Biological Conservation 306 (2025) 111112

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Expanding a network of marine protected areas based on functional rather than structural connectivity is more profitable

Sylvain Blouet[a,b], Thibaud Tournadre[a], Skandar Hentati[a], Katell Guizien[a,*]

[a] CNRS-Sorbonne Université, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB, Observatoire Océanologique de Banyuls Sur Mer, 66650 Banyuls sur Mer, France

[b] Ville d'Agde, Aire marine protégée de la côte agathoise, 34300 Agde, France

ARTICLE INFO

Keywords:
Marine functional connectivity
Systematic conservation planning
Hard bottom habitat
Marxan connect
Gorgonian
NW Mediterranean Sea

ABSTRACT

One strategy to boost population resilience and stop the long-term loss of ocean biodiversity is to establish networks of interconnected, highly protected areas. In this study, we assess the relationship between profitability and adequacy brought about by structural and functional connectivity in systematic conservation planning (SCP). Twelve sets of conservation plans were explored to protect the hard bottom habitat of the Gulf of Lion (NW Med Sea), varying conservation objectives (10 % and 30 % of the surface area), human activity pressures (including or ignoring existing highly protected areas) and connectivity types: (i) structural connectivity (ii) early summer and (iii) late summer connectivity arising from a week-long larval dispersal. These connectivity are likely estimates of the functional connectivity of gorgonians. Conservation plan profitability - which was defined as the ratio of the population part under protection to protection cost - was assessed using observations of the spatial distribution (that were not used in the SCP) of five gorgonian species *Eunicella singularis, Leptogorgia sarmentosa, Eunicella cavolinii, Paramuricea clavata and Corallium rubrum*. When functional connectivity replaced structural connectivity, the spatial distribution of highly protected areas was altered, systematically targeting the center of the Gulf of Lion whatever the conservation objective. Profitability drastically increased with functional compared to structural connectivity for four of the five species in the 10 % conservation objective. Including existing highly protected areas also improved profitability but differently according to the species in 10 and 30 % objective. No plan was profitable for *P. clavata*.

1. Introduction

The ongoing collapse of marine biodiversity underscores the urgent need to revise the current marine protected areas (MPAs) system to ensure the long-term conservation of nature, ecosystem services, and cultural values (Watson et al., 2009; Halpern et al., 2019). As of 2024, designated MPAs cover 8.4 % of the global ocean surface (ProtectedPlanet, 2024). However, the level of protection varies significantly, with only 2.9 % of the ocean classified as fully or highly protected (Grorud-Colvert et al., 2021; The Maritime Protection Atlas, 2024). To address this, the Global Biodiversity Framework has set an ambitious target to protect at least 30 % of the ocean by 2030 (CBD, 2022). This target is based on biodiversity distribution assessments, which suggest that protecting 30 % of a habitat could conserve 60–80 % of its species (Zhao et al., 2020). At the national level, France has aligned with this goal, aiming to protect 30 % of its marine areas, including 10 % as highly protected, by 2030 (Ministère de la Transition Ecologique et de la Cohésion des Territoires, 2023).

While area-based targets are easy to communicate, they are insufficient for prioritizing conservation efforts. Effective conservation planning requires a scientifically sound approach that ensures the representativeness of biodiversity and the long-term persistence of species and ecosystems (Wilson et al., 2009). Systematic Conservation Planning (SCP) provides a methodological framework for making objective decisions about the spatial arrangement of conservation actions. SCP uses iterative optimization algorithms to identify areas with the highest conservation value, meeting targets while minimizing costs and incorporating stakeholder input (Kirckpatrick, 1983). A 30 % protection target is often adopted in SCP studies (Schill et al., 2015; Chen et al., 2022), but achieving this requires careful consideration of ecological criteria, including connectivity.

Ecological connectivity—the degree to which the movement of

* Corresponding author.
E-mail address: guizien@obs-banyuls.fr (K. Guizien).

https://doi.org/10.1016/j.biocon.2025.111112
Received 8 October 2024; Received in revised form 15 February 2025; Accepted 23 March 2025
Available online 8 April 2025

organisms and ecological processes are facilitated within an ecosystem—is critical for the effectiveness of MPAs (Crooks and Sanjayan, 2006; Goetze et al., 2021). However, connectivity is often overlooked in MPA design, with only 11 % of MPAs incorporating it as a criterion (Balbar and Metaxas, 2019). When connectivity is considered, it typically refers to structural connectivity (physical continuity through corridors), which is easier to map and integrate into SCP tools like Marxan and Zonation (Ball et al., 2009; Lehtomäki and Moilanen, 2013; Casati, 2024). However, scientific literature emphasizes the importance of population connectivity (the exchange of individuals across generations) for ensuring long-term species persistence and resilience (Hastings and Harrison, 1994; Hanski, 1998). Population connectivity, which results from the interaction of ocean currents and organism motility, is more challenging to represent but is essential for adequate MPA siting (Carr et al., 2017; Bandelj et al., 2020).

In marine environments, population connectivity often involves directional fluxes between distant locations, which are difficult to track due to the vastness of the ocean and the challenges of monitoring early life stages. While some SCP studies have used observational data like telemetry tracking and genetic metrics (Beger et al., 2014; Lea et al., 2016), most rely on larval dispersal modeling to estimate connectivity (White et al., 2014; Schill et al., 2015; Álvarez-Romero et al., 2018). Recent advancements in SCP tools, such as Marxan Connect and Coco, now allow for the integration of spatial dependencies in connectivity networks (Daigle et al., 2020; van Mantgem et al., 2023), addressing previous limitations.

This study explores how the profitability of conservation plans—measured in terms of cost and the proportion of regional populations under protection—varies with the adequacy of connectivity criteria. The study focuses on the Gulf of Lion, a biodiversity hotspot in the NW Mediterranean, targeting hard bottoms (rocky and coralligenous habitats). These habitats are among the most biodiverse in the Mediterranean, supporting species like sponges, gorgonians, mollusks, and fish (Laubier, 1966; Ballesteros, 2006). Gorgonians, in particular, play a key role in structuring these ecosystems, forming underwater forests that enhance biodiversity and biomass (Gili and Coma, 1998; Rossi et al., 2017). They also attract scuba divers, contributing to the coastal economy (Ballesteros, 2006). However, their erect structures make them vulnerable to anthropogenic pressures like fishing, diving, and boat anchoring (Font and Lloret, 2014; Sala et al., 1996; Milazzo et al., 2002), highlighting the need for effective conservation measures.

We developed twelve sets of plans with protection objectives of either 10 % (aligned with French national targets) or 30 % (aligned with the Global Biodiversity Framework) of hard bottom habitats. These plans varied in connectivity criteria: (i) structural connectivity, (ii) early summer functional connectivity, and (iii) late summer functional connectivity, derived from week-long larval dispersal simulations. We also assessed the impact of including or excluding existing highly protected areas. Functional connectivity was integrated as spatial dependency, reflecting the directional fluxes of larval dispersal.

The profitability of each plan was evaluated based on its effectiveness in protecting five gorgonian species: *Eunicella singularis*, *Leptogorgia sarmentosa*, *Eunicella cavolini*, *Paramuricea clavata*, and *Corallium rubrum*. Abundance data for these species, collected independently from the SCP process, were used to assess the proportion of regional populations included in the plans. This approach allowed us to compare the performance of different connectivity criteria and protection objectives, providing insights into the trade-offs between cost, coverage, and ecological adequacy in marine conservation planning.

2. Material and methods

2.1. Study area

The Gulf of Lion is a wide, micro-tidal continental shelf (<200 m), in the French national waters of the North-western Mediterranean, delineated by a steep shelf-break along which the Northern Current—a return flow of the cyclonic circulation in the western Mediterranean basin—moves southwestward along this boundary (Fig. 1, Millot, 1990). The coastal circulation in the Gulf of Lion is driven by two strong northern winds, the Tramontane and Mistral, which erratic variability results into highly variable currents in both space and time, with localized up- and down-wellings throughout the area and mesoscale eddies. It has been identified as a disconnected hydrodynamical province for dispersal lasting <30 days (Rossi et al., 2014). In the Gulf of Lion, the coastal benthic habitat is mainly made up of large and contiguous soft bottoms, with a few small patches of hard bottom habitat ranging in size from 0,5 to 34 km^2, totalling a surface of 80 km2. The study area comprises a set of eight hard bottom sites (Côte Bleue, Aigues Mortes, Aresquiers, Agde, Valras, Leucate, Saint-cyprien, Côte Vermeille; Fig. S1). Four sites include a highly protected area (according to the classification of Horta e Costa et al., 2016: Fully protected) with different surface areas (Côte Bleue: 289 ha, Aigues-Mortes: 100 ha; Agde: 310 ha, Côte Vermeille: 69 ha; Fig. S1), representing 5.45 % of the coastal hard bottom habitat surface.

2.2. MPA network design

We used Marxan (V 4.0.6) and Marxan Connect (V 1.0.0) to design marine conservation networks by optimizing planning unit (PU) layouts, balancing ecological objectives, costs, and connectivity. PUs are geospatial units that partition the ocean into smaller, more manageable units, and used to assemble a conservation plan, each requiring data on conservation features (e.g., habitat area, species biomass) and costs (e.g., management, opportunity costs). The Marxan implementation section below details PUs definition and cost dataset used.

Marxan prioritizes structural connectivity, minimizing conservation area fragmentation by favoring clustered PUs with shared boundaries, thus reducing perimeter length (Ball et al., 2009). This approach benefits habitat-following species and lowers monitoring costs (Ardron et al., 2010). Compactness is controlled by the boundary length modifier (BLM): higher BLM values prioritize compactness, while lower values allow fragmentation to reduce costs.

Marxan Connect instead integrates functional connectivity, linking ecologically interdependent PUs (e.g., via species migration or larval dispersal) even if spatially distant (Daigle et al., 2020). Marxan Connect deals with functional connectivity in two ways. One way is to integrate functional connectivity (symmetrical or asymmetrical) through links between PUs by creating high penalties in conservation plans that fail to protect a pair of highly connected PUs (Beger et al., 2010). The other way is to integrate functional connectivity in the form of a feature ranking PUs according to their influence in the connectivity network (e.g. degree of entry, intermediate centrality, local retention, Google pagerank, https://marxanconnect.ca/). In the present study, functional connectivity was implemented as spatial dependency with asymmetrical connectivity (see the Marxan connect implementation section below for the description of the functional connectivity dataset). Like the BLM, the connectivity strength modifier (CSM) adjusts the importance of connectivity in the conservation plan design by applying a penalty when connected PUs are not included (Beger et al., 2010).

Both tools employ simulated annealing to iteratively generate cost-efficient PU portfolios meeting conservation targets. The algorithm minimizes a score combining PU costs, connectivity penalties, and unmet objective penalties. Structural connectivity prioritizes compactness (minimizing boundary length), while functional connectivity emphasizes ecological linkages (Ball and Possingham, 2000). The simulated annealing algorithm is repeated several times (number of runs) to obtain several optimal prospective conservation plans.

2.3. Marxan implementation

As PUs, we targeted square plots of about 1 km^2, which is in the order

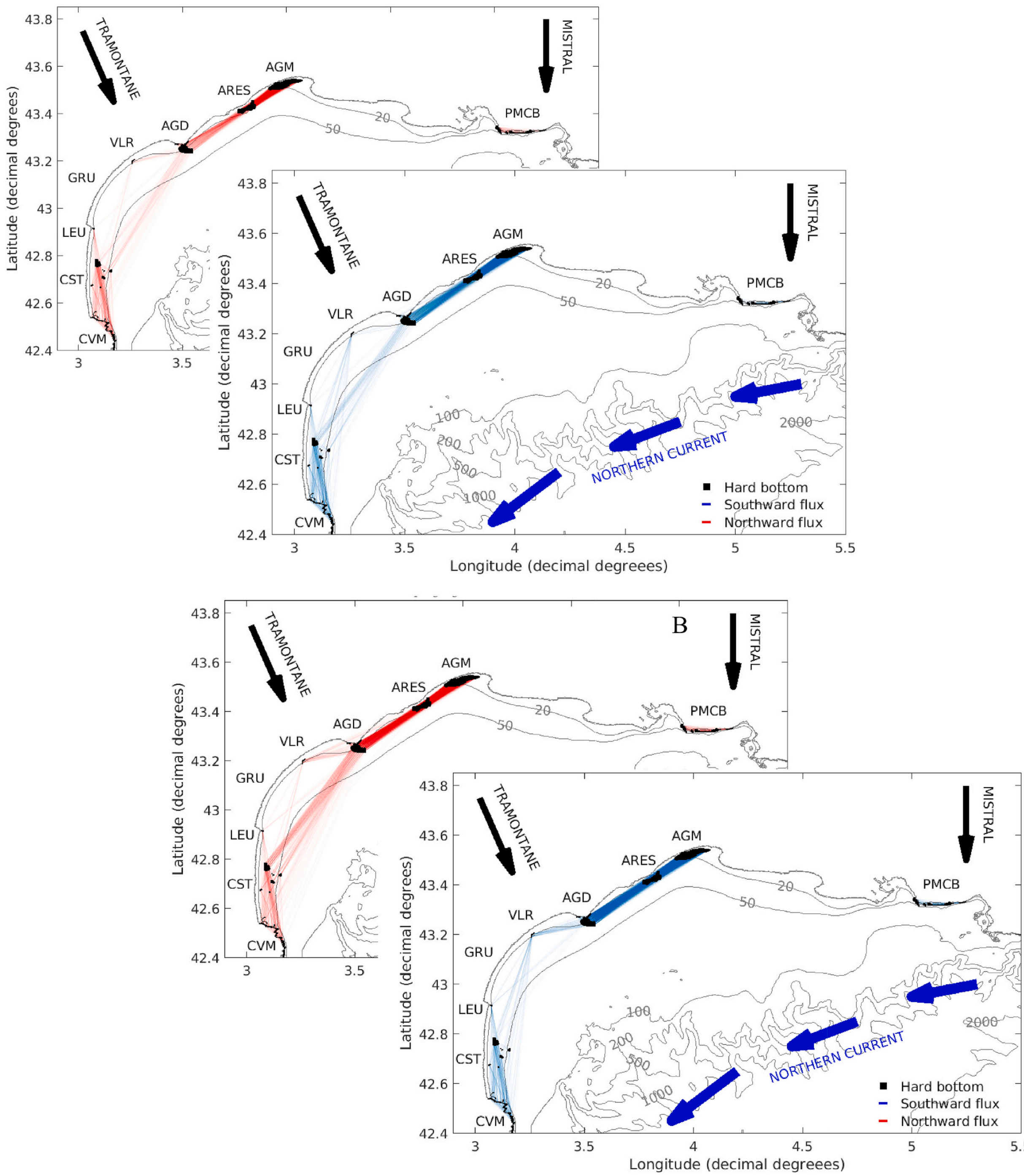

Fig. 1. Median larval transport (probability of transfer) in the study area after a pelagic dispersal duration of 7 days for a release from June 1 to July 10 (early summer, A) and from August 1 to September 10 (late summer, B) during the 3 summers (2010, 2011 and 2012) between each of the 138 hard bottom habitat planning units (black polygons). The blue lines correspond to southward larval transport. The red lines correspond to northward larval transport. Lines transparency is proportional to transport intensity. Black arrows display the dominant winds Mistral and Tramontane and blue arrows display the Northern Current which in combination drive the circulation over the Gulf of Lion shelf (PMCB = Côte Bleue, AGM = Aigues-Mortes, ARES = Aresquiers, AGD = Agde, VLR = Valras, GRU = Gruissan, LEU = Leucate, CST = Saint-Cyprien, CVM = Côte Vermeille). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of magnitude of the smallest surface area of current strong protection zones and a spatial scale consistent with the variability of local retention linked to marine currents in the Gulf of Lion (Fig. S1, Briton et al., 2018). In total, the 8 sites were described by 138 PUs with surface areas ranging from 0.01 to 1.4 km^2, most of which are squares except those around the edges of the sites whose shapes and sizes have been adapted to match the contour of the habitat and its natural fragmentation (Fig. S1).

Maritime activities data for calculating costs per PU were extracted from IMPACTS (Modeling coastal anthropogenic pressures and vulnerability thresholds; 20 × 20 m resolution; https://medtrix.fr/, Holon et al., 2015). We selected activities known to have a direct or indirect impact on hard-bottom biodiversity. Four activities were selected: small boat (<24 m) and large boat (>24 m) mooring, artisanal fishing and beach tourism. The maximum value for each activity was extracted for each PU.

The mapping of anthropogenic impacts, obtained by interpolating pressure as a function of distance between proven pressure sites (100 %) and habitat boundaries (0 %), did not take into account existing activity regulation. Existing activity regulations could be taken into account by setting fishing and beach tourism pressures to zero in PUs located in highly protected areas (www.medamp.org). For PUs that overlap two types of zoning (protected and unprotected), the value of the pressures is proportional to the surface area of the type of zoning. The final cost for each PU was calculated by summing the pressure values of the activities. Two cost scenarios were considered for setting up conservation plans, one including existing highly protected areas and one ignoring them, in order to test for the relevance of existing highly protected areas that were proposed long before pressures and connectivity assessments (Fig. S2 A and B).

2.4. Marxan Connect implementation: functional connectivity scenarios

Functional connectivity by larval dispersal were estimated from three-dimensional larval dispersal simulations. Larval dispersal was simulated by a Lagrangian method integrating the transport by ocean currents of virtual particles of neutral buoyancy, according to measured larval traits of *E. singularis* (Guizien et al., 2020). Three-dimensional currents were simulated on a curvilinear grid with high horizontal spatial resolution (from 80 m to 300 m near the coast) and temporal resolution (every 1 h) in the Gulf of Lion during 3 consecutive summer periods (from June to October, in 2010–2011 and 2012, Briton et al., 2018). A virtual particle is released at 1 m above the seabed every hour and every 100 m in all PUs from June 1 to July 10 for early summer and from August 1 to September 10 for late summer in the three years (2010, 2011 and 2012). The early summer corresponded to *E. singularis* and *Paramuricea clavata* (Gori et al., 2007; Guizien et al., 2020) and the late summer corresponded to *Leptogorgia Sarmentosa* and *Corallium rubrum* (Rossi and Gili, 2009; Guizien et al., 2020). A week-long PLD was chosen reflecting the competency of *E. singularis*, *P. clavata* and *C. rubrum* (Zelli et al., 2020). The probability of larval transfer between all directed pairs of PU was computed as the median of the probability of larval transfer obtained after a one-week PLD for twelve (four per year) 10-day release periods per species. Larval transfer probability was calculated as the ratio of the number of particles that were released in a source PU and reached a destination PU to the total number of particles released in the source PU, multiplied by the ratio of surface areas of source PU to destination PU. In summary, the functional connectivity by larval dispersal for the two species only varied in terms of the release periods, resulting in a greater number of PUs connected in late summer than in early summer (Fig. 1).

2.5. Configurations and simulations with Marxan

The simulations were carried out considering two conservation targets of 10 % and 30 % of the hard bottom habitat surface area (Tables 1 and S1). Species Penalty Factor which controls how much priority is given to achieving the conservation objective versus minimizing the cost of the solution, was set to 5.5 in all simulations and allowed for not reaching the objective if cost becomes prohibitive. Twelve configurations were tested (Tables 1 and S1). In each configuration, the model sensitivity to the scaling factor (BLM or CSM) between cost and connectivity measure that adjusts the score's sensitivity to these two quantities was explored. The most compact solution was explored by setting BLM value equal to 1 and the least cost solution was explored by setting BLM value equal to 0. The optimal BLM of 0.004 in the structural connectivity configurations was calibrated using ©Qmarxan software (Fig. S3A). In the functional connectivity configurations, the sensitivity to the choice of the CSM was explored, varying its value from 3 (medium penalty), 10 (high penalty) to 100 (very high penalty) and finally set to 3, this value leading to a reasonable compromise between cost and connectivity (Stewart and Possingham, 2005).

In all configurations, the number of executions was set to 100 times with 10 million iterations ensuring to consistently detect an optimal solution in each of them (calibrated using ©Qmarxan software, Fig. S3B). This led to a 100 optimal conservation plans and a selection frequency across all plans was calculated for each PU, yielding a resolution of 1 % on the selection frequency. Selection frequency was preferred to best solution as it enables to distinguish essential PUs with higher frequency selection from optional PUs with lower frequency selection. In addition, selection frequencies distribution indicates the robustness of the conservation plan options as a dominance of high selection frequency means robust plans with drastic cost/target gain while a dominance of low selection frequency means flexible plans with equivalent cost/target trade-offs. If selection was random and all PUs had a same size, each PU would be selected at a frequency equal to the conservation objective. Thus, selection frequency lower than the conservation objective were considered not significantly different from random sorting and only selection frequencies larger than the conservation objective were ranked into 5 classes from low to high on selection frequency maps produced using GIS software (©QGIS). In the conservation objective of 10 % of hard bottom surface area, the classes were: 10–20 % (low), 20–40 %, 40–60 %, 60–80 %, 80–100 % (high). In the conservation objective of 30 % of hard bottom surface area, the classes were: 30–44 % (low), 44–58 %, 58–72 %, 72–86 %, 86–100 % (high). Similarity between conservation plans in the different configurations was estimated by the Pearson coefficient between PU selection frequencies.

2.6. Conservation plans assessment

For each of the 100 conservation plans, the proportion of individuals of the known population of *Eunicella singularis*, *Leptogorgia sarmentosa*, *Eunicella cavolini*, *Paramuricea clavata*, and *Corallium rubrum* was calculated. The five gorgonian species display different spatial distributions in the hard bottom habitat (Blouet et al., 2024). The population density of the five species was assessed in 2013 and in 2021 at 601 georeferenced stations spaced by 100 m to 800 m, depending on the bathymetric gradient of each zone and covering the hard bottom habitat

Table 1

Cost, proportion of the hard bottom habitat surface (average for the 100 conservation plans) and achievement rate (AR) of the objective in the three connectivity scenarios (structural connectivity, functional connectivity of early summer, functional connectivity of late summer) and with or without existing highly protected areas in the objective of fully protecting 10 % or 30 % of the hard bottom habitat surface.

	TARGET 10 %						TARGET 30 %					
	Including existing highly protected areas			Ignoring existing highly protected areas			Including existing highly protected areas			Ignoring existing highly protected areas		
	Cost	Area (%)	AR (%)	Cost	Area (%)	AR	Cost	Area (%)	AR (%)	Cost	Area (%)	AR (%)
Structural connectivity (BLM = 0.004)	12.0	10.2	98	14.1	10.1	95	37.3	30.1	96	40.6	30.1	96
Functional connectivity of early summer (CSM = 3)	9.7	10.1	89	9.8	10.1	83	25.2	30.1	78	31.0	30.1	80
Functional connectivity of late summer (CSM = 3)	5.1	10.1	69	9.8	10.1	82	24.9	30.1	82	30.6	30.1	87

at all sites (Guizien et al., 2022; https://cardobs.mnhn.fr/). *E. singularis* is frequently observed and abundant throughout the hard bottom habitat of the Gulf of Lion (Fig. S4 A). *L. sarmentosa* is eight times less abundant than *E. singularis* in the hard bottom habitat, mainly distributed in the western part of the Gulf of Lion (Fig. S4 B). *P. clavata*, *C. rubrum* and *E. cavolinii* are rare species, distributed in Côte Vermeille and Côte Bleue only for *P. clavata* and *C. rubrum* and in the Plateau des Aresquiers and Côte Bleue only for E. cavolinii (Fig. S4 C, D and E, respectively). The mean population density for each species was calculated across the 102 PUs where data from either the 2013 or 2021 surveys were available. To account for transient demographic collapses occurring between the two surveys in certain areas, the higher value from the two surveys was used for each PU. The abundance of each species per PU was then calculated by multiplying the mean population density values assessed in each PU by the surface area within the PU.

For each of the 100 conservation plans, the proportion of the total cost in the PUs selected in the plan was calculated as well and conservation plan profitability was defined as the ratio between the proportion of individuals of the known population that are proposed to be put under protection and the proportion of the total cost.

3. Results

On average across the 100 conservation plans, the surface area objective was achieved, whaveter the scenario (Table 1). However, achievement rates of the surface area objective were notably higher with structural (95 % to 98 %) than with functional connectivity, whatever the target or cost scenario (69 % to 89 %, Table 1). Under the 10 % objective, surface area coverage ranged from 9.84 % to 10.56 % of hard bottom habitats, while in the 30 % objective, it ranged from 29.87 % to 33.89 % across the 100 plans. Conservation plans using functional connectivity were systematically cheaper than those with structural connectivity, reducing costs by 20–135 %, with the largest savings observed under the 10 % objective when extending existing highly protected areas (Table 1).

The spatial layout of conservation plans differed markedly between structural and functional connectivity, with a correlation <0.38 in planning unit (PU) selection frequencies (compare panels A vs. B and C vs. D in Figs. 2 and 3). Including or ignoring existing highly protected areas did not alter the spatial layout of conservation plans (correlation > 0.8 in planning unit (PU) selection frequencies; Figs. 2A vs. C; 3A vs. C; 3B vs. D), except in the 10 % objective with functional connectivity (correlation < 0.31 in planning unit (PU) selection frequencies. Fig. 2B

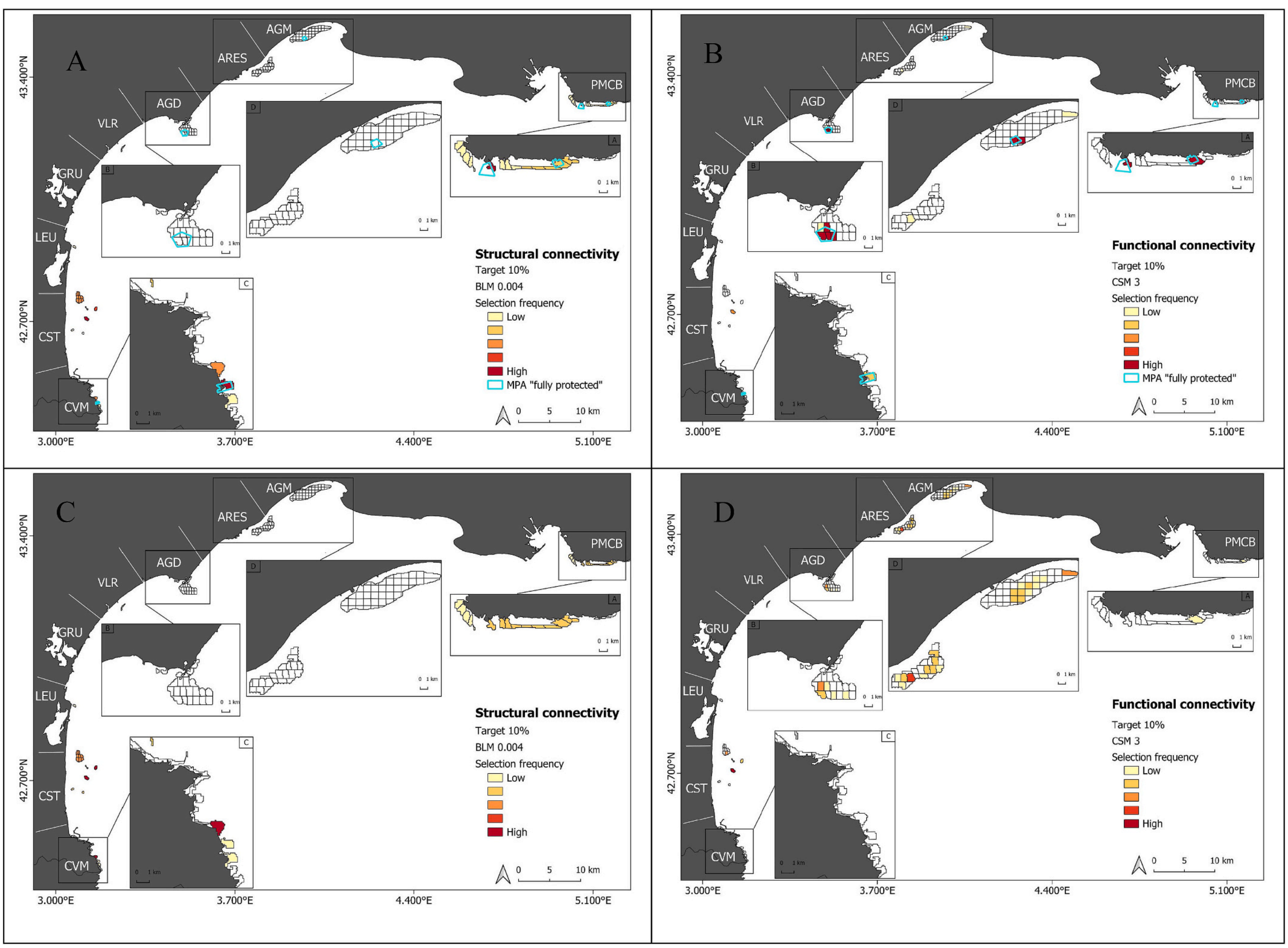

Fig. 2. Selection frequency of planning units obtained with Marxan in the objective of fully protecting 10 % of the hard bottom habitat surface in 4 configurations: including existing highly protected areas (upper panels) and structural connectivity (A, BLM = 0.004) or early summer functional connectivity as asymmetric spatial dependence (B, CSM = 3) and ignoring existing highly protected areas (lower panels) and structural (C, BLM = 0.004) or early summer functional connectivity as asymmetric spatial dependence (D, CSM = 3). The five classes of selection frequencies obtained from the 100 runs used were: 10–20 % (low), 20–40 %, 40–60 %, 60–80 %, 80–100 % (high). (PMCB = Côte Bleue, AGM = Aigues-Mortes, ARES = Aresquiers, AGD = Agde, VLR = Valras, GRU = Gruissan, LEU = Leucate, CST = Saint-Cyprien, CVM = Côte Vermeille).

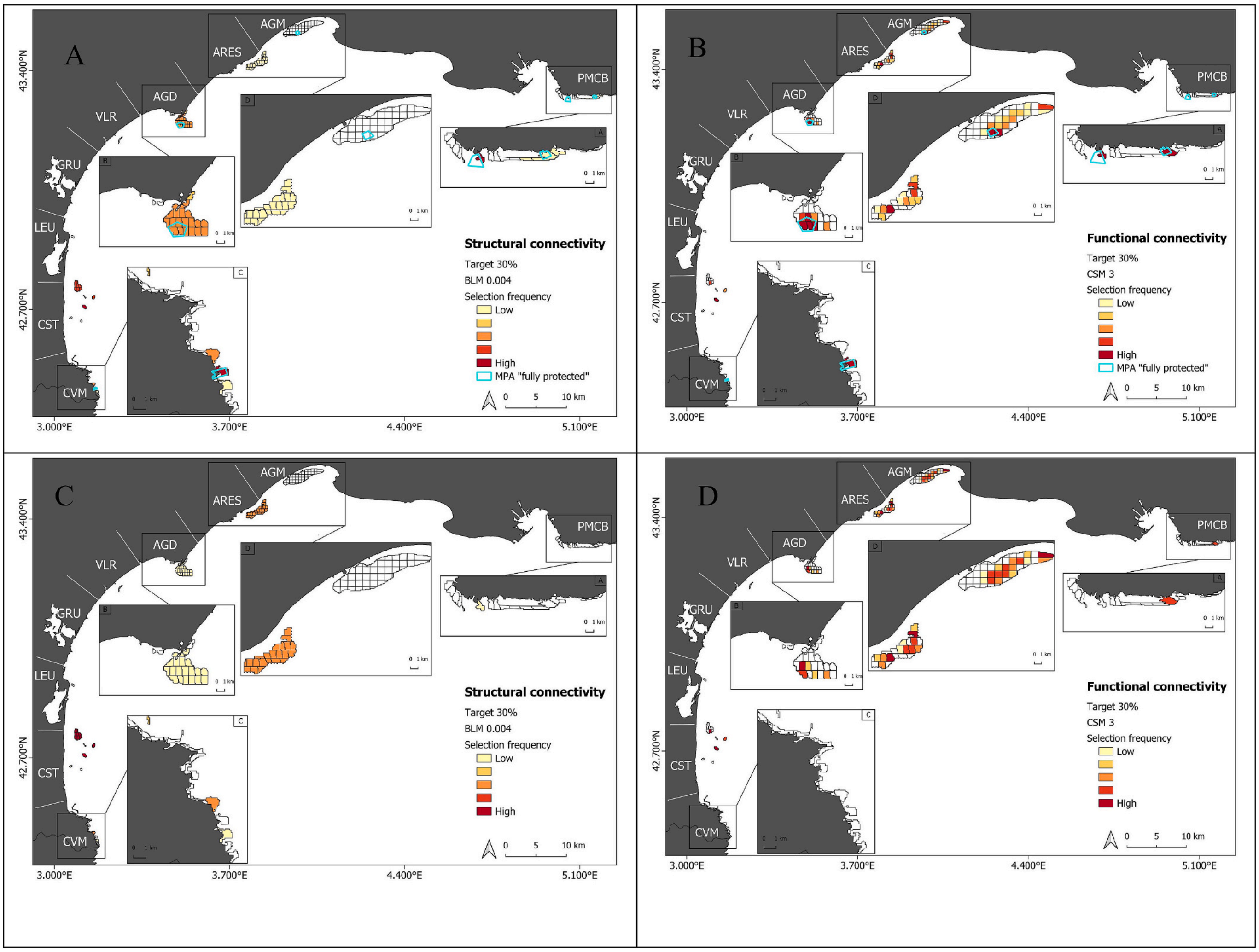

Fig. 3. Selection frequency of planning units obtained with Marxan in the objective of fully protecting 30 % of the hard bottom habitat surface in 4 configurations: including existing highly protected areas (upper panels) and structural connectivity (A, BLM = 0.004) or early summer functional connectivity as asymmetric spatial dependence (B, CSM = 3) and ignoring existing highly protected areas (lower panels) and structural (C, BLM = 0.004) or early summer functional connectivity as asymmetric spatial dependence (D, CSM = 3). The five classes of selection frequencies obtained from the 100 runs used were: 30–44 % (low), 44–58 %, 58–72 %, 72–86 %, 86–100 % (high). (PMCB = Côte Bleue, AGM = Aigues-Mortes, ARES = Aresquiers, AGD = Agde, VLR = Valras, GRU = Gruissan, LEU = Leucate, CST = Saint-Cyprien, CVM = Côte Vermeille).

vs. D).

In the conservation objective of 10 %, conservation plans with structural connectivity, targeted isolated PUs in Côte Bleue, Saint-Cyprien and Côte Vermeille (Fig. 2A and C). These plans obtained with BLM set to 0.004 did not select PUs from the center of the Gulf of Lion, in contrast with those obtained with BLM set to 0 (Fig. S5A and C) or 1 (Fig. S5B and D). The former being least cost oriented selected large PUs in Agde, Aresquiers, and Aigues-Mortes that had the lowest cost (Fig. S5A and C). The latter being compact oriented priviledged PUs in all large continuous habitat sites with little selectivity, excluding the fragmented habitat of Saint-Cyprien and Côte Vermeille (Fig. S5B and D). In contrast, conservation plans with functional connectivity included PUs from the center of the Gulf of Lion (Fig. 2B), and mainly them if ignoring existing highly protected areas (Fig. 2D), similarly to the most compact solutions (BLM = 0) but more selectively. Noteworthy, with functional connectivity, PUs from Côte Vermeille were not prioritized in conservation plans in the 10 % objective when ignoring existing highly protected areas. As expected, conservation plans tended to favor existing highly protected areas, when taking into account their reduced cost, resulting in little variability among conservation plans in the conservation objective of 10 %.

In the conservation objective of 30 %, with structural connectivity, PUs in Saint-Cyprien and existing highly protected areas (when their reduced cost was considered) were highly selected, complemented by PUs moderately selected in Agde (Fig. 3A and C). Selection frequency of PUs in Plateau des Aresquiers and Aigues-Mortes was low or unsignificant (Fig. 3A and C). In contrast, with functional connectivity, conservation plans were consistently selecting the same set of PUs distributed throughout the region, including the center of the Gulf of Lion (Fig. 3B and D). Like in the conservation objective of 10 %, conservation plans in the 30 % objective selected all existing highly protected areas, when their reduced cost was considered (Fig. 3B). Notably, PUs corresponding to existing highly protected areas of Agde, Aigues-Mortes, and Côte Bleue were also selected in conservation plans in the 30 % objective when ignoring existing highly protected areas (Fig. 3D). With functional connectivity, no PUs from Côte Vermeille were selected in conservation plans in the 30 % objective when ignoring existing highly protected areas (Fig. 3D).

Conservation plans obtained using early or late summer functional connectivity were very similar to each other, under the same conditions of costs and conservation objectives, sharing over 70 % of the variance in PU selection frequencies (Fig. S6A versus Fig. 2B – $R^2 = 0.82$; Fig. S6C versus Fig. 2D - $R^2 = 0.73$; Fig. S6B versus Fig. 3B – $R^2 = 0.89$; Fig. S6D versus Fig. 3D – $R^2 = 0.76$).

In terms of protection effect, there was a large variability in the proportion of the Gulf of Lion individuals concerned by conservation plans with 10 % objective whatever the connectivity type, varying from 0 % to 30.4 % for *E. singularis,* 39.1 % for L. *sarmentosa,* 54.2 % for *E. cavolinii,* 24.5 % for *P. clavata,* and 71.6 % for *C. rubrum* (Fig. S7). Using structural connectivity to extend existing highly protected areas, a minimum of 3 % (0.5 %, 2.1 %, 6.6 %) of the Gulf of Lion individuals of *E. singularis* (*L. sarmentosa, P. clavata* and *C. rubrum*, respectively) was included in conservation plans, while ignoring existing highly protected areas could lead to no protection at all (Fig. S7). Using functional connectivity to extend existing highly protected areas, a minimum of 4.6 % and 6.1 % of the Gulf of Lion individuals of *E. singularis* and L. *sarmentosa* was included in conservation plans, while ignoring existing highly protected areas could lead to no protection at all (Fig. S7). For the other three species, using functional connectivity could lead to no protection at all, including or ignoring existing highly protected areas. In the 10 % conservation plans, the proportion of the Gulf of Lion individuals for *E. singularis* and L. *sarmentosa* was at least 14.1 % and 15.3 % with functional connectivity compared to 4.4 % and 1.6 % with structural connectivity in half of plans (Fig. S7). The proportion of the Gulf of Lion individuals for *E. cavolinii* and *C. rubrum* was at least 17.9 % and 26 % in half of plans, whatever the connectivity as long as existing highly protected areas were included. In contrast, conservation plans with 10 % objective were in most cases uneffective for *P. clavata* with <3.5 % of the Gulf of Lion individuals protected in half of plans, whatever the connectivity and whether existing highly protected areas were included or not. It was still the case in conservation plans with 30 % objective for this rare species in the region. For the other four species, raising the conservation objective to 30 % had different effect. For *E. singularis* and L. *sarmentosa*, protection effect was still larger when including existing highly protected areas compared to ignoring them whatever the connectivity, and this effect was bigger with structural connectivity (46 % and 81 %, respectively in half of the plans) than with functional connectivity (41.5 % and 38 %, respectively in half of the plans). It could reach up to 71 % of the *E. singularis* and 93 % of L. *sarmentosa* individuals of the Gulf of Lion in some plans with structural connectivity while yielding a maximum of 50 % of *E. singularis* and 75 % for L. *sarmentosa* with late summer functional connectivity. However, some 30 % objective conservation plans with structural connectivity could also protect <20 % of the L. *sarmentosa* Gulf of Lion individuals (Fig. S8). For *E. cavolinii* and *C. rubrum,* raising the conservation objective to 30 % had the same protection effect wether including or not existing highly protected areas, but increased more with functional connectivity (25.7 % and 26.3 %, respectively in half of the plans) than with structural connectivity (19.2 % and 11.7 %, respectively in half of the plans). However, as for *E. singularis* and *L. sarmentosa*, in the 30 % objective, the protection effect could reach up to 78.1 % of the *E. cavolinii* and 76.6 % of *C. rubrum* individuals of the Gulf of Lion in some plans with structural connectivity while yielding a maximum of 43.3 % of *E. cavolinii* and 50.5 % for *C. rubrum* with functional connectivity (Fig. S8). In summary, a functional connectivity criterion improved protection effect compared to a structural one in the conservation objective of 10 % for four of the five species, and this effect was enhanced when including the existing highly protected areas. In the conservation objective of 30 %, functional connectivity did better than stuctural connectivity for only two of the four species while for the other two species including existing highly protected areas had the most importance. Very few plans would protect the fifth and most rare species, whatever the scenarios. In addition, it is highlighted that the structural connectivity criterion lead to highly variable protection effect for the five species.

In terms of protection cost, the functional connectivity (early or late summer) criterion reduced it compared to structural connectivity by a factor 1.5 to 3, and even more when extending existing highly protected areas, whatever the conservation objective (Figs. S7 and S8).

By combining reduced costs with effective protection, the median profitability of 10 % conservation plans increased significantly when structural connectivity was replaced with functional connectivity (early or late summer) and existing highly protected areas were included, for four of the five species. For *E. singularis*, profitability rose from 0.6 to 4.1 using early summer functional connectivity (or to 6.3 using late summer functional connectivity, Fig. 4A). Similarly, for L. *sarmentosa*, it increased from 2 to 4.6 (or to 6.9 under the same conditions, Fig. 4B), for *E. cavolinii*, it improved from 2.3 to 5.5 (or to 5.6, Fig. 4C) and for *C. rubrum*, it improved from 4.4 to 8.1 (or to 8.7, Fig. 4E). In all cases, the median profitability of 10 % conservation plans was close to zero for *P. clavata* (Fig. 4D).

Raising the conservation objective to 30 % reduced the median profitability of conservation plans, regardless of the connectivity criteria used. For *E. singularis*, profitability increased less than in the 10 % objective, from 2 to 2.7 with early summer functional connectivity (or to 2.8 with late summer functional connectivity; Fig. 4A) under the 30 % objective. For L. *sarmentosa*, structural connectivity resulted in more efficient conservation plans than functional connectivity in more than half of the cases, though it could also lead to entirely inefficient plans in others (Fig. 4B), resulting in comparable median profitability. In contrast, for *E. cavolinii*, profitability increase was a factor two as in the 10 % objective, from 0.8 to 1.7 (or to 1.7 under the same conditions,; Fig. 4C), and for *C. rubrum*, profitability increase was a factor four (twice

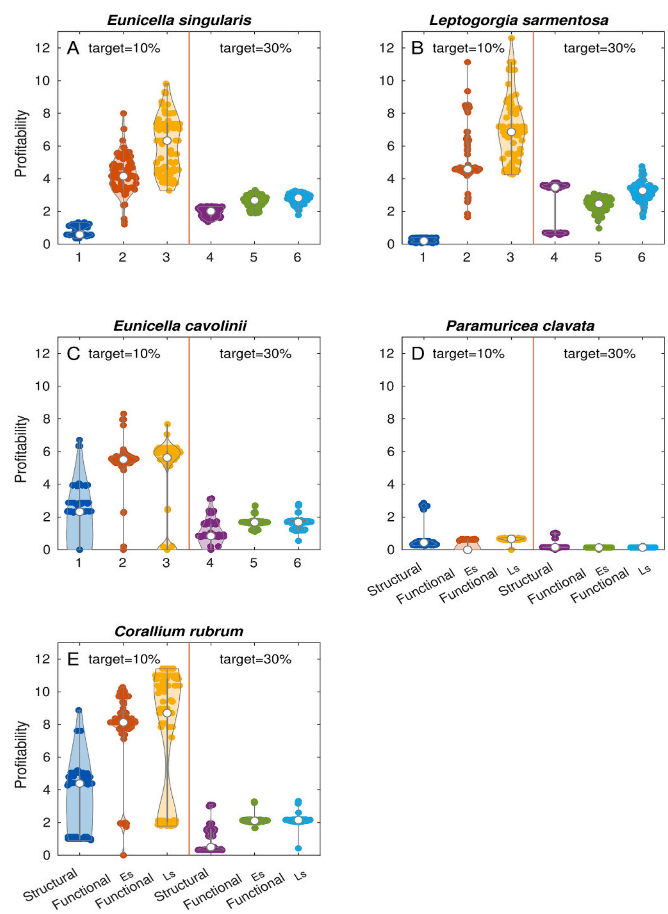

Fig. 4. : Violin plots of the profitability of the 100 conservation plans in protecting *Eunicella singularis* (A), *Leptogorgia sarmentosa* (B), *Eunicella cavolinii* (C), *Paramuricea clavata* (D) and *Corallium rubrum* (E) for the targets of 10 % and 30 % protection of the hard bottom habitat in the different connectivity scenarios: structural (BLM = 0.004), functional in the early summer (Es, CSM = 3), functional in the late summer (Ls, CSM = 3), extending the current highly protected. Cost of the conservation plans were calculated using the current cost with HPAs.

the one in the 10 % objective), from 0.5 to 2.1 (or to 2.1; Fig. 4E). As with the 10 % objective, the median profitability of 30 % conservation plans remained close to zero for *P. clavata*.

When existing highly protected areas were excluded, replacing structural connectivity with functional connectivity still increased the profitability of conservation plans for both conservation objectives and the four target species. However, the profitability gains were smaller (Fig. S9).

4. Discussion

This study demonstrates that systematic conservation planning (SCP) for protecting 10 % or 30 % of hard bottom habitats in the Gulf of Lion, while minimizing costs and conflicts with resource users, yields different outcomes depending on the connectivity criteria used. The inclusion or exclusion of existing highly protected areas had a greater impact on the 10 % objective than on the 30 % objective. Plans incorporating functional connectivity consistently recommended extending highly protected areas in Agde (southeastern part), Aigues-Mortes (central part), and adding a new protected area in Aresquiers, connecting distant hard bottom habitats. These findings support the long-standing consensus that a network of small to medium-sized MPAs, which achieve persistence through mutual offspring exchange, is more socially acceptable and cost-effective than relying on large, self-sustaining MPAs (Halpern and Warner, 2003). Functional connectivity proved more profitable than structural connectivity, reducing costs and improving protection for most gorgonian species, except for the rarest species, *Paramuricea clavata*, which remained unprotected. Overall, profitability was lower under the 30 % objective compared to the 10 % target.

4.1. Habitat-based conservation and its limitations

In marine conservation, habitats are often used as surrogates for biodiversity due to limited knowledge of species distributions (Costello et al., 2010). The assumption is that protecting a representative sample of habitats will also protect associated biodiversity (Ward et al., 1999). This principle underpins international biodiversity goals. Recent SCP studies incorporating functional connectivity, often derived from larval dispersal models, have focused on habitat-based conservation targets (Schill et al., 2015; Krueck et al., 2017; Muenzel et al., 2022a, 2022b). However, the effectiveness of habitat-based approaches in ensuring population persistence remains understudied. Insufficient representation of species within protected areas can accelerate genetic and demographic collapse (Allee, 1931). This study highlights that relying solely on broad habitat descriptors, such as hard bottom habitats, can lead to ineffective conservation plans, particularly for patchily distributed species like the five gorgonians studied. Including existing highly protected areas, informed by biodiversity inventories (e.g., Laubier, 1966 in Côte Vermeille), improved plan effectiveness. Larger protection targets (e.g., 30 %) mitigated the risks associated with species patchiness, but refining habitat maps at the species level using distribution models could also enhance conservation outcomes (Combes et al., 2021). For example, mapping the restricted extent of suitable habitat for *P. clavata* and *Corallium rubrum* would improve their protection (Blouet et al., 2024). In contrast, for the other three species, suitable habitat maps are less informative while functional connectivity constraints proved critical to capture the abundance patchiness within suitable habitats. These results suggest that smaller protection targets require more precise data on both suitable habitats and functional connectivity.

4.2. Challenges in integrating connectivity into SCP

Despite advances in connectivity modeling, integrating population connectivity into SCP remains challenging, particularly in marine environments (Virtanen et al., 2020; Beger et al., 2022). Marine connectivity, driven by larval dispersal in ocean currents, is directional and often spans large distances, transcending habitat fragmentation (Kinlan and Gaines, 2003). Early SCP tools like Marxan and Zonation (Lehtomäki and Moilanen, 2013) could not handle connectivity as a directed flux and required transforming directed connectivity into hierarchical maps using metrics like betweenness centrality, self-recruitment, or out-degree (Treml and Halpin, 2012; White et al., 2014) or a cost using an inverse measure of connectivity (Krueck et al., 2017; André et al., 2022). However, different metrics can lead to varying PU hierarchies, reducing the reliability of decision-support tools (Magris et al., 2016). Combining multiple metrics (e.g., local retention, outflux, and betweenness centrality) has been proposed to improve robustness (Magris et al., 2018). Recent tools like Marxan Connect allow for direct integration of spatial dependencies, offering a more direct approach to connectivity (Beger et al., 2010, 2015; Muenzel et al., 2022a). In this study, we prioritized spatial dependencies to preserve functional loops across generations, ensuring long-term species persistence (Hastings and Botsford, 2006). However, neither method fully captures the long-term persistence of metapopulations, as they do not account for flux intensity or population history (Moilanen, 2011). Hence, spatially explicit metapopulation modeling have been used to test those methods (Magris et al., 2018; Muenzel et al., 2022a). Spatial dependency methods are particularly suitable for degraded habitats, limited dispersal or low conservation targets, while site-based metrics perform better in well-connected, high-quality habitats or high conservation targets (Muenzel et al., 2022a). However, evaluating the way to integrate connectivity versus metapopulation modeling based on the same connectivity do not inform on the reliability of the connectivity structure itself, which might be incomplete or uncertain. To our knowledge, this is the first SCP study in a marine setting crossing real cost estimates with directed connectivity estimates that showed using population census data that integrating functional connectivity using spatial dependencies is more profitable than structural connectivity.

4.3. Spatial scales and uncertainties in connectivity modeling

Integrating connectivity into SCP requires examining connections across all relevant spatial scales, which can range from a few kilometers for adult fish movements to hundreds of kilometers for larval dispersal (D'Aloia et al., 2015; Jessopp and McAllen, 2007; Palumbi, 2004). However, only scales compatible with those at which protection measures can be implemented in practice are relevant for SCP (Watson et al., 2009). Larval dispersal models, while useful, are sensitive to the accuracy of parameters like flow speed, release timing, and larval duration. In this study, flow speeds were resolved at an 80-m resolution, validated at eight locations in the Gulf of Lion (Vissenaekens et al., 2023). Despite this precision, uncertainties remain due to limited knowledge of biological traits, such as larval duration and buoyancy. For *Eunicella singularis*, *P. clavata*, and *C. rubrum*, field and laboratory studies have provided some data, but for *Leptogorgia sarmentosa* and *Eunicella cavolinii*, information is scarce (Gori et al., 2007; Guizien et al., 2020; Zelli et al., 2020). A week-long dispersal duration was validated for *E. singularis* using genetic data (Padrón et al., 2018). For *P. clavata* and *C. rubrum,* genetic differentiation between populations dwelling at the two extreme tips of the Gulf of Lion suggests limited connectivity across the Gulf of Lion (Ledoux et al., 2010; Mokhtar-Jamaï et al., 2011). Refining habitat delineation at the species level would have helped filter out irrelevant connectivity estimates *(*Blouet et al., 2024*)*. Combining multiple connectivity estimates in SCP is desirable but still methodologically challenging (D'Aloia et al., 2017).

4.4. Robustness of prioritization and policy implications

Despite uncertainties in larval traits, the prioritization of highly protected areas in the central Gulf of Lion appears robust. This region has been identified as critical for both local and regional persistence across a range of dispersal durations and buoyancy behaviors for soft-bottom species (Guizien et al., 2012, 2014). These findings have been shared with national and regional decision-makers to inform the extension of highly protected areas in the Gulf of Lion, with the goal of raising the status of the Agde area as a National Reserve.

CrediT authorship contribution statement

Sylvain Blouet: Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Investigation, Data curation, Conceptualization. **Thibaud Tournadre:** Writing – review & editing, Validation, Investigation, Data curation. **Skandar Hentati:** Writing – review & editing, Resources, Investigation, Data curation. **Katell Guizien:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Impact statement

First tested operational systematic conservation planning integrating functional connectivity due to larval dispersal in the NW Mediterranean sea

Declaration of competing interest

The authors of this publication declare that they have no financial conflicts of interest with the content of this article.

Acknowledgements

This work was funded by the Programme National Français LITEAU IV of the Ministère de l'Ecologie et de l'Environnement Durable as part of the RocConnect project - Connectivité des habitats rocheux fragmentés du golfe du Lion (PI, K. Guizien, Project Number 12-MUTS-LITEAU-1-CDS-013) and by the Agence de l'Eau Rhône-Méditerranée-Corse as part of the ICONE project - Impacts actuels et potentiels de la CONnectivité Ecologique ajoutés par les récifs artificiels sur la biodiversité fixée des substrats durs du Golfe du Lion (PI, K. Guizien, Convention 2018 0697). The authors would like to thank R. Bricout, B. Hesse, L. Lescure, J.-C. Roca, and the staff of the Aire marine protégée de la côte agathoise, the Réserve nationale marine de Cerbère-Banyuls and the Parc marin de la Côte bleue and Thomas Bockel from Andromède océanologie for making available the MEDTRIX data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111112.

Data availability

Data will be made available on request.

References

Allee, W.C., 1931. Animal Aggregations, a Study in General Sociology. The University of Chicago Press, Chicago. https://doi.org/10.5962/bhl.title.7313.
Álvarez-Romero, J.G., Mills, M., Adams, V.M., Gurney, G.G., Pressey, R.L., Weeks, R., Ban, N.C., Cheok, J., Davies, T.E., Day, J.C., Hamel, M.A., Leslie, H.M., Magris, R.A., Storlie, C.J., 2018. Research advances and gaps in marine planning: towards a global database in systematic conservation planning. Biol. Conserv. https://doi.org/10.1016/j.biocon.2018.06.027.
André, L.V., Chinain, M., Cmi, Gatti, Liao, V., Van Wynsberge, S., Tedesco, P., Andréfouët, S., 2022. A systematic prioritization approach for identifying suitable pearl oyster restocking zones following a mass mortality event in Takaroa Atoll. French Polynesia. Marine Pollution Bulletin. 176, 113472.
Ardron JA, Possingham HP, Klein CJ. 2010. Marxan Good Practices Handbook, Version 2. Pacific Marine Analysis and Research Association, Victoria, BC, Canada. 165 pages. www.pacmara.org.
Balbar, A.C., Metaxas, A., 2019. The current application of ecological connectivity in the design of marine protected areas. Global Ecology and Conservation 17, e00569.
Ball, I., Possingham, H., 2000. Marine Reserve Design using Spatially Explicit Annealing.
Ball IR, Possingham HP, Watts ME. 2009. Marxan and Relatives: Software for Spatial Conservation Prioritization: in Spatial conservation prioritisation: Quantitative methods and computational tools., Eds : A. Moilanen, K.A. Wilson, and H.P. Possingham. Oxford University Press: 185–195.
Ballesteros, E., 2006. Mediterranean coralligenous assemblages: A synthesis of present knowledge. Oceanogr. Mar. Biol. Annu. Rev. 44, 123–195.
Bandelj, V., Solidoro, C., Laurent, C., Querin, S., Kaleb, S., Gianni, F., Falace, A., 2020. Cross-scale connectivity of macrobenthic communities in a patchy network of habitats: The Mesophotic Biogenic Habitats of the Northern Adriatic Sea. Estuar. Coast. Shelf Sci. 245, 106978.
Beger, M., Linke, S., Watts, M., Game, E., Treml, E., Ball, I., Possingham, H.P., 2010. Incorporating asymmetric connectivity into spatial decision making for conservation. Conserv. Lett. 3, 359–368.
Beger, M., Selkoe, K.A., Treml, E., Barber, P.H., Von Der Heyden, S., Crandall, E.D., Toonen, R.J., Riginos, C., 2014. Evolving coral reef conservation with genetic information. Bull. Mar. Sci. 90 (1), 159–185. https://doi.org/10.5343/bms.2012.1106.
Beger, M., McGowan, J., Treml, E.A., Green, A.L., White, A.T., Wolff, N.H., Klein, C.J., Mumby, P.J., Possingham, H.P., 2015. Integrating regional conservation priorities for multiple objectives into national policy. In: Nature Communications 6:8208. Nature Publishing, Group.
Beger, M., Metaxas, A., Balbar, A.C., McGowan, J.A., Daigle, R., Kuempel, C.D., Treml, E. A., Possingham, H.P., 2022. Demystifying ecological connectivity for actionable spatial conservation planning. Trends Ecol. Evol. 37, 1079–1091.
Blouet, S., Bramanti, L., Guizien, K., 2024. Ecological niche modelling of five gorgonian species within the shallow rocky habitat of the french mediterranean coast. Vie et Milieu / Life & Environment 2024 (7), 1–43.
Briton, F., Cortese, D., Duhaut, T., Guizien, K., 2018. High-resolution modelling of ocean circulation can reveal retention spots important for biodiversity conservation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 28, 882–893.
Carr, M.H., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E.J., Williams, M., 2017. The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. Aquat. Conserv. Mar. Freshwat. Ecosyst. 27, 6–29.
Casati R (2024) The cognitive life of maps. The MIT Press. 256 pp. ISBN: 9780262547086.
CBD, 2022. Kunming-Montreal Global Biodiversity Framework. Draft decision submitted by the President. Fifteenth meeting – Part II of the Conference of the Parties to the Convention on Biological Diversity. 7–19 December 2022, Montreal, Canada. CBD/COP/15/L.25. Available at. https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf.
Chen, Z., Zhang, H., Xu, M., Liu, Y., Fang, J., Yu, X., Zhang, S., 2022. A study on the ecological zoning of the Nantong coastal zone based on the Marxan model. Ocean Coast. Manag. 229, 106328.
Combes, M., Vaz, S., Grehan, A., Morato, T., Arnaud-Haond, S., Dominguez-Carrió, C., Fox, A., González-Irusta, J.M., Johnson, D., Callery, O., Davies, A., Fauconnet, L., Kenchington, E., Orejas, C., Roberts, J.M., Taranto, G., Menot, L., 2021. Systematic Conservation Planning at an ocean basin scale: Identifying a viable network of deep-sea protected areas in the North Atlantic and the Mediterranean. Front. Mar. Sci. 8, 611358. https://doi.org/10.3389/fmars.2021.611358.
Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., Miloslavich, P., 2010. A census of marine biodiversity knowledge, resources, and future challenges. PLoS One 5, e12110.
Crooks, K.R., Sanjayan, M.A., 2006. Connectivity Conservation: Maintaining Connections for Nature. In: Crooks, K.R., Sanjayan, M. (Eds.), Connectivity Conservation. Cambridge University Press, Cambridge, pp. 1–20. https://doi.org/10.1017/cbo9780511754821.001.
D'Aloia, C.C., Bogdanowicz, S.M., Francis, R.K., Majoris, J.E., Harrison, R.G., Buston, P. M., 2015. Patterns, causes, and consequences of marine larval dispersal. Proc. Natl. Acad. Sci. 112, 13940–13945.
D'Aloia, C.C., Daigle, R.M., Côté, I.M., Curtis, J.M.R., Guichard, F., Fortin, M.-J., 2017. A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biol. Conserv. 216, 93–100.
Daigle, R.M., Metaxas, A., Balbar, A.C., McGowan, J., Treml, E.A., Kuempel, C.D., Possingham, H.P., Beger, M., 2020. Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. Methods Ecol. Evol. 11, 570–579.
Font, T., Lloret, J., 2014. Biological and ecological impacts derived from recreational fishing in Mediterranean coastal areas. Rev. Fish. Sci. Aquac. 22 (1), 73–85.
Gili, J.M., Coma, R., 1998. Benthic suspension feeders: Their paramount role in littoral marine food webs. Trends Ecol. Evol. 13, 316–321. https://doi.org/10.1016/S0169-5347(98)01365-2.
Goetze, J.S., et al., 2021. Increased connectivity and depth improve the effectiveness of marine reserves. Glob. Chang. Biol. 27, 3432–3447.
Gori, A., Linares, C., Rossi, S., Coma, R., Gili, J.M., 2007. Spatial variability in reproductive cycle of the gorgonians *Paramuricea clavata* and *Eunicella singularis* (Anthozoa, Octocorallia) in the Western Mediterranean Sea. Mar. Biol. 151, 1571–1584.
Grorud-Colvert, K., et al., 2021. The MPA Guide: A framework to achieve global goals for the ocean. Science 373 (6560), 1–10 eabf0861.
Guizien, K., Belharet, M., Marsaleix, P., Guarini, J.M., 2012. Using larval dispersal simulations for marine protected area design: Application to the Gulf of Lions (northwest Mediterranean). Limnol. Oceanogr. 57, 1099–1112.
Guizien, K., Belharet, M., Moritz, C., Guarini, J.M., 2014. Vulnerability of marine benthic metapopulations: implications of spatially structured connectivity for conservation

practice in the Gulf of Lions (NW Mediterranean Sea). Divers. Distrib. 20, 1392–1402.
Guizien, K., Viladrich, N., Martínez-Quintana, Á., Bramanti, L., 2020. Survive or swim: different relationships between migration potential and larval size in three sympatric Mediterranean octocorals. In: Scientific Reports 10:18096. Nature Publishing, Group.
Guizien K et al. 2022. Database of sea fans spatial distribution in the northwestern Mediterranean sea. [dataset] SEANOE. Doi :10.17882/86176. Available from https://www.seanoe.org/data/00750/86176/.
Halpern BS, Warner RR. 2003. Review Paper. Matching marine reserve design to reserve objectives. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:1871–1878. Royal Society.
Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C., Scarborough, C., Selkoe, K.A., 2019. Recent pace of change in human impact on the world's ocean. In: Scientific Reports 9:11609. Nature Publishing, Group.
Hanski, I., 1998. Metapopulation dynamics. In: Nature 396:41–49. Nature Publishing, Group.
Hastings, A., Botsford, L., 2006. Persistence of spatial populations depends on returning home. Proc. Natl. Acad. Sci. USA 103, 6067–6072.
Hastings, A., Harrison, S., 1994. Metapopulation dynamics and genetics. Annu. Rev. Ecol. Evol. Syst. 25, 167–188. https://doi.org/10.1146/annurev.es.25.110194.001123.
Holon, F., Mouquet, N., Boissery, P., Bouchoucha, M., Delaruelle, G., Tribot, A.-S., Deter, J., 2015. Fine-Scale Cartography of Human Impacts along French Mediterranean Coasts: A Relevant Map for the Management of Marine Ecosystems. PLoS One 10, e0135473.
Horta e Costa, B., Claudet, J., Franco, G., Erzini, K., Caro, A., Gonçalves, E.J., 2016. A regulation-based classification system for Marine Protected Areas (MPAs). Mar. Policy 72, 192–198.
Jessopp, M., McAllen, R., 2007. Water retention and limited larval dispersal: implications for short and long distance dispersers in marine reserves. Mar. Ecol. Prog. Ser. 333, 27–36.
Kinlan, B.P., Gaines, S.D., 2003. Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. In: Ecology 84:2007–2020. America, Ecological Society of.
Kirckpatrick, J.B., 1983. An lterative Method for Establishing Priorities for the Selection of Nature Reserves: An Example From Tasmania. Biol. Cons. 25, 127–134.
Krueck, N.C., Ahmadia, G.N., Green, A., Jones, G.P., Possingham, H.P., Riginos, C., Treml, E.A., Mumby, P.J., 2017. Incorporating larval dispersal into MPA design for both conservation and fisheries. Ecol. Appl. 27, 925–941.
Laubier, L., 1966. Le coralligène des Albères: monographie biocénotique. Annales de l'Institut Océanographique de Monaco 43, 139316.
Lea, J.S.E., Humphries, N.E., Von Brandis, R.G., Clarke, C.R., Sims, D.W., 2016. Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. Proc. R. Soc. B Biol. Sci. 283, 20160717.
Ledoux, J.B., Mokhtar-Jamaï, K., Roby, C., Feral, J.P., Garrabou, J., Aurelle, D., 2010. Genetic survey of shallow populations of the Mediterranean red coral [Corallium rubrum (Linnaeus, 1758)]: new insights into evolutionary processes shaping nuclear diversity and implications for conservation. Mol. Ecol. 19, 675–690.
Lehtomäki, J., Moilanen, A., 2013. Methods and workflow for spatial conservation prioritization using Zonation. Environ. Model Softw. 47, 128–137.
Magris, R.A., Treml, E.A., Pressey, R.L., Weeks, R., 2016. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography 39, 649–664.
Magris, R.A., Andrello, M., Pressey, R.L., Mouillot, D., Dalongeville, A., Jacobi, M.N., Manel, S., 2018. Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. Conserv. Lett. 11, e12439.
van Mantgem, E.S., Hillebrand, J., Rose, L., Klau, G.W., 2023. Coco : conservation design for optimal ecological connectivity. Front. Ecol. Evol. 11, 1149571. https://doi.org/10.3389/fevo.2023.1149571.
Milazzo, M., Chemello, R., Badalamenti, F., Camarda, R., Riggio, S., 2002. The impact of human recreational activities in marine protected areas: what lessons should be learnt in the Meditteranean Sea? Mar. Ecol. 23, 280–290.
Millot, C., 1990. The Gulf of Lion's hydrodynamics. Cont. Shelf Res. 10 (9–11), 885–894.
Ministère de la Transition Ecologique et de la Cohésion des Territoires. 2023. Stratégie Nationale Biodiversité 2030. https://biodiversite.gouv.fr/la-strategie-nationale-biodiversite-2030, accessed Sept. 11, 2024.
Moilanen, A., 2011. On the limitations of graph-theoretic connectivity in spatial ecology and conservation. J. Appl. Ecol. 48, 1543–1547.
Mokhtar-Jamaï, K., Pascual, M., Ledoux, J.B., Coma, R., Féral, J.P., Garrabou, J., Aurelle, D., 2011. From global to local genetic structuring in the red gorgonian Paramuricea clavata : the interplay between oceanographic conditions and limited larval dispersal. Mol. Ecol. 20, 3291–3305.
Muenzel D, Critchell K, Cox C, Campbell S, Jakub R, Chollett I, Krueck N, Holstein D, Treml E, Beger M. 2022a. Comparing spatial conservation prioritization methods with site versus spatial dependency-based connectivity. Conservation BiologyDOI: https://doi.org/10.1111/cobi.14008.
Muenzel D, Critchell K, Cox C, Campbell S, Jakub R, Suherfian W, Sara L, Chollett I, Treml E, Beger M. 2022b. Integrating larval connectivity into the marine conservation decision-making process across spatial scales. Conserv. Biol.DOI: https://doi.org/10.1111/cobi.14038.
Padrón, M., Costantini, F., Baksay, S., Bramanti, L., Guizien, K., 2018. Passive larval transport explains recent gene flow in a Mediterranean gorgonian. Coral Reefs 37.
Palumbi, S.R., 2004. Marine reserves and ocean neighborhoods : the Spatial Scale of Marine Populations and Their Management. Annu. Rev. Environ. Resour. 29, 31–68.
ProtectedPlanet, 2024. https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas, accessed Sept. 11, 2024.
Rossi, S., Gili, J.-M., 2009. The cycle of gonadal development of the soft bottom-gravel gorgonian Leptogorgia sarmentosa in the NW Mediterranean sea. Invertebr Reprod Dev. Invertebr. Reprod. Dev. 53, 175–190.
Rossi S, Bramanti L, Gori A, Orejas C (Eds.) 2017. Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots. Springer, Cham, 505p. https://www.springer.com/gp/book/9783319210117.
Rossi, V., Ser Giacomi, E., Lopez Cristobal, A.A., Hernandez-Garcia, E., 2014. Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. Geophys. Res. Lett. 9 (41), 2883–2891.
Sala, E., Garrabou, J., Zabala, M., 1996. Effects of diver frequentation on Mediterranean sublittoral populations of the bryozoan Pentapora fascialis. Mar. Biol. 126, 451–459.
Schill, S.R., Raber, G.T., Roberts, J.J., Treml, E.A., Brenner, J., Halpin, P.N., 2015. No reef is an island: integrating coral reef connectivity data into the design of regional-scale marine protected area networks. PLoS One 10, e0144199.
Stewart, R.R., Possingham, H.P., 2005. Efficiency, costs and trade-offs in marine reserve system design. Environ. Model. Assess. 10, 203–213.
The Marine Protection Atlas. 2024. https://mpatlas.org/, accessed Sept. 11, 2024.
Treml, E.A., Halpin, P.N., 2012. Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle. Conserv. Lett. 5 (2012), 441–449.
Virtanen, E.A., Moilanen, A., Viitasalo, M., 2020. Marine connectivity in spatial conservation planning: analogues from the terrestrial realm. Landsc. Ecol. 35, 1021–1034.
Vissenaekens, E., Guizien, K., Durrieu de Madron, X., Pairaud, I., Leredde, Y., Puig, P., Bourrin, F., 2023. Accuracy of high resolution coastal flow speed simulations during and outside of wind, wave and stratification events (Gulf of Lion, NW Mediterranean). J. Mar. Syst. 239 (103845), 1–13. https://doi.org/10.1016/j.jmarsys.2022.103845.
Ward, T., Vanderklift, M., Nicholls, A., Kenchington, R., 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. Ecol. Appl. 9, 691–698.
Watson JEM, Grantham HS, Wilson KA, Possingham HP. 2009 'Systematic conservation planning: Past, present and future'. in Atte Moilanen, Kerrie A Wilson, and Hugh P Possingham, Spatial Conservation Prioritization: Quantitative Methods and Computational Tools, doi:https://doi.org/10.1093/oso/9780199547760.003.0002.
White, J.W., Schroeger, J., Drake, P.T., Edwards, C.A., 2014. The Value of Larval Connectivity Information in the Static Optimization of Marine Reserve Design. Conserv. Lett. 7, 533–544.
Wilson KA, Cabeza M, Klein CJ. 2009. Fundamental Concepts of Spatial Conservation Prioritization. Page 0 in Moilanen A, Wilson KA, Possingham HP, editors. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press. Available from doi:https://doi.org/10.1093/oso/9780199547760.003.0002 (accessed September 26, 2024).
Zelli, E., Quéré, G., Lago, N., Di Franco, G., Costantini, F., Rossi, S., Bramanti, L., 2020. Settlement dynamics and recruitment responses of Mediterranean gorgonians larvae to different crustose coralline algae species. J. Exp. Mar. Biol. Ecol. 530–531, 151427.
Zhao, Q., Stephenson, F., Lundquist, C., Kaschner, K., Jayathilake, D., Costello, M.J., 2020. Where Marine Protected Areas would best represent 30% of ocean biodiversity. Biol. Conserv. 244, 108536.