ROV”, “underwater vehicle technologies”), water circulation (e.g., “flow regime”, “upwelling”) and hydrodynamic modelling (e.g., “circulation model”, “mathematical model”) as well as the influences of near “coastal areas”, while the La Jolla studies were more focused on the sedimentary processes and features (e.g., “hemipelagic sedimentation”, “sedimentary features”) and “demersal fish”.

Lastly, in this list of the most studied canyons, the single example from the Asian margin is the Gaoping (Kaoping) Canyon, mostly described in terms of the river inputs (e.g., "river floods”, “river sediments”), sediments, hydrodynamics (e.g., “water circulation”) and tectonics related topics (e.g., "forearc and backarc”, “thrust zone”, Figure 2.1.7).

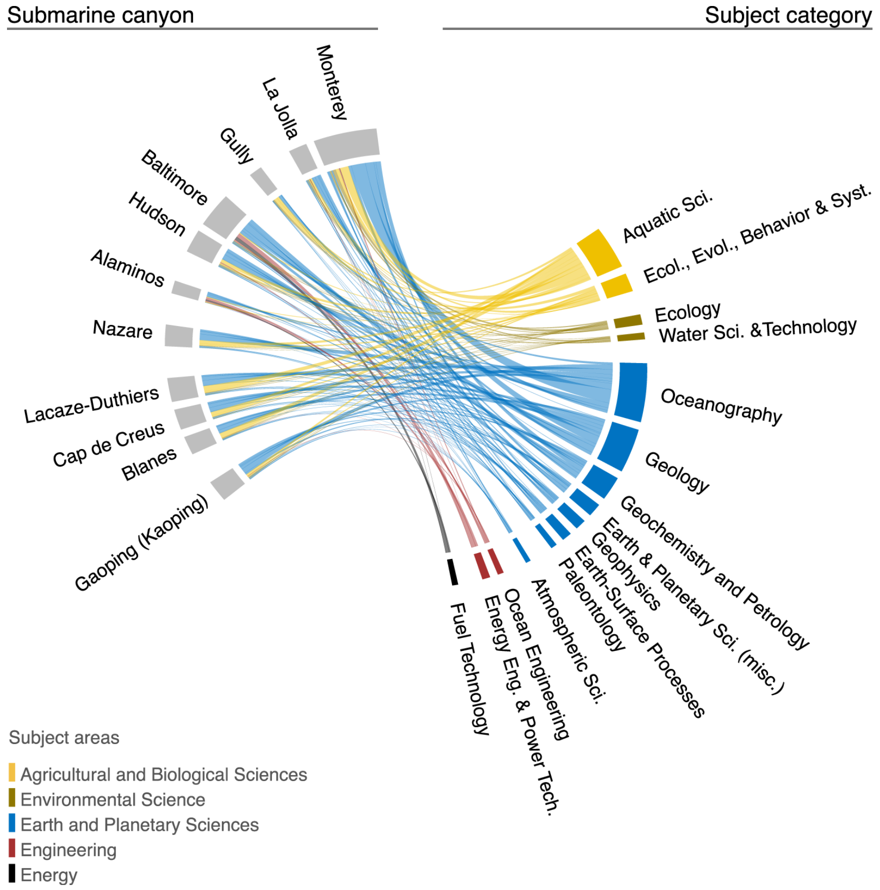


Figure 2.1.7 – Chord-diagram with the most well-studied submarine canyons in the corpus and related top 15 subject categories addressed. The arc length and the chord thickness are scaled to represent the number of documents associated to each entity while the colours correspond to the subject area where categories occur. Sci. – Sciences; Ecol. – Ecology; Evol. – Evolution; Syst. – Systematics; Misc. – Miscellaneous; Tech. – Technology.

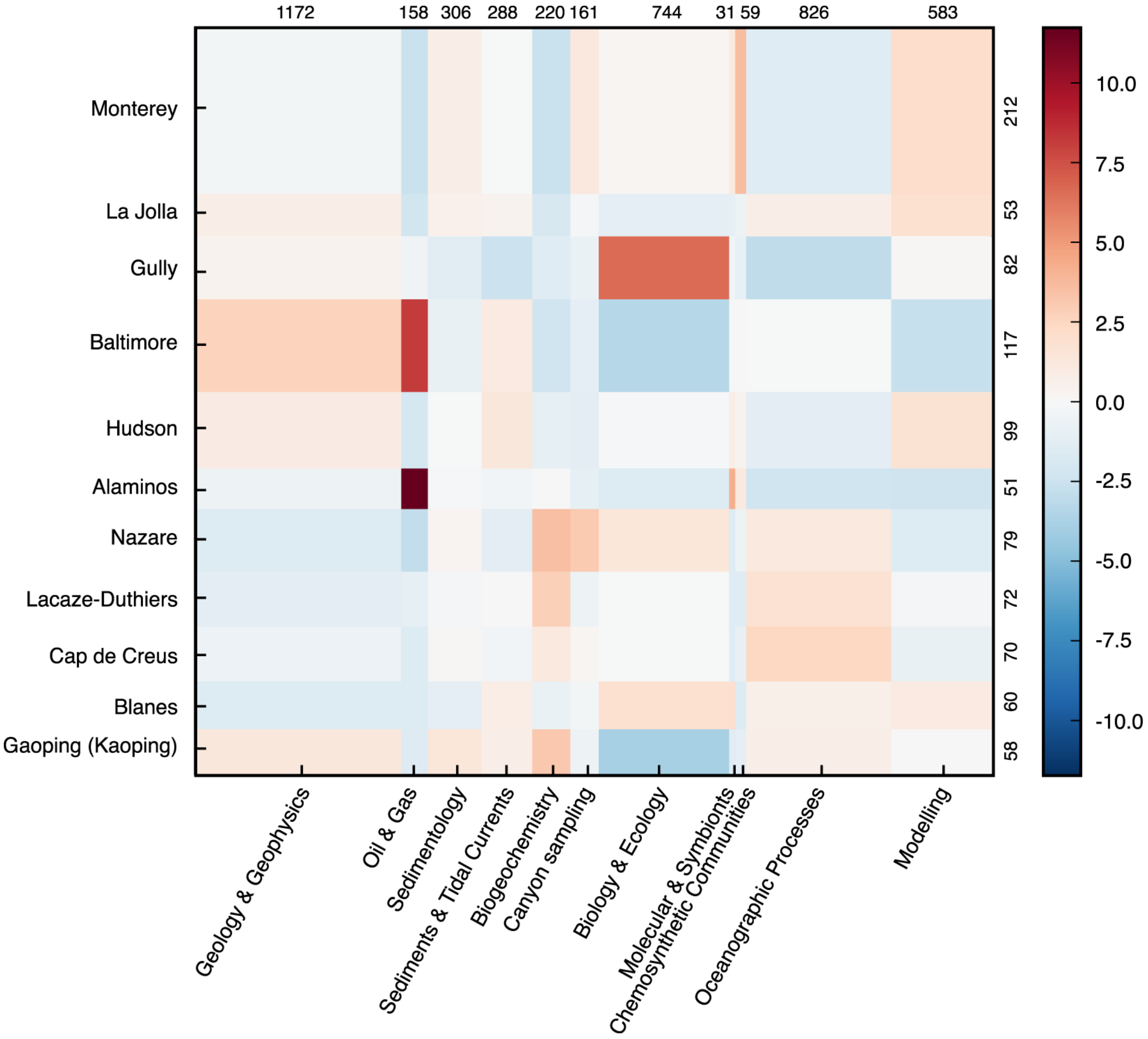


Figure 2.1.8 - Contingency matrix showing the correlation degree (chi-square score) between the top 11 submarine canyons and the topical clusters identified in the semantic network. The size of each cell is proportional to the number of documents. The colour scale encodes how submarine canyons are positively correlated (red), not correlated (white) or negatively correlated (blue) with the topical clusters.

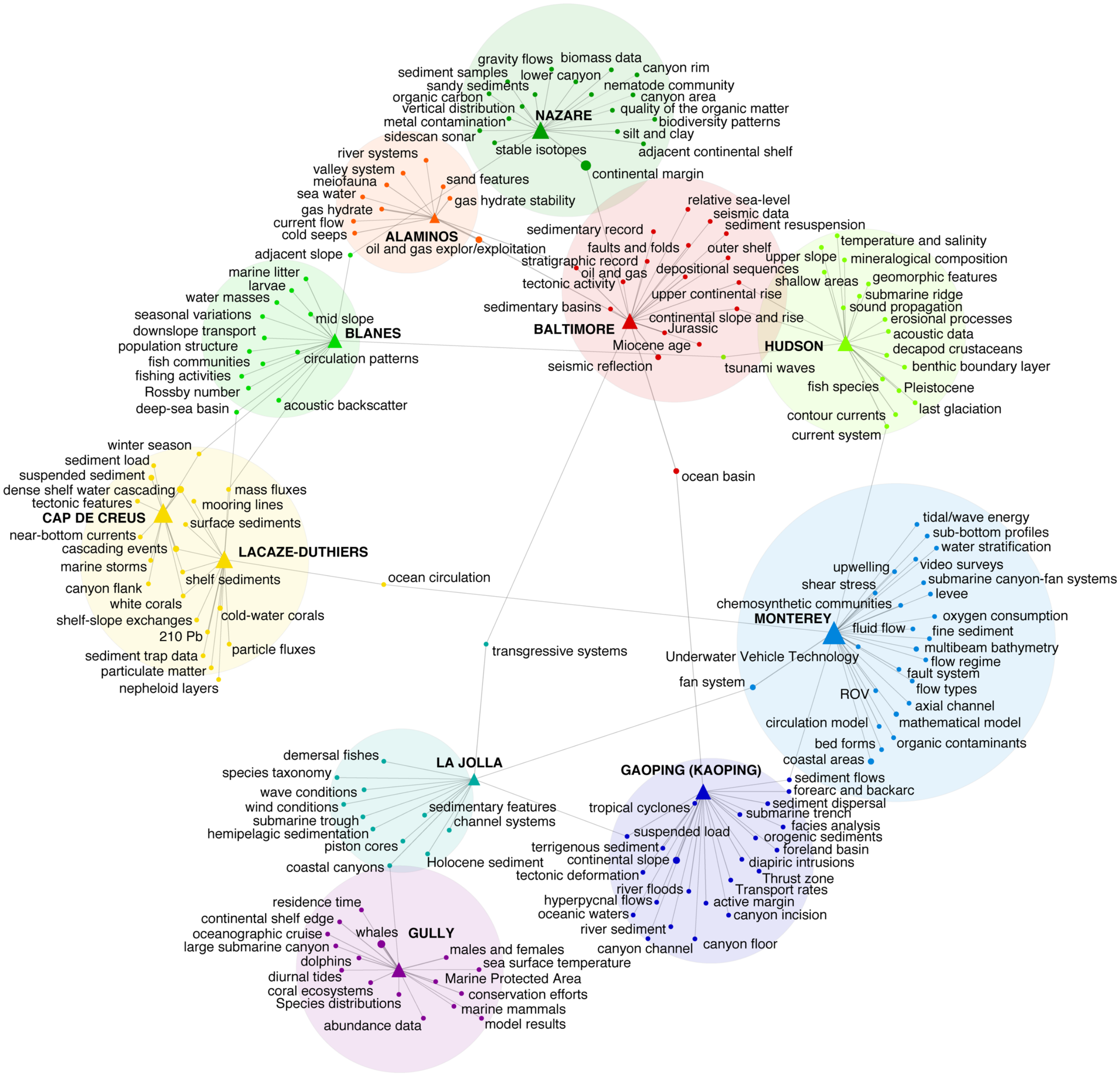


Figure 2.1.9 - The top 11 submarine canyons (triangles) and the top 300 most common terms in the abstracts (dots). Network built using the distributional proximity measure; no filter was applied.

2.1.6.3.2 - International networking

International collaboration is strongly implemented in canyon research (Figure 2.1.10), and the leading institutions were identified by the top 100 authors collaboration network (Figure 2.1.11). The ten most prominent institutions were (by decreasing order; Figure 2.1.12) the ICM-CSIC (Spain), US Geological

Survey (USA), MBARI (USA), University of Barcelona (Spain), NOCS (UK), Scripps Institution of Oceanography (USA), IFREMER (France), Woods Hole Oceanographic Institution (USA), NIOZ (Netherlands) and University of Washington (USA). Although academia and governmental agencies were the main players in the canyon research arena, we also identified private companies operating primarily in the energy sector and geophysical studies (e.g., Chevron Energy Technology Company, AOA Geophysics Inc.) among the 100 most relevant contributors to canyon research.

We tagged the groups detected in the collaboration network with the five most relevant abstract terms in order to highlight the main research topics carried out by each one. The results suggest that the research networking tends to concentrate on specific subjects, also demonstrated by the high correlation of some institutions with the main knowledge clusters. Examples are the correlation of the US Geological Survey with "Geology & Geophysics" and "Oil & Gas", the University of Washington with "modelling hub", and the NIOZ with "Biogeochemistry". Some cross-disciplinary collaboration revealed by the links between clusters was also observed between institutions (Figure 2.1.11 and 2.1.12).

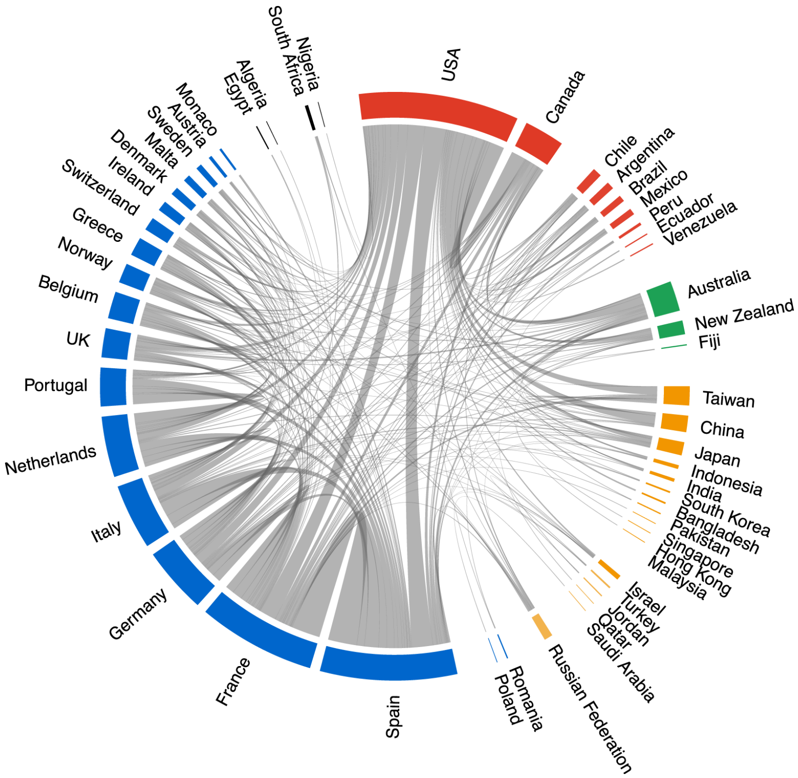


Figure 2.1.10 – Chord diagram of the international collaboration network at the country level, grouped by geographical region. When multiple institutions of the same country were present in the same reference, the country contribution was only counted once. The arc length is scaled to represent the total number of collaborations endorsed (an indicative measure of the countries investment in canyons research) while chord thickness between bands encodes the collaboration frequency between countries detected in the corpus.

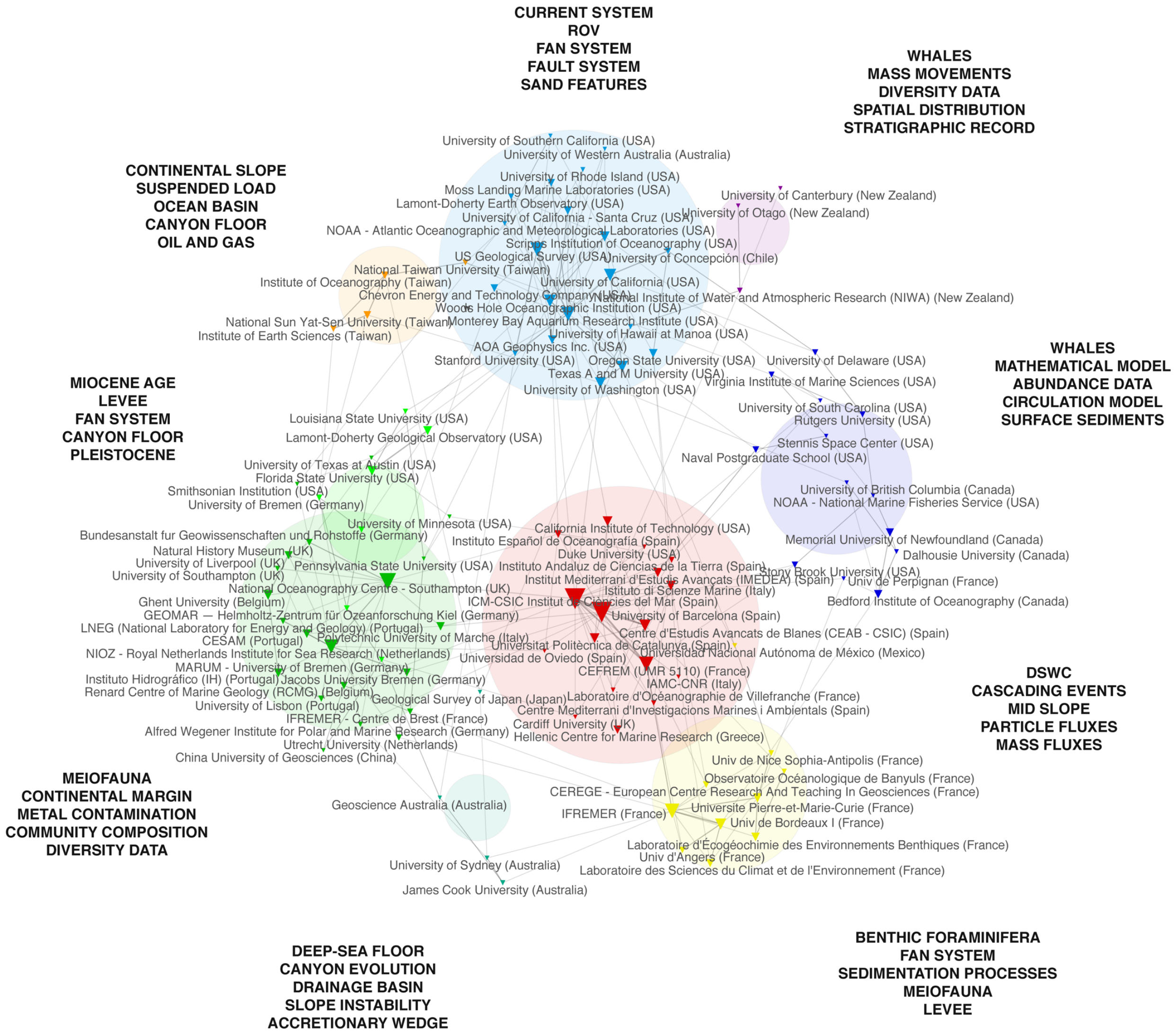


Figure 2.1.11 - Institutional collaboration network (top 100 authors affiliation from a total of 1092 institutions (measure: raw, threshold: top-3 neighbours). The clusters are tagged with the top 5 related abstract terms (chi-square metric). DSWC - Dense shelf water cascading.

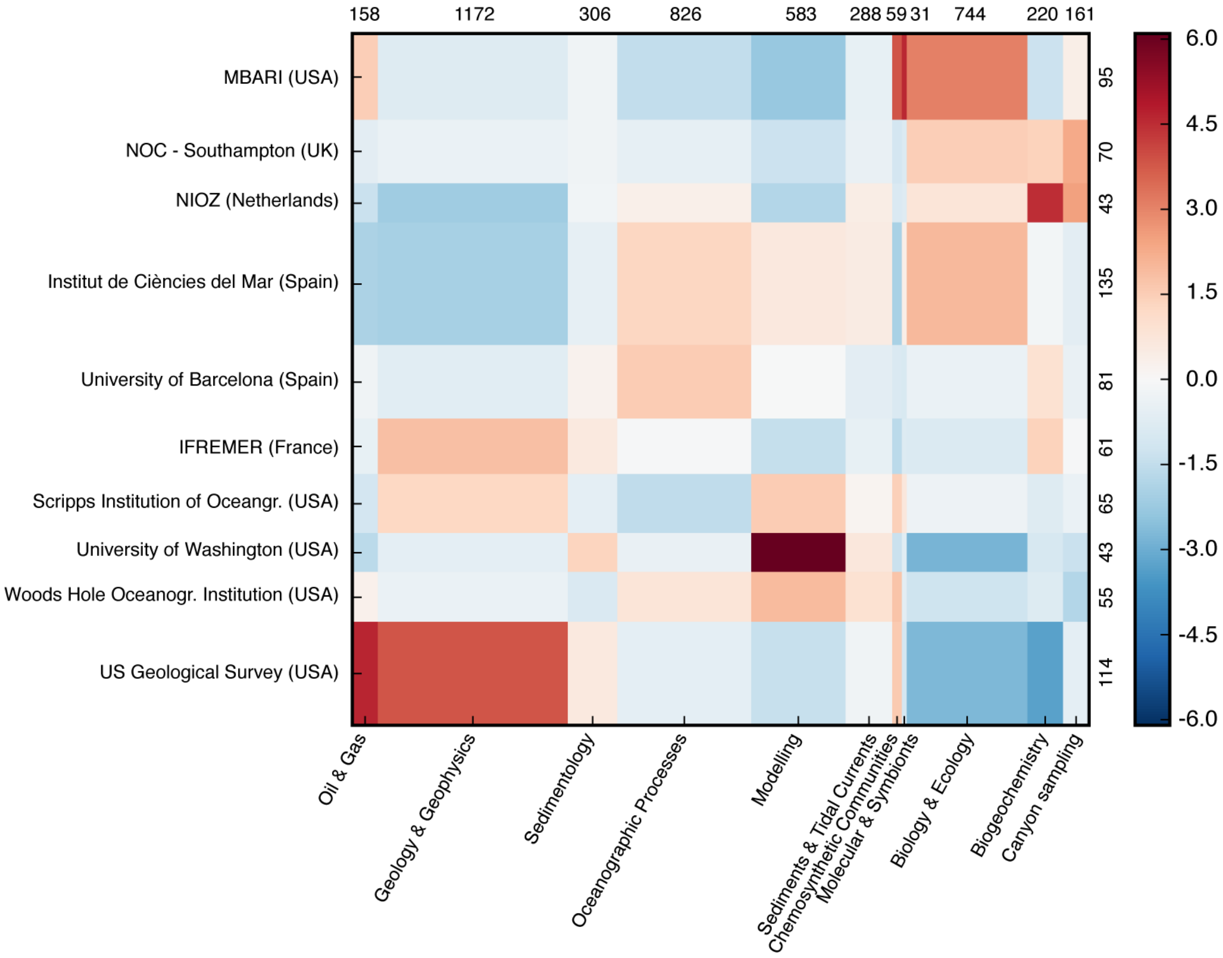


Figure 2.1.12 - Contingency matrix (chi-square measure) between knowledge clusters detected in the semantic network and the top10 institutions.

2.1.7 - Discussion

The investments in submarine canyon research over the last 87 years have resulted in the development of a series of research fields, which is illustrated by a steady increase of research publications, especially in the past two decades. Although peer reviewed journal articles are the main vector for disseminating scientific results, topics regarding technology and resource assessment can be underestimated in this study because they are published in more difficult to access technical reports or other document types only for internal use within an organization. The early years are also less represented in the corpus, partly an artefact resulting from the absence of older works in digital format, but also a consequence of early difficulties imposed by greater technological and operational limitations. Furthermore, we only considered abstracts written in English, and therefore, some governmental and institutional documents written in other languages were possibly excluded. Despite these limitations, we believe that the main trends in canyon research were captured by our analyses, particularly in the most recent years where the number of documents was considerably high. As observed by Huvenne and Davies (2014) and corroborated by our results, the research effort committed to submarine canyons is unevenly distributed, not only geographically (11 canyons dominating the efforts) but also thematically. In general, most canyons are almost completely unknown. Of the 9500 canyons listed in Harris et al. (2014), we identified studies conducted in less than a tenth of those. This preference towards particular canyons may be due to practical reasons like the ease of access and consequently reduced costs, a common caveat in deep-sea research (Oldham et al. 2014a), or scientific reasons because biologically productive or geologically unique canyons have long been recognized as the most relevant. This geographical and thematic bias coincides with the location of the leading research institutions and the expertise or fields of interest of their scientific teams, further enhanced by the scientific funding frameworks and amount of investment by each country or region. Moreover, once a specific canyon has been studied to a certain level, the accumulation of background data makes it easier and more attractive to continue further detailed studies or to conduct long-term time-series, a phenomenon described as the *Matthew effect* (Perc 2014). The disproportionate efforts towards the study of some canyons may be a necessary step for research development. Continuous and multidisciplinary studies in some pilot systems optimize limited resources, allow understanding more factors and variables, identify new directions for future research and increase the robustness of the interpretation of new studies.

The most determinant traits of submarine canyon research are captured in the 11 knowledge clusters identified by the semantic network analysis. However, a sustained investment in canyon research will probably result in the development of fields still poorly explored (e.g., biogeochemistry, molecular studies), or the rise of new research lines. In fact, emergent topics (e.g., conservation and ecosystems services) requiring multidisciplinary approaches and/or the integration of social sciences, virtually absent in today's canyon research, will probably gain momentum in view of the growing societal concerns that drive present-day research funding.

The early interests leading the scientific exploration of submarine canyons and the prominent nature of physical processes operating therein resulted in a predominance of geological and geophysical studies. The most cited works in the corpus appear to be seminal in canyon research and, therefore, determined the evolution of different research lines. Landmark publications, concerning sediment sampling (Ericson et al. 1961), their transport (Gardner 1989) and deposition (Curray and Moore 1971; Damuth and Kumar 1975), turbidity currents (Komar 1971) and landslides (McAdoo et al. 2000), marked the stride of canyon research in geology, geophysics and sedimentology. Technological improvements in sampling methodologies (e.g., remote sensing, core sampling, ROVs) and, later, the economic interest associated with exploration for hydrocarbons likely contributed to maintaining the effort towards these knowledge clusters. The study of present-day processes with, for instance, moored instruments, instrumented tripods, or multibeam systems, revealed a significant dynamism in some submarine canyons shifting the paradigm about canyons' activity (e.g., Palanques et al. 2006; Canals et al. 2006) and attracting new disciplines. Many topics related to oceanography and biology started to be explored only more recently, also benefiting from technological developments in sampling (e.g., remote sensing, underwater vehicles, multi-parameter observatories) and modelling (e.g., computers' processing capacity, data access, big data). However, the links between "Modelling" and "Biology & Ecology" in the network are weaker or indirect reflecting the low number of studies already using modelling approaches to ecological problems. On the other hand, the close links between "Modelling" and "Oceanographic Processes", and to some extent also "Geology & Geophysics", reflect the development of fields such as operational oceanography dedicated to the systematic and long-term measurement of the oceans and forecasting. Ever more national or regional data portals provide useful forecasts and data products from operational oceanography based on a swift interpretation of ocean data and their dissemination to the public, governmental institutions and industry.

Oceanography arises as a central cluster, well embedded in the canyon research landscape and connected by the nodes with highest betweenness centrality. The evolution of oceanography in canyon research is not completely independent from other research lines, and it is difficult to track along the historical record. This might be because it shares many connections with other knowledge clusters, and it has been used as a fundamental tool to better understand complex interdisciplinary problems rather than being studied for its own merit. In the study of oceanographic processes, the work of Millot (1990) on dense water formation coincided with the origin of a stream system in the river plot (cyan bars; Figure 2.1.6) focused on transport mechanisms of water and sediments. More recently, the works by Palanques et al. (2006) and Canals et al. (2006) highlighted the importance of climate driven extreme events (dense shelf water cascading) and the concern regarding global change which was reflected in a two-fold increase in publications.

Biological research in canyon ecosystems derived initially (mostly during the 1990s) from opportunistic sampling of infaunal (macrofauna and meiofauna) and foraminiferal assemblages in campaigns focused on characterization of the seabed. A strong relationship with the "Biogeochemistry" knowledge cluster is reflected by the importance of the nodes "organic carbon" and "burial efficiency". Pioneer studies were focused on community composition and structure. In one of the most cited canyon biology papers, Vetter and Dayton (1998) bring to the fore the importance of organic matter enrichment and its influence on benthic communities. Canyons as hotspots of biomass and productivity remained a central topic in canyon research as demonstrated by the often cited works of Schmiedl et al. (2000), Croll et al. (2005) and De Leo et al. (2010). Many studies (e.g., Ross et al. 2015; Demopoulos et al. 2017) tested for a possible *canyon effect* by comparing the biological assemblages of canyons and the "adjacent slopes" (a node with central importance in the network) in relation to their respective environmental settings. During the past decade, this knowledge cluster evolved continually with biology topics becoming greatly diversified and more interconnected with other disciplines through the study of biological processes (e.g., population connectivity, Perez-Portela et al. 2016) and the use of multi-disciplinary data retrieved from observatory networks (Matabos et al. 2014). The implementation of the ecosystem principles approach in deep-sea research (Jobstvogt et al. 2014) and the growing concerns regarding conservation and management issues, anthropogenic impacts and climate change (Fernandez-Arcaya et al. 2017), projected biology as a current hot topic in canyon research.

In the earliest periods of canyon research history, the lack of continuity in research lines, and their diversity despite the low number of studies, are consistent with the initially worldwide spatially fragmented research on canyons. However, we cannot ignore that this low number of studies may reduce the probability of terms co-occurrence. Furthermore, the distinctive nature of the canyons investigated (active vs. inactive canyons, size, topography), as well as the different scientific interests and research priorities of the teams involved, may have also contributed to this initial lack of connectedness. This pattern further developed into a thematic and geographical bias in canyon research with a preference of the canyon scientific community to address specific questions and specific canyons. These findings uncover a strong limitation, locally and regionally, to our interdisciplinary understanding of submarine canyons. Besides, since patterns captured from a single canyon may not be universally transposable to other canyons (Huvenne and Davies 2014), this fragmented view hinders knowledge integration and prevents a comprehensive assessment of the patterns and processes that shape these outstanding geomorphological features and their associated ecosystems. Still, the international collaboration within the scientific community is becoming more deeply implemented in the current landscape, actively contributing to the research topic diversification, fundamental to the understanding of canyon systems (e.g., Amaro et al. 2016). In fact, the evolution pattern described here for canyon research follows some of the theoretical principles of scientific progress – the paradigm shifts, the knowledge spreading and the reinforcement of scientific collaboration increase the interdisciplinarity while developing and consolidating research lines (Salatino et al. 2017).

We now understand better the geological evolution and the structural and functional components of several canyon systems. However, the historical imbalance among disciplines, the lack of standardized approaches and paucity of robust inter-disciplinary research have hindered further advances in other topics, such as understanding functional interactions between the biota and canyon environment, or perceiving patterns of spatial and temporal variability within and between canyons. Progress in intrinsically cross-disciplinary fields like biogeochemistry, ecology and conservation as well as the growing utilization of modelling and molecular techniques, may help counteract these limitations. Moreover, the implementation of multidisciplinary ocean observatory networks and other concerted initiatives at the international level that use a standardized set of sensors and equipment to collect data on essential ocean variables (Lindstrom et al. 2012) are important steps towards the integration of knowledge at large temporal and spatial scales.

2.1.8 - Conclusion

The geological and geophysical characterization, including processes involved in canyon formation and evolution, represent the main research topics addressed in submarine canyon research over the last 87 years. This emphasis is likely to persist with the worldwide increase in studies conducted in canyons and the technological advances in environmental surveys and habitat mapping. Even so, the historical disparity between the number of studies focused on the physical environment and on the biological component is starting to decrease.

The triad “canyons - research topics - leading institutions” typifies the canyon research landscape and is translated into regionalization and thematic bias: specific topics have been consistently addressed in the same submarine canyon by a given leading institution, typically based geographically close to that canyon. The lack of coherence in the set of traits and essential variables covered in different canyons hinders knowledge integration and a comprehensive assessment of submarine canyons’ physical and biological structure and functioning. However, continuous and multidisciplinary studies in some canyon model systems may have ensured the necessary background knowledge for the development of future research directions. Our results, based on an extensive and multidisciplinary set of submarine canyon publications, revealed that synergies between knowledge clusters have developed only recently. The investment in fields that are interdisciplinary by nature, technological advances and a strong international collaboration network should enable future comparative studies at regional and global levels and contribute to successfully addressing conservation issues and complex emergent research topics, such as the effects of anthropogenic impacts and climate change on submarine canyons.

This work depicts the status and historical trends of canyon research; the results are available through an open access, interactive online platform, offering the scientific community and stakeholders an informative tool to identify knowledge gaps, find key players in the global collaboration network and facilitate planning of future research in submarine canyons.

2.2 - Mediterranean seascape suitability for *Lophelia pertusa*: challenging the physiological limits

2.2.1 - Abstract

Ecological niche modelling is used in deep-sea research to investigate the environmental preferences and potential distribution of data-poor species. We present a mesoscale assessment of Mediterranean seascape suitability for the cold-water coral *Lophelia pertusa*. We estimated seascape suitability and uncertainty maps using an ensemble approach of three machine-learning algorithms (Generalized Boosting Model, Random Forest, Maximum Entropy) based on environmental predictors. Bathymetry, aragonite saturation and temperature were the most important predictors for the models. Overall the models reached good to excellent performance and the uncertainty of the ensemble forecast was low, with a very reliable prediction of the most suitable and most unsuitable areas. In the Mediterranean Sea, *L. pertusa* encounters environmental settings close to its physiological limits but, despite the highly variable quality of the seascape, we identified high suitability areas mostly at submarine canyons and along the upper slope of the Western and Central margins. The existing MPAs do not overlap with high suitability areas and therefore *L. pertusa* is only protected at the deepest fringe of its potential distribution by the Bottom Trawl Closure. This seascape suitability assessment may assist future research, including high-resolution modelling targeting high-suitability areas, investigation on the resilience of *L. pertusa* populations and development of conservation actions.

2.2.2 - Introduction

The geographical distributions of species in the deep sea remain largely unknown mainly due to the extent and remoteness of their habitats, and to the expensive and highly technology-dependent deep-sea surveys. This knowledge deficit has hindered the development of effective management measures framed by recent policy initiatives (e.g., European Habitats and Marine Strategy Framework Directives) that aim to preserve biodiversity and functioning of ecosystems. Conservation options heavily rely on spatial explicit information (Savini et al. 2014; Reiss et al. 2015), and depend on modelling approaches at large spatial scales (Burgman et al. 2005) to capture the multiple interactions between the organisms and their habitats and the spatial-temporal dynamics of the landscape (Turner et al. 1995).

Cold-water corals (CWC) are among the most emblematic deep-sea organisms and play an important role in the structure and functioning of marine ecosystems. CWC increase the complexity of the habitat and support attendant assemblages with significantly enhanced biodiversity and biomass when compared to the surrounding environment (Linley et al. 2017). The provision of spawning, nursery and feeding areas by CWC is well documented for hundreds of species (e.g., Buhl-Mortensen et al. 2010; Gianfranco et al. 2016). CWC are also involved in the provision of other important ecosystem functions and services including nutrient cycling and carbon sequestration (Soetaert et al. 2016). Due to their low tolerance to disturbance, slow growth rates, and consequently poor resiliency, these organisms can be highly impacted by anthropogenic activities (Fabri et al. 2014) and climate change (Georgian et al. 2016).

Among the reef-building CWC species, *Lophelia pertusa* is one of the most studied. Classified as deep-sea cosmopolitan in the Atlantic Ocean, the presence of living colonies is less frequently reported in the Mediterranean Sea. The restricted distribution of *L. pertusa* in the Mediterranean Sea has been considered to result from the geologic history of the region and the present-day physical barriers to dispersal (Delibrias and Taviani 1984; Freiwald 2002). However, recent studies reporting the occurrence of living colonies in the Alboran Sea (Iacono et al. 2014b), the Western (Freiwald 2002) and Central Mediterranean basins (Tursi et al. 2004; Freiwald et al. 2009; Maier et al. 2012), and the Adriatic Sea (Angeletti et al. 2014) contradict the initial perception of a highly restricted Mediterranean distribution of *L. pertusa*. Furthermore, its distribution is still probably underestimated since very few surveys targeting *L. pertusa* were conducted in the Mediterranean Sea in comparison to other oceanic regions (Zibrowius 2003).

Recent studies have successfully used ecological niche models (ENMs) to estimate the potential distribution and the environmental suitability of various deep-sea species, including CWC (Davies and

Guinotte 2011; Iacono et al. 2018; Bargain et al. 2018), sponges (Howell et al. 2016), echinoderms (González-Irusta et al. 2015) and crustaceans (Basher et al. 2014). The panoply of ENMs available encompasses different approaches (e.g., correlative, mechanistic), modelling techniques (e.g., regression-based, machine learning methods), occurrence data inputs (e.g., presence-absence, presence-only), and ecological concepts (Valverde et al. 2008; Peterson et al. 2015). Differences between these methodological and conceptual aspects may result in model outputs with different interpretations (Peterson et al. 2015).

Correlative ENM forecasts based on presence-only data rely on a set of ecologically-relevant predictors and provide meaningful results even with a limited number of species occurrences. The modelling process consists in determining statistically the species environmental profile based on the values of predictors for the known occurrence locations and then project this profile over the model geographical space (Miller 2010; Guillera-Arroita et al. 2015). The output is a continuous representation of the species potential distribution. However, it may overestimate the species actual distribution since it excludes relevant parameters such as biotic interactions and the dispersal capacity of the species (Miller 2010). Model predictions depend not only on the adopted modelling technique and settings defined by practitioners, but are also subjected to different types of uncertainties related to data quality and quantity (e.g., sample size, sampling bias, spatial resolution issues; Burgman et al. 2005; Zhang et al. 2015). These issues and their implications on the model performance have prompted the use of ensemble forecasting frameworks that combine the output of multiple models into a single estimation and produce more accurate predictions, also reducing their uncertainty (Araújo and New 2007).

The main objective of this work is to predict and map the seascape environmental suitability for *L. pertusa* in the Mediterranean Sea using a multiple model ensemble forecasting approach. Here, we provide a succinct and easily readable prediction of the seascape suitability, assess the performance of the model and derive the prediction uncertainty maps. Previous studies estimated the *L. pertusa* potential distribution using ENMs regionally (Howell et al. 2011; Rengstorf et al. 2013; Georgian et al. 2014; Robert et al. 2016; Bargain et al. 2018) and worldwide (Davies and Guinotte 2011), but not encompassing the whole Mediterranean basin and none used a multi-algorithm approach that provides both the prediction of seascape suitability and a measure of uncertainty of the forecast.

2.2.3 - Material and methods

2.2.3.1 - Modelling area and occurrence data

Considering the low number of occurrences historically reported for the Mediterranean Sea (61), we opted to extend the modelling area to also include the extensive records of the species reported along the European Atlantic margin from the Iberian Peninsula to Norway (i.e., 30ºN and 70ºN and the 33ºW and 38ºE; Figure 2.2.1). This option will allow us to better determine the species environmental profile and thus improve the prediction power and the ecological plausibility of our model.

The living colonies records were extracted from the Global Distribution of Cold-Water Corals database (Freiwald et al. 2005), further updated with recent records for the Mediterranean Sea obtained from the literature (Table S 2.2.1). Colony records referring to transects covering a distance greater than 1 km were excluded. For shorter transects (26 out of 34), the starting coordinates were considered as the colony location. Considering the modelling resolution (~1 km^2), this lack of accuracy was assumed as negligible. In order to remove duplicates and spatially auto-correlated occurrences we applied a filter using the SDMtoolbox (Brown 2014), that reduced multiple occurrences within 1 km^2 to a single record. The locations of living colonies are unevenly distributed over the modelling area. From the initial 747 presences, a total of 403 occurrences, but only 36 for the Mediterranean Sea, were retained. This procedure minimizes the sampling bias and prevents over-fitting of predictions without losing an excessive amount of information.

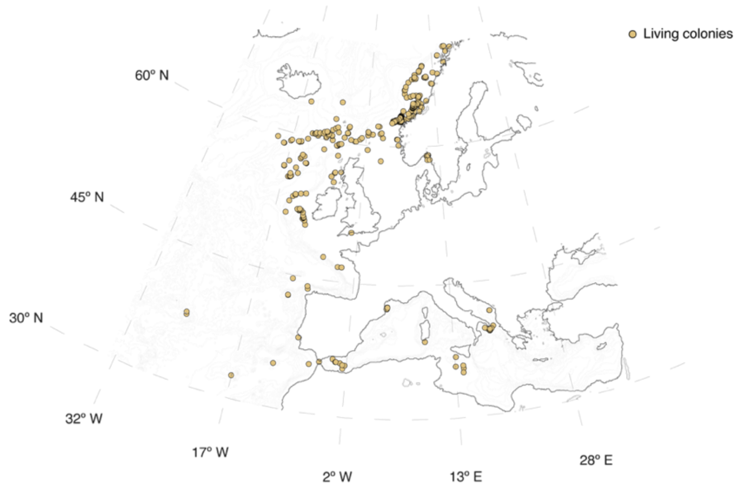


Figure 2.2.1 - The distribution of the living colonies of *L. pertusa* across the model fitting area.

2.2.3.2 - Environmental predictors

The selection of environmental variables was based on the species ecology and on previous modelling studies for *L. pertusa* (Table 2.2.1). The topographic variables are among the most important for this species (Georgian et al. 2014); the bathymetry (meters) and the bathymetric slope (degrees) data products were obtained from Sbrocco & Barber (2013) and derived from the SRTM30_PLUS high resolution bathymetry (Becker et al. 2009). Other variables known to physiologically constrain the distribution of CWC such as the aragonite saturation state (Ω_{ARAG}), salinity (pss), temperature (ºC) and dissolved oxygen concentration (ml l^{-1}), were estimated for the seafloor conditions by Davies & Guinotte (2011). Although salinity, dissolved oxygen, temperature and Ω_{ARAG} were correlated ($r \geq 0.7$; Figure S 2.2.1), we opted to retain all these variables since they are generally considered as fundamental for the species occurrence (Guinotte et al. 2006; Dodds et al. 2007; Naumann et al. 2014).

The topographic variability interacting with hydrodynamics is particularly relevant for species that depend on currents for feeding. The water circulation setting, characterized here by the current velocity (m s^{-1}) was extracted from the HYCOM products (Chassignet et al. 2009) and processed using the Marine Geospatial Ecological Tools (Roberts et al. 2010) as a continuous representation of conditions at the seafloor. The current velocity data was then interpolated to match the model cell resolution and fill areas with information gaps using the inverse weighted distance in the software ArcGIS, following the methodology used by Davies & Guinotte (2011).

Table 2.2.1 – Details of the environmental predictors used in the models fitting and respective sources.

Variable (units)	Resolution	Derived from	Source	Reference
Bathymetry (m)	0.0083°	SRTM30 Plus Bathymetry	MARSPEC	Sbrocco and Barber 2013
Bathymetric slope (°)		Bathymetry		
Aragonite Saturation State (Ω_{ARAG})			Marine Conservation Institute & Davies and Guinotte 2011	Orr et al. 2005
Dissolved Oxygen (ml l^{-1})				Garcia et al. 2006
Salinity (pss)				Boyer et al. 2005
Temperature (°C)				
Current velocity (m s^{-1})	0.08°	2009-2013 cumulative mean	HYCOM	Chassignet et al. 2009

2.2.3.3 - Modelling

The modelling process was conducted using R (R Core Team 2016) and the "Biomod2" package (Wilfried et al. 2009; version 3.3-15) which supports different modelling techniques. The ensemble model output resulted from the consensus of three machine-learning algorithms: Generalized Boosting Model (GBM, also known as Boosted Regression Trees), Random Forest (RF), and Maximum Entropy (MaxEnt). The machine-learning class algorithms are among the most appropriate for mapping and discriminating areas with different suitability degrees while keeping a high predictive performance (Reiss et al. 2015; Scales et al. 2016; Mi et al. 2017; Carvalho et al. 2017). Moreover, their predictions are considered highly robust to predictors correlations (Anderson et al. 2016).

The selected algorithms require pseudo-absence or background information for building the models. We generated ten datasets with 1000 randomly sampled pseudo-absences each for GBM and RF algorithms, following the recommendations by Barbet-Massin *et al.* (2012). A minimum distance of 10 km from any presence point was imposed using the geographical constraint strategy offered in “Biomod2” to avoid pseudo-replicates. The procedure applied to MaxEnt models differed slightly from the previous – 10000 random background points were selected to reach the optimal performance of the algorithm (2008), and no geographic constraints were applied.

Although an adjustment to the complexity of the model is recommended (Merow et al. 2013), we maintained the default settings supplied by “Biomod2” because of the lack of truly independent evaluation data for model tuning. The tuning process is fundamental for models aiming high transferability (i.e., to be projected to other areas or periods) but it is less important in studies aiming to project the prediction of the model to the same area used for its calibration (Anderson and Gonzalez 2011). Each observation (either presence or pseudo-absence/background point) was equally weighted during the calibration process.

2.2.3.3.1 - Evaluation of models performances

A total of 300 single models were generated resulting from ten runs of the three algorithms for the ten pseudo-absences (GBM and RF) or background point (MaxEnt) datasets. The evaluation of the models was performed using a 10-fold cross-validation approach, splitting randomly the original datasets into two subsamples: 75% of all data were selected for the calibration of the models and the remaining 25% were used to test their predictions.

There is no consensus on the most appropriate metrics to assess the accuracy of a model and, instead, a multi-metric approach is encouraged. We chose three of the most commonly used metrics: the area under the curve values of the Receiver Operator Characteristic (ROC), the True Skill Statistic (TSS), and the Boyce Index. The ROC is a threshold independent metric, neutral to species prevalence, which measures the discrimination capacity in terms of relative proportions of correctly and incorrectly classified predictions (Pearce and Ferrier 2000). The ROC values range from 0 to 1, with 1 corresponding to a perfect classification. The TSS is also independent of the species prevalence and compares the number of correct predictions subtracted by those assigned by chance in a theoretical perfect forecast (Omri et al. 2006); this statistics ranges from -1 to 1, with values near 1 indicating a good agreement between predictions and observations. The Boyce Index (Boyce et al. 2002; Hirzel et al. 2006), calculated separately using the "ecospat" package (Di Cola et al. 2017) for R, is a threshold independent evaluator ranging also from -1 to 1. Values close to 1 indicate a good agreement between the model predictions and the presences distribution in the evaluation dataset, i.e., areas with high suitability values coincide with areas where presences are more frequent (Hirzel et al. 2006). Conversely, values close to-1 indicate that the model scored with low suitability values areas with a high number of occurrences, and thus performed poorly, while values close to zero indicate that the model is not different from a random forecast. The mean of each metric was calculated for each algorithm.

The contributions of the variables to the models can differ between algorithms and between runs. We estimated the importance of each predictor using the built-in method in "Biomod2" that is independent of the modelling techniques and thus allows direct comparisons (Wilfried et al. 2009). This procedure was repeated 10 times for each predictor during the modelling process.

2.2.3.4 - Ensemble modelling

The ensemble forecasting was performed combining a subset of the single models. Only models with a TSS equal or greater than 0.8 were retained to build the consensus maps. As for the evaluation of models, there is no consensus on the most appropriate metric to select the single models used to build the ensemble model (Scales et al. 2016). However, the TSS and the ROC are among the metrics most frequently used. We opted to use the TSS over the ROC because the reliability of the latter has been heavily criticized (Lobo et al. 2008).

We combined and mapped the habitat suitability values of each grid cell using three consensus algorithms (Wilfried et al. 2009): 1) the mean of the probabilities over the selected models; 2) the binary models committee averaging; and 3) the coefficient of variation of probabilities. The first algorithm provides the prediction of seascape suitability while the other two provide a measure of uncertainty of the predictions.

The ensemble model based on the mean of probabilities of the selected models (TSS ≥ 0.8) is a continuous representation of the habitat suitability index (HSI) ranging from 0 to 1000, with values close to 1000 representing the most suitable areas. The committee averaging returns the average of binary prediction (transformation of the models output to presence/absence estimations) based on a threshold that maximizes the values of TSS; it gives both a prediction and a measure of uncertainty. Values close to 1 or 0, mean that all models agree to predict presence and absence, respectively, while values around 0.5 correspond to the highest uncertainty in the predictions. The coefficient of variance (i.e., standard deviation/mean of probabilities) can also be used as measure of the model uncertainty: lower scores correspond to better predictions and higher scores to higher levels of uncertainty.

In order to rank the seascape features by suitability, we intersected the output of the mean ensemble model with the seafloor geomorphological classification produced by Harris *et al*. (2014), the authors used the nomenclature defined, primarily, by the International Hydrographic Organisation for the seafloor feature types. According to the terminology used by Harris *et al*. (2014; and references therein) we identified the following features in the Mediterranean Sea:

- Shelf valleys - features incising the continental shelves or intersecting the shelf breaks no longer than 10 km in length.
- Terraces on the continental slope - "isolated or group of relatively flat horizontal or gently inclined surfaces, sometimes long and narrow, which are bounded by a steeper ascending slope on one side and by a steeper descending slope on the opposite side".
- Continental rise - identifiable by the occurrence of a smooth sloping seabed adjacent to the base of the continental slope, in general, with a sediment layer > 300 m thick.
- Sills - "sea floor barriers of relatively shallow depth restricting water movement between basins".
- Seamounts - "discrete or group of large isolated elevations, greater than 1000 m in relief above the sea floor, characteristically of conical form".
- Guyots or tablemounts - "isolated or group of seamounts having a comparatively smooth flat top".
- Submarine canyons - "steep-walled, sinuous valleys with V-shaped cross sections, axes sloping outwards as continuously as river-cut land canyons and relief comparable to even the largest of land canyons".
- Ridges - "isolated or group of elongated narrow elevations of varying complexity having steep sides, often separating basin features".
- Troughs: "long depressions of the sea floor characteristically flat bottomed and steep sided and normally shallower than a trench".
- Trenches: "long narrow, characteristically very deep and asymmetrical depressions of the sea floor, with relatively steep sides".
- Bridges - blocks of material that partially infill trenches and troughs.

- Fans - “relatively smooth, fan-like, depositional features normally sloping away from the outer termination of a canyon or canyon system”.

Additionally, we used the MPAtlas database of the Marine Conservation Institute (www.mpatlas.org) to analyse the overlap between areas of suitability and the existing marine protected areas (MPAs) in the Mediterranean Sea.

The datasets generated during the current study will be made available in the Mendeley Data repository.

2.2.4 - Results

We estimated the environmental suitability of the Mediterranean seascapes for *L. pertusa* from models fitted using a wider geographical area encompassing the European Atlantic margin (Figure 2.2.1). The locations of living colonies, used as input data, were unevenly distributed over the modelling area with the records mainly spread along the Norwegian Atlantic margin and the continental slope around the British and Ireland Islands. In the Mediterranean Sea, the occurrences were more clustered and sparsely represented (36 out of 403).

2.2.4.1 - Environmental profiling

The intersection of the presences record with the values of the environmental predictors (Figure 2.2.2) illustrates how the species distribution is related to these variables. On the other hand, the response curves (Figure 2.2.3 and Supplementary Figure S 2.2.2) describe the suitability variation along the observed range of values for the different predictors. The MaxEnt models returned the most complex behaviour but possibly the best representation of the species response to the extremes of environmental gradients (with predicted responses close to zero; Figure S 2.2.2). The GBM and RF models, showed smoother response curves and similar trends, but a lower sensitivity to the environmental gradient variation. The response curves of the ensemble model (Figure 2.2.3) combine the responses of the selected single models. The species occurrences in the Atlantic Ocean and the Mediterranean Sea were observed at similar ranges of the physiographic variables (Figure 2.2.2, bathymetry and slope): the colonies of *L. pertusa* were essentially concentrated at depths between 150 and 900 m, and in areas of gentle slope. According to our model (Figure 2.2.3), suitability is high between 150 and 1100 m and peaks at depths close to 150 m; it rises sharply with increasing slope and maintains high values at slopes >0.4°. Regarding the oceanographic variables, the ranges differed according to the region (Atlantic vs Mediterranean) where colonies were located (Figure 2.2.2, temperature, salinity, dissolved oxygen, aragonite, current velocity). This result expresses the distinct properties of the Atlantic and

Mediterranean water masses, a difference also noticeable by the multimodal response curves of our model (Figure 2.2.3, same predictors): the most suitable conditions were predicted for values matching the properties of Atlantic water masses but the predictors' ranges observed in Mediterranean water masses also encompassed favourable conditions. The Mediterranean colonies were mainly found in warmer (>13ºC), saltier (>38.3) and aragonite supersaturated waters (>2.13 Ω_{ARAG}; Figure 2.2.2), near the upper limits of the optimal suitability ranges of the predictors (Figure 2.2.3) while the Atlantic counterparts were found at temperatures between 7-10 ºC, salinities from 34.7 to 36 (close to the suitability peaks) and Ω_{ARAG} >1.5 (closer to the lower limit of the optimal suitability range, Figure 2.2.2 and 2.2.3). Contrarily, for the dissolved oxygen (DO) and current velocity (4.06 to 5.08 ml l^{-1} and below 0.05 m s^{-1}, respectively), Mediterranean colonies were detected closer to the lowest values of the optimal range (Figure 2.2.3), occurring in areas less oxygenated and exposed to lower current velocities (DO: 4.8-6.9 m l^{-1}; current velocities up to 0.23 m s^{-1}) than the ones observed for Atlantic records (Figure 2.2.2 and 2.2.3).

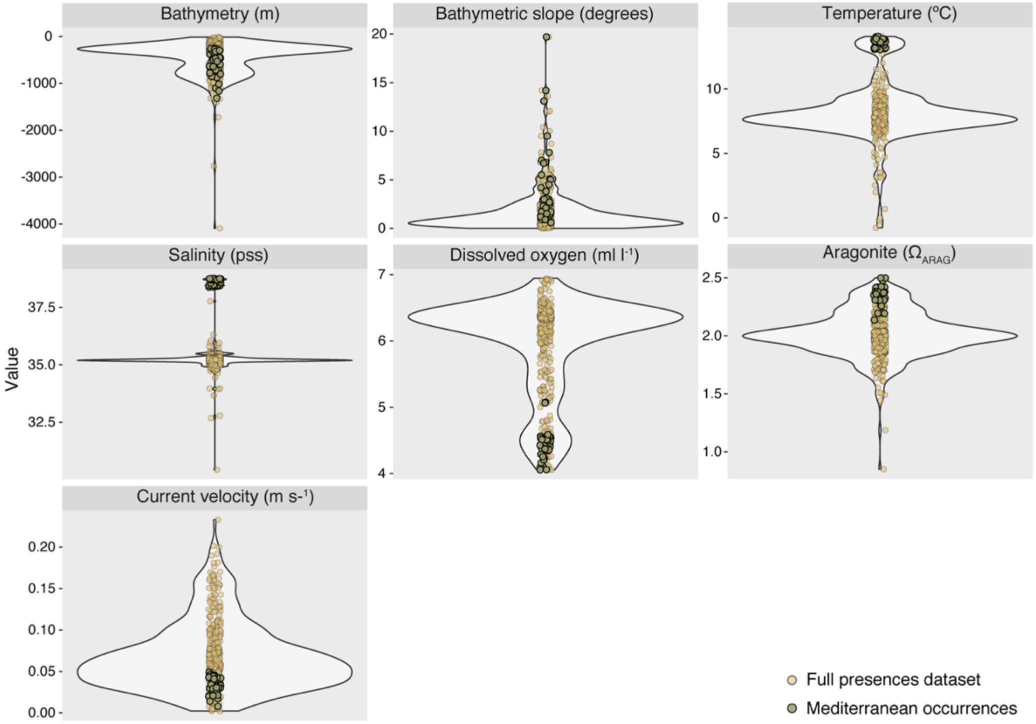


Figure 2.2.2 – Violin plots showing the distribution of the species occurrences (white area illustrates the relative frequency of occurrence) intersected with the environmental predictors. Lighter dots correspond to the whole dataset of presences and, the darker circles, the records for the Mediterranean Sea.

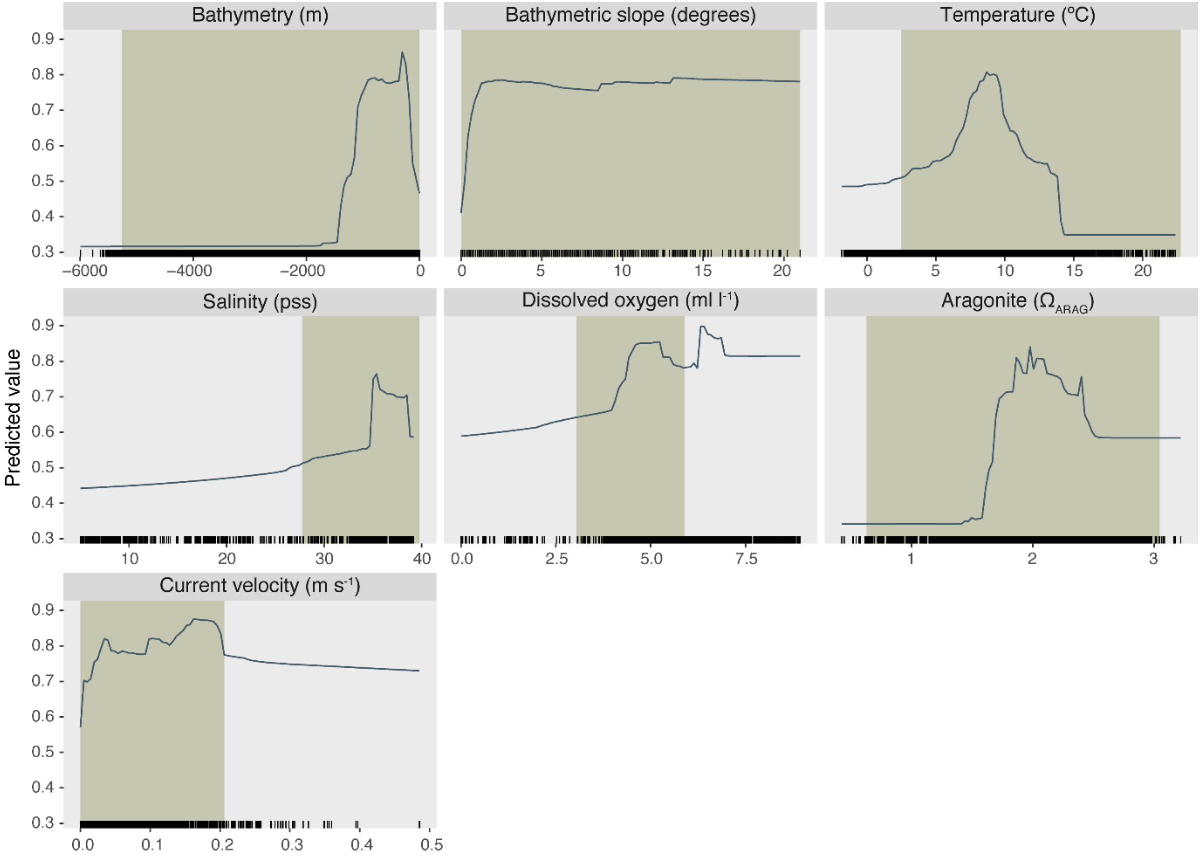


Figure 2.2.3 - Univariate response curves for each environmental predictor according to the mean ensemble model. The variables environmental gradients are represented in the xx-axis and the suitability prediction values in the yy-axis. The shaded areas correspond to the ranges of values observed in the Mediterranean Sea.

The contributions of the variables to the predictions differ between algorithms (Figure 2.2.4). Aragonite saturation and bathymetry were the variables with the highest contribution for GBM and RF estimates, while bathymetry and temperature were the most important for MaxEnt estimates. For all algorithms, the current velocity showed the lower scores. The variables contributions to the ensemble model are not presented because this model is composed of a combination of the results from different algorithms and therefore such contributions cannot be interpreted in a meaningful way (Aguirre-Gutiérrez et al. 2013).

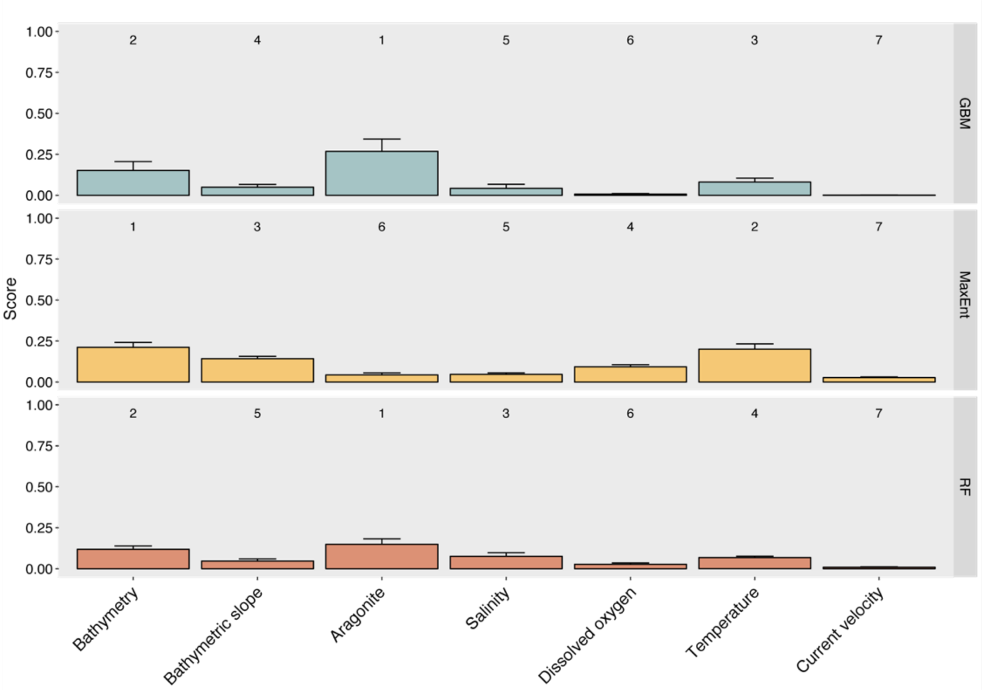


Figure 2.2.4 – Predictors contributions scored as the relative importance to models considering all pseudo-absence datasets and evaluation runs by algorithm (ranging between 0 and 1). The highest the value, the more important is the variable for the model, while the value zero means no influence at all. The interaction between predictors was not considered.

2.2.4.2 - Performance of the models

The performance of the models was assessed using ROC, TSS and Boyce index (Figure 2.2.5). ROC values greater than 0.95 and TSS scores equal or greater than 0.8, were considered highly accurate. Overall, the single models reached good to excellent average predictive scores, however, according to the Boyce index individual performance was lower for GBM and MaxEnt (the latter, in a less extent) than for RF which attained high levels of agreement between the presence dataset and grid cells with high HSI.

The ensemble model forecast was built from the consensus of 258 out of the 300 simulated models, selected according to the defined TSS threshold (0.8). For the three metrics, the scores of the ensemble model were higher than the average scores of the single models indicating that it over-performed the estimation of the single algorithms.

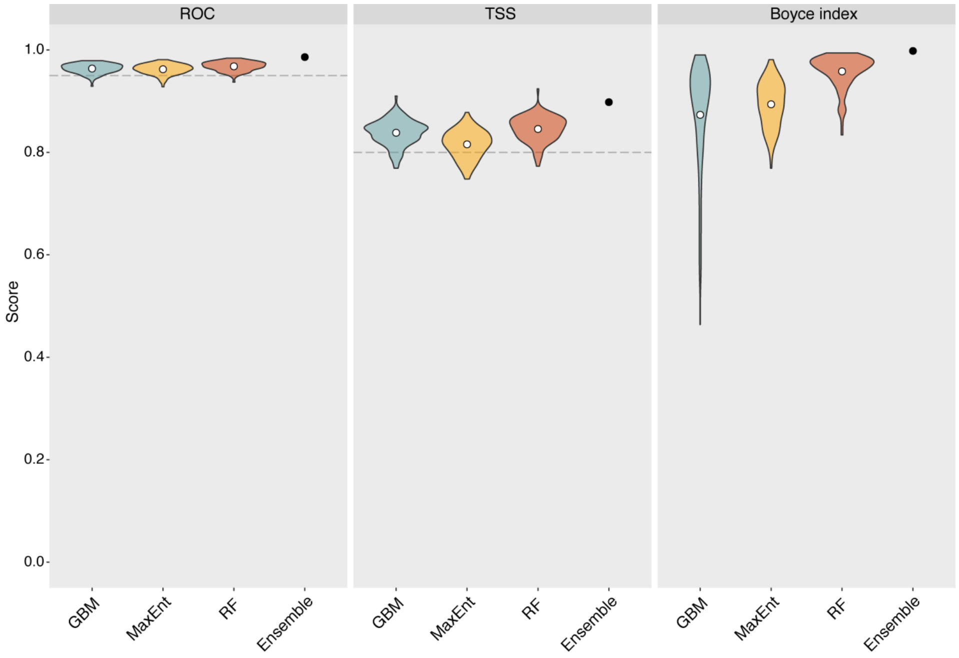


Figure 2.2.5 – Performances of the models grouped by modelling algorithms (presence/pseudo-absence datasets and repetitions pooled) according to ROC, TSS and Boyce evaluation scores. The models scores above the threshold indicated by the dashed lines are considered highly accurate. The average scores of single models are indicated by the white dots (n = 100). Black dots are the scores for the ensemble model.

2.2.4.3 - Seascape suitability

The highest HSI values were found mainly along the upper slope of the Mediterranean margins, in the Western region characterised by the presence of many submarine canyons (e.g., the Gulf of Lion), in the Central region off the Malta Island, in the North of the Ionian Sea (deep-water coral provinces of Santa Maria di Leuca) and the South Adriatic Sea (Figure 2.2.6a). The HSI values decreased towards the Eastern Mediterranean region (e.g., the Aegean Sea) and reached values close to zero in shallower (e.g., North Adriatic, and Tunisian and Libyan continental shelves) and abyssal depths.

The result of the committee averaging (Figure 2.2.6b) model indicates a high reliability of the ensemble forecast for the most suitable and most unsuitable areas and high uncertainty (values around 0.5) for the Aegean Sea and overall for the upper slope of the Eastern Mediterranean region. On the other hand, the coefficient of variance returned overall a low uncertainty of the ensemble forecast with the exception of small areas in the Levantine Sea (Figure 2.2.6c).

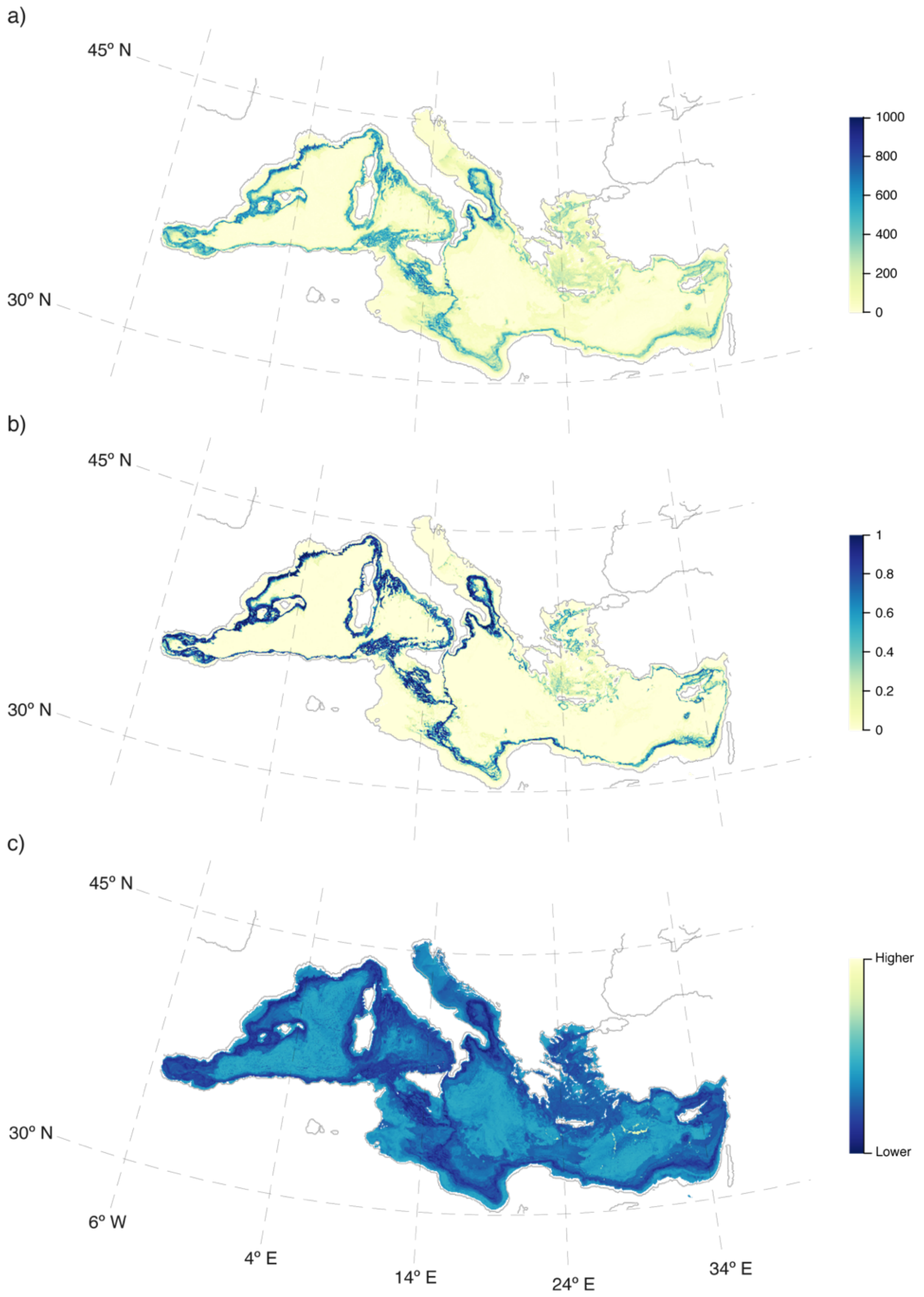


Figure 2.2.6 - a) Ensemble model based on the mean probabilities of the selected models and expressed as HSI (ranging from 0 to 1000, representing the least and the most suitable areas, respectively). b) Map of the committee averaging score; this map offers a measure of uncertainty of the ensemble model (values close to 1 or 0 indicate a good agreement among the single models predictions regarding the potential presence or absence, respectively; values around 0.5 mean that the estimates of the models are evenly distributed by 0 and 1 values). c) The coefficient of variance (i.e., standard deviation/mean) of the probabilities estimated for the selected models is also a measure of uncertainty: lower scores correspond to better predictions, while higher scores mean that prediction uncertainty is high.

Among the 15 geomorphologic features identified by Harris *et al.* (2014) in the Mediterranean Sea, trenches, seamounts, guyots, bridges and sills represent individually less than 0.5% of the seascape area (0.4, 0.3, 0.1, 0.01, <0.01%, respectively). The continental slopes and submarine canyons are, in terms of area covered, the two most relevant features with high HSI values estimated by our model (Figure 2.2.7); together with troughs, terraces and ridges they cover 34.1% of the Mediterranean seascape. The variation of the HSI estimates within each category was large, indicating a highly heterogeneous environment, and the limits of the third quartile remained below 460 for all categories. The geomorphologic categories showing the highest proportions of low suitability habitats (in all cases the third quartile showed HSI scores lower than 52) were the abyssal areas, continental shelves and rise, and submarine fans, in total accounting for 64.1% of the Mediterranean seascape.

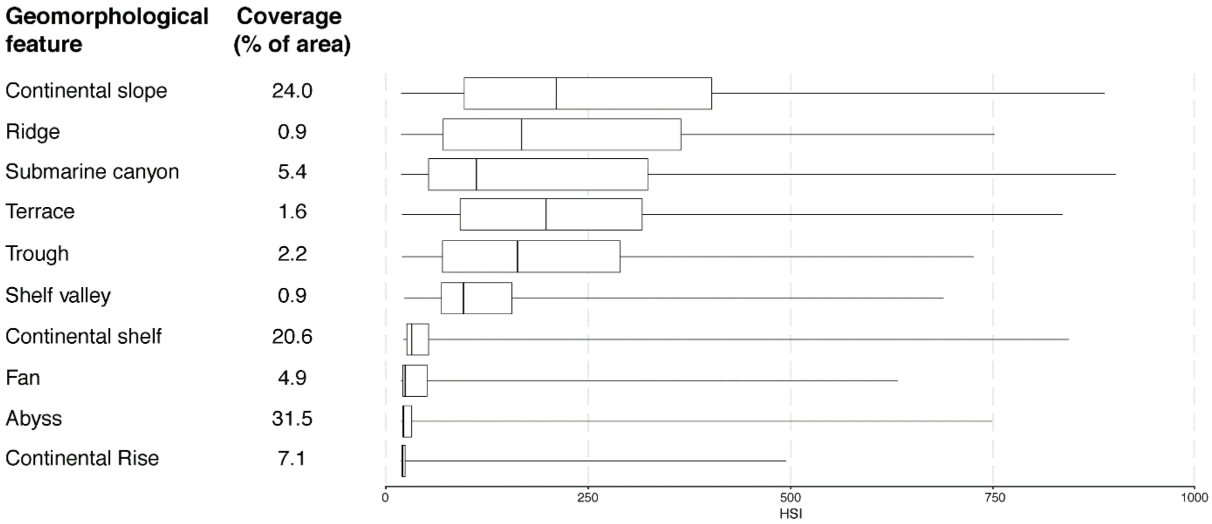


Figure 2.2.7 - Classification of seascape suitability of the geomorphologic feature categories (Harris et al. 2014) present along the Mediterranean Sea by decreasing order of the 3rd quartile. The lines indicate the HSI value ranges and the boxplots show the 1st quartile, the median and the 3rd quartile. The coverage percentages were given by the area of the polygons shape that defined the individual features in Harris *et al.* (2014). Features with an area lower than 0.5% were omitted.

A total of 898 MPAs, mostly encompassing coastal and shelf depths, confer some type of legal protection within the modelling region. From these MPAs, a clear majority allows multiple uses, and only 6.46%, covering a total area of 9863 km^2, have some type of fishing restriction or are no take zones (Figure S 2.2.3). Note that these values exclude the vast Bottom Trawl Closure, the largest non-fishing area in the Mediterranean Sea, covering depths greater than 1000 m, as well as the Shark and Cetacean Habitat Protected Areas and the Marine Mammal Sanctuary where the allowed fishing activities do not affect significantly the seabed. The analysis of the overlap between high seascape suitability and Mediterranean MPAs showed that the vast majority of the areas with high HSI were not covered by any MPA (Figure S 2.2.3). The exceptions were the deepest areas (>1000 m depth), namely in the South of Italy and in the Western Mediterranean (e.g., Gulf of Lion), which were obviously included within the Bottom Trawl Closure.

2.2.5 - Discussion

The output of a presence-only model is an estimation of the species environmental preferences (Guillera-Arroita et al. 2015) and can be interpreted as a measure of habitat suitability for the species occurrence. Species respond differently to a large variety of processes and environmental constraints at local, regional and global scales, hence, the analysis of the organisms distributions should take into consideration different levels of the environment spatial hierarchy (Mackey and Lindenmayer 2001). Our aim was not to provide a fine-scale assessment of the Mediterranean seascape suitability for *L. pertusa*, for which the spatial resolution of the ensemble model is not adequate. Instead we present a continuous assessment of the environmental conditions, confront the empirical knowledge on the Mediterranean distribution of *L. pertusa* and provide relevant information to identify focal areas for future efforts using higher resolution models currently only applicable at local scales. To our best knowledge, this work is the first mesoscale (seascape level) estimation of the habitat suitability for *L. pertusa* that encompasses the whole Mediterranean Sea using an ensemble ENM with a multi-algorithm approach that provides both the prediction of seascape suitability and a measure of uncertainty of the forecast.

The concept of ecological niche is central for the ENM approach and the quality of the forecast can be partly inferred from the response curves and their ecological plausibility. Despite some variations between algorithms the bathymetry, aragonite saturation and temperature showed the highest contributions to the forecasts. These results agree with previous global and regional modelling studies that used at least one of these predictors to estimate the environmental suitability for *L. pertusa* (Davies and Guinotte 2011; Rengstorf et al. 2013; Georgian et al. 2014; Bargain et al. 2018). A strong link between CWC occurrence and the hydrodynamic regime has been often reported (e.g., Rengstorf et al. 2014) but our results indicate current velocity as the predictor contributing less for the model predictions. This can be partially explained by the relatively coarse resolution of the source data (0.08º) that is insufficient to represent the fine-scale local hydrodynamics and its complex interaction with topography, probably underestimating the actual influence of this predictor on the species distribution (Davies and Guinotte 2011; Rengstorf et al. 2014). Surrogates of food availability (e.g., POC flux), and terrain variables derived from bathymetry are also widely recognized as important proxies for habitat suitability in local, high-resolution models (e.g., Bargain et al. 2018). However, we intentionally excluded these because: i) the amount of food reaching the seafloor can only be poorly estimated owing to the spatial offset between surface productivity and the influence of lateral transport in the POC flux (Georgian et al. 2014); ii) terrain attributes such as ruggedness, aspect, and bathymetric position index are highly scale-dependent and their computation at coarse resolutions results in significant differences between the derived data and the local characteristics (Rengstorf et al. 2012). The univariate response curves reproduce only partially the multivariate environmental space where species occur, are susceptible of incorporating inaccuracies derived from input data (Cory et al. 2014), and also show differences depending upon which algorithm is used (Figure S 2.2.2). However, our mesoscale ensemble model showed ecologically plausible response curves and are therefore expected to accurately predict the relationship between the environmental gradients and species occurrence (Vierod et al. 2014).

The distribution of living CWC in the Mediterranean Sea has been historically considered as restricted, partly owing to the near homoeothermic conditions (12.7-14.5 ºC) and the high salinity of its deep waters (38.4-39, Delibrias and Taviani 1984). Our results show that in the Mediterranean Sea, *L. pertusa* encounters temperature and salinity values close to the upper limit of the optimal range of the response curves and dissolved oxygen concentrations close to the lower limit. Beyond these limits, suitability values in the ensemble response curves for the predictors suffer a sharp drop. Although *L. pertusa* shows some biogeographic physiological plasticity to face environmental changes (Georgian et al. 2016), the populations in the Mediterranean Sea may be already subjected to the limits of their physiological tolerance (Figure 2.2.2 and 2.2.3). Studies on the thermal tolerance of *L. pertusa*, revealed significant effects on its physiological response when subjected to temperature variations outside the species natural thermal range (Naumann et al. 2014). The species distribution is also determined by the concentration levels of dissolved oxygen and aragonite, and distributional constraints by these variables may be even more important in the context of future global changes (Georgian et al. 2016). *Lophelia pertusa* shows some capacity to regulate oxygen consumption (Dodds et al. 2007), but the synergy between lower concentrations of dissolved oxygen and higher temperatures can amplify the effects of these stressors. Moreover, although in the Mediterranean Sea the aragonite unsaturated waters are confined to the deeper water masses (Figure S 2.2.4), this situation can change with the increasing acidification of sea water and subsequent shallowing of the Ω_{ARAG} horizon, which may threaten the species survival (Guinotte et al. 2006).

The good performance scores of the single models were surpassed by the ensemble model scores in all metrics, strengthening our confidence in its predictive capacity. The estimates of the committee averaging and coefficient of variance, indicating overall low uncertainty levels for the forecast of the ensemble model further support the advantages of using this modelling approach. The projection of the ensemble model over the Mediterranean Sea (Figure 2.2.6a) encompasses an almost continuous area of medium to high HSI scores, mostly located along the upper slope, extending from the Alboran Sea to the Central Mediterranean region. The lowest HSI values cover vast areas including the continental shelves (<100 m depth) and the deepest regions (>1500 m). The environmental constraints to *L. pertusa* distribution seem to be stronger in the Eastern Mediterranean Sea, following the well-documented gradient of increasing temperature, salinity and oligotrophy from the Western to the Eastern region (Azov 1991; Sardà et al. 2004).

We are aware that the species distribution is not continuous nor uniform and therefore ground-truthing surveys are always required. ENMs are scale-dependent and predictions are overestimated for larger grid cells (Seo et al. 2009). Moreover, regardless of their performance, ENMs commonly overestimate the species potential distributions since they assume that their occurrence is largely influenced by the ecological niche, ignoring other important drivers for species prevalence (Georgian et al. 2014). A species may be absent in areas with suitable conditions owing to biotic interactions, oceanographic barriers (e.g., water column stratification, prevailing currents) and other complex ecological mechanisms preventing dispersal and/or colonization (Rogers 2003).

ENM predictions are always coupled with a certain level of uncertainty associated to the data characteristics (i.e., quality and quantity) and to the methodological decisions made during the modelling process. For instance, the spatial filter applied to diminish sample spatial clustering and avoid pseudo-replication, is expected to provide an adequate representation of the full range of environmental conditions in which *L. pertusa* occurs. Nevertheless, the influence of various limitations on the models forecasts are difficult to quantify. Among the main sources of uncertainty affecting deep-sea ENM are the limitations in the occurrence datasets which, in the case of *L. pertusa*, derive from an insufficient coverage by surveys targeting CWC in the Mediterranean Sea (e.g. the absence of occurrence data for the easternmost Mediterranean Sea may partly explain the higher uncertainty of the forecast for this region). Moreover, field observations show that *L. pertusa* is less common in the Mediterranean than in other oceans and has a more patchy distribution, often occurring as isolated colonies (Orejas et al. 2009; Howell et al. 2011). The increasing number of biological surveys in the Mediterranean Sea and the growing tendency to use remote sensing and underwater technologies in oceanographic cruises, is likely to increase the number of coral areas detected in this region (Taviani et al. 2017). Recent efforts to catalogue coral occurrences in the Mediterranean Sea highlighted the existence of an “almost uninterrupted, albeit patchy, belt of CWC sites” along the south-western Adriatic margin (Angeletti et al. 2014) and a coral reef of considerable size was observed in the Lacaze-Duthiers submarine canyon

(Gori et al. 2013). These and other well-known CWC areas were scored with high HSI by our model: the Santa Maria di Leuca coral province (e.g., Tursi et al. 2004), the South Adriatic (e.g., Freiwald et al. 2009; Angeletti et al. 2014), Ionian Sea (e.g., Savini et al. 2014), South of Malta Island (e.g., Maier et al. 2012), the Melilla CWC Province (Iacono et al. 2014b), and several submarine canyons (e.g., Cap de Creus (Orejas et al. 2011), Lacaze-Duthiers (Fabri et al. 2014), Nora (Taviani et al. 2017), Bari (Freiwald et al. 2009).

The ranking of submarine canyons with some of the highest HSI scores confirms previous indications that, as a consequence of their complex topography and influence on hydrodynamics, these geomorphologic features may be considered CWC hotspots (Orejas et al. 2009; Van den Beld et al. 2017). The high-energy environments and roughed topography commonly associated with canyons can result in low sediment coverage and a higher availability of hard substrates for reef development (Sánchez et al. 2014). Such conditions may also be frequently found in escarpments and rocky outcrops at continental slopes. Seamounts (and guyots) are also recognized as preferential areas for CWC development (Roberts et al. 2009) but they were not considered in our analysis owing to the low percentage cover they occupy in the Mediterranean Sea. Moreover, the size of these geomorphologic structures is difficult to capture at the scale of our ensemble model or by regional and global models with relatively coarse resolutions.

Apart from the ecological reasons mentioned above, species distributions can be constrained by the type, intensity and frequency of anthropogenic disturbance. Human activities can lead to local extinctions of vulnerable species from otherwise environmental suitable locations (Clark et al. 2016). Many studies exposed severe impacts on *L. pertusa* populations (Orejas et al. 2009; Fabri et al. 2014; Lastras et al. 2016) that result from fishing activities, litter accumulation and waste disposal. Conservation measures to mitigate some of these detrimental activities are implemented in areas classified as Sensitive Habitats by the European Commission and/or marine Sites of Community Importance (p-SCI) included in the Natura 2000 network (Madurell et al. 2012). However, these examples correspond mainly to MPAs covering coastal and shelf regions and therefore not effectively protecting *L. pertusa*. The Bottom Trawl Closure is a clear exception, but despite its great importance and extent, the exclusion of fishing activities below the 1000 m may only provide a partial protection to *L. pertusa* since it barely overlaps with the deepest fringe of the most suitable areas. Considering these issues, the conservation of *L. pertusa* habitat and the persistence of its Mediterranean populations could be at risk with serious consequences for the biodiversity and functioning of deep-sea ecosystems (particularly at the continental slopes). In this context, canyons may have a supplementary conservation value acting as natural refuges for CWC to some of the anthropogenic impacts (e.g., bottom trawling, Van den Beld et al. 2017), particularly because the Mediterranean Sea is one of the world's regions where canyons are more densely and closely spaced (Harris and Whiteway 2011) occupying naturally delimited and therefore potentially more manageable areas for conservation purposes.

Regardless of their limitations, ENMs are important to compile and interpret information on the species ecology, provide insights on their potential distributions, and are particularly relevant for research on data-poor species (Vierod et al. 2014). Our seascape suitability assessment broadens the perception of the Mediterranean distribution of *L. pertusa*, and its ecological constraints, previously based on fragmented information from punctual biological surveys and local modelling efforts. The results show that the Mediterranean populations of *L. pertusa* seem to be already subjected to the environmental limits of the species physiological tolerance which may compromise their resilience with an intensification of stressful conditions. This is a scenario likely to occur under the current climate change trend, increasing anthropogenic pressure and lack of effective protection of CWC habitats in the Mediterranean Sea. The mapping of the seascape environmental suitability of *L. pertusa* may assist future research efforts, including further modelling studies with higher resolution data on the areas identified as most suitable, the development of action plans for their conservation and the investigation of the mechanisms governing the persistence *L. pertusa* populations in the Mediterranean Sea. The potential connectivity between the Mediterranean populations of *L. pertusa* and the connectedness between suitable habitats areas (seascape connectivity) is currently being estimated using a biophysical model and the outputs presented herein (Chapter 2.3 of this thesis).

2.2.6 - Supplementary material

SUPPLEMENTARY TABLE

Table S 2.2.1 - Records of *L. pertusa* living colonies from the Mediterranean Sea. Coordinates in decimal degrees and depth in meters.

Start Lon	Start Lat	End Lon	End Lat	Start Depth	End Depth	Location	Structure	Notes	Source
-2.253	35.794	-2.254	35.795	318	419	Cabliers II–Banco de Cabliers			(Pardo et al. 2011)
-2.574	35.829	-2.573	35.835	363	470	Catifas I–Banco de Cabliers			(Pardo et al. 2011)
-3.974	36.393	-3.969	36.397	320	398	El Algarrobo – banco de Djibuti			(Pardo et al. 2011)
-2.922	36.522	-2.909	36.537	243	486	Seco de los Olivos			(Pardo et al. 2011)
18.691	41.648			505		Lacaze-Duthiers	Canyon	ROV transects	(Angeletti et al. 2014)
18.674	41.648			441	443	Off Montenegro		ROV transects	(Angeletti et al. 2014)
18.92	39.891			786		Off Tricase		ROV transects	(Angeletti et al. 2014)
2.833	41.583	2.85	41.585	900		Blanes	Canyon		Ayma et al., in press
17.688	39.765			1100					Carlier et al. 2009
18.398	39.587			520					Carlier et al. 2009
18.437	39.565			550	700	Reef A			Carlier et al. 2009
3.398	42.564			343	369	Lacaze-Duthiers	Canyon	ROV transects	Fabri et al. 2014
3.408	42.552			387	468	Lacaze-Duthiers	Canyon	ROV transects	Fabri et al. 2014
17.179	41.297	17.166	41.292	306	508	Bari	Canyon	Approximated location	Freiwald et al. 2009
17.277	41.291	17.276	41.283	374	640	Bari	Canyon	Approximated location	Freiwald et al. 2009
18.08	39.621	18.084	39.625	603	744	Gallipoli escarpment		Approximated location	Freiwald et al. 2009
17.047	41.725	17.061	41.72	674	714	Gondola slide		Approximated location	Freiwald et al. 2009
13.044	35.767	13.043	35.765	669	679	Linosa Trough		Approximated location	Freiwald et al. 2009
14.11	35.512	14.107	35.515	453	576	off Malta		Approximated location	Freiwald et al. 2009

Start Lon	Start Lat	End Lon	End Lat	Start Depth	End Depth	Location	Structure	Notes	Source
18.453	39.565	18.437	39.565	556	604	Santa Maria di Leuca		Approximated location	Freiwald et al. 2009
18.456	39.555	18.451	39.564	590	624	Santa Maria di Leuca		Approximated location	Freiwald et al. 2009
13.156	36.84	13.154	36.838	509	600	Urania Bank		Approximated location	Freiwald et al. 2009
3.315	42.394	3.313	42.391	191	280	Cap de Creus	Canyon	ROV transects	Gori et al. 2013
3.319	42.385	3.321	42.387	311	230	Cap de Creus	Canyon	ROV transects	Gori et al. 2013
3.334	42.357	3.334	42.357	243	235	Cap de Creus	Canyon	ROV transects	Gori et al. 2013
3.399	42.567	3.399	42.561	320	379	Lacaze-Duthiers	Canyon	ROV transects	Gori et al. 2013
3.403	42.583	3.402	42.583	271	276	Lacaze-Duthiers	Canyon	ROV transects	Gori et al. 2013
3.406	42.578	3.407	42.582	198	360	Lacaze-Duthiers	Canyon	ROV transects	Gori et al. 2013
3.421	42.546	3.414	42.54	199	537	Lacaze-Duthiers	Canyon	ROV transects	Gori et al. 2013
3.329	42.379	3.329	42.38	279	325	Cap de Creus	Canyon	ROV and sumersible JAGO transects	Gori et al. 2013; Orejas et al. 2009
3.338	42.369	3.337	42.371	257	293	Cap de Creus	Canyon	ROV and sumersible JAGO transects	Gori et al. 2013; Orejas et al. 2009
-3.53	36.088	-3.536	36.1	710	284	Alboran		ROV	Hebbeln et al. 2009
-2.922	36.024			404		Alboran		ROV, exact location	Hebbeln et al. 2009
-2.515	35.436			349		Alboran		ROV, exact location	Hebbeln et al. 2009
-3.496	36.156	-3.508	36.132	662	289	El Idrissi Bank, NE flank		ROV	Hebbeln et al. 2009
-3.553	36.091	-3.553	36.096	366	309	El Idrissi Bank, S flank		ROV	Hebbeln et al. 2009
-3.488	36.105	-3.495	36.109	687	388	El Idrissi Bank, SE flank		ROV	Hebbeln et al. 2009
3.421	42.545			520		Lacaze-Duthiers	Canyon	In situ experiments	Lartaud et al. 2014
3.42	42.55			267	500	Lacaze-Duthiers	Canyon	Approximated location	Maier et al. 2012
14.082	35.83			690		southwest off the		Approximated location	Maier et al. 2012

Start Lon	Start Lat	End Lon	End Lat	Start Depth	End Depth	Location	Structure	Notes	Source
						island of Malta			
3.315	42.39			214-218					Orejas et al. 2008
3.317	42.388	3.314	42.39	185	240	Cap de Creus	Canyon	ROV transects	Gori et al. 2013; Orejas et al. 2008
14.05	35.059	14.053	35.063	395	444			Approximated location	Schembri et al. 2007
14.105	35.508	14.1	35.514	420	617			Approximated location	Schembri et al. 2007
8.909	38.708	8.908	38.707	350	350	Nora	Canyon	ROV	Taviani et al. 2017
8.912	38.703	8.913	38.703	415	380	Nora	Canyon	ROV	Taviani et al. 2017
8.912	38.703	8.912	38.704	440	440	Nora	Canyon	ROV	Taviani et al. 2017
8.912	38.703	8.912	38.703	432	340	Nora	Canyon	ROV	Taviani et al. 2017
3.321	42.386			300		Cap de Creus	Canyon		Tsounis et al. 2010; Naumann et al. 2014
18.39	39.583					Santa Maria di Leuca		ROV	Vertino et al. 2010
18.508	39.612					Santa Maria di Leuca		ROV	Vertino et al. 2010
18.378	39.48			784		Santa Maria di Leuca			Yakimov et al. 2006

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SUPPLEMENTARY FIGURES:

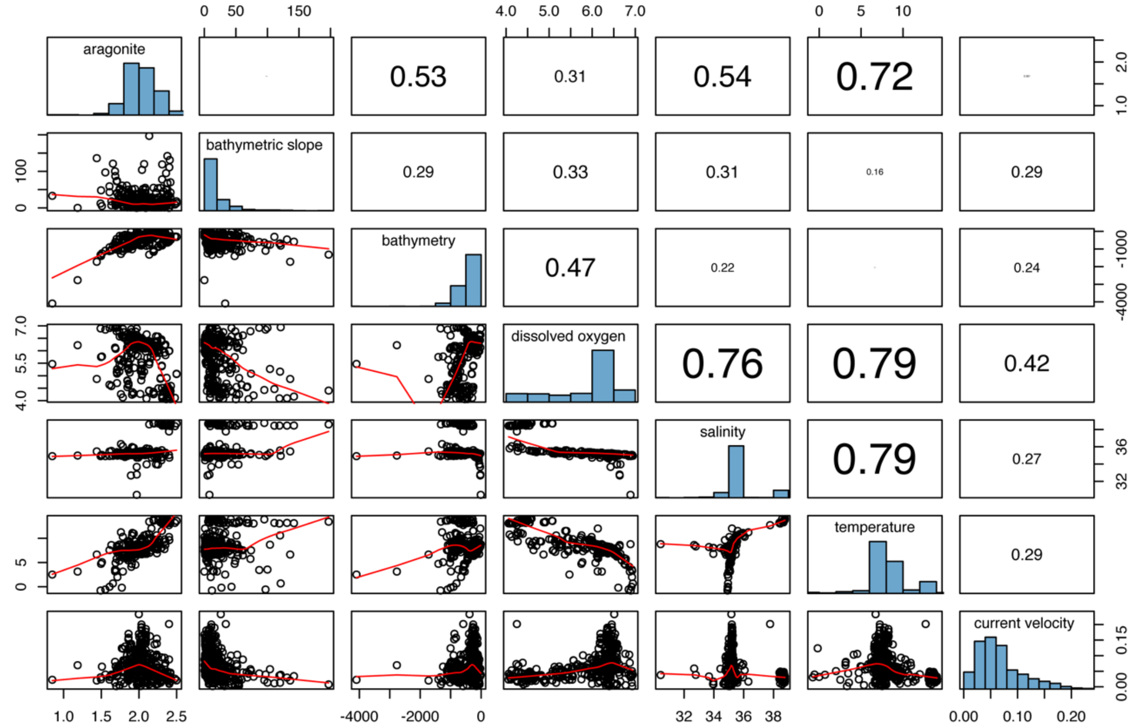

Figure S 2.2.1 - Variables correlation using the occurrence data points.

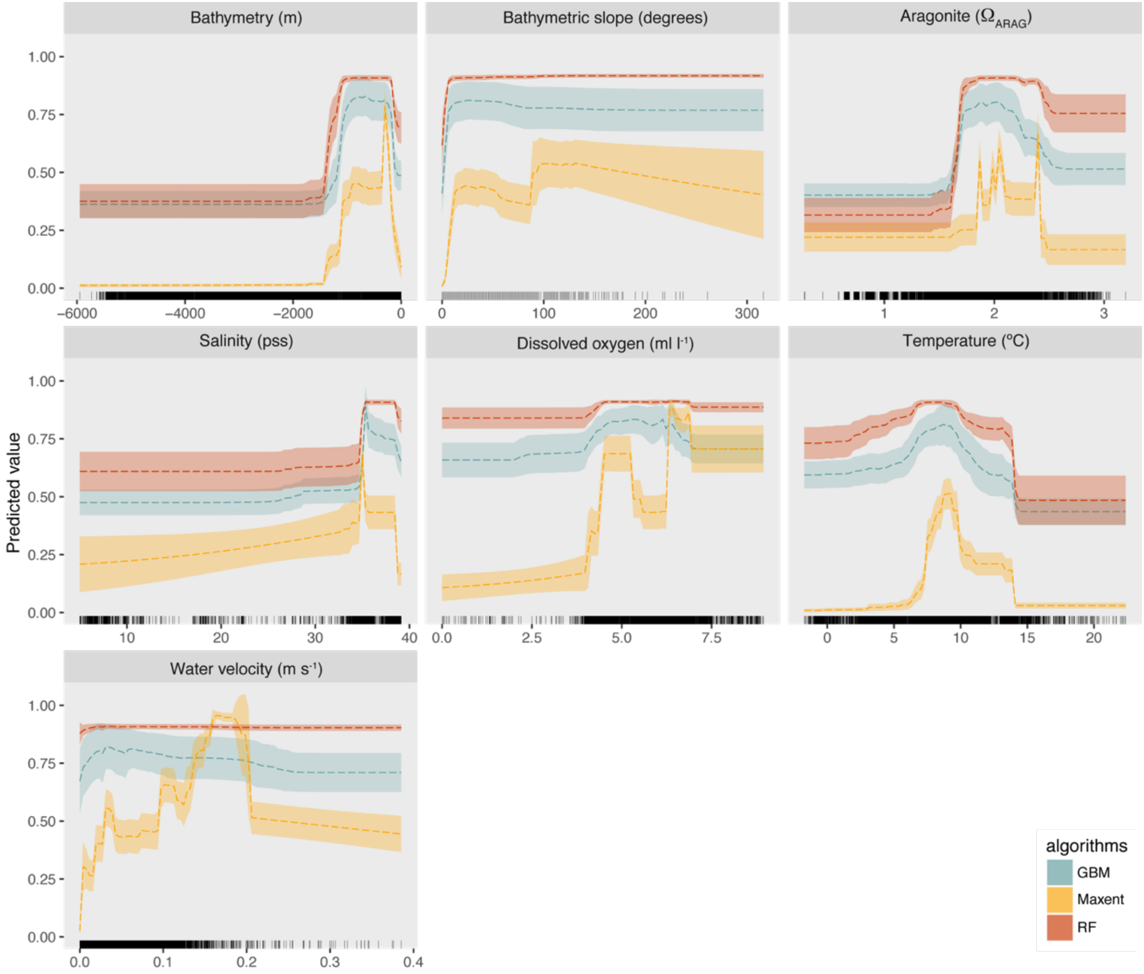

Figure S 2.2.2 – Response curves for each algorithm. The line corresponds to the mean of the single models and the shaded area to the standard deviation.

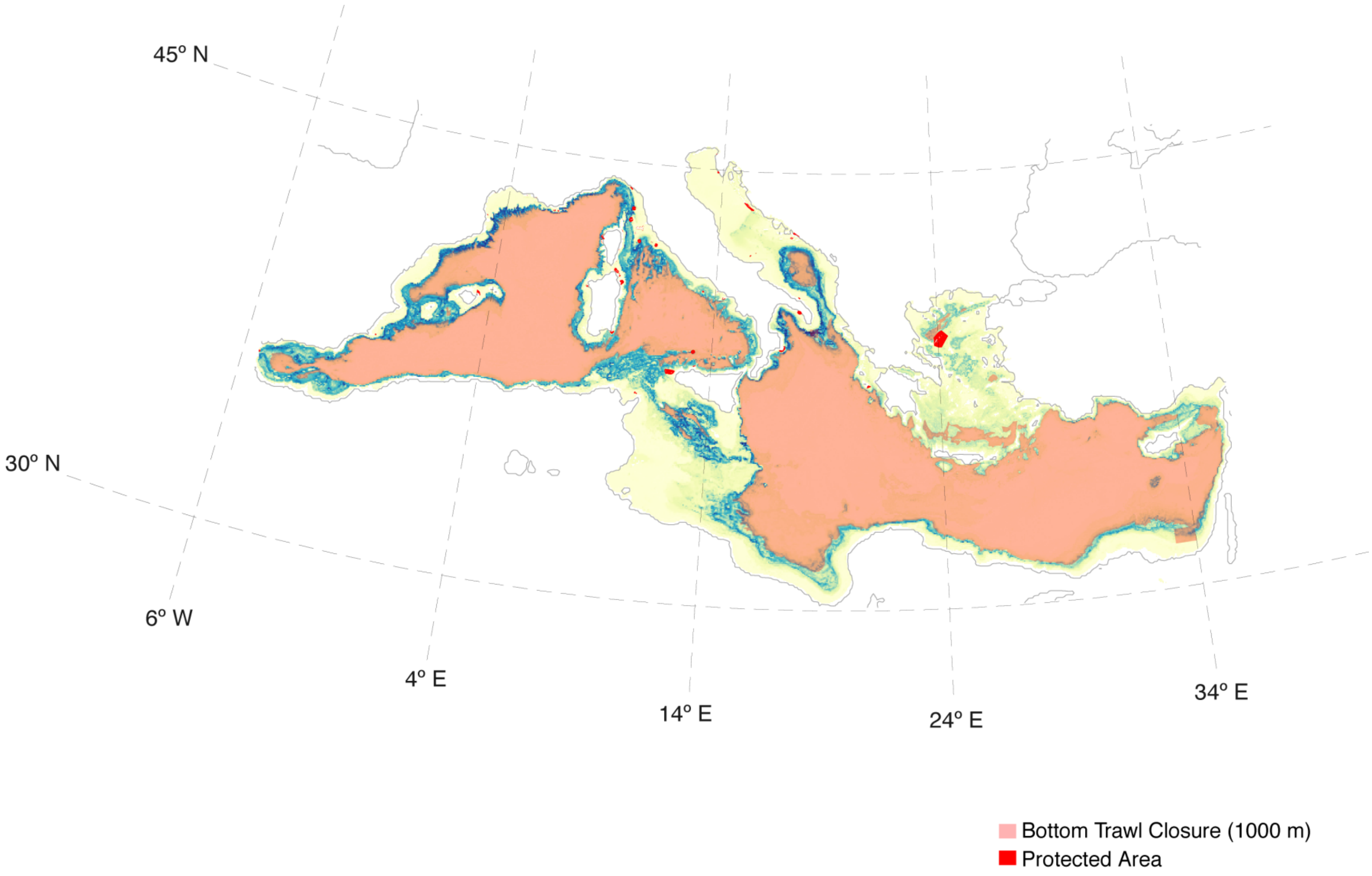

Figure S 2.2.3 – Marine protected areas with restrictions to fishing activities according to the MPAtlas of the Marine Conservation Institute.

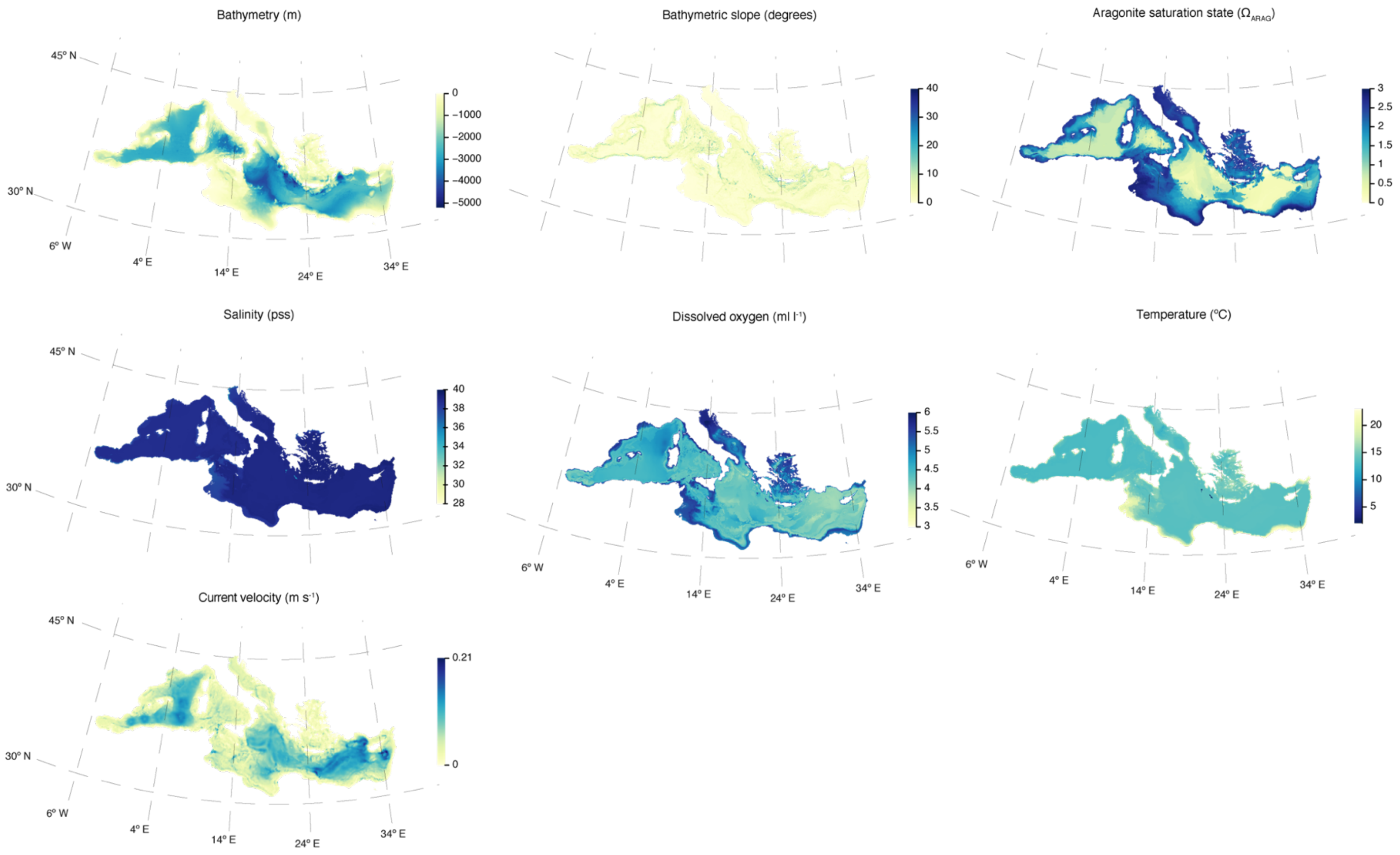

Figure S 2.2.4 – Predictors environmental range across the Mediterranean Sea.

2.3 - Gone with the stream: connecting dots across the Mediterranean seascape of *Lophelia pertusa*

2.3.1 - Abstract

Ecosystem connectivity determines the species distribution, the metapopulation dynamics and population resilience. It is a guiding principle in marine conservation planning, particularly for spatial prioritization and the design of networks of marine protected areas. Cold-water corals (CWC) are among the most vulnerable deep-sea ecosystems. In this work, we simulate transport of *Lophelia pertusa* larvae in the Mediterranean Sea, estimate their potential dispersal and the habitat availability, based on the suitability and spatial configuration of the seascape. The larval transport simulations were performed using a biophysical modelling tool built in a Lagrangian framework and accounted for inter-annual variability of Mediterranean Sea. Habitat availability was analysed using a graph-based approach taking into consideration the attributes of habitat areas. We concluded that connectivity among Mediterranean ecoregions was weak and that the intensification of climate-driven events (e.g., dense shelf water cascading) may worse this scenario. The potential exchange of larvae between colonies within the same ecoregion was significant, favouring population resilience to local disturbances. The analyses of larval transport and habitat availability allowed identifying the Gulf of Lion, the Catalan and Apulian margins, and the Bari Canyon as habitat areas playing an important role in the connectivity of *Lophelia pertusa* Mediterranean populations. However, these habitat areas are subjected to intense anthropogenic pressures, which allied to the effects of climate change, may impose greater challenges to their conservation. We discuss the potential application of our results in designing future target surveys targeting *L. pertusa* and as a framework for future empirical studies based on spatial explicit information with interest for the policy and management of Mediterranean seascape.

2.3.2 - Introduction

Cold-water corals (CWC) are among the most iconic deep-sea organisms and provide refuge, nursery grounds and physical support for a remarkable diversity of other life forms (Henry and Roberts 2016). Because of their ecological significance and high vulnerability to fishing activities (Ramirez-Llodra et al. 2011), CWC are classified as Vulnerable Marine Ecosystems (VME; FAO 2009). Among the CWC species, *Lophelia pertusa* is one of the most studied. *Lophelia pertusa* is a broadcast spawner, with multiple and asynchronous gamete releases within the same population (Brooke and Järnegren 2013; Larsson et al. 2014). Spawning season varies among colonies from the NE Atlantic Ocean (Waller and Tyler 2005; Brooke and Järnegren 2013; Larsson et al. 2014), the Gulf of Mexico (Brooke and Schroeder 2007) and in the Brazilian coast (Pires et al. 2014). No larvae of this species have ever been collected in nature (Roberts et al. 2016), however, some were successful reproduced in laboratory and provided essential and novel information on larval development and behaviour (Larsson et al. 2014; Strömberg and Larsson 2017). According to Larsson *et al* (2014), the larvae of *L. pertusa* show an ontogenetic vertical migration behaviour and a high dispersal potential (Strömberg and Larsson 2017). However, estimates of larval longevity vary considerably within and between studies, with temperature exerting a significant control on larval development (Strömberg and Larsson 2017). An increase in temperature of three degrees halved the development period from 3-5 weeks to approximately two weeks. These results suggest that, in addition to spawning season, the pre-competency period and the pelagic larval duration (PLD) are also likely to vary with the latitudinal gradients in water temperature.

In the Atlantic Ocean, *L. pertusa* shows a widespread distribution but in the Mediterranean Sea, despite the existence of areas with high seascape suitability (Chapter 2.2), its known occurrences are more restricted and patchier (Gori et al. 2013; Angeletti et al. 2014; Iacono et al. 2014a; Savini et al. 2014; Fabri et al. 2016; Taviani et al. 2017). This distribution pattern has been considered to result from changes in the Mediterranean environmental conditions, most favourable in the past (e.g., lower seawater temperature), and to present-day physical barriers to dispersal (Delibrias and Taviani 1984; Freiwald 2002). In fact, the known living colonies in the Mediterranean Sea are considered as reminiscent refugia of the species from a more widespread and thriving distribution during the Younger Dryas (10–11 kyr BP) when the Mediterranean Sea was characterised by 4–8ºC cooler waters than today (Wienberg et al. 2009). The present environmental settings of the Mediterranean water masses challenge the physiological limits of *L. pertusa* (Chapter 2.2) and the topography and oceanographic patterns impose barriers to its dispersal and limit the seascape connectivity which may further be affected in a future scenario of climate change

Species distributions and the persistence of their populations are closely related with ecosystem connectivity. The concept of connectivity can be approached by three broad typologies (Treml and Kool 2017): the structural, functional and realized connectivity. The structural connectivity, often referred as "connectedness", incorporates only information about the physical attributes of the landscape (e.g., habitat location, size and shape) and refers to the physical links between their elements (Opermanis et al. 2012). In addition to the physical relationships between landscape elements, functional connectivity includes species-level characteristics (e.g., environmental tolerance and life-history traits) and the organisms' response (e.g., larval behaviour. post-settlement mortality) to the landscape patterns (Treml and Kool 2017). The realized connectivity refers to the actual population connectivity patterns which result from the transference of individuals and genetic material among sub-populations of a species (Opermanis et al. 2012; Treml et al. 2015). Realized connectivity is usually described from empirical approaches such as direct observations, larval tracking and genetic data (Calabrese and Fagan 2004). Because empirical data on marine species are scarce, and life-history traits and environmental tolerances are often unknown many connectivity studies focus on functional connectivity, commonly measured as the potential population connectivity, using mainly ecological modelling approaches (e.g. numerical biophysical models, network analysis) that incorporate the few available or inferred species attributes.

Biophysical models have been used as an indirect approach to simulate trajectories of virtual larvae, estimate dispersal probabilities and contribute to the knowledge on connectivity of populations and ecosystems (Schill et al. 2015; Kough et al. 2016; Ross et al. 2017a; Henry et al. 2018). The dispersal of larvae in the marine environment results from the interaction of physical transport with the organisms' behaviour and life-history traits (Pineda et al. 2007; Treml and Kool 2017). Biophysical modelling integrates oceanographic data with the species life-history traits, allowing to test ecological hypotheses and plan targeted field sampling strategies (Kool and Nichol 2015). Empirical techniques based on genetics and microchemistry of organismal structures have provided valuable insights on dispersal and the extent of realized population connectivity. However, despite the technical and methodological advances in these fields their application is limited, especially with deep-sea species (Génio et al. 2015), while biophysical modelling allows to embrace, simultaneously, large spatial and temporal scales in a degree not possible by purely empirical studies (Brown et al. 2016).

Like biophysical modelling, network analysis based on graph theory became a popular and powerful tool to study ecosystem connectivity (Cowen et al. 2006; Treml et al. 2008; Lookingbill et al. 2010) and it has also been used to prioritize seascape elements for conservation (e.g., Engelhard et al. 2016). In ecosystem connectivity studies using this technique, the landscape dimensionality is mimicked in a spatial graph. The habitat patches are represented as a set of nodes potentially connected by links expressing the degree of connectivity (Urban and Keitt 2001; Fall et al. 2007). Different graph-based metrics can be then applied to estimate the habitat availability at the seascape level (Pascual-Hortal and Saura 2006; Saura et al. 2014). Habitat availability metrics integrate in a single index the connected habitat area within a patch with the habitat made available by connections with other habitat patches in the seascape (Saura and Torne 2009).

One of the greatest challenges of using ecological modelling, and particularly biophysical approaches, for the study of larval dispersal and population connectivity in the deep sea is the large knowledge gap on deep-sea species life-history traits (Hilário et al. 2015). Because *L. pertusa* is one of the most studied deep-sea species in terms of biology and ecology, relevant information on the larval life-history traits is currently available and can be used for the biological parameterization of biophysical models. *Lophelia pertusa* is therefore one of the best available model organisms to study connectivity of deep-sea ecosystems.

The main objective of this work is to assess the Mediterranean seascape connectivity for *L. pertusa*. We will use a Lagrangian biophysical model to estimate the potential dispersal of *L. pertusa* considering the best available information on larval biology and behaviour as well as the spatiotemporal variability of the oceanographic conditions observed in the study area. Additionally, we will use a graph-based network analysis to: i) assess the habitat availability for *L. pertusa* in the Mediterranean seascape; ii) understand how habitat availability is affected by different climate-driven oceanographic scenarios and iii) identify and prioritise habitat areas that are highly relevant for the maintenance of seascape connectivity. Finally, we will discuss the potential application of our results in designing future surveys targeting *L. pertusa* and in assisting the management and conservation of deep-sea ecosystems in the study area.

2.3.3 - Methods

2.3.3.1 - Study area

The Mediterranean Sea is a semi-enclosed water body, connected to the Atlantic Ocean by the narrow Strait of Gibraltar and divided into two major basins, Western and Central-Eastern, by the Strait of Sicily (Robinson et al. 2001; Sardà et al. 2004). The water circulation is markedly influenced by topography, wind stress and the buoyancy flux resulted from the fresh-water inputs and heat fluxes, and the hydrodynamics complex between the water masses (i.e., eddies, current meanders and bifurcations).

In the Western basin, the less dense water flowing from Atlantic Ocean dominates the upper layers of the Mediterranean Sea. At intermediate deeps, the water masses are mainly influenced by Levantine Intermediate Water running from the Central-Eastern basin through the Strait of Sicily, whilst at greater depths, the Western Mediterranean Deep Water prevails (Sardà et al. 2004; Schroeder et al. 2012). Entering the Mediterranean Sea, the Atlantic water flows eastwards along the North African slope forming the Algerian Current, with a generally counter-clockwise circulation pattern (Schroeder et al. 2012). The Algerian Current diverges then into two branches, a larger one that follows North to the Tyrrhenian Sea through the Sardinia Channel (Western Mediterranean), and a smaller one which inflows through the Sicilian Chanel into the Ionian Sea and the Central-Eastern Mediterranean basin. In the Tyrrhenian Sea, the circulation follows the northern coast of Sicily running afterwards along the Ligurian and Provençal coasts, and then offshore, along the Catalan margin closing a mostly cyclonic path with several eddies and meanders (Tanhua et al. 2013). A set of eddies develops from the Algerian Current and occasional interacts with the central Western Mediterranean waters promoting their mixture within the basin.

In the Central-Eastern Mediterranean, the general circulation is characterized by well-defined gyres (forced by topography and wind) which are linked by jets and follow multiple paths into the Levantine basin. An overall clockwise circulation is clear in the Southern Ionian Sea, branching through the Libyan and Egyptian coasts and propagating then northwards (Schroeder et al. 2012). The surface water running through the Central-Eastern Mediterranean convects latterly with the Levantine Intermediate Water at mid-depths, spreading then eastwards into the Levantine basin, and to westwards to the Ionian and northwards to the Adriatic Seas (Tanhua et al. 2013).

Mesoscale variability is generalized across the Mediterranean Sea resulting in changes of the water masses properties and current patterns, both with important consequences for the Mediterranean biota and environmental setting (Sardà et al. 2004; Tecchio et al. 2013). This variability is more evident during exceptionally cold winters, when the formation of deep-water masses is particularly strong at both basins of the Mediterranean Sea. The deep water formation via the occurrence of dense shelf water cascading (DSWC) is a climate-driven phenomenon with a decadal frequency in the study area. DSWC occurs predominantly in the Western Mediterranean along the Gulf of Lion (Puig et al. 2013). and in the Central-Eastern basin, this process happens mainly at the Otranto Strait (Adriatic Sea, Robinson et al. 2001).

In terms of biogeography, the Mediterranean Sea is classified according to Spalding *et al.* (2007) into seven ecoregions (Figure 2.3.1): Alboran Sea, Western Mediterranean, Tunisian Plateau/Gulf of Sidra, Ionian Sea, Adriatic Sea, Aegean Sea and Levantine Sea. Marine ecoregions, as defined by Spalding *et* *al*. (2007) are: *"Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features. The dominant biogeographic forcing agents defining the ecoregions vary from location to location but may include isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, (…) currents, and bathymetric or coastal complexity".*

2.3.3.2 - Biophysical modelling

We simulated the larval trajectories using the open-source Connectivity Modelling System (CMS version 2.0, Paris et al. 2013). The CMS is a multiscale stochastic Lagrangian framework composed by different modules allowing to track the individual path of particles based on oceanographic and biological information. The particles position is estimated using the fourth-order Runge-Kutta integration and the tri-cubic interpolation methods according to a defined time step (3600 seconds, in our model). In addition to the advection transport provided by current velocity from the oceanographic data, the particles were diffused stochastically using a random walk process (10 $m^2 s^{-1}$ every 4 hours, Sayol et al. 2014; Rossi et al. 2014) to account for the turbulent motion of seawater. Besides the common oceanographic and biological modules, CMS is capable of reproducing the tri-dimensionality of the seascape.

We used the outputs of the CMS to identify the preferential dispersal pathways of *L. pertusa* in the Mediterranean Sea and perform the analyses of functional connectivity. CMS simulations were run using the High-Performance Computing cluster ARGUS of the University of Aveiro and R software (R Core Team 2016) was used to perform the data analysis and visualization.

2.3.3.2.1 - Oceanographic module

We ran the oceanographic module of CMS with the daily mean values of the horizontal velocity fields, water temperature and salinity provided by the Mediterranean Forecasting System. These products are available through the Copernicus Marine Environment Monitoring Service and supplied by the Nucleus for European Modelling of the Ocean (NEMO v3.6). To account for the effects of oceanographic variability on the species potential dispersal, simulations were performed for six years. The "typical" oceanographic conditions (non-DSWC years) in the Mediterranean Sea were simulated using oceanographic data for the years 2015-2016, 2016-2017, 2017-2018, with a horizontal resolution of 1/24° (ca. 4 km) and divided over 141 unevenly spaced vertical levels (Clementi et al. 2017). The effects of changes in the oceanographic conditions during exceptional cold winters (DSWC years) were tested using data from 1999-2000, 2004-2005 and 2011-2012. For this oceanographic scenario, the simulations were performed using a coarser data resolution (1/16°, 72 unevenly spaced vertical levels, Oddo et al. 2009) since before 2015 higher resolution of data covering the whole Mediterranean Sea are currently unavailable. The oceanographic data for DSWC years simulations applies only to the Mediterranean Sea, while for non-DSWC years the modelling area also includes the Iberian Peninsula margin.

2.3.3.2.2 - Seascape module

The habitat mosaic for *L. pertusa* was derived from the seascape suitability map estimated for the species in the Chapter 2.2. We used the lowest value of habitat suitability index (HSI) observed in Mediterranean locations with known living colonies as the threshold to separate potential *L. pertusa* habitat from low suitability locations (i.e. locations with a low probability of recruitment success). Locations with HSI values equal or greater than the threshold were retained (Figure 2.3.1) and re-gridded to polygons with 8×8 km size. In total, 16270 polygons with HSI above the threshold were treated independently as discrete potential habitat patches (hereafter designated as habitat polygons). The seascape tri-dimensionality in the biophysical model was addressed by allocating the polygons to depth strata of 50 m. When a polygon intersected multiple depth strata, it was accounted for in each one of the intersected strata. A habitat polygon was considered as successfully reached only when a competent virtual larva (section 2.3.3.2.3) was located at the same depth strata of this given habitat polygon.

2.3.3.2.3 - Biological module

The biological module was programmed to incorporate the life traits reported on the literature for *L. pertusa* and adjusted to the Mediterranean environmental conditions. The 59 release locations used (Table S 2.3.1) coincide with living colonies of *L. pertusa* identified in the study area (Figure 2.3.1). We estimated the most probable spawning season for *L. pertusa* in the Mediterranean Sea since no information for this region is currently available and regional differences were documented. This estimation was inferred from the spawning pattern observed on populations from regions other than the Mediterranean Sea and according to the net primary production record (Figure S 2.3.2). Each simulation was extended for 62 days starting on December 1st of each year and the spawning frequency was set in a daily basis. The same number of virtual larvae (3000 day^{-1}) was released in each location. The number of larvae released in each simulation was defined based on a sensitivity test of habitat polygon reachability. Despite their relevance for the species distribution and persistence, variables such larval mortality and post-settlement processes were not included since no reliable information about these parameters are currently available. We limited the PLD to 25 days, approximately half of the estimated duration for colder areas. We based our estimation on the unified model proposed by O'Connor (2007) for the temperature dependency of larval development in marine metazoans and used the temperature range crossed by the virtual larvae/particles during their simulated trajectories. We programmed the larvae to undertake a vertical migration profile according to the information in the literature (Larsson et al. 2014; Ross et al. 2017a) and assumed varying swimming speeds (up to approximately 60 m day^{-1}; Strömberg and Larsson 2017). Larvae were considered competent from the 13th day of simulation up to the limit of the PLD.

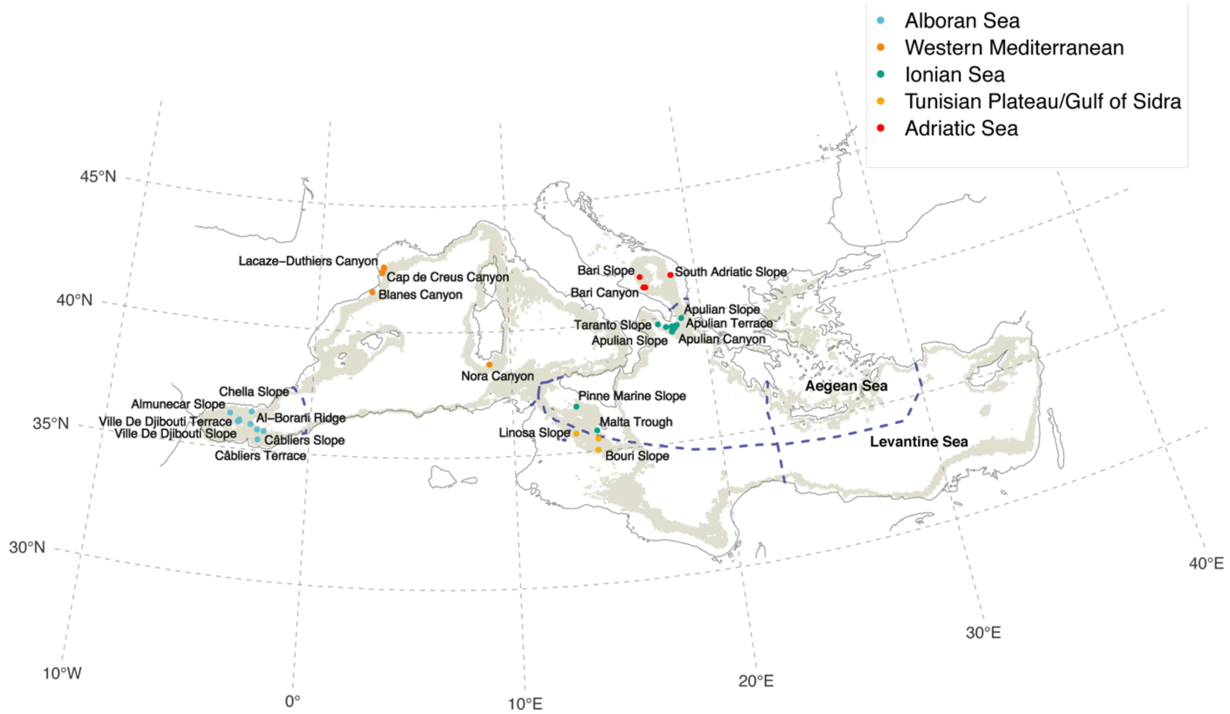

Figure 2.3.1 – Map of the study area with the release location coloured-coded by ecoregion. The areas shaded showed HSI above the threshold of (237, Chapter 2.2). The limits of the ecoregions were defined by the dashed lines.

2.3.3.3 - Network analysis of the L. pertusa seascape

We used a network analysis approach based on graph theory to estimate habitat availability and identify the potential links between known locations of *L. pertusa* living colonies and habitat polygons within the Mediterranean seascape. In order to facilitate the readability of our results, we delimited 1178 geographic areas by intersecting the centroids of the 16270 habitat polygons with the Mediterranean seafloor geomorphic features in the map developed by Harris *et al.* (2014). These areas (hereafter designated as habitat areas) were named after the nearest undersea feature identified in the GEBCO – Gazetteer of undersea feature names (see also Chapter 2.1). Each habitat area was allocated to one of the 7 Mediterranean ecoregions considered and classified based on two attributes: the size (total number of polygons, both habitat and non-habitat) and quality (sum of the HSI of the habitat polygons divided by the total number of polygons). In the spatial graph, each habitat area is represented by a node.

The habitat availability of *L. pertusa* in the Mediterranean Sea was estimated using the Conefor 2.6 (Saura and Torne 2009) for directed networks, a software that quantifies the importance of habitat areas and links for the maintenance of connectivity. This software version was designed for the analysis of asymmetric networks, i.e., a graph in which the probability of dispersal from the area *i* to *j* is different from the probability of dispersal from the area *j* to *i*. We used the "Probability of Connectivity" index (PC; Saura and Pascual-Hortal 2007), that integrates in a single measure the intrapatch connectivity based on the intrinsic characteristics of the habitat area such as quality, and the interpatch connectivity as the quantity of habitat made available by direct connections between the nodes of the network. In our network, direct connections are only established between a release area *i* (area with one or more locations with known living *L. pertusa* colonies) and any other habitat area *j* based on the CMS outputs. Each direct connection was weighted as a probability (number of larvae reaching habitat polygons in area *j*, divided by the total number of larvae released in area *i*).

The overall PC value for the entire seascape has three components with relative contributions that can be expressed as a percentage of the total value (Saura et al. 2014): the *PCintra* corresponding to the intrapatch connectivity; the *PCdirect* that quantifies the connectivity resulting from direct connections among habitat areas; and the *PCstep* which accounts for the interpatch connectivity resulting from "stepping-stone" connections. The importance of each individual habitat area (*dPC*) can be calculated as the change in PC value when that node is removed from the network. The *dPC* can also be partitioned in three components (Saura and Lidón 2010): the *dPCintra* related to the quality of the habitat area; the *dPCflux* resulting from the dispersal flux to and from the habitat area and depending both on its attributes and its topological position in the network; and the *dPCconnector* that evaluates the impact that the loss of the habitat area would have on the network connectivity. Additionally, we used the Area-weighted flux (*dAWF*) index, calculated as the sum of the products of the direct dispersal probability between each pair of habitat areas (p_{ij}) and the attributes of those habitat areas *i* and *j* (Urban and Keitt 2001; Saura and Pascual-Hortal 2007); *dAWF* captures the amount of flux originated through those connections.

2.3.4 - Results

2.3.4.1 - Biophysical modelling output

The density maps of the simulated trajectories show the preferential dispersal pathways for the larvae released from locations with known living *L. pertusa* colonies in the Mediterranean Sea (Figure 2.3.2). These pathways follow the general pattern of the water circulation in the study area with some inter-annual variability of the trajectories direction and distance travelled (Figure 2.3.3). The changes in oceanographic conditions (non-DSWC vs. DSWC years) affected differently the larval transport from different release locations. Larvae released in the Alboran Sea, albeit some may have been exported through the Strait of Gibraltar to the Atlantic Ocean, were mostly retained within the source region or were transported by the Algerian Current travelling along the African coast. Despite variations in the trajectory directions, the linear distances travelled by the larvae were in general shorter during DSWC years when compared to the distances travelled during years without DSWC (Figure 2.3.2 and 2.3.3). In the Western Mediterranean, changes in the oceanographic setting during DSWC years constrained the transport of the larvae and induced shifts in their trajectories especially pronounced in the Gulf of Lion and Catalan margin canyons (Figure 2.3.3b). Larvae released in the Alboran Sea and in the Gulf of Lion during non-DSWC years, are among the ones that travelled greatest distances (Figure 2.3.3a and b). In general, the larvae released in colonies located in the TP/GoS and Ionian Sea showed more erratic trajectories when compared to the other ecoregions and were transported for shorter distances from the source during DSWC years (Figure 2.3.3c and d). The exceptions were the Taranto slope, with larvae traveling in opposite directions in different oceanographic scenarios, and the Malta Trough, where the trajectories of the larvae were apparently unaffected by the oceanographic conditions (Figure 2.3.3d). For the colonies located in the Adriatic Sea (Figure 2.3.3e), the dispersal pattern was identical for the six spawning seasons regarding the direction of trajectories and distances travelled by the larvae, which were shorter in DSWC years than in non-DSWC years. No larvae released from colonies included in the simulations entered the Aegean and the Levantine ecoregions, the easternmost regions of the Mediterranean Sea.

The simulation of the six spawning events resulted in 65 844 000 larval trajectories, from which 41.5% successfully reached a habitat polygon (note that mortality rates were not accounted for). The number of simulated trajectories that could lead larvae to reach a habitat polygon varied between ecoregions (Table 2.3.1): trajectories originated in the TP/GoS and in the Western Mediterranean were more likely to reach a habitat polygon when compared to other ecoregions and the chances of success were also greater during non-DSWC years than during DSWC years, except for the Ionian and Adriatic seas.

Noteworthy this exception resulted in an overall increase of the number of larvae reaching habitat polygons during DSWC years (44.8%) compared to non-DSWC years (38.3%).

Table 2.3.1 - Percentage of simulated trajectories (larvae mortality not accounted for) that coincided with a habitat polygon within the estimated competence period of a *L. pertusa* larva. Results are grouped by ecoregion and oceanographic scenario.

Ecoregion of release	**% of larvae reaching a habitat area**	
	non-DSWC years	***DSWC years***
Alboran Sea	40.0	35.1
Western Mediterranean	54.5	51.8
TP/GoS	61.2	54.8
Ionian Sea	17.8	40.6
Adriatic Sea	41.1	46.9
Whole modelling area	38.3	44.8

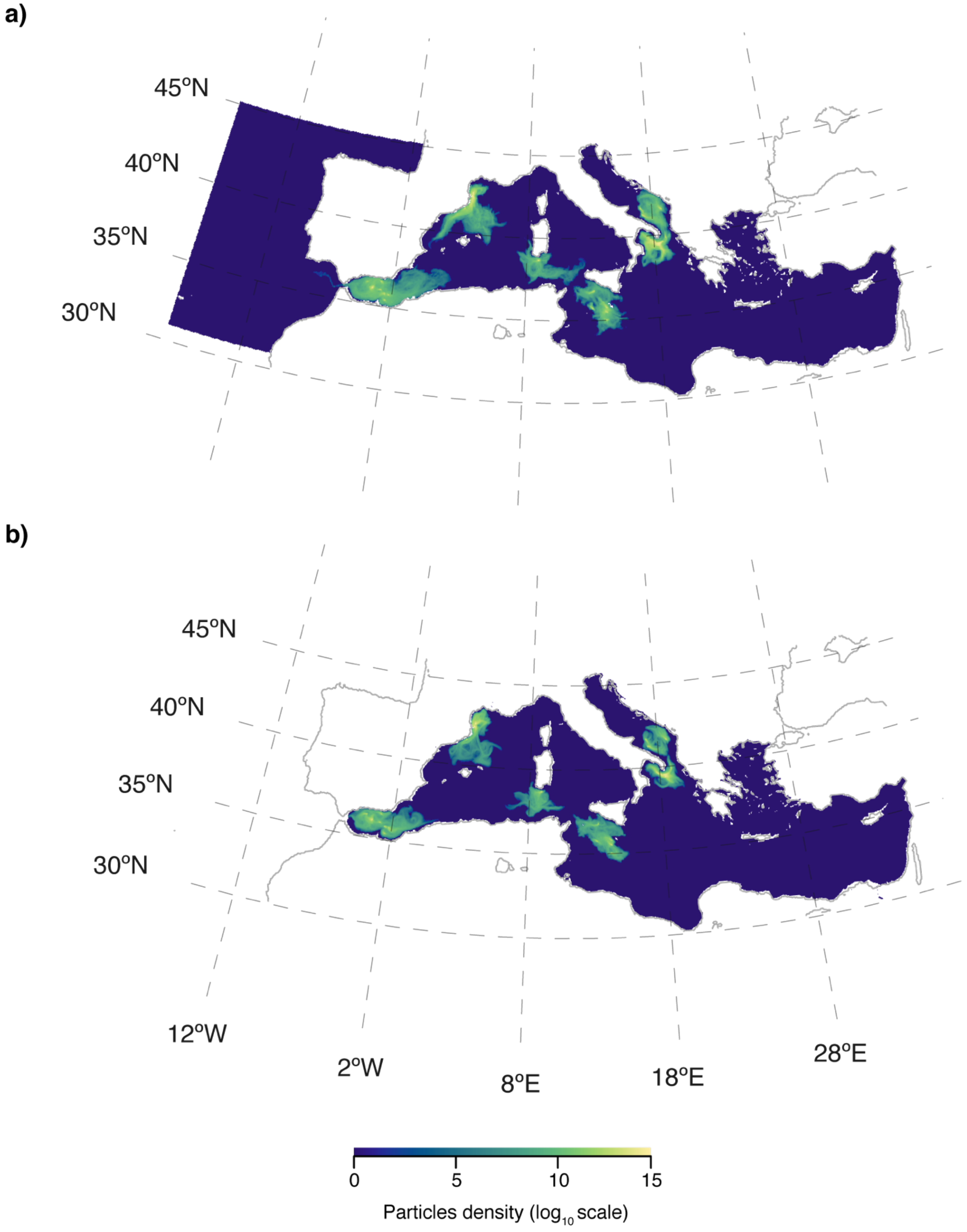

Figure 2.3.2 - Map of the preferential dispersal pathways of larvae in non-DSWC years (a) and years with DSWC events (b). Trajectories density was calculated as the total number of trajectories in three years passing through each cell on a 1/16° grid (ca. 6-7 km).

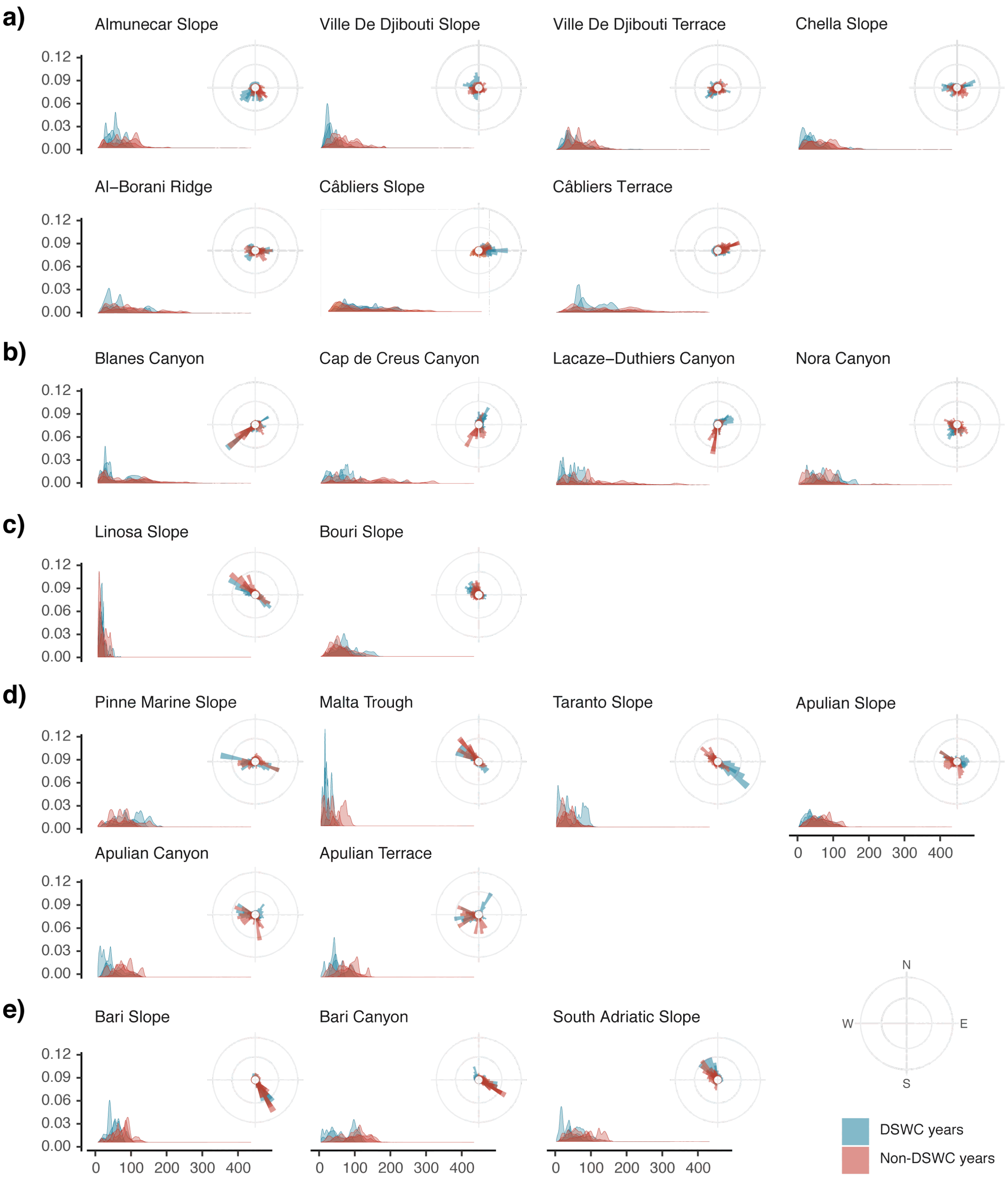

Figure 2.3.3 - Estimated dispersal kernels for the travelled linear distance (density plots) and direction of trajectories (angular histograms) for particles released in 22 release areas in 3 years for each oceanographic scenario (typical oceanographic conditions coloured in red and years with DSWC events in blue, darker shades indicate overlap of two or more years). The xx-axis of the density plots are in kilometres and the yy-axis refers to the density of the estimated dispersal kernel. The circles on the angular histograms correspond to 0, 25 and 50% of larval density. a – Alboran Sea, b – Western Mediterranean, c – Tunisian Plateau/Gulf of Sidra, d – Ionian Sea, and e – Adriatic Sea.

2.3.4.2 - Connectivity between ecoregions and habitat areas

The probability of a larva reaching a habitat polygon in an ecoregion other than its source was in general low, but slightly higher during non-DSWC years (Figure 2.3.4). Some connections between ecoregions occurred in both oceanographic settings: Alboran Sea - Western Mediterranean, TP/GoS - Ionian Sea, Ionian Sea - TP/GoS, Ionian Sea - Adriatic Sea, and Adriatic Sea - Ionian Sea. On the other hand, the connection from the Western Mediterranean to habitat polygons in the Ionian Sea and the TP/GoS was only observed during non-DSWC years, while larvae released in the Ionian Sea were only able to reach habitat polygons in the Western Mediterranean during DSWC years.

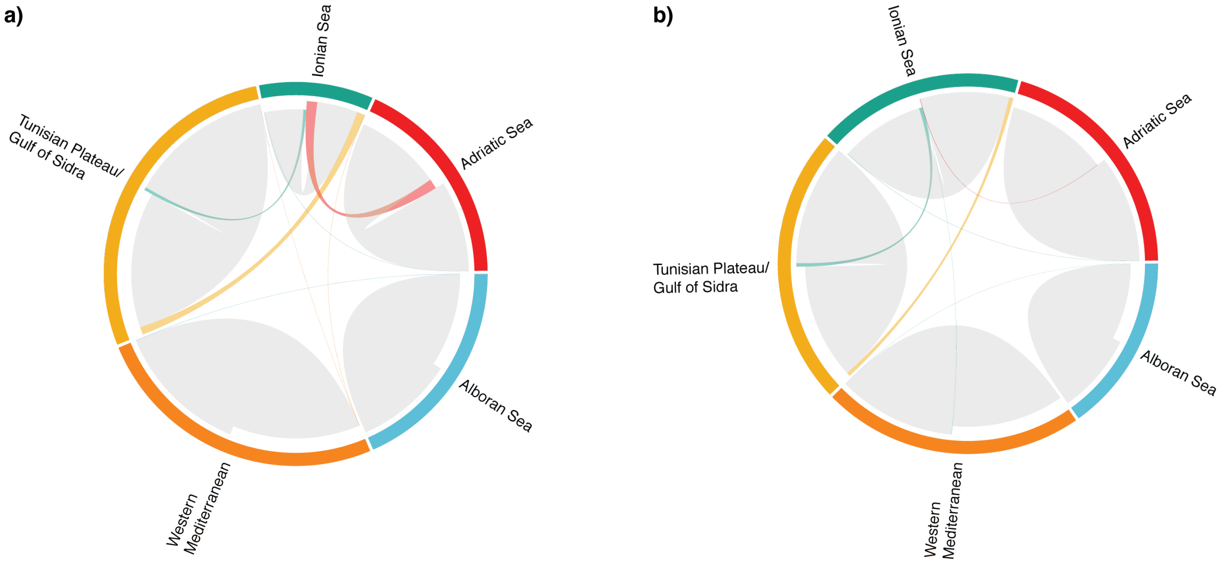

Figure 2.3.4 - Chord-diagram showing the geographical partition of larvae that reached habitat polygons. Each arc segment is colour coded by ecoregion. The large gap between the arc segment and the chord indicates the larvae released while the shorter gap indicates the larvae received. The chords that link different ecoregions are colour-coded by release ecoregion while the grey chords represent the larvae released and received within the same ecoregion. The thickness of the chords encodes the percentage of larvae that successfully reached a habitat polygon within an ecoregion during: a) three non-DSWC years and, b) three DSWC years.

When habitat areas are grouped by seascape feature typology, the continental slopes represent more than 60% of the total area (Table 2.3.2), followed by submarine canyons (10.41%), the abyss (7.64%) and continental shelf (6.89%) with slopes and canyons showing also the highest percentages of habitat polygons. Over 90% of the habitat polygons reached by larvae during our simulations in both oceanographic scenarios were concentrated in only four typologies: most were located again in slopes followed by shelves, terraces, and canyons. However, when the suitability of the habitat areas is considered, submarine canyons are the most relevant geomorphological category in the Mediterranean seascape, followed by continental shelf and slope, all with HSI mean values of habitat polygons higher than 400.

Table 2.3.2 – Percentage of habitat area, habitat polygons and habitat polygons reached by larvae grouped by geomorphological category.

Geomorphologic category	Area of the seascape including habitat & non-habitat areas (%)	Area of habitat polygons (%)	Habitat polygons reached by larvae (%)	
			non-DSWC	DSWC
Slope	61.36	67.29	66.56	67.42
Shelf	6.89	2.63	11.17	9.71
Terrace	3.84	4.32	8.35	8.95
Canyon	10.41	11.05	6.63	6.49
Abyss	7.64	6.18	2.13	2.98
Shelf Valley	0.98	0.76	2.03	0.95
Trough	4.46	4.29	1.86	2.41
Ridge	2.38	2.38	1.27	1.09
Fan	0.28	0.10	-	-
Guyot	0.20	0.17	-	-
Rise	1.08	0.56	-	-
Seamount	0.47	0.26	-	-
Sill	0.01	0.01	-	-
Trench	0.01	>0.01	-	-
Total number of polygons	949494	568232	2910	2112

Regarding the percentage of larvae (Figure 2.3.5), the vast majority reached habitat polygons on continental slopes (54.37%) and shelves (16.90%) during Non-DSWC years while, in DSWC years, the slopes remained as the most important type of feature (54.21%) but the terraces (14.85%) exceeded the relative importance of the continental shelves (11.24%). The importance of submarine canyons also varied between oceanographic scenarios, gaining more relevance during DSWC years. Submarine canyons are especially important in the Western Mediterranean ecoregion where they are the top seascape feature reached by larvae during DSWC years (Figure 2.3.5b). It also noticeable that canyons act mostly as larval suppliers to the shelves and slopes, while shelves appear to act as sinks (no known living colonies reported in the Mediterranean Sea).

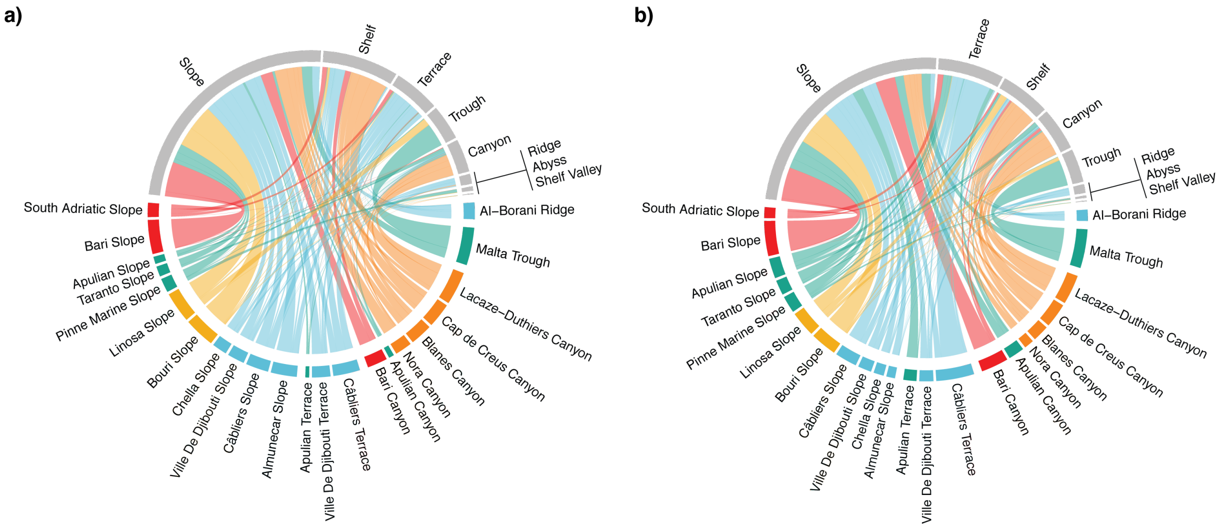

Figure 2.3.5 - Chord-diagrams showing the relative distribution of larvae that successfully reached a habitat polygon by geomorphological categories during typical oceanographic conditions in the Mediterranean Sea (a) and during years with DSWC events (b). Chords and release habitat areas are colour-coded by ecoregion.

The percentage of larvae reaching habitat polygons in non-release habitat areas (Figure 2.3.6) was greater during non-DSWC years (68.1%) than during DSWC years (42.8%). The percentage of larvae that reached a habitat polygon in a different release habitat area varied from <1% to 0% (non-DSWC and DSWC years, respectively) in the Nora Canyon to 25.01% in the Câbliers Terrace (Non-DSWC) and 26.64% in the Apulian Slope during DSWC years. The percentage of larvae that reached a habitat polygon in a release habitat area located in a different ecoregion was slightly higher (3.63%) during non-DSWC years than during DSWC years (0.29%) when the isolation of different ecoregions is most evident (Figure 2.3.6). Overall, this trend was also observed for connections between release habitat areas within the same ecoregion except for the Ionian Sea, where the larval exchange between release habitat areas was more common and intense during DSWC years.

At least a part of the larvae that reached a habitat polygon remained in the same release habitat. Overall, these numbers were higher during DSWC years than during non-DSWC years (19.4% and 29.0% in non-DSWC and DSWC years, respectively). The highest proportions of retention were observed in the Bari Slope, Linosa Slope and Malta Trough during non-DSWC years (92.0%, 67.8% and 59.7%, respectively), and Bari Slope, Malta Trough and Câbliers Terrace during DSWC year (97.8%, 62.1% and 54.6%, respectively). In contrast, no larvae were retained in the Nora Canyon during DSWC years.

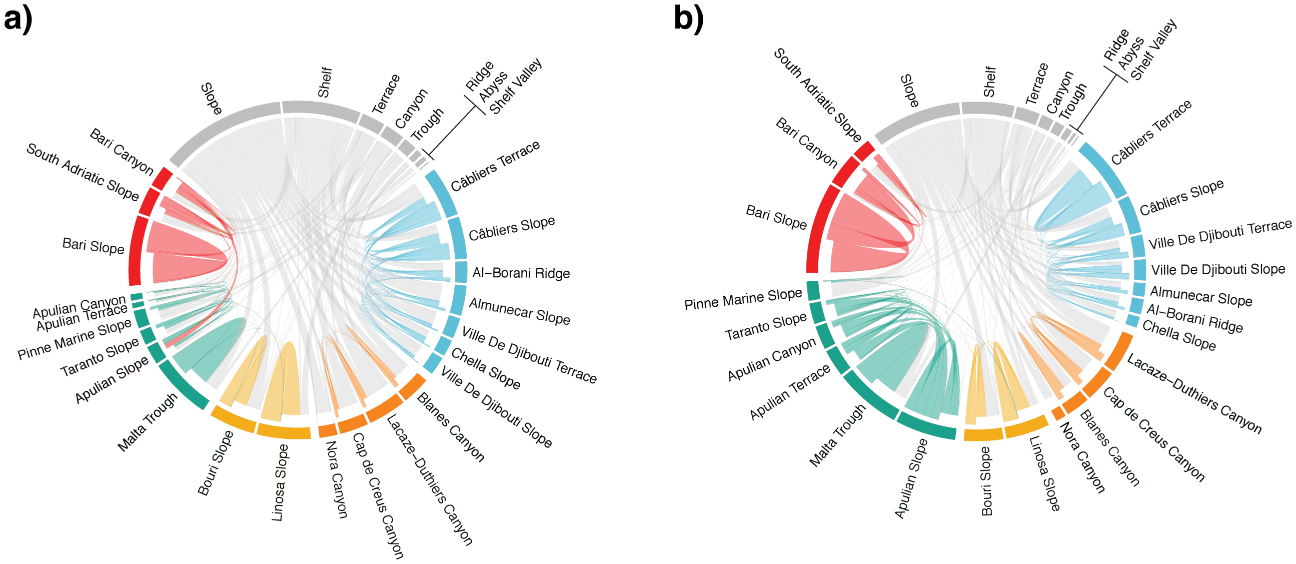

Figure 2.3.6 – Chord-diagrams showing the relative distribution of larvae among release habitat areas, including the number of larvae retained in the same habitat area, during non-DSWC years (a) and years DSWC events (b). Chords are colour-coded by ecoregion for the larvae reaching any release habitat area. Connection to other habitat areas are coloured in grey.

The prevalence of the connections between habitat areas, ecoregions and oceanographic scenarios is shown in the matrices in Figure 2.3.7. Within each ecoregion, a core of habitat areas was regularly reached regardless of the oceanographic setting, while others were only reached in one of the oceanographic scenarios. Overall, the number of connected habitat areas was higher and more stable during non-DSWC years. The isolation between the Western and Central-Eastern basins is evident in both scenarios, with very rare exceptions of connections established between the Western Mediterranean ecoregion and both TP/GoS and the Ionian Sea ecoregions. The number and frequency of habitat areas reached during non-DSWC years is higher than during DSWC years. However, when both scenarios are combined the total number habitat areas reached is higher because different areas are reached during non-DSWC and DSWC years.

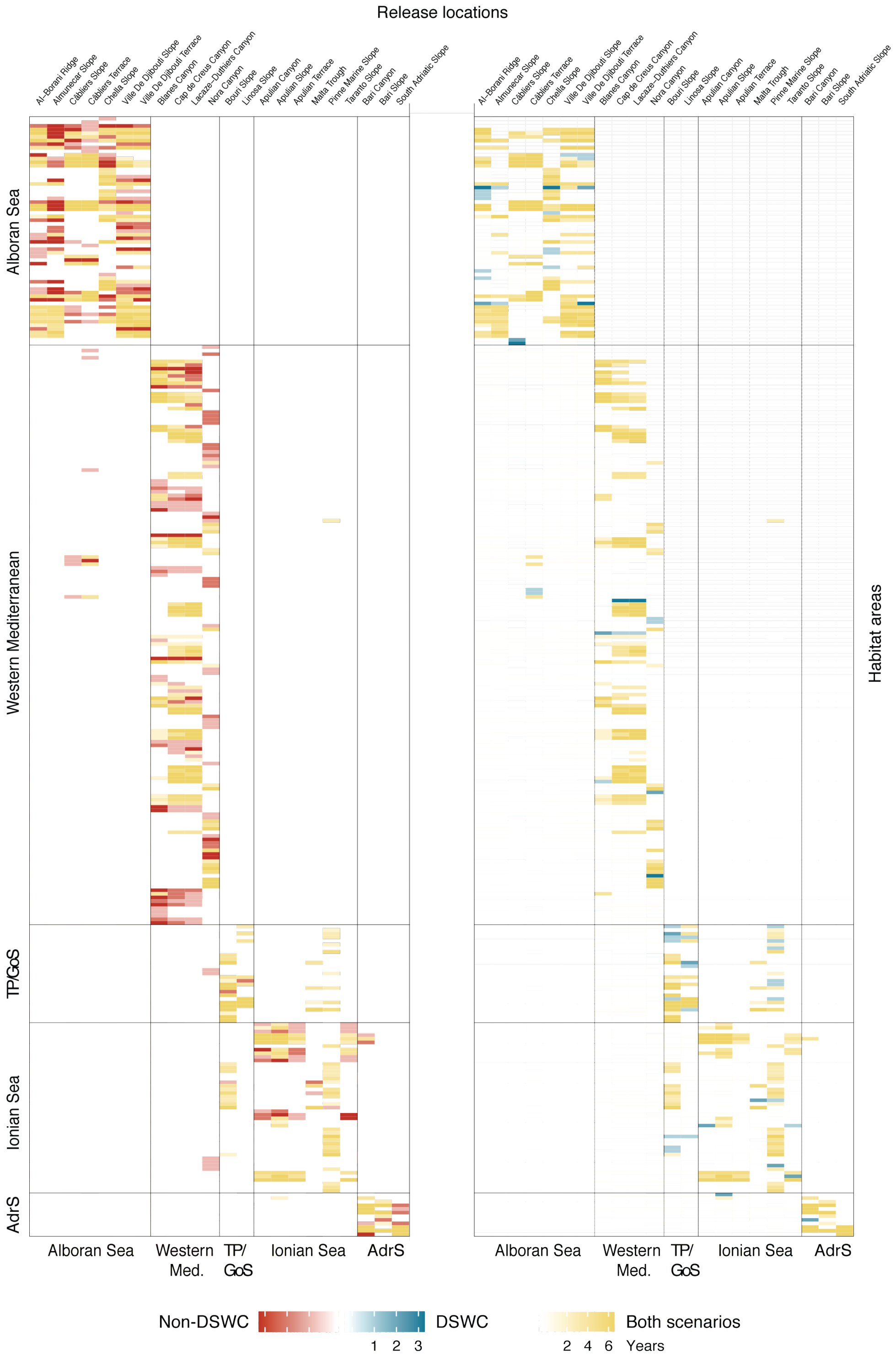

Figure 2.3.7 – The prevalence of the connections between habitat areas, ecoregions and oceanographic scenarios. Within each ecoregion, the habitat areas reached were ordered by latitude. The colour gradient encodes the number of years with larvae reaching habitat polygons in each area. Cells classified as “Both scenarios” received larvae at least in one non-DSWC and one DSWC simulation years. TP/GoS – Tunisian Plateau/Gulf of Sidra; AdrS – Adriatic Sea; DSWC – Dense-shelf water cascading.

2.3.4.3 - Network analysis of the L. pertusa seascape

The network analysis of *L. pertusa* seascape connectivity (*PC*) shows that more than 99% of the habitat availability during non-DSWC years is explained by intrapatch connectivity (*PCintra*) and only 0.86% by interpatch connectivity (*PCdirect*). During DSWC years, the importance of direct connections for the seascape connectivity increases to 0.93%. In both cases, less than 0.01% of the habitat availability resulted from intermediated/stepping-stone connections (*PCstep*).

The prioritizing of individual habitat areas (*dPC*) also varied among ecoregions and between oceanographic conditions. Most of the habitat areas accounted with very low contributions for the seascape connectivity, especially in the Aegean and the Levantine Seas (Figure 2.3.8 and Table 2.3.3). However, a small set of 55 habitat areas in a total of 1178 (the top 5%) contributed with ca. 20% to the bulk of Mediterranean seascape connectivity. These high ranked habitat areas were located mainly in the Western Mediterranean (47 in non-DSWC and 45 in DSWC years) while a much smaller number was located in other ecoregions: the Ionian Sea (3 and 5; e.g., Pantellaria Abyss, Linosa Abyss, Apulian Slope), the Adriatic Sea (Bari Slope, Bari Canyon and South Adriatic Slope), and the Alboran Sea (Tofiño Ridge) and TP/GoS (Bouri Trough), darker areas in Figure 2.3.8. Most of the top 10 priority habitat areas (Table 2.3.3) correspond to locations currently with no records of living colonies, and only 13 release habitat areas are also listed. The release habitat areas spotlighted were common to both oceanographic scenarios, except for the Apulian Canyon and the Almunecar Slope, ranked only in non-DSWC and DSWC years, respectively.

The partition of the *dPC* shows that the importance of each habitat area resulted mainly from the *dPCintra* component. In fact, the importance of some of the top 10 ranked habitat areas in each ecoregion consisted only in this component of *dPC,* owing to their remarkable quality (habitat suitability and extension) albeit the absence of larval flux from the release habitat areas. High interpatch connectivity indicates a high potential to harbour unknown records of *L. pertusa*: the Alborán Ridge (Alboran Sea), Rec del Basos Slope (Western Mediterranean), Malta Slope (TP/GoS), Hurd Through (Ionian Sea), and Bari Shelf (Adriatic Sea). Not surprisingly, in habitat areas that include release locations, the importance of the d*PCflux* component reached the highest values: it varied from 13.00% on the South Adriatic Slope to 44.28% on the Apulian Slope during non-DSWC years, and from 13.64% of the Linosa Slope to 32.03% in the Câbliers Slope during DSWC years. The *dPCconnector* component related to stepping-stone connections was irrelevant (always lower than 0.003%). The highest values of *dPCflux* were also mirrored in the *dAWF* values.

Table 2.3.3 – Top-10 habitat areas in each ecoregion ranked by *dPC* value (ranging 0–1) calculated by the Conefor analysis. Values lower than 0.001 (●) or equal to zero (–) were omitted. *dAWF* – Area-Weighted Quality Flux, *dPC* – Probability of Connectivity of each individual patch. Areas including release locations are highlighted in bold.

	Non-DSWC years						**DSWC years**					
Ecoregion	**Habitat area**	**dPC**	**dPC Components**			**dAWF**	**Habitat area**	**dPC**	**dPC Components**			**dAWF**
			intra	**flux**	**connector**				**intra**	**flux**	**connector**	
Alboran Sea	Tofiño Ridge	0.356	0.347	0.009	–	0.938	Tofiño Ridge	0.350	0.347	0.003	–	0.314
	Alborán Ridge	0.272	0.256	0.016	–	1.678	Alborán Ridge	0.274	0.256	0.017	–	2.027
	Xauen Canyon	0.264	0.264	●	–	0.029	Xauen Canyon	0.265	0.264	●	–	0.083
	Câbliers Slope	**0.250**	**0.180**	**0.070**	●	**7.456**	**Câbliers Slope**	**0.265**	**0.180**	**0.085**	●	**9.853**
	Avenzoar Slope	0.245	0.241	0.004	–	0.472	**Almunecar Slope**	**0.256**	**0.176**	**0.080**	●	**9.193**
	Tofiño Canyon	0.244	0.239	0.006	–	0.609	Avenzoar Slope	0.247	0.241	0.006	–	0.727
	Ceuta Canyon	0.242	0.242	–	–	–	Ceuta Canyon	0.243	0.242	●	–	0.057
	Ville De Djibouti Terrace	**0.235**	**0.175**	**0.061**	●	**6.471**	Tofiño Canyon	0.239	0.239	●	–	●
	Abubacer Ridge	0.232	0.232	–	–	–	**Ville De Djibouti Terrace**	**0.235**	**0.175**	**0.060**	●	**6.952**
	Abubacer Slope	0.208	0.208	–	–	–	Abubacer Ridge	0.232	0.232	–	–	–
Western Mediterranean	Rec del Basos Slope	0.493	0.476	0.017	–	1.846	Morras Canyon	0.498	0.492	0.006	–	0.679
	Morràs Canyon	0.492	0.492	●	–	0.061	Berenguera Slope	0.490	0.488	0.003	–	0.308
	Berenguera Slope	0.487	0.487	●	–	0.015	Rec del Basos Slope	0.483	0.476	0.007	–	0.831
	Besò`s Canyon	0.475	0.473	0.002	–	0.183	Besos Canyon	0.475	0.474	●	–	0.108
	Tortuga Canyon	0.459	0.459	–	–	–	Tortuga Canyon	0.461	0.459	0.002	–	0.235
	San Feliu Terrace	0.454	0.454	●	–	0.023	San Feliu Terrace	0.455	0.454	0.001	–	0.135
	Narbone Canyon	0.451	0.434	0.017	–	1.863	Narbone Canyon	0.438	0.434	0.004	–	0.446
	Cap de Creus Canyon	**0.445**	**0.343**	**0.101**	●	**10.844**	**Cap de Creus Canyon**	**0.433**	**0.343**	**0.089**	●	**10.396**
	Tortosa Canyon	0.414	0.414	–	–	–	Morras Slope	0.425	0.407	0.018	–	2.102
	Morras Slope	0.413	0.406	0.007	–	0.731	Tortosa Canyon	0.414	0.414	●	–	0.071

	Non-DSWC years						DSWC years					
Ecoregion	Habitat area	dPC	dPC Components			dAWF	Habitat area	dPC	dPC Components			dAWF
			intra	flux	connector				intra	flux	connector	
Tunisian Plateau/ Gulf of Sidra	Bouri Trough	0.335	0.334	0.001	–	0.112	Bouri Trough	0.334	0.334	–	–	–
	Alfil Trough	0.273	0.265	0.008	–	0.817	Alfil Trough	0.269	0.265	0.004	–	0.507
	Alfil Abyss	0.246	0.246	●	–	0.023	Alfil Abyss	0.247	0.246	●	–	0.090
	Linosa Slope	**0.240**	**0.196**	**0.044**	**●**	**4.465**	**Linosa Slope**	**0.227**	**0.196**	**0.031**	**●**	**3.607**
	Bouri Slope	**0.224**	**0.164**	**0.058**	**0.002**	**6.145**	**Bouri Slope**	**0.205**	**0.164**	**0.041**	**●**	**4.719**
	Misurata Canyon	0.174	0.174	–	–	–	Misurata Canyon	0.175	0.175	–	–	–
	Malta Slope	0.167	0.123	0.044	–	4.643	Hurd Slope	0.165	0.153	0.012	–	1.440
	Hurd Slope	0.159	0.153	0.006	–	0.629	Malta Slope	0.164	0.123	0.041	–	4.749
	Linosa Trough	0.138	0.131	0.007	–	0.778	Linosa Trough	0.154	0.131	0.023	–	2.633
	Alfil Terrace	0.137	0.136	●	–	0.096	Alfil Terrace	0.136	0.136	●	–	●
Ionian Sea	Pantelleria Abyss	0.430	0.430	–	–	–	Pantelleria Abyss	0.430	0.430	–	–	–
	Linosa Abyss	0.361	0.361	–	–	–	Linosa Abyss	0.361	0.361	–	–	–
	Apulian Slope	**0.312**	**0.171**	**0.138**	**0.003**	**14.823**	Bovalino Canyon	0.306	0.306	–	–	–
	Bovalino Canyon	0.306	0.306	–	–	–	Corigliano Terrace	0.244	0.240	0.005	–	0.501
	Apulian Terrace	**0.295**	**0.199**	**0.097**	**–**	**10.046**	Hurd Trough	0.233	0.219	0.013	–	1.531
	Apulian Canyon	**0.251**	**0.177**	**0.074**	**–**	**7.627**	**Apulian Slope**	**0.226**	**0.171**	**0.052**	**0.003**	**6.061**
	Corigliano Terrace	0.240	0.240	●	–	0.001	Talbot Canyon	0.224	0.224	●	–	0.002
	Hurd Trough	0.237	0.219	0.017	–	1.862	Cumecs Canyon	0.222	0.222	–	–	–
	Talbot Canyon	0.224	0.224	–	–	–	**Apulian Terrace**	**0.214**	**0.199**	**0.015**	**–**	**1.759**
	Cumecs Canyon	0.222	0.222	–	–	–	Caulonia Slope	0.211	0.211	–	–	–

	Non-DSWC years						DSWC years					
Ecoregion	Habitat area	dPC	dPC Components			dAWF	Habitat area	dPC	dPC Components			dAWF
			intra	flux	connector				intra	flux	connector	
Adriatic Sea	**Bari Canyon**	**0.479**	**0.330**	**0.149**	●	**15.765**	**Bari Canyon**	**0.418**	**0.331**	**0.087**	●	**9.835**
	Bari Slope	**0.417**	**0.296**	**0.120**	●	**12.847**	**South Adriatic Slope**	**0.347**	**0.290**	**0.057**	●	**6.650**
	South Adriatic Slope	**0.334**	**0.289**	**0.043**	**0.001**	**4.658**	**Bari Slope**	**0.328**	**0.297**	**0.032**	●	**3.611**
	South Adriatic Canyon	0.208	0.208	●	–	0.010	South Adriatic Canyon	0.209	0.208	●	–	0.041
	Bari Terrace	0.145	0.143	0.001	–	0.108	Bari Terrace	0.145	0.143	0.002	–	0.223
	Apulian Abyss	0.127	0.127	●	–	0.003	Apulian Abyss	0.127	0.127	–	–	–
	Bari Abyss	0.100	0.099	●	–	0.022	Bari Abyss	0.099	0.099	●	–	●
	South Adriatic Abyss	0.081	0.081	●	–	0.038	South Adriatic Abyss	0.081	0.081	●	–	0.024
	South Adriatic Terrace	0.049	0.035	0.014	–	1.374	South Adriatic Terrace	0.043	0.035	0.009	–	0.962
	Bari Shelf	0.018	0.016	0.002	–	0.261	Bari Shelf	0.020	0.016	0.004	–	0.439
Aegean Sea	Amfitríti Canyon	0.098	0.098	–	–	–	Amfitríti Canyon	0.098	0.098	–	–	–
	Ira Trough	0.089	0.089	–	–	–	Ira Trough	0.089	0.089	–	–	–
	Brooker Trough	0.073	0.073	–	–	–	Brooker Trough	0.073	0.073	–	–	–
	Mansell Trough	0.059	0.059	–	–	–	Mansell Trough	0.059	0.059	–	–	–
	Thermaicos Canyon	0.055	0.055	–	–	–	Thermaicos Canyon	0.055	0.055	–	–	–
	Truva Trough	0.051	0.051	–	–	–	Truva Trough	0.052	0.052	–	–	–
	Venus Canyon	0.051	0.051	–	–	–	Venus Canyon	0.051	0.051	–	–	–
	Venus Trough	0.048	0.048	–	–	–	Venus Trough	0.048	0.048	–	–	–
	Amfitríti Trough	0.042	0.042	–	–	–	Amfitríti Trough	0.042	0.042	–	–	–
	Truva Canyon	0.040	0.040	–	–	–	Truva Canyon	0.040	0.040	–	–	–

	Non-DSWC years						DSWC years					
Ecoregion	Habitat area	dPC	dPC Components			dAWF	Habitat area	dPC	dPC Components			dAWF
			intra	flux	connector				intra	flux	connector	
Levantine Sea	Nile Canyon	0.090	0.090	–	–	–	Nile Canyon	0.090	0.090	–	–	–
	Cyprus Canyon	0.083	0.083	–	–	–	Cyprus Canyon	0.083	0.083	–	–	–
	Ashdod Canyon	0.080	0.080	–	–	–	Ashdod Canyon	0.080	0.080	–	–	–
	Nile Slope	0.078	0.078	–	–	–	Nile Slope	0.079	0.079	–	–	–
	Ashdod Slope	0.068	0.068	–	–	–	Ashdod Slope	0.068	0.068	–	–	–
	Hecataeus Ridge	0.067	0.067	–	–	–	Hecataeus Ridge	0.067	0.067	–	–	–
	Cyprus Trough	0.064	0.064	–	–	–	Cyprus Trough	0.064	0.064	–	–	–
	Qishon Slope	0.061	0.061	–	–	–	Qishon Slope	0.061	0.061	–	–	–
	Latakia Trough	0.059	0.059	–	–	–	Latakia Trough	0.059	0.059	–	–	–
	Afiq Slope	0.054	0.054	–	–	–	Afiq Slope	0.054	0.054	–	–	–

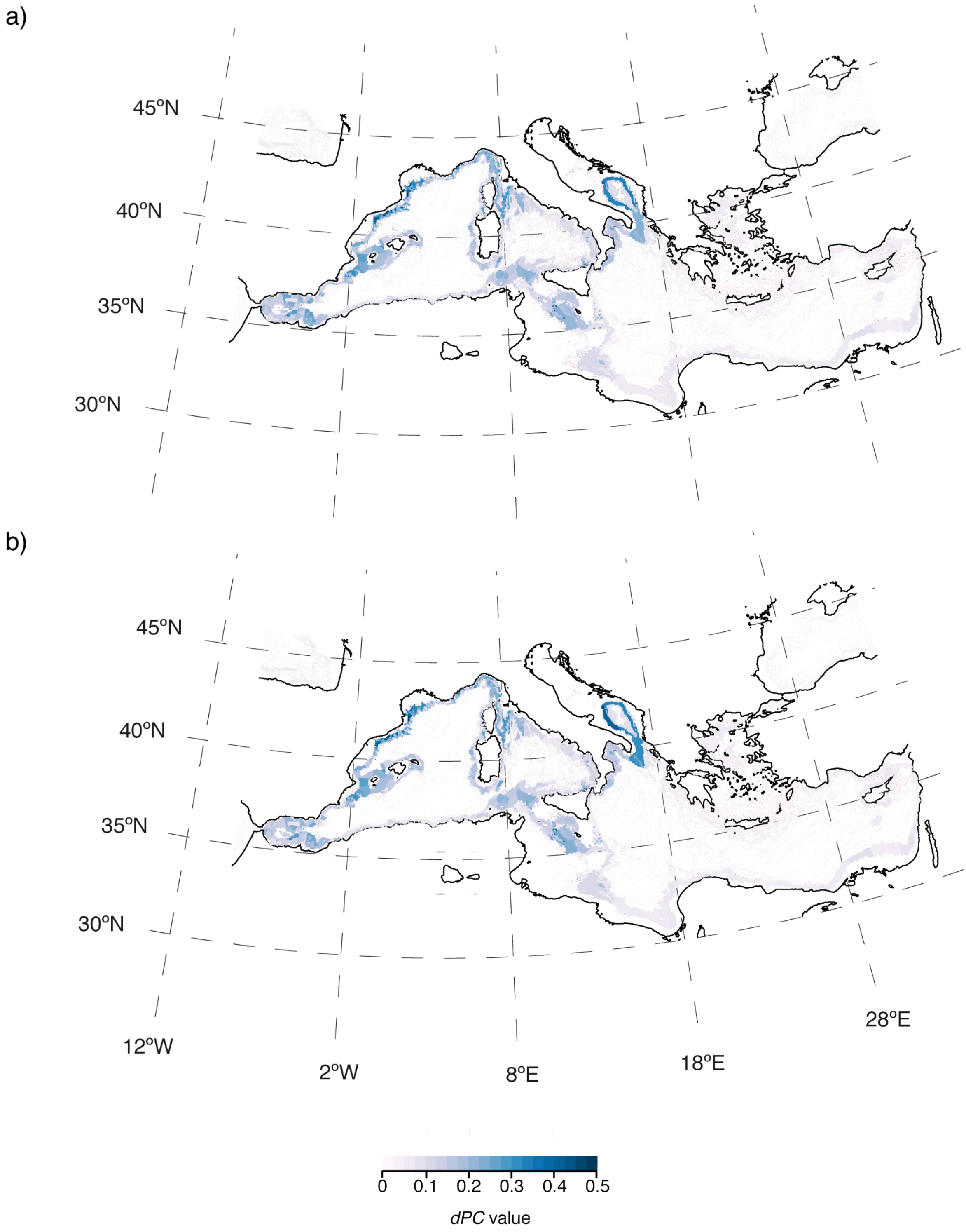

Figure 2.3.8 – Prioritisation of *L. pertusa* habitat areas in the Mediterranean seascape according of the *dPC* values in non-DSWC (a) and DSWC years (b). Darker colour indicates the areas with the highest conservation value for *L. pertusa*.

2.3.5 - Discussion

Connectivity is known to be affected by the variability of oceanographic conditions, seascape spatial arrangement and habitat patch attributes (e.g., Treml et al. 2008; Engelhard et al. 2016; Weeks 2017). Knowledge on the different aspects of ecosystem connectivity is crucial for marine conservation and it is evermore required for supporting conservation policies and the design of spatial management strategies (Morrison et al. 2015; Hidalgo et al. 2017). To our best knowledge, this paper is the first assessing the seascape connectivity and habitat availability for a deep-sea species using a Lagrangian framework and network analysis. The relative coarse resolution of the oceanographic model limits the representation of fine scale oceanographic mechanisms known to influence the larval transport and retention (e.g., the estimates of larvae reaching continental shelves may be affected by the unresolved the circulation in these areas). However, this option was required to estimate the seascape connectivity for the model species in the Mediterranean Sea at the whole-basin scale. As in all modelling approaches, our results can only be strengthened by empirical validation, for instance, by field surveys and complementary methodologies such as genetic characterization. The putative detection of undiscovered colonies of *L. pertusa* in the Mediterranean Sea will allow a better knowledge of the species distribution and improved estimations of seascape connectivity

As for most deep-sea species, the life cycle of *L. pertusa,* our model organism, has not yet been fully described. This required the inference of the most probable period for larval spawning and PLD of *L. pertusa* in the Mediterranean Sea (Table S 2.3.1) based on the best scientific knowledge available. We assumed that the spawning season for the Mediterranean populations precedes the months with higher primary productivity at the surface waters because the increasing levels of food availability in the water column, and presumably reaching the seafloor, have been pointed as factors that maximize the chances of survival of larvae and new recruits of *L. pertusa* (Waller and Tyler 2005; Brooke and Järnegren 2013). The PLD was fixed based on the variation in seawater temperature during the larval vertical migration, a condition that may significantly affect the metabolic rate of larvae (Hilário et al. 2015). This hypothesis is supported by laboratory observations that reported an acceleration of the embryonic development rate of *L. pertusa* larvae when exposed to higher seawater temperatures (Strömberg and Larsson 2017). Both spawning timing and PLD are known to affect the scale of dispersal and therefore connectivity (Selkoe and Toonen 2011; Donahue et al. 2015) and consequently, the estimated dispersal kernels obtained in our simulations were considerably smaller than the ones estimated for the NE Atlantic by Ross et al. (2017a) who used a similar vertical migration profile for larvae but a longer PLD. Other important life-history traits such as larval mortality were not included similarly to other studies (e.g., Fox et al. 2016; Ross et al. 2017a). The integration of mortality would have decreased the total number of larvae able to reach a habitat polygon within their competence period. However, the main pathways for dispersal would have remained similar.

The degree of larval retention provides a useful index of how much the populations of *L. pertusa* in the Mediterranean Sea are linked or isolated. This mechanism favours auto-recruitment and complements larval exchange to ensure population persistence (Jones et al. 2009). Considering the vertical swimming behaviour described for the larvae of *L. pertusa,* the dispersal potential is considered high (Strömberg and Larsson 2017) and the probabilities of larvae settling in the same area of the source reef are virtually low (Larsson et al. 2014). In the Mediterranean Sea, this assumption seems to be not applicable at the habitat area scale of our simulations as we observed an important number of larvae being retained within the same habitat area of the source populations. The approach used to assess connectivity may partly explain this result since we defined habitat areas with a considerable extent (e.g., Bari Slope – 6848 km^2, Linosa Slope – 3904 km^2, Malta Trough – 2432 km^2). The extension of some habitat areas in conjunction with the interactions of local hydrodynamics, geomorphology and the shorter PLD of *L. pertusa* in the Mediterranean Sea, increase the chances of larvae to remain within their release habitat areas. Nevertheless, most of the larvae were transferred to non-native habitat areas and most frequently during non-DSWC to habitat areas without reported living colonies.

At the ecoregion scale, the exchange of larvae was weak. The patterns of connectivity among habitat areas and the preferential dispersal pathways matched roughly the limits of the ecoregions defined by Spalding et al. (2007), emphasizing the prevalence of oceanographic (e.g., currents) and topographic features (e.g., Strait of Sicily) as the main drivers explaining larval dispersal in the Mediterranean Sea. The most glaring example is the absence of larvae reaching the most eastern sections of the Mediterranean Sea. This result may contribute to explain the absence of reported living colonies of *L. pertusa* in these low environmental suitability areas of the seascape (Chapter 2.2). Although the presence of subfossils of *L. pertusa* in these ecoregions suggests the species presence in the recent past (Taviani et al. 2017), the lack of new recruits may have contributed to the populations demise. Considering the high susceptibility of the Mediterranean Sea to climate change (Danovaro 2018), this scenario can be extended to other ecoregions and accentuate the isolation of *L. pertusa* populations. Not only the water temperature increase has important implications on shortening the larval development (Strömberg and Larsson 2017) of *L. pertusa* but also paleoclimate studies showed that increases in water temperature during past geologic periods coincided with CWC declining in the Mediterranean Sea (Delibrias and Taviani 1984; Wienberg et al. 2009).

The intensification and higher frequency of climate-driven events such as DSWC may also affect the distribution of *L. pertusa* by reducing the potential dispersal of larvae and the habitat availability for this species in the Mediterranean seascape. The shifts observed in the larval trajectories during DSWC years may enhance the demographic stochasticity and expand the potential for *L. pertusa* to disperse in the present-day Mediterranean seascape. However, the constraints to larval dispersal may be stronger during DSWC events. Our results indicate a considerable decrease in the linear distance travelled and an overall reduction in the extension of habitat areas reached by larvae, leading to an increase in the spatial isolation both within and between ecoregions. These results highlight the importance of conservation efforts of this VME and associated fauna in the study area.

In the Mediterranean Sea, the *L. pertusa* seascape connectivity consists largely on intrapatch (quality of the habitat areas) rather than interpatch connectivity (probability of connections between habitat areas). Areas with potential to harbour unknown colonies of *L. pertusa* were identified, however the establishment of colonies at a given location will depend on post-settlement processes not considered in this study and also on the level of anthropogenic impacts that they may be subjected to. In such scenario, habitat areas with high environmental suitability may have a higher relevance for conservation. Habitat areas located in the Gulf of Lion and along the Catalan continental margin were ranked as the most important elements in the Mediterranean seascape connectivity. In the Cap de Creus Canyon, for instance, the presence of both medium to large-sized colonies of *L. pertusa* and recurrent small-sized colonies that suggest regular colonization pulses (Gori et al. 2013) are in agreement with our estimates of high habitat quality and great potential to be reached by a considerable number of larvae. In the Central-Eastern basin, the high density of connections to habitat areas identified along the South-Western area of the Apulian margin (Ionian Sea) coincides with the well-known ground of Santa Maria de Leuca Coral Province. As proposed by Angeletti et al. (2014), links between the Adriatic colonies and those inhabiting the Apulian margin are likely to occur, particularly by larvae released from populations close to the Bari Canyon.

Some of the habitat areas identified as the most important for *L. pertusa* seascape connectivity (e.g., the Catalan margin, Apulian margin, South Adriatic Sea) are subjected to intense anthropogenic activity and lack effective conservation measures (Company et al. 2012; Puig et al. 2012; Lastras et al. 2016; D'Onghia et al. 2017; Capezzuto et al. 2018). A rare example of effective protection of habitat areas identified in our study are the French MPAs in Gulf of Lion which encompass the Lacaze-Duthiers Canyon (Fabri et al. 2014). In fact, among the geomorphological features in the Mediterranean Sea, canyons provide suitable environmental conditions (e.g., hard substrate) to the development of *L. pertusa* (Huvenne et al. 2011; Van den Beld et al. 2017); they are known locations of living colonies, they act as larval suppliers to other habitat areas and, therefore, may have a supplementary conservation value. This information is particularly relevant since the Mediterranean Sea is one of the world's regions where canyons are more densely and closely spaced (Harris and Whiteway 2011) occupying natural delimited and therefore potentially more manageable areas for conservation purposes. The prioritization of habitat areas indicated some of the highest *dPC* values for canyons in the Western Mediterranean. Although canyons are known to offer refuges from anthropogenic impacts they are also prone to high pressures (e.g., bottom trawling). The Besòs and Morràs canyons (Catalan margin), for instance, are among the most relevant habitat areas in the Western Mediterranean ecoregion but without any records of living *L. pertusa* colonies. These areas hold important fishing grounds and are affected by increased sedimentation rates resulting from bottom trawling fishing (Paradis et al. 2017). Although the reasons for the absence of the species in these high suitability areas are unknown, the intensity and the direct impact on the seafloor of trawling gears may compromise the successful settlement of the larvae. Increased sediment loads are known to cause significant larval mortality (Järnegren et al. 2017). Adults of *L. pertusa* show efficient cleaning mechanism but the sediment accumulation and burial of coral may also result in damage to *L. pertusa* colonies (Larsson and Purser 2011).

As mentioned above, the intensification of climate changes may induce important alterations in the oceanographic circulation and in the habitat suitability for *L. pertusa*, which in the Mediterranean Sea encounters environmental conditions close to its physiological limits (Chapter 2.2). This underscores the need for connectivity studies at the basin-wide scales to understand the species extinction risk, particularly in scenarios of global habitat loss and rapid climate change (Henry et al. 2014).The synergy of climate change and anthropogenic pressures may impose significant challenges to the larval dispersal capacity and limit distribution of *L. pertusa* by disrupting dispersal pathways. These are pressing issues that highlight the importance of the documented living colonies and the urgency of their protection. The conservation and management of the *L. pertusa* in the Mediterranean Sea is totally under the countries direct jurisdiction considering that the entire region is covered by Economic Exclusive Zones. This fact requires the national commitment of the concerned countries to the preservation of the species in this region and a trans-boundary international conservation strategy (Howell et al. 2016).

2.3.6 - Supplementary material

Table S 2.3.1 – Release location of virtual larvae. Release depth adjusted to the oceanographic model datasets.

Ecoregion	Release location	Long	Lat	Release depth (m)	
				non-DSWC	DSWC
Alboran Sea	Al-Borani Ridge	-2.922	36.024	365	360
	Almunecar Slope	-3.974	36.393	453	517
	Câbliers Slope	-2.253	35.794	398	525
		-2.574	35.829	579	596
	Câbliers Terrace	-2.515	35.436	276	280
	Chella Slope	-2.922	36.522	453	386
	Ville De Djibouti Slope	-3.53	36.088	416	615
		-3.553	36.091	416	615
		-3.488	36.105	602	266
	Ville De Djibouti Terrace	-3.496	36.156	453	266
Western Mediterranean	Blanes Canyon	2.833	41.583	284	386
	Cap de Creus Canyon	3.334	42.357	182	156
		3.315	42.394	182	156
		3.319	42.385	182	156
		3.329	42.379	182	156
		3.338	42.369	182	156
		3.315	42.39	182	156
		3.317	42.388	182	156
		3.321	42.386	182	156
	Lacaze-Duthiers Canyon	3.398	42.564	143	123
		3.408	42.552	203	146
		3.399	42.567	93	123
		3.421	42.546	203	146
		3.421	42.545	203	146
		3.42	42.55	203	146
		3.403	42.583	93	123
		3.406	42.578	93	123
	Nora Canyon	8.909	38.708	270	244
		8.912	38.703	270	244
Tunisian Plateau/Gulf of Sidra	Bouri Slope	14.05	35.059	493	491
		14.11	35.512	453	493
		14.105	35.508	453	493

Ecoregion	Release location	Long	Lat	Release depth (m)	
				non-DSWC	DSWC
	Linosa Slope	13.044	35.767	756	794
Ionian Sea	Apulian Canyon	18.5348	39.5517	784	855
		18.5185	39.6123	646	600
		18.508	39.612	626	600
	Apulian Slope	18.36	39.3998	1076	1216
		18.3937	39.453	843	1061
		18.3992	39.4547	843	1061
		18.4018	39.4625	729	1061
		18.378	39.48	754	812
		18.3977	39.5322	651	602
		18.398	39.587	493	602
		18.39	39.583	556	602
		18.437	39.565	576	608
		18.453	39.565	596	658
		18.456	39.555	626	658
		18.3857	39.6163	434	389
		18.92	39.891	784	810
	Apulian Terrace	18.6482	39.6448	651	661
	Malta Trough	14.082	35.83	971	1005
	Pinne Marine Slope	13.156	36.84	426	311
	Taranto Slope	18.08	39.621	814	796
		17.688	39.765	971	1078
Adriatic Sea	Bari Canyon	17.179	41.297	434	394
		17.277	41.291	276	644
	Bari Slope	17.047	41.725	676	704
	South Adriatic Slope	18.691	41.648	434	333
		18.674	41.648	453	453

Supplementary material S1

Inference of the most probable spawning season for *L. pertusa* in the Mediterranean Sea

Considering the trends observed for populations located in other regions (Figure S 2.3.1), the period between December and the end of January may be the most suitable for the larval release in the Mediterranean Sea. This timeframe precedes the months when primary productivity at the surface waters reaches the highest values. During this period the increasing levels of food availability in the water column and reaching the seafloor probably maximize the chances of survival of larvae and the new recruiters (Waller and Tyler 2005; Brooke and Järnegren 2013).

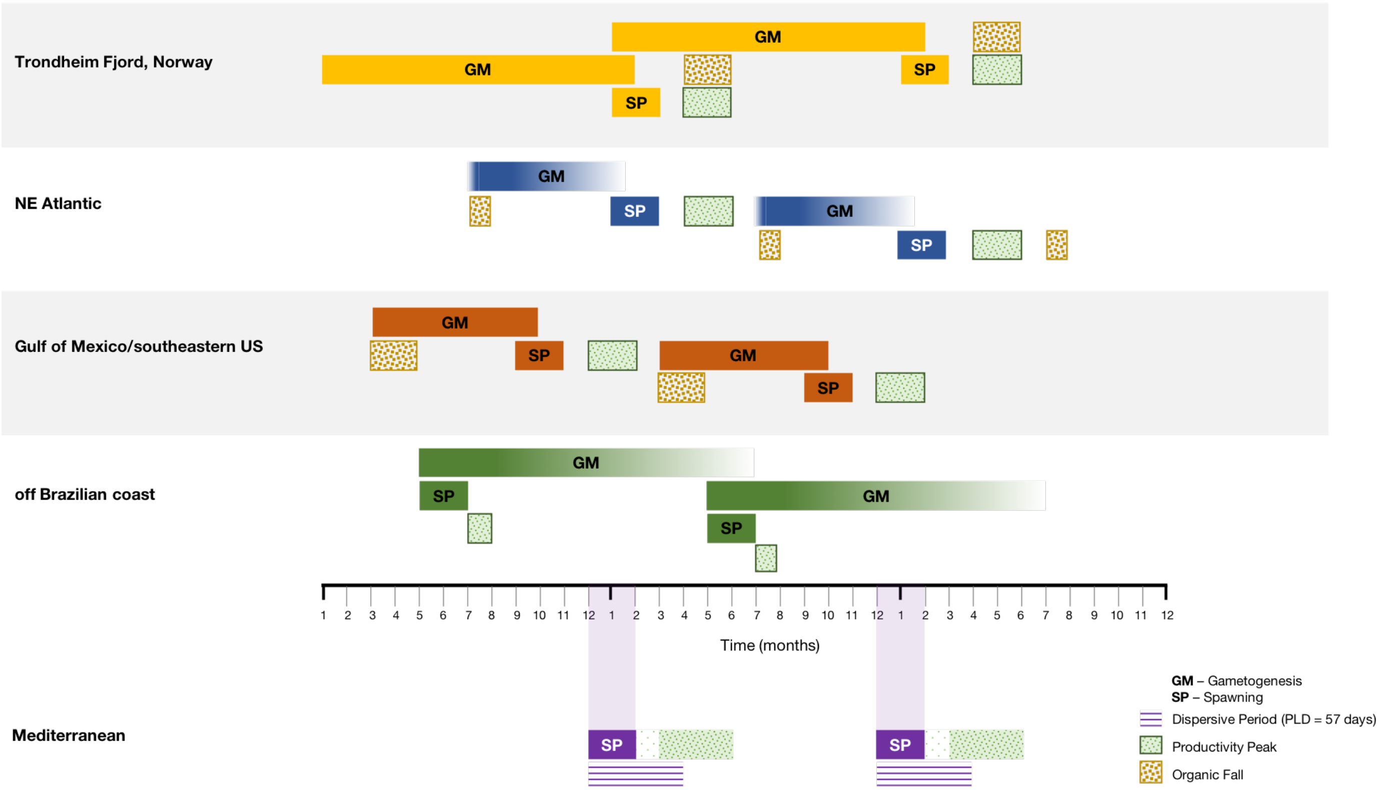

Figure S 2.3.1- Spawning scheme derived from the literature. In the NE Atlantic Ocean, the spawning season was estimated between January and March (Waller and Tyler 2005; Brooke and Järnegren 2013; Larsson et al. 2014), while in the Gulf of Mexico and off Brazilian coast, the spawning is most likely to occur between September and November (Brooke and Schroeder 2007) and from May to July (Pires et al. 2014), respectively.

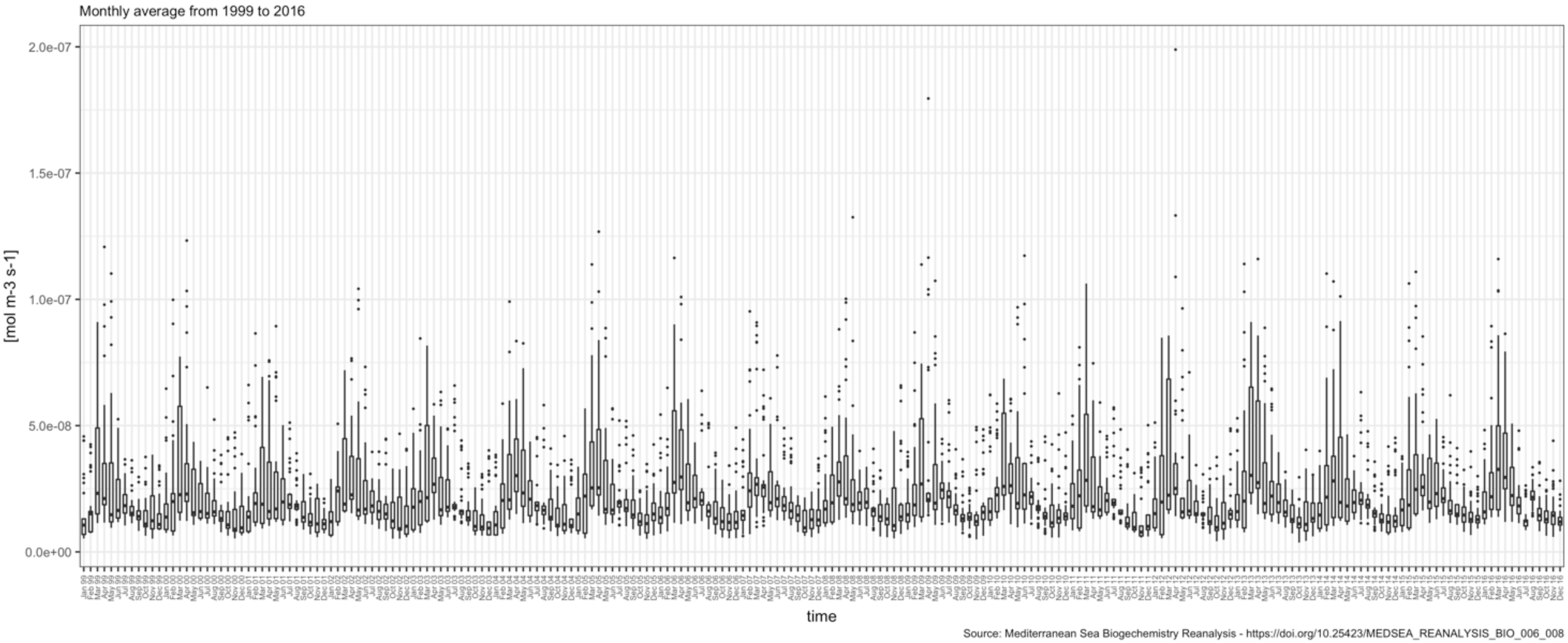

Figure S 2.3.2 – Variation of the net primary production on location with known colonies of *L. pertusa* in the Mediterranean Sea between January of 1999 and December of 2016.

Section 3 - General discussion

Submarine canyons are geomorphological features characterized by their spatially and temporally dynamic and complex interactions in the wider biogeochemical and oceanographic settings (Liu et al. 2002; Allen and Durrieu de Madron 2009; Masson et al. 2010; Puig et al. 2014), and by their habitat heterogeneity which harbours productive and diversified but mostly undescribed biological communities (De Leo et al. 2010; Cunha et al. 2011; Kavanaugh et al. 2015). These distinctive and iconic ecosystems, distributed worldwide along continental and island margins (Harris et al. 2014), are bridging the coastal areas to the deep sea and act as natural traps and conduits both for natural and anthropogenic materials (Weaver et al. 2004; Canals et al. 2006; Castro-Jimenez et al. 2013; Pham et al. 2014). Canyons are often subjected to intense fishing pressures and to the impacts of various anthropogenic activities (Yoklavich et al. 2000; Company et al. 2012; Puig et al. 2012; Paradis et al. 2017) that may operate synergistically with the effects of natural disturbance (Almeida et al. 2017) and climate change (Danovaro 2018). Submarine canyons are therefore a fascinating research subject but their complexity and the existing knowledge gaps (Huvenne and Davies 2014; Amaro et al. 2016) require integrative, multidisciplinary and broad-scale approaches.

In this thesis I reviewed the existing bibliographic information on submarine canyons and characterised the scientific canyon research landscape. Taking into account the scope of the thesis, i.e. contribute to the knowledge on the role of submarine canyons in (deep) seascape connectivity and provide scientific evidence to support decision-making in marine spatial planning and conservation, the bibliographic revision allowed identifying the Mediterranean Sea and the CWC *L. pertusa* has the most suitable protagonists for my work. A unifying characteristic of my thesis is the use of network analysis as a framework both for scientometrics and for ecological modelling. Below I provide a summary and brief overall discussion of the main results.

3.1 - Submarine canyons research landscape

The number of publications on the different aspects of submarine canyons and the evolution observed over the 20th century reflect a persistent interest for these geomorphological features. The network analyses of the abstracts content revealed the main topics addressed in the literature and constraints to the development of canyons research in the near future. Despite of the exploration of deep sea being a relatively recent science field, an international network of scientific collaboration on canyon research is well implemented and encompasses disciplines such as geology, biology and oceanography. Among the most important findings mentioned on the first manuscript is the uneven distribution of the research efforts committed to submarine canyons worldwide, not only geographically but also thematically.

Although much progress has been achieved, this bias uncovers a strong limitation in the knowledge integration that jointly with the lack of robust inter-disciplinary and standardized approaches and hinders our understanding on submarine canyons processes and functioning. The implementation of multidisciplinary cable observatories (e.g., Barkley Canyon - British Colombia, Canada) has, in part, overcame some of these issues and contributed to the understanding of long-term trends of water mass properties, currents and faunal community composition and distribution (Juniper et al. 2013; Matabos et al. 2014; De Leo et al. 2018). This investment allows the scientific community to face some of the greatest challenges for the future research on submarine canyons, including the demand for protecting and management measures of biodiversity that arise from a higher societal awareness on the human impacts on deep-sea ecosystems (Glover et al. 2010; Ressurreição et al. 2011; Jobstvogt et al. 2014).

Concerns regarding conservation and management issues, anthropogenic impacts and climate change, albeit recent as a canyon research topic, were already detected by the semantic analysis. Recent works of Palanques et al. (2006) and Canals et al. (2006) highlighted the importance of climate driven extreme events (dense shelf water cascading) on and the functioning of canyon ecosystems. The impacts of fishing activities on the canyons morphology (Puig et al. 2012; Lastras et al. 2016), the litter concentration (Mordecai et al. 2011; Tubau et al. 2015) and waste disposal (Fabri et al. 2014) are evermore reported. Multi- and interdisciplinary approaches will be required to address these threats and understand how to minimize their impacts. The use of modelling approaches to study the physical environment in submarine canyons, particularly regarding oceanography, is well established but their application to biological topics is poorly explored. The second and third manuscripts of this thesis contribute to fill the gaps detected on canyon research regarding biodiversity conservation and ecological modelling.

3.2 - Case study

An integrated perspective of canyon relevance in the seascape connectivity requires an ocean scale analysis. The only study on connectivity among submarine canyons and its implications for conservation planning was conducted by Kool et al. (2015), in the SW marine region of Australia using ophiuroid larvae as a model organism. The work that I conducted is the first study assessing the seascape connectivity and habitat availability for a deep-sea species using a Lagrangian framework and network analysis at an ocean basin scale. The selection of the study area and the model species used in this thesis was based on particular attributes. As a study area, the Mediterranean Sea is an interesting option because of the high concentration of submarine canyons and their close proximity (Harris and Whiteway 2011; Harris et al. 2014). Simultaneously, the Mediterranean Sea has the potential to serve as a natural laboratory to study effects of global change on oceans (Lejeusne et al. 2010). A CWC was selected as the modelling organism because these animals are frequently associated with submarine canyons. *Lophelia pertusa* is one of the most studied species; it plays an important role on deep-sea ecosystems as an ecosystem engineering species and it is classified as a VME. The development of conservation measures aiming to protect and minimize impacts on these species resulting from the global change will be amplified and extended to their associated biological communities and, indirectly also to other organisms (Lavergne et al. 2010).

I assessed and mapped for the first time the potential distribution of *L. pertusa* considering the whole Mediterranean Sea. Habitat mapping provides a way to measure and explore the spatial heterogeneity of seascape at ecological meaningful scales that are also operationally relevant for conservation and management planning (Lecours et al. 2015; Lecours 2017). The assessment of the Mediterranean seascape suitability for *L. pertusa* constituted a fundamental step to estimate the seascape connectivity for this species and to determine the relative importance of submarine canyons in the study area. An almost continuous area of medium to high HSI scores was delimited along the upper slope, from the Alboran Sea to the Central-Eastern Mediterranean. The lowest HSI values were concentrated along vast areas of the continental shelves (<100 m depth) and the deepest regions of the Mediterranean Sea (>1500 m). The environmental constraints to *L. pertusa* distribution seem to be stronger towards the Eastern Mediterranean Sea, following the well-documented gradient of increasing temperature, salinity and oligotrophy (Azov 1991; Sardà et al. 2004). Moreover, the simulations of larval dispersal from colonies closer to the eastern part of Mediterranean Sea, showed that no larva is able to reach these sections of the study explaining in part the absence of reported living colonies. Although some physiological plasticity to environmental changes was reported for *L. pertusa* species (Dodds et al. 2007; Naumann et al. 2014; Georgian et al. 2016), the populations in the Mediterranean Sea may be already subjected to the limits of their physiological tolerance regarding temperature, salinity and dissolved oxygen. This finding is even more worrying knowing that the habitat availability for *L. pertusa* in the Mediterranean Sea may be largely determined by the quality of the habitat areas (intrapatch connectivity) rather than from the larval flux between habitat areas (interpatch connectivity). In other words, this means that although there are relatively vast areas of suitable habitat for *L. pertusa*, many of these habitat areas are not likely to be reached by the larvae released in the currently known living colonies making the Mediterranean populations overall less resilient to natural and anthropogenic disturbances.

Despite the estimation of an almost continuous area of medium to high suitability, along the upper slope of the Western and Central Mediterranean Sea, it is unlikely that *L. pertusa* occurs uniformly across the suitable seascape. I identified the areas with higher potential to harbour unknown colonies of *L. pertusa* based on the environmental quality and larval flux. However, the effective occurrence of colonies in these habitat areas will depend on stochastic events various other factors such as biological processes, occurrence of oceanographic barriers (e.g., water column stratification, prevailing currents; Rogers 2003) and the level of anthropogenic impacts that those area may be subjected to (e.g., fishing activities, litter accumulation and waste disposal; Orejas et al. 2009; Fabri et al. 2014; Clark et al. 2016; Lastras et al. 2016). The conservation *L. pertusa* in the study area may be seriously compromised since the protection measures implemented so far only partially coincide with high suitability areas.

The results that I present in this thesis derive from modelling approaches and therefore they require empirical validation and ground-truthing surveys. The relative coarse resolution of the models (seascape level) limits the representation of some processes such as the fine-scale oceanographic mechanisms known to influence the larval transport or the role of fine-scale topographic variations on the environmental suitability of an area (Lecours et al. 2015). However, habitat mapping and connectivity studies at the ocean-basin scale allows also to better infer the species extinction risk, particularly in scenarios of global habitat loss and rapid climate change (Henry et al. 2014). The continuous assessment of the environmental conditions in the whole Mediterranean Sea also allows detecting focal areas for future efforts using higher resolution models currently only applicable at local scales. Field surveys and complementary methodologies such as genetic characterization will contribute to assess the realized distribution and connectivity of *L. pertusa* in the Mediterranean Sea. The detection of new colonies in the study area will allow improving the estimates reported in this thesis.

The intensification of climate-driven processes such as DSWC that presently occur with a decadal frequency in some of the Mediterranean canyons (Canals et al. 2013) may act synergistically with other environmental changes (e.g., temperature, dissolved oxygen, seawater acidifications) and affect the distribution of *L. pertusa* by reducing the potential dispersal of larvae and the environmental suitability of the seascape. This highlights the importance of submarine canyons in the Mediterranean seascape such as refuges for the conservation of *L. pertusa* and their associated fauna. In fact, submarine canyons were ranked among the most suitable features for the occurrence of *L. pertusa* in the study area. This result confirms previous indications that, as a consequence of their complex topography and influence on hydrodynamics, these geomorphologic features may be considered CWC hotspots (e.g., Orejas et al. 2009; Van den Beld et al. 2017). The most important canyon systems in the Mediterranean Sea are located on the European continental slopes of the western basin (Ceramicola et al. 2015). This region coincides not only with the occurrence of the strongest DSWC events (Gulf of Lion) but also with intense anthropogenic activities such as trawling fisheries along the Catalan coast. Locations that are already severely damaged or under threat (Ceramicola et al. 2015) correspond to potential habitats areas for *L.*

pertusa identified in my work. The Besòs and Morràs canyons in the Catalan margin, for instance, are among the most relevant habitat areas in terms of habitat availability for *L. pertusa* in the Mediterranean Sea but coincide with important fishing grounds. The trawling activities on these areas increase the sedimentation rates (Paradis et al. 2017) potentially affecting *L. pertusa* survival of adults (Larsson and Purser 2011; Larsson et al. 2013) and larvae (Järnegren et al. 2017). Moreover, the direct impact of trawling gears on the seafloor (Puig et al. 2012), besides being able to remove established colonies, may compromise the recruitment of new individuals.

Marine Protected Areas (MPAs) cover only about 4% of the Mediterranean Sea (CIESM 2011) and the overall protection of hundreds of vulnerable Mediterranean submarine canyon habitats is negligible. The only exception are the Lacaze-Duthiers and Cassidaigne submarine canyons, which receive some protection provided by the French MPAs on this region (Fabri et al. 2014). The conservation and management of the Mediterranean Sea biodiversity is totally under national jurisdiction since the entire region is covered by the Economic Exclusive Zones of the coastal countries. This fact requires the national commitment of the concerned countries and a responsible trans-boundary international conservation strategy in order to the preserve biodiversity in the Mediterranean Sea (Howell et al. 2016). The successful management of Mediterranean canyons will depend on the coordination between countries and the application of an ecosystem-based approach for the design of a comprehensive, effective and representative network of MPAs to ensure the conservation and integrity of submarine canyon processes and functioning (Ceramicola et al. 2015). The geomorphological boundaries of these features define natural limits that make these areas potentially more manageable and facilitate their conservation.

Section 4 - References

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