Photo credit: Steve Lonhart

Assessing Connectivity Across the California Marine Protected Area Network

Final Report to the Ocean Protection Council/C0752002

Principal investigator: Peter Raimondi
Co-Principal investigator: Will White
Co-Principal investigator: Mark Carr
Lead Analyst and Report Author: Mallarie Yeager
Associate Investigator: Dan Malone

AUTHORS

Mallarie Yeager
U.C. Santa Cruz

Will White
Oregon State University

Mark Carr
U.C. Santa Cruz

Dan Malone
U.C. Santa Cruz

Peter Raimondi
U.C. Santa Cruz

ACKNOWLEDGMENTS

We would like to thank Chris Edwards and Patrick Drake for providing us ROMS simulations, Tom Bell for help on obtaining environmental and kelp Landsat variables, Chris Free for help with the spatial fishing pressure metrics, and Emily Saarman for help with bathymetry and habitat calculations

SUGGESTED CITATION

Yeager ME, White W, Carr MH, Malone D and Raimondi P. 2023. Assessing connectivity across the California Marine Protected Area Network.

Table of Contents

Executive Summary

The 1999 Marine Life Protection Act mandated that California's array of Marine Protected Areas be designed to operate as a network, and that they should be monitored, evaluated, and adaptively managed to ensure that they are doing so. In this report we present the first such evaluation of network functionality in California's MPAs. What it means to operate 'as a network' is not legislatively defined so we proceeded with two operational definitions. First, from an ecological perspective, we considered connectivity within the metapopulations of fished species protected within the MPA network and asked how the MPAs affect long-term projections of population persistence. Essentially this asks whether, on average, each adult fish replaces itself with at least one offspring over its lifetime, so that the population can be expected to remain at a constant level. To evaluate this, we built a spatially realistic model of the population dynamics of five rocky reef/kelp forest fishes. This model included the habitat associations of each species (based on bathymetry, water temperature, etc.), size-dependent demography (growth, mortality, fecundity), and spatially realistic fishing pressure based on logbook data (importantly, this analysis assumes that fishing is kept to sustainable levels, consistent with contemporary management plans). The five species have negligible movement between habitat patches as adults, but widespread connectivity between patches during the pelagic larval stage. We therefore estimated the connectivity between habitat patches in the model by simulating the movement of particles ('larvae') within the ocean current field generated by a high-resolution ocean circulation model. Based on this analysis, we found that overall, all five species are predicted to have persistent metapopulations within California, and moreover focusing just the portions of those populations within the MPAs themselves (ignoring habitat where fishing is allowed) are also projected to be persistent. This analysis also allows us to call attention to the particular habitat patches that contribute most to population persistence; some of these are protected within MPAs but some are not, and this information could be used for adaptive management recommendations. Our second analysis considered the full suite of benthic habitat types (not just shallow rocky reefs) and examined 'environmental connectivity' in terms of the movement of particles alone within the ocean circulation model; these particles could represent larvae of other species but also nutrients, chemicals, or other particles. Overall, this analysis estimates that there is greater transport of particles into MPAs than into non-MPAs on a per-area basis. That calculation includes particles originating in both MPAs and non-MPAs, and the result was consistent across habitat types and depths and was relative insensitive to the time the dispersing particles spent in the water column. Overall, these analyses indicate that California's MPA network is well-connected both demographically and environmentally, and our report provides detailed information on how those connections could be strengthened to further enhance network performance.

Technical Summary

Background

The California Marine Life Protection Act (MLPA) stipulated that the state create a network of marine protected areas (MPAs), and evaluate how well the MPAs function as a network. The purpose of this study was to develop and apply a modeling approach to evaluate the performance of the MPA network. The ecological network comprises populations of species that are distributed both inside and outside of MPAs across the state. Those local populations inside and outside of MPAs are connected by the transport of their propagules (spores, eggs, larvae) from one population to another (“population connectivity”). For each species, these collections of connected populations constitute a “metapopulation”.

Our evaluation asks two overarching questions. Question 1 (**Q1**) asks “*What are the population consequences of* ***ecological connectivity*** *across the MPA network?”* This question considers connectivity in the ecological sense, as the process of demographic replacement in metapopulations. For the MPA network to be effective, the replacement capacity and resulting population persistence should be enhanced by the presence of the MPAs. Question 2 (**Q2**) asks "*How does network design, habitat availability, and particle transport over different timescales contribute to* ***environmental connectivity*** *across the network?"* This question focuses solely on the environmental factors affecting patterns of propagule abundance and transport across the network for several different habitats and propagule durations, and is not linked to particular species. MPA networks are more effective in contributing to population persistence when the modeled population connectivity via propagule transport is greater than would be expected based on the relative habitat area included within the MPAs.

Definitions Table

ROMS	Regional Ocean Modeling System. A numerical ocean modeling framework that uses environmental data inputs (e.g., surface winds) and fluid dynamics equations to produce descriptions of the three-dimensional current field in a particular ocean region over some time period.
ROMS cell Site Patch	To track the movement of simulated larvae within the ROMS ocean circulation fields, it is necessary to define starting and ending locations for larval pathways. For this purpose, California state waters were divided into 365 ROMS 'cells' which are on average 90,000 m^2 in size. Other terms refer to the same spatial unit of a ROMS cell but are used in different ecological contexts. *Site* is used when referring to the value of a ROMS cell based on its effectiveness to the network, while the term *patch* is in reference to one of the two site value metrics, patch importance.
MPA vs. non-MPA	In the context of our demographic model, an MPA is a location where a particular model species does not experience fishing mortality. This is distinct from California statutory language that distinguishes State Marine Reserves, State Marine Conservation areas, etc. In the model, locations that are SMCAs but fishing for a particular species is permitted are considered non-MPAs. The ROMS cell boundaries were arranged so that each MPA is completely contiguous within a single ROMS cell.

Environmental connectivity	Connectivity pertaining to the transport of particles via ocean currents interacting with the geography of varying habitats
Ecological connectivity	Connectivity pertaining to the transport and dispersal of larvae, which affects the population dynamics and demography of that species.
Metapopulation persistence	The condition under which, on average, each individual within the metapopulation successfully replaces itself with at least one offspring during its lifetime.
Replacement capacity	The metapopulation's growth rate if brought to very low abundance values (levels low enough that density-dependent competition is not operating)

Approach

To answer our first question (**Q1**) we quantified metapopulation persistence for five ecologically and economically important species that inhabit shallow rocky reefs and kelp forests along different geographic portions of the MPA network: Black Rockfish (*Sebastes melanops*), Blue Rockfish (*S. mystinus*), Kelp Rockfish (*S. atrovirens*), Kelp (a.k.a. Calico) Bass (*Paralabrax clathratus*) and California Sheephead (*Bodianus pulcher*; formerly known as *Semicossyphus pulcher*). Fundamentally, Q1 asks how the MPA network supports the demographic persistence of these species. This leads to multiple sub-questions to explore the projected effects of MPAs. First, (**Q1a**) *what is the replacement capacity of the full coastal network (i.e., entire metapopulation) and how does it vary across the 5 species?* Second, *(**Q1b**) what is the replacement capacity of the MPA portion of the network alone?* Third, *(**Q1c**) what would the replacement* *capacity of the full coastal network be in the absence of MPAs, all else being equal?* Finally, ***(Q1d)*** *which cells (MPAs and non-MPA areas) contribute most to the effectiveness of the network?*

To answer the suite of Q1 questions and better understand the population consequences of ecological connectivity across the MPA network, we constructed a spatially explicit demographic population model that incorporates information about fish demography, habitat associations, fishing, and larval transport. The model tracked both the abundance and size of fish in each habitat patch, using an ecological modeling approach known as an Integral Projection Model. Because we also account for larval connectivity we refer to the entire model as an Integral Projection Connectivity Model, or IPCM. The connectivity across the metapopulation is simulated via movement of each species' larval stage via ocean currents. The IPCM functions similar to an age- or stage-based population model with the exception that size or age is a continuous integral and not allocated to discrete bins. Our IPCM uses size-based metrics as this would allow for smooth comparisons to length-based monitoring data in future implementations. The model was run separately for each of the five target species. For each species we parameterized the model with information about their larval stages interacting with ocean currents, their specific habitat associations across California's rocky reefs, the spatial distribution of fishing pressure and other demographic data on growth, mortality and reproduction.

We modeled the first stages of these fish populations' life cycle by simulating larval dispersal using a particle tracking routine using output from a Regional Ocean Model System (ROMS) solution for the California Current (see Definitions table). California state waters were divided up into 365 'cells' within the ROMS model domain, with each cell being the potential origin or destination of a dispersing larvae. These cells were selected to be larger than the spatial scale of adult fish movements, and ROMS cells containing MPAs were constrained to be exactly contiguous with MPA boundaries. Simulated larvae were released at each local population (i.e., ROMS cell) every year, and allowed to passively disperse within the ROMS flow field for a period of time corresponding to that species' larval development time. At the conclusion of that time period, if the simulated larva is close to a ROMS cell containing suitable habitat, it is assumed to settle into the benthic population in that destination cell. Those calculations provided estimates of the probability of a larvae traveling from one cell to any other cell.

In order to represent the distribution of suitable habitat for each species across the MPA network, we built Species Distribution Models (SDMs) to quantify the habitat associations of each species in each ROM cell. We quantified the associations of habitat with shallow subtidal rocky reef fish species, using underwater SCUBA surveys conducted for the MPA kelp forest monitoring program across their long-term monitoring sites (1999-2022), paired with a suite of environmental variables. Finally, we used aggregated Commercial Passenger Fishing Vessel logbook data from along the coast to approximate relative harvest rates in non-MPA locations within the IPCM.

We used the SDMs for each species to describe the habitat distribution for the IPCM for each species, and then used this combined model framework to simulate the population dynamics of each species in California waters, and to calculate various quantities needed to answer Q1.

To answer Q1a, we calculated replacement capacity at the **Full network** scale, which is the entire California coast network which contains all areas of MPAs and areas of fishing across. For Q1b, we only calculated replacement capacity across the **MPA sub-network**, which excludes reproductive contribution from anywhere else besides the MPAs. For Q1c, we calculated replacement capacity on the **Full network with no MPAs**, which is the entire California coast network where all areas of MPAs are open to fishing (as if the California coastline did not have MPAs established). To answer Q1d, we determined, for each species, the percent change in replacement capacity from the full network with a focal region MPAs only to the full network without MPAs (fishing everywhere).

In interpreting the responses to Q1 it is important to point out that because the fish metapopulations in the California MPA network span both MPAs and fished locations, questions about population persistence and metapopulation capacity are inextricably linked to fishery management (at least for the species we considered that are targeted by fisheries). We assumed in our model that fisheries management operates in the manner it is currently intended to under the Marine Life Management Act and the Nearshore Fishery Management plan, with a precautionary approach and harvest rates that – all else being equal – should lead to sustainable harvest. Therefore, our answers to Q1 reveal how much we can expect the MPA network to function to *improve* metapopulation capacity and persistence relative to a baseline without MPAs, rather than whether the MPA network is a replacement for or a substitute for precautionary, sustainable fisheries management.

To answer our second question (**Q2**) we examined environmental connectivity across the California coastline as the contribution of particles connected via similar habitats of either rocky intertidal, sandy beaches, shallow subtidal rocky reefs, and varying depths of both rock and soft bottom habitats across donor and recipient sites. In this context we are considering the potential transport of any type of waterborne particle, including propagules, nutrients, sediments, or pollutants. In that context we asked: *(**Q2a**) How does environmental connectivity vary across both transport duration and connectivity pathways within shallow rocky reef and kelp forest habitats? (**Q2b**) How does environmental connectivity vary across both transport duration and connectivity pathways within other coastal and subtidal habitats found within the California MPA network?*

Output of the total number of larvae and total number of recruits at the last timestep across each ROMS cell was used to calculate the contribution estimates across 10 habitats: (1) rocky intertidal, (2) shallow subtidal rocky reef, (3) rock in 30-100 meter depth, (4) rock in 100-200 meter depth, (5) rock in greater than 200 meter depth, (6) sandy beaches, (7) soft bottom in 0-30 meter depth, (8) soft bottom in 30-100 meter depth, (9) soft bottom in 100-200 meter depth and (10) soft bottom in greater than 200 meter depth. For habitat estimates we calculated the total summed area (km2) of a habitat type within every ROMS cell using multibeam sonar by the California Seafloor Mapping Project (CSMP).

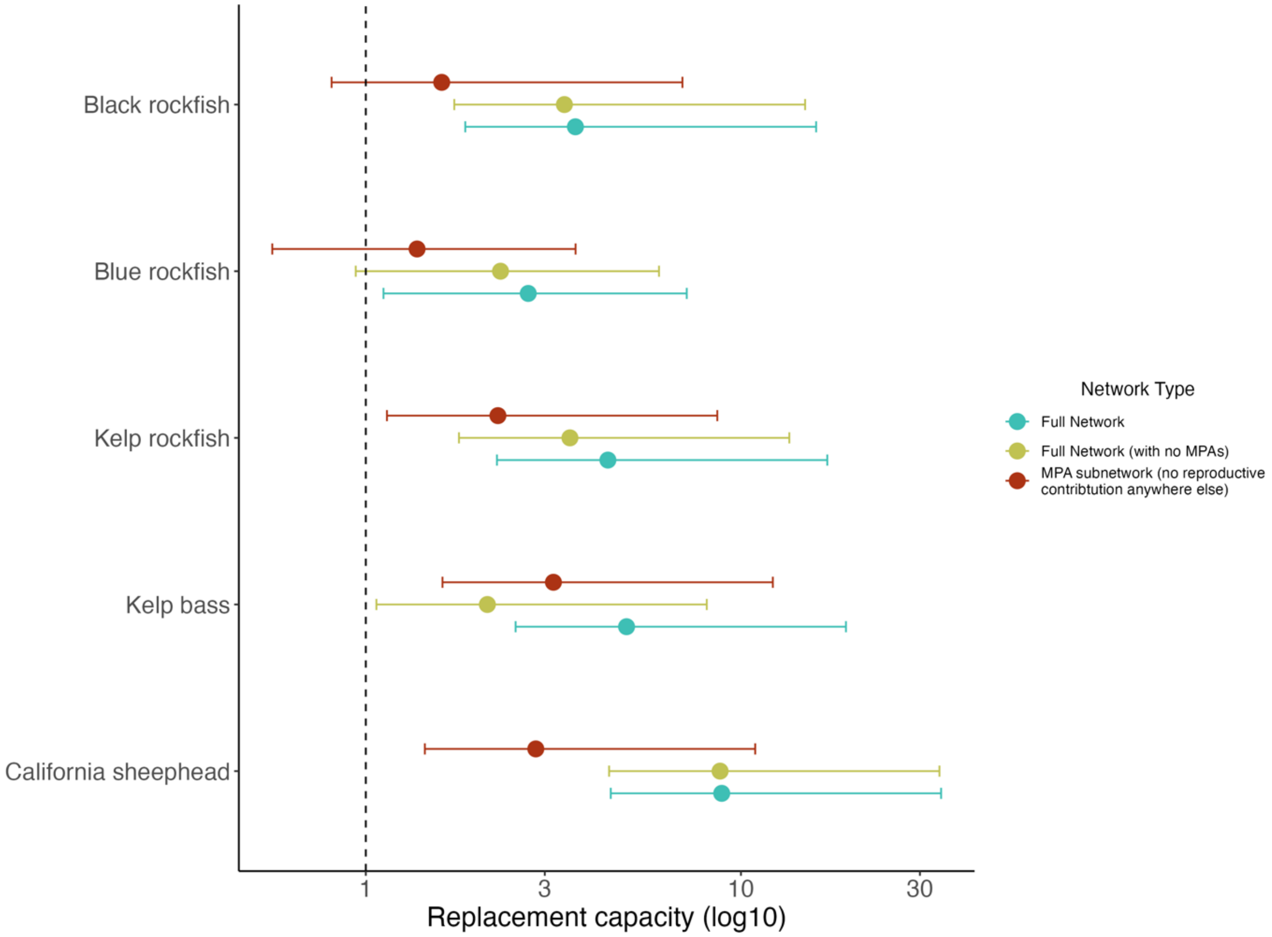
To answer question, Q2a and Q2b, we calculated contribution estimates of particle transport across the same 10 habitats we examined for question Q1 and applied four PLD ranges: 5-15 days, 30-60 days, 60-90 days, and 90-150 days. We tested how transport from and transport to an MPA relates to the transport from or transport to a non-MPA, which allows us to directly understand the role of larval transport across the different connectivity pathways within the network: into or out of an MPA or non MPA. We first calculated the expected proportion of habitat in an MPA and in an non-MPA and then calculated it amongst the four pathways of connectivity: (1) MPA to MPA, (2) MPA to non MPA, (3) non MPA to MPA and (4) non MPA to non MPA. We then took the ratio of observed versus expected contribution, which specifically controls for habitat and allows us to examine the role of connectivity across these four pathways. With quantifying particle transport across 4 connectivity pathways and controlling for habitat area across MPA and non-MPAs we were able to test how environmental connectivity varies across PLD and different connectivity pathways (**Q2a**) within rocky reef habitats, and (**Q2b**)within the other coastal and subtidal habitats found within the California MPA network.

Results

Q1a: What is the replacement capacity of the full coastal network (i.e., entire metapopulations) and how does it vary across the 5 species?

We found that all species are projected to have persistent metapopulations, with replacement capacity for all species being above one (i.e., full replacement; **Figure ES1, blue points**).

Figure ES1. Replacement capacity across varying network types: Full network (MPAs and fished areas), Full network (no MPAs - all areas are fished), and the MPA sub-network (Only the MPAs, no reproductive contribution from fished areas), by the five species: Black Rockfish, Blue Rockfish, Kelp Rockfish, Kelp Bass and California Sheephead. If the point lies to the right of the dashed line (1), the metapopulation is persistent. The error bars represent the total variation in the steepness parameter, h.



Q1b: What is the replacement capacity of the MPAs portion of the network alone?

We found that when evaluating replacement capacity across only the MPA sub-network that all species are projected to have persistent metapopulations with Kelp Bass having the highest replacement capacity of the species we considered. To assess the role of connections between MPAs and non-MPAs we compared the magnitude of change in replacement capacity between the full network and the MPA sub-network and found that the presences of non-MPA and MPA connections substantially enhanced replacement capacity for all species (**Figure ES1 comparing blue and red points**), with the degree of projected increase ranging from 57% to >200%, depending on the species modeled.

Q1c: What would the replacement capacity of the full coastal network be in the absence of MPAs?

We found that when evaluating replacement capacity of the full network in the hypothetical scenario with no MPAs that all species had persistent metapopulations, though with lower replacement capacity than we calculated in the scenario with MPAs. To quantify the role of the MPAs in the replacement capacity of network we compared the magnitude of change in replacement capacity between the full network with MPAs and the full network without MPAs; this increase ranged from 1% (for California Sheephead) to 135% (for Kelp Bass; **Figure ES1 comparing blue and yellow points**).

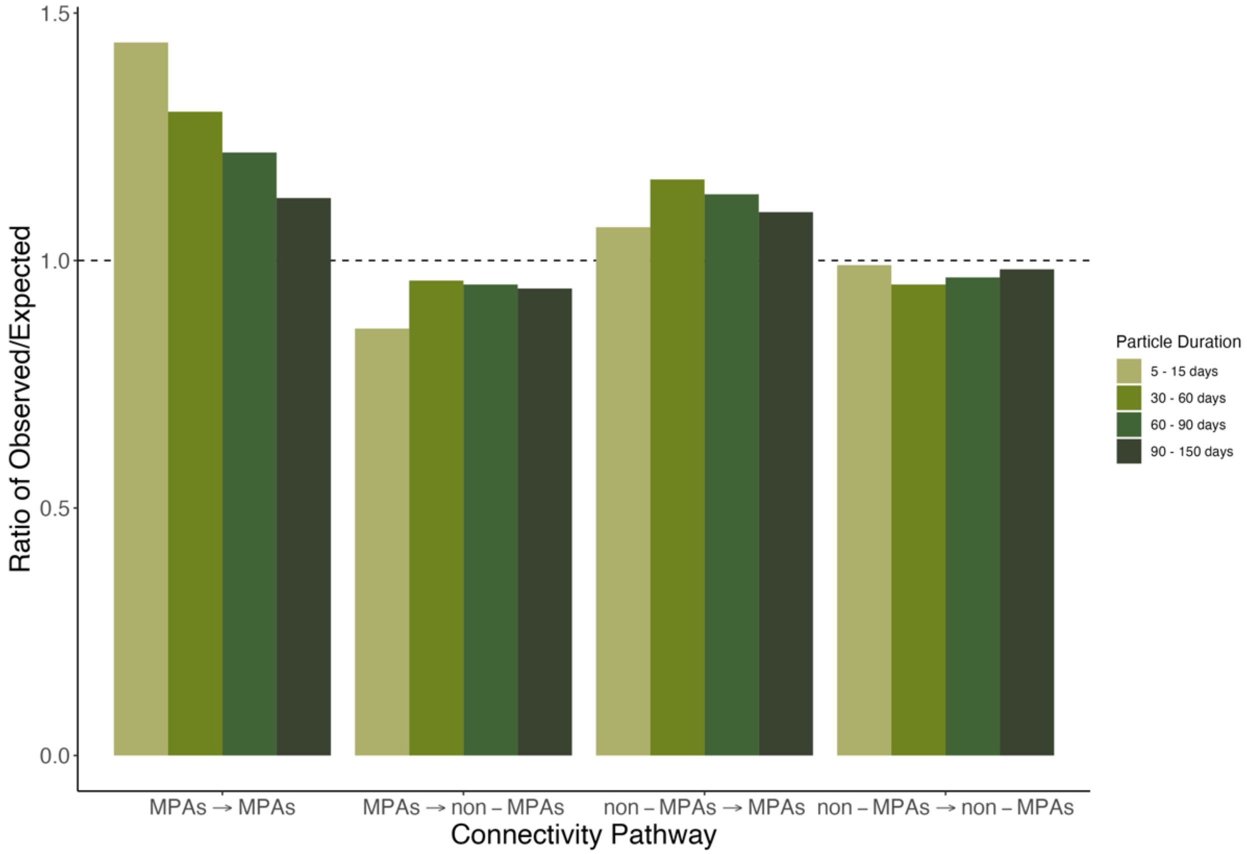
Q1d: Which MPAs contribute more to the effectiveness of the California ecological network?

Examining the two metrics of site importance to the effectiveness of the network, we were able to identify (1) the top ten important sites for each species **(Table 3-7 of main text)**, (2) general trends for which regions displayed the highest site values across the two metrics within a species **(Table 8-9 of main text**) and (3) site designation differences (whether the site is a SMR, SMCA, a special closure or a non-MPA; **and Table 10-11 of main text**). The full list of sites for both relative realized export and relative patch importance values for each species can be found in Table S3 to S7. Additionally, we have identified for each species the top ten MPAs for each site value metric (**Table S2**)

Q2a: How does environmental connectivity vary across both transport duration and connectivity pathways within shallow rocky reef and kelp forest habitats?

We found that particle transport contribution across shallow rocky reef and kelp forest habitats differed across the 4 connectivity pathways (**Figure ES2**). Pathways of particle contribution into MPAs (MPAs into other MPAs and non-MPA into MPAs) had higher levels of particle contribution than expected based on habitat area alone. Given that finding, it was mathematically inevitable that the pathways of particle contribution into non-MPAs (MPAs into non-MPAs or non-MPAs into other non-MPAs) had lower contributions than expected based on habitat area alone. There was not a strong effect of larval duration (PLD) on the estimated levels of proportional contribution based on habitat area across all connectivity pathways (i.e., the bars in **Figure ES2** were always found either all above or all below the 1 line across all PLDs within each pathway), however there is a trend for decreasing contribution from MPAs into other MPAs with increasing PLD.

Figure ES2. The ratio of proportional observed to expected shallow rocky reef and kelp forest habitat contribution estimates of transport across the four connectivity pathways, while controlling for differences in habitat area. Each colored bar represents the pelagic larval duration of the simulation. If the value is greater than 1, there is more particle transport than expected by habitat area alone.



Q2b: How does environmental connectivity vary across both transport duration and connectivity pathways within other coastal and subtidal habitats found within the California MPA network?

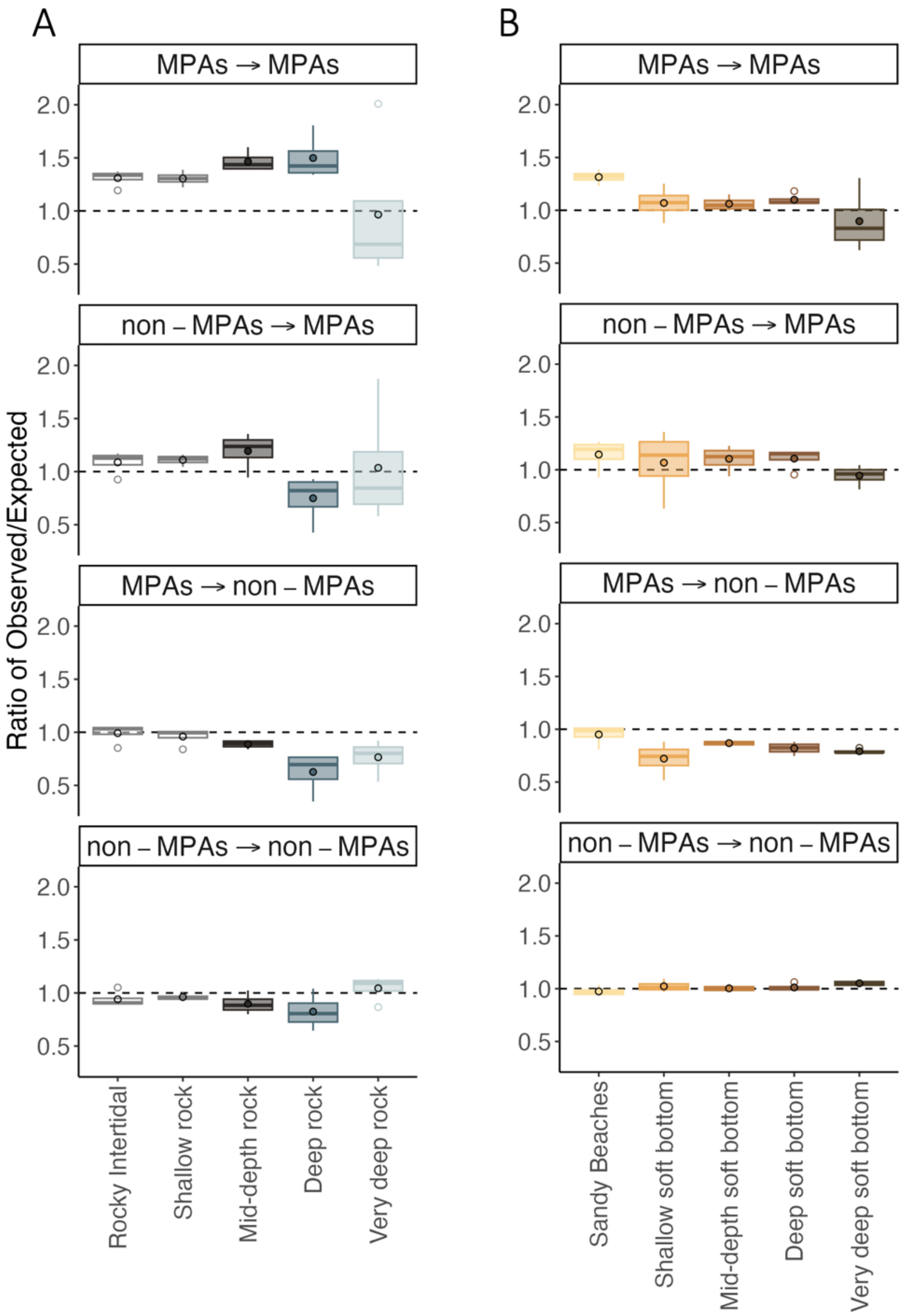
For both rocky intertidal (**Figure ES3a**) and sandy beaches (**Figure ES3b**), we found the contribution of transport into MPAs (from both other MPAs and non-MPAs) to be higher than expected based on area for all transport durations except 5-15 days from non-MPAs (Figure S15) . The contribution of transport into non-MPAs had approximately the same amount, or slightly less than expected by area, from MPAs and lower contribution of transport than expected by area from other non-MPAs (besides the 5-15 day duration where we observed the opposite trend).

For subtidal shallow, mid-depth and deep rock habitats we found contribution of particle transport into MPAs from other MPAs to be higher than expected based on area across all particle durations (**Figure ES3a**). Similarly, shallow and mid-depth rock had higher contributions of particle transport into MPAs from non-MPAs than expected by habitat area (except for the mid-depth rock particle duration of 5-15 days; Figure S16), while the transport of particles from non-MPAs into MPAs at deep rock was less than expected by habitat area. Very deep rock also had higher contributions of transport into MPAs (from both other MPAs and non-MPAs), but only for the particle duration of 5-15 days. For all subtidal rock habitats, we found the contribution of particle transport into non-MPAs (from both other MPAs and non-MPAs) to be less than expected based on habitat area (except for non-MPA into other non-MPA for very deep rock habitat).

Subtidal shallow, mid-depth and deep soft bottom habitats also had higher contributions of particle transport into MPAs (from both other MPAs and non-MPAs) than predicted by habitat area alone **(Figure ES3b**; besides 30-60 days of particle duration from MPAs in shallow soft bottom and 5-15 days from non-MPAs in shallow, mid-depth and deep soft bottom habitats, Figure S16). The very deep soft bottom habitat had lower contributions of particle transport into MPAS (from both other MPAs and non-MPAs) than predicted by habitat area (with the exception of the 5-15 day particle duration for MPA into MPAs). Across all soft bottom habitats, particle transport into non-MPAs from MPAs was lower than expected based on habitat area and transport to non-MPAs from other non-MPAs were all around what is expected based on habitat area.

Overall, these results based on the particle transport analysis suggest that there is high sub-network connectivity in the different habitats in the system (i.e., high MPA-to-MPA environmental connectivity) and that MPAs were generally placed in locations favored to receive high levels of propagule replenishment based on environmental transport alone.

Figure ES3. The ratio of proportional observed to expected contribution of transport across rocky and soft bottom habitats based on habitat area. (A) The blue-gray color palette signifies rocky habitats, while (B) the brown color palette signifies soft bottom habitats. If a value is greater than 1 (above the horizontal dashed line), there is more particle transport than expected by habitat area alone. The filled point signifies the mean ratio across the 4 particle durations for each treatment. The centerline of the boxplot is the median, lower and upper lines indicate the 25% and 75% quantiles of the distribution, and the unfilled points indicate outliers.


A
B
MPAs → MPAs
non – MPAs → MPAs
MPAs → non – MPAs
non – MPAs → non – MPAs
Ratio of Observed/Expected
2.0
1.5
1.0
0.5
Rocky Intertidal
Shallow rock
Mid-depth rock
Deep rock
Very deep rock
Sandy Beaches
Shallow soft bottom
Mid-depth soft bottom
Deep soft bottom
Very deep soft bottom

Conclusions

Most broadly, we can say that for both ecological and environmental connectivity *we found that the California MPAs are working as an effective network.* We found that all five fish species were predicted to exist in metapopulations that exhibit long-term persistence, with varying strengths of replacement capacity. For environmental connectivity we found higher than predicted particle transport into MPAs based on the habitat area. As we found no self-persistence in any individual MPA for any of the species analyzed, we conclude that the spatial configuration of MPAs leading to high connectivity amongst the MPAs is supporting a persistent metapopulation. Lastly, we were able to identify the highest leverage sites, specific to connectivity and found differences across species, region and site designation. From an adaptive management lens, these metrics can help us understand which MPA and non-MPAs are most critical in supporting connectivity across the network and potentially highlight areas to sustain or enhance protection and management.

Given the persistence of all five species examined within the subnetwork of MPAs (i.e. with no contribution from MPAs outside the MPAs), and the disproportionate reception of larvae by most, not all, MPAs relative to their habitat area, we conclude that the spatial configuration of MPAs has led to high MPA connectivity and is supporting persistent metapopulations. In our models, the total MPA area makes up 15.5 - 18% (depending on the species' range) of the total potential habitat in the California model domain. This speaks to the success of the MLPA planning process.

We found that for three of the five species, protection from fishing inside MPAs considerably enhanced the replacement capacity of their metapopulations. This was particularly true for Kelp Bass which were estimated to have 135% greater replacement capacity with MPAs present relative to the hypothetical no-MPA baseline. This suggests that the protection MPAs provide for these three species substantially enhance biomass and larval production, supporting greater demographic replenishment across the metapopulation networks. The lower effect of MPAs on the replacement capacity of Black Rockfish can be explained by the observing that the areas where black Rockfish are in highest abundance (i.e. the North Coast) have lower fishing pressure than other regions of the state, so the effect of MPAs on reducing fishing is lower. California Sheephead also did not have a large change in replacement capacity in our models. This is a consequence of the female-first sex-changing life history of that species; the greater biomass found inside in MPAs consists primarily of male fish, and thus would not substantially enhance spawning output or larval production in those MPAs.

Using metrics of realized export and patch value we identified high leverage sites for each fish species, accounted for differences across site designation, and explained regional mechanisms of connectivity. We saw 14% more SMRs relative to SMCAs Among the high-valued sites for these five species, 34% were SMRs and 20% were SMCAs. Almost all of those SMCAs were areas of no-take for the modeled species. Understanding which SMRs and SMCAs are critical for connectivity across these metapopulations can help guide which locations to prioritize continual management and protection. Although MPAs made up a majority of high leverage sites for connectivity across these five species' metapopulations, there were a considerable number of non-MPA regions which came out as important sites. These high value sites that are not MPAs might be considered for future protection, specific to enhancing connectivity.

The period (1999-2012) that informed the ROMS model output supporting our analyses was characterized largely by 'typical' historical oceanographic conditions. To better understand how atypical oceanographic periods (e.g., El Niño, marine heatwaves) alter patterns of network connectivity and metapopulation persistence, future studies should apply ROMS model solutions that have been updated to include those more recent events. Our analyses also integrated seasonal variation in oceanographic conditions. Because species release young (spawn) in particular seasons, seasonal releases of young tailored to spawning seasons will better estimate connectivity metrics and the replacement capacity of particular species. Understanding how climate change will influence network connectivity and population persistence will require ROMS models that predict future responses of ocean conditions to climate dynamics (e.g., changes in current patterns, including coastal upwelling, changes in temperature and nutrient concentrations) that influence larval production, transport processes, pelagic larval durations, and larval survival. The current study lays the foundation for incorporating these refinements to better estimate metapopulation performance now and into the future.

Overall, our analyses provide strong evidence that California's planning process created a network of ecologically connected MPAs and that this connectivity is enhancing the long-term resilience and persistence of the species examined in this study and those that occupy many of the habitats targeted for protection. It also identifies the relative contribution of individual MPAs and non-MPA areas to the persistence of species metapopulations, which can predict how species would respond to potential adaptive management actions (i.e., the addition or removal of MPAs or changes in MPA regulations). The approaches developed in the study add to the growing efforts to better understand the conservation consequences of MPA networks and their adaptive management.

Project Narrative

Introduction

A central concern in any type of spatial resource management application is connectivity: the movement of organisms between habitat patches and between areas with more or less protections or levels of harvest (Carr et al. 2017, White et al. 2019, Hilty et al. 2020). For many coastal marine ecosystems, it is appropriate to examine questions about connectivity in the context of metapopulation dynamics (Kritzer and Sale 2010). This is because many species have relatively sedentary demersal or benthic adult stages that occupy discrete habitat patches (e.g., kelp forests, rocky reefs) and the local populations on different patches are linked by dispersal of a planktonic spore (algae) or larval (animal) life stage (White et al. 2019).

In 2007-2012, California created the world's second largest network of marine protected areas (MPAs) via iterative, science-informed, stakeholder-driven design processes in each of four regions of the state's coastline (White et al. 2023, Kirlin et al. 2013, Botsford et al. 2014, Yaffee 2020). The result was a network of 124 MPAs along the coast; many of these are State Marine Reserves that prohibits all fishing and resource extraction, while others are State Marine Conservation Areas or other types of MPAs that allow selected types of fishing to continue (White et al. 2023, CDFW website). The legislation enabling the creation of this MPA network was the 1999 Marine Life Protection Act (MLPA). The MLPA mandated that the new MPAs be designed and function as a network. During the implementation phase, that directive led to science guidelines that recommended maximum distances between MPAs, with the intention of ensuring that there would be larval connectivity between MPAs (those distances were based primarily on estimates of genetic isolation-by-distance and inferred from empirical dispersal estimates; Shanks et al. 2003, Kinlan and Gaines 2003, Saarman et al. 2013). The design was also informed by spatial metapopulation models in which larval connectivity was based on information from ocean circulation models, similar to the work described in this report (White et al. 2013). The MLPA legislation also specified that the MPA network should be managed adaptively. The basic premise of adaptive management is that any management action should have an expected or hoped-for outcome (e.g., achieving the goals of the MLPA legislation), the system should be monitored following a management action, and then monitoring data are compared to the expectation, to see if adjustments to management are necessary to achieve the goal (Walters 1996). In 2023 a statewide effort was made to assemble monitoring data and other information to support an adaptive management review of the MPA network. This work described in this report centers on evaluating the degree to which the MPAs *function as a network*. We assess connectivity across the MPA network by examining (1) general connectivity as the transport of propagules among patches with mutual habitats, and (2) through species metapopulation connectivity as incorporating more species-specific information along the network.

Assessing how well the metapopulations protected in California's MPAs function in a network sense requires understanding and estimating how larvae move between habitat patches (the nodes in the network). This is a notoriously difficult undertaking, because larvae of most species are both extremely small, transparent, incredibly numerous and can travel long distances, transported by ocean currents as well as vertical and/or horizontal swimming (Cowen and Sponaugle 2009, White et al. 2019). It is possible to use genetic tags or trace element signatures in calcified body parts to detect evidence of movement between local populations (reviewed by White et al. 2019), and there are examples of such methods being used to reveal connectivity patterns among MPAs and from MPAs to fished areas, or to examine the network dynamics of metapopulations (Baetscher et al. 2019, Harrison et al. 2020, Dedrick et al. 2021). However, the spatial and temporal scope of such efforts is limited, and they require tremendous resources. A different approach that allows estimates of connectivity at the scale of the state of California is to simulate the transport and dispersal of larvae in the current fields generated by ocean circulation models (White et al. 2019b, examples include James et al. 2002, (James et al. 2002, Cowen et al. 2006, Watson et al. 2011, Garavelli et al. 2018). We took that approach to generate estimates of the probability of larval connectivity between all of the different habitat patches in California waters. We then used those estimates to inform spatially explicit demographic metapopulation models for five particular species in order to address questions about network function from a metapopulation perspective.

A fundamental question about the dynamics of any metapopulation is whether it is persistent (Hanski 1998, Ovaskainen and Hanski 2001, Hastings and Botsford 2006). That is, are the organisms in the metapopulation replacing themselves over time, such that a consistent population size is maintained, and such that if the population were reduced to a low level, it would rebound (Botsford et al. 2019). There are two ways persistence could arise in a metapopulation: *self persistence* and *network persistence*. Self persistence occurs when organisms in one single patch produce enough offspring (i.e., larvae) that remain in that patch to replace the adult population in that patch. In the context of marine populations, this requires both extremely high fecundity in the patch and an extremely high rate of local retention of larvae; i.e., most larvae do not disperse (Botsford et al. 2009, White et al. 2010, Burgess et al. 2014). If those conditions are not met, then the metapopulation may still persist via network persistence, which occurs when replacement occurs among multiple patches over multiple generations. Essentially one can imagine that larvae from patch A disperse to patch B, settle, mature, and reproduce, producing the next generation of larvae that disperse back to patch A or replenish other populations that in turn replenish patch A. If those larvae are sufficient in number to replace the adult population in patch A, then the system can persist despite the lack of high local retention of larvae. To understand whether a population is persistent, and what persistence mechanism is at play, one must have both estimates of larval connectivity and a demographic model describing the survival, maturation, and reproductive output of the adults. Garavelli et al. (2018) applied this method to the Caribbean population of spiny lobster, finding both that the Caribbean-wide metapopulation was persistent but that there were also self-persistent sub-networks within the region that were self-replenishing despite the large spatial scale of dispersal in that species. Alternatively, Dedrick et al. (2021) applied this method to an Indo-Pacific metapopulation of anemonefishes (though they used dispersal estimates based on genetic tags, not a circulation model) and determined that the apparently isolated metapopulation was not network persistent, and must be dependent on immigration from populations elsewhere in the region in order to exhibit the stable population size that it had. The strength of a metapopulation's persistence value can be described as the **replacement capacity** or the metapopulation's growth rate if that population was brought to very low abundance values (i.e., no density dependence present). We used similar logic and methodology to ask whether populations of fished species protected in California's MPAs are persistent and what the level of replacement capacity was for each species' metapopulation.

Once we have an understanding of whether the metapopulation is persistent, we may want to know specific information about which MPAs (or non-MPAs) are having the highest influence on metapopulation connectivity. This may be particularly important for adaptive management if decisions are being made on the future of managing specific MPAs or adding or removing MPAs. To do this we can adopt metrics from network theory to quantify specific site-level values to the effectiveness of connectivity across the network. The two metrics we used in this report are **realized export** and **patch importance**. Realized export can be defined as the total contribution of larval export from one focal patch to its neighbors. Patch importance on the other hand considers the population structure via the reproductive capacity of a population in concert with the level of connectedness a focal site has to other sites.

General connectivity, as in the transport of particles via ocean currents interacting with the geography of varying habitats, is important for quantifying realized environmental connectivity across different ecosystems. This can generally inform how species that are reliant on or associated with specific habitats are connected across the California MPA network. Whether a habitat patch (e.g., an MPA) receives more or less particles than we expect based on the amount of habitat in a patch allows us to understand the role connectivity plays in bolstering or diminishing a population's persistence. For instance, if the ocean was a well-mixed larval pool, we would predict that the amount of propagules spawning from or recruiting to a patch would be equivalent to the amount of habitat area that exists in said patch. So, if our results show more or less particles than expected by area, we can assume that connectivity, via oceanography or currents between two locations, is a potential mechanism behind sustaining a population.

In this report, we centered on two main questions. First, (**Q1**) *What are the population consequences of **ecological connectivity** across the MPA network?* This question considers connectivity in the ecological sense, as the process of demographic replacement in metapopulations (Burgess et al. 2014); thus it includes network design (i.e. the size, protection level, and distribution of the MPAs), the environmental attributes (ocean circulation, distribution and abundance of habitat) that affect propagule transport across the network, and the demographic consequences of protection in MPAs and fishing in non-MPA areas. Second, we ask (**Q2**) *How does network design, habitat availability, and particle transport over different timescales contribute to **environmental connectivity** across the network?* This question focuses solely on the environmental factors affecting patterns of propagule abundance and transport across the network for several different habitats and propagule durations and is not linked to particular species.

For the first question we quantified metapopulation persistence for five species: Black Rockfish (*Sebastes melanops*), Blue Rockfish (*S. mystinus*), Kelp Rockfish (*S. atrovirens*), Kelp (a.k.a. Calico) Bass (*Paralabrax clathratus*) and California Sheephead (*Bodianus pulcher*; formerly known as *Semicossyphus pulcher*). These five species inhabit shallow rocky reefs and kelp forests along different geographic portions of the MPA network and are all commercially or recreationally fished. Fundamentally, Q1 is asking how the MPA network supports the demographic persistence of these species.

This leads to multiple sub-questions to explore the projected effects of MPAs. First, (**Q1a**) what is *the replacement capacity of the full coastal network (i.e., entire metapopulations) and how does it vary across the 5 species?* This addresses the role of MPAs as components of the larger managed populations. Second, ***(Q1b)** what is the replacement capacity of the MPAs portion of the network alone?* This addresses a question that originally arose during the MLPA Initiative, which is whether the MPAs are self-sustaining without outside contributions from fished areas. Third, ***(Q1c)** what would the replacement capacity of the full coastal network be in the absence of MPAs?* This helps understand the role of MPAs in supporting the replacement capacity identified in Q1b. Finally, ***(Q1d)** Which sites (MPAs and non-MPA areas) contribute more to the effectiveness of the network?* This question could inform future adjustments to the network in an adaptive management process.

*F*or the second question (Q2) we examined environmental connectivity across the California coastline as the contribution of particles connected via similar habitats of either rocky intertidal, sandy beaches, shallow subtidal rocky reefs, and varying depths of both rock and soft bottom habitats across donor and recipient sites. With this we asked: ***(Q2a)** How does environmental connectivity vary across both transport duration and connectivity pathways within shallow rocky reef and kelp forest habitats?* ***(Q2b)** How does environmental connectivity vary across both transport duration and connectivity pathways within other coastal and subtidal habitats found within the California MPA network?*

Methods

Modeling Framework

What are the population consequences of ecological connectivity across the network?

To understand the population consequences of ecological connectivity across the MPA network, we constructed a spatially realistic demographic population model that incorporates information about fish demography, habitat associations, fishing, and larval transport. The model is a discrete-time, spatially explicit, size-structured population model which tracks the dynamics of a local fish population in each model cell. The model assumes that organisms in their benthic stage do not move between cells (and the cells were chosen to have a spatial extent large enough to support that assumption), so the dynamics of each local population are dependent on the local features of the cell (e.g., the habitat, protection status, and level of fishing). Connectivity between model cells in the metapopulation was assumed to be solely by larval dispersal, which we represented by between-cell dispersal probabilities estimated from Lagrangian particle tracking within a ROMS circulation field. The size-structured within-cell dynamics were represented using a type of model known as an integral projection model (Easterling et al. 2000, Ellner et al. 2016, White et al. 2016), so we term the spatially realistic version an Integral Projection Connectivity Model, or IPCM. The IPCM functions similar to an age- or stage-based population model with the exception that size or age is a continuous integral and not allocated to discrete bins. Our IPCM uses size-based metrics as this allows for smooth comparisons to length-based monitoring data in future applications.

We selected five fish species which are commonly found in shallow rocky reefs and kelp forests, occupy varying geographic ranges throughout California, display different levels of larval duration and are important commercial and/or recreational fisheries in the state: Black Rockfish (*Sebastes melanops*), Blue Rockfish (*S. mystinus*), Kelp

Rockfish (*S. atrovirens*), Kelp (a.k.a. Calico) Bass (*Paralabrax clathratus*) and California Sheephead (*Bodianus pulcher*; formerly known as *Semicossyphus pulcher*). The model is run separately for each species and has a one year time step. For each species we parameterized the model with information about their larval stages interacting with ocean currents, their specific habitat associations across California's rocky reefs, the spatial distribution of fishing pressure and other demographic data on growth, mortality, and reproduction. Next, we will summarize the varying components of the model however a more thorough explanation of these methods can be found in the appendix.

In the model, we represented the dynamics of growth, mortality, fishing harvest, and reproduction within each discrete habitat patch with an integral projection model with density-dependent post-settlement mortality, and larval connectivity among patches, following the methods and equations in Garavelli et al. (2018), Nickols et al. (2019), and Dedrick et al. (2021). The model domain was divided up into model 'cells', or patches, that were large enough to justify the assumption that adult fish did not have substantial movement between cells. The cells were defined such that each MPA occupied an entire cell, and other non-MPA areas were assigned to similar-sized spatial cells.

We modeled the larval stages of these fish populations' life cycle using Langrangian particle tracking within a Regional Ocean Model System (ROMS) solution for the California Current (Drake et al. 2013). To estimate the probability of larval connectivity between each cell, we simulated the release of larval particles from each ROMS cell every year of the ROMS time domain. The particles dispersed in the ROMS flow field for their pelagic larval duration (PLD, which was species-dependent; Table 1), and the particles were assumed to be able to settle in a particular patch if they are in that patch within a range of 10% of their PLD (e.g for PLD of 30 days: 27-33 days). We then calculated the probability of connectivity between patches as the number of simulated propagules that dispersed to each patch, divided by the number released from that patch, averaged over all model months and years.

To estimate the amount of suitable habitat in each model cell, we built Species Distribution Models (SDMs) to quantify the habitat associations of each species in each ROM cell. We quantified the associations of habitat with shallow subtidal rocky reef fish species, using underwater SCUBA surveys from the Partnership for Interdisciplinary Studies of the Coastal Oceans (PISCO; https://www.piscoweb.org/) and Reef Check California (RCCA; https://www.reefcheck.org/country/usa-california/) across their long-term monitoring sites (1999-2022), paired with a suite of environmental variables which would ecologically explain fish presence and/or abundance across California. Once we built the best models for each species (Appendix Table S1), we used these models to predict fish biomass across the California coast (Appendix Figure S1-S5). This was used in the model to set the maximum carrying capacity of larval recruits of each species via dividing the total biomass by the calculated biomass per recruit (BPR; Table 1). This value was used as the asymptotic maximum number of recruits that could settle into each local population.

Table 1. Life history parameters used in the IPCM.

Parameter	Definition	California sheephead	Kelp Bass	Kelp Rockfish	Blue Rockfish	Black Rockfish
		Larval dispersal and recruitment				
PLD	Pelagic Larval Duration	30 – 60 days	20 – 30 days	60 – 90 days	90 – 150 days	90 – 150 days
EPR	Eggs per recruit	2.82×10^{3}	9.46×10^{5}	7.156×10^{5}	9.60×10^{4}	2.90×10^{5}
BPR	Biomass per recruit	5.75×10^{3}	3.01	10.42	20.75	4.43
α	Density-independent Beverton-Holt settler survival- based on steepness parameter ‘h’	2.27×10^{-2}	3.468×10^{-5}	1.9×10^{-4}	1.5×10^{-3}	8.86×10^{-4}
h	Steepness parameter	0.097	0.097	0.097	0.13	0.0734
		Growth				
k	von Bertalanffy growth rate	0.068	0.06	0.23	0.17	0.33
L_{∞}	von Bertalanffy asymptotic length (cm)	83.86	69.8	37.8	38.15	45.11
L_{0}	Larval size at recruitment (cm)	13.5	6	4	7	7.2
		Mortality				
M	Natural mortality	0.25	0.18	0.20	0.14	0.14
F	Total fishing mortality – spatially divided	0.25	0.12	0.16	0.16	0.05
L_{f}	Length at which there is a 50% chance a fish will be removed	30.5	24	25	34	32
		Reproduction				

v	Constant in allometric fecundity relationship	4.0×10^{-12}	2.01×10^{-5}	2.1×10^{-5}	1.14×10^{-8}	1.14×10^{-8}
w	Exponent in allometric fecundity relationship	6.337	4.123	4.123	4.816	4.816
L_c	Length at which 50% of fish change sex	30	N/A	N/A	N/A	N/A
L_m	Size at maturity	19	18	18	22.26	30

Fish settle from larval to benthic stages via a Beverton-Holt density dependent model.

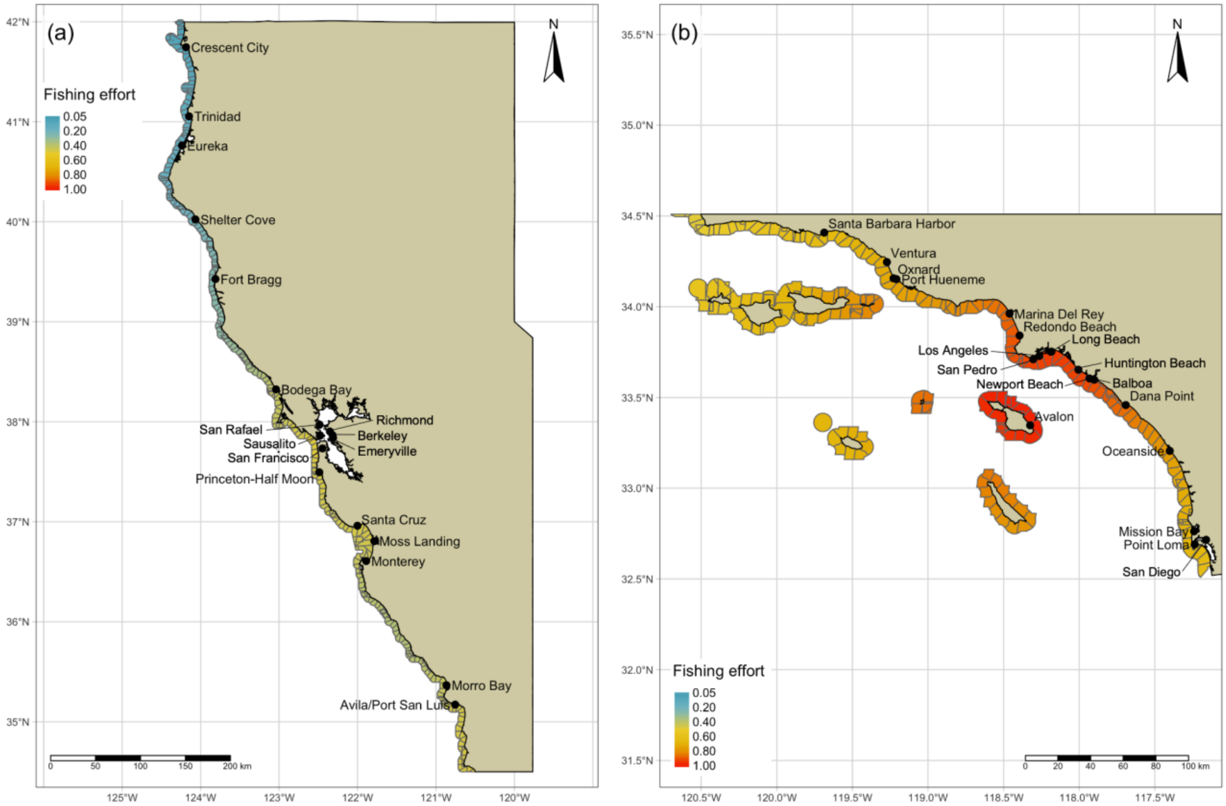
$$R = \frac{\alpha S}{1 + \beta S}$$

This model sets the relationship between the number of settlers (S) coming into a cell and the number of recruits (R) surviving to benthic stages. The survival parameter, α, which accounts for mortality in spatial explicit models (i.e., the product of larval survivorship, retention and density independent settlement), can be calculated from the steepness parameter 'h' in the stock assessment which is the number of recruits when the unfished population reaches 20% of its stock, accounting for the loss of larvae during the dispersal phase in the Lagrangian simulations, as described in White (2010). Using steepness, we can calculate the slope of the stock recruitment function at zero, (1-h)/4h. The term which sets the carrying capacity (or the maximum number of recruits a cell can contain) in the Beverton-Holt function, β, is calculated as the ratio of predicted biomass (from the SDM) to the biomass per recruit. This gives us the total number of recruits that can settle into each ROMS cell based on habitat quality (via the SDM).

Once the fish settle into their benthic stages, they undergo processes at the local ROMS-spatial scale, within an integral projection model. Within a ROMS cell they experience growth via a size dependent Von Bertalanffy growth function. Mortality is calculated as the sum of natural and fishing mortality, where MPAs experience only natural mortality (fishing mortality = 0). Fishing mortality was calculated through building a spatial fishing fleet model which combines: (1) The distance from each major fishing port and the overall effort (# of trips) from CDFW logbooks (Figure 1). We used the mean F from stock assessments (Table 1) and spatially distributed this effort across the coastline based on the relative number of trips reported from each port in the logbook data, and a negative exponential function of effort by distance that we fit to the spatially explicit logbook data. Lastly, reproduction, via the total larval production across the population structure, was quantified using a fecundity-length relationship which combines size at maturity with species-specific constants. This reproduction quantifies the amount of larvae which are released from each ROMS cell and enter the larval stage and disperse via the ROMS connectivity calculations. We ran each species metapopulation model until the population abundances were brought to equilibrium. Output of the total number of larvae and total number of recruits at the last timestep across each ROMS cell was used in the analysis section below.

Figure 1. The relative spatial fishing effort across (a) the northern, central and (b) the southern regions of the California coastline. Each polygon is the ROMS cell's relative mean fishing effort calculated as the sum of the distance from each major fishing port

(labeled points on the map) and the overall effort (# of trips) from CDFW logbooks.



How does particle transport contribute to environmental connectivity across the network?

To answer questions about environmental connectivity we examined contributions of propagules based on the particle transport (informed by the ocean circulation models) in combination with the amount of specific habitat area that exists at donor and recipient sites. We calculated these contribution estimates across 10 habitats: (1) rocky intertidal, (2) shallow subtidal rocky reef, (3) rock in 30-100 meter depth, (4) rock in 100-200 meter depth, (5) rock in greater than 200 meter depth, (6) sandy beaches, (7) soft bottom in 0-30 meter depth, (8) soft bottom in 30-100 meter depth, (9) soft bottom in 100-200 meter depth and (10) soft bottom in greater than 200 meter depth. A more thorough explanation of these methods can be found in the appendix, but next we will summarize the varying components.

To calculate estimates of environmental connectivity we need to quantify where propagules or particles come from and where they go in regards to ocean currents as well as the amount of habitat (which can be a proxy for how many propagules a site may receive or donate) at each location. For the connectivity component, we used the same solutions for the ROMS ocean circulation model as described above in the IPCM. For habitat estimates we calculated the total summed area (km2) of a habitat type within every ROMS cell using multibeam sonar by the California Seafloor Mapping Project (CSMP; https://www.usgs.gov/centers/pcmsc/science/california-seafloor-mapping-program) to calculate all rock and soft-bottom habitats, as well as kelp extent from CDFW flyover data (composite of years: 1989, 1999, 2002-2006, 2008, 2009, 2013-2016). Using a union of the 0-30 meter depth rock layer and the kelp layer, we calculated the shallow rocky reef habitat. Using both the environmental connectivity and habitat area maps we calculated total contribution as explained in the analysis below.

Analyses

What are the population consequences of ecological connectivity across the network?

To better understand the population consequences of ecological connectivity across the network for each of the five focal fish species, we examined metapopulation replacement capacity across varying organizational network structures. To answer **Q1a** (*What is the replacement capacity of the full coastal network and how does it vary across the 5 species?)* we calculated replacement capacity at the **Full network** scale, which is the entire California coast network which contains all areas of MPAs and areas of fishing across. For **Q1b** (*What is the replacement capacity of the MPAs portion of the network alone?)* we only calculated replacement capacity across the **MPA sub-network**, which excludes reproductive contribution from anywhere else besides the MPAs. For **Q1c** (*What would the replacement capacity of the full coastal network be in the absence of MPAs?)* we calculated replacement capacity on the **Full network with no MPAs**, which is the entire California coast network where all areas of MPAs are open to fishing (as if the California coastline did not have MPAs established).

To address these questions we quantified replacement capacity values across all five species at each of the three organizational network structures. If a value is below one, it suggests that metapopulation will not persist. If it is above one, the metapopulation is persistent and the value signifies the amount of replacement the metapopulation will receive if its abundances crash, possibly due to a large disturbance. We also explored how variation in one parameter, called steepness (Table 1) which can be thought of as a nondimensional descriptor of the stock-recruitment curve affects replacement capacity. We used ranges from the standard deviation in stock assessments to set the upper and lower limits of steepness.

To answer ***Q1d*** *(Which MPAs contribute more to the effectiveness of the network?),* we determined, for each species, the influence of regional MPA sub-networks on metapopulation connectivity by examining the percent change in replacement capacity from the full network with a focal region MPAs only to the full network without MPAs (fishing everywhere). To identify the importance of each MPA to the effectiveness of connectivity across the California ecological network, we calculated the following two metrics.

How does particle transport contribute to environmental connectivity across the network?

We calculated contribution estimates of particle transport across 10 habitats: rocky intertidal, shallow rocky reef (subtidal rock 0-30m and kelp union), subtidal rock 30-100m, subtidal rock 100-200m, subtidal rock >200m in depth, sandy beaches, subtidal sediment 0-30m, subtidal sediment 30-100m, subtidal sediment 100-200m and subtidal sediment >200m in depth and 4 PLD ranges: 5-15 days, 30-60 days, 60-90 days, and 90-150 days. We tested how transport from and transport to an MPA relates to the transport from or transport to a non-MPA. Our calculation controls for habitat area amongst MPAs and non-MPAs, which allows us to directly understand the role of larval transport across the different connectivity pathways within the network: into or out of an MPA or non MPA.

Specifically for each habitat type and PLD level we first calculated the expected proportion of habitat in an MPA and in an non-MPA and then calculated it amongst the four pathways of connectivity: (1) MPA to MPA, (2) MPA to non MPA, (3) non MPA to MPA and (4) non MPA to non MPA. The same calculations were made for observed proportions via converting the total summed relative contribution estimates across the four connectivity pathways into a proportion. We then took the ratio of observed versus expected contribution which specifically controls for habitat and allows us to examine the role of connectivity across these four pathways. With quantifying particle transport across 4 connectivity pathways and controlling for habitat area across MPA and non-MPAs we were able to test *how environmental connectivity varies across PLD and different connectivity pathways (**Q2a**) within rocky reef habitats, and (**Q2b**) within the other coastal and subtidal habitats found within the California MPA network?*

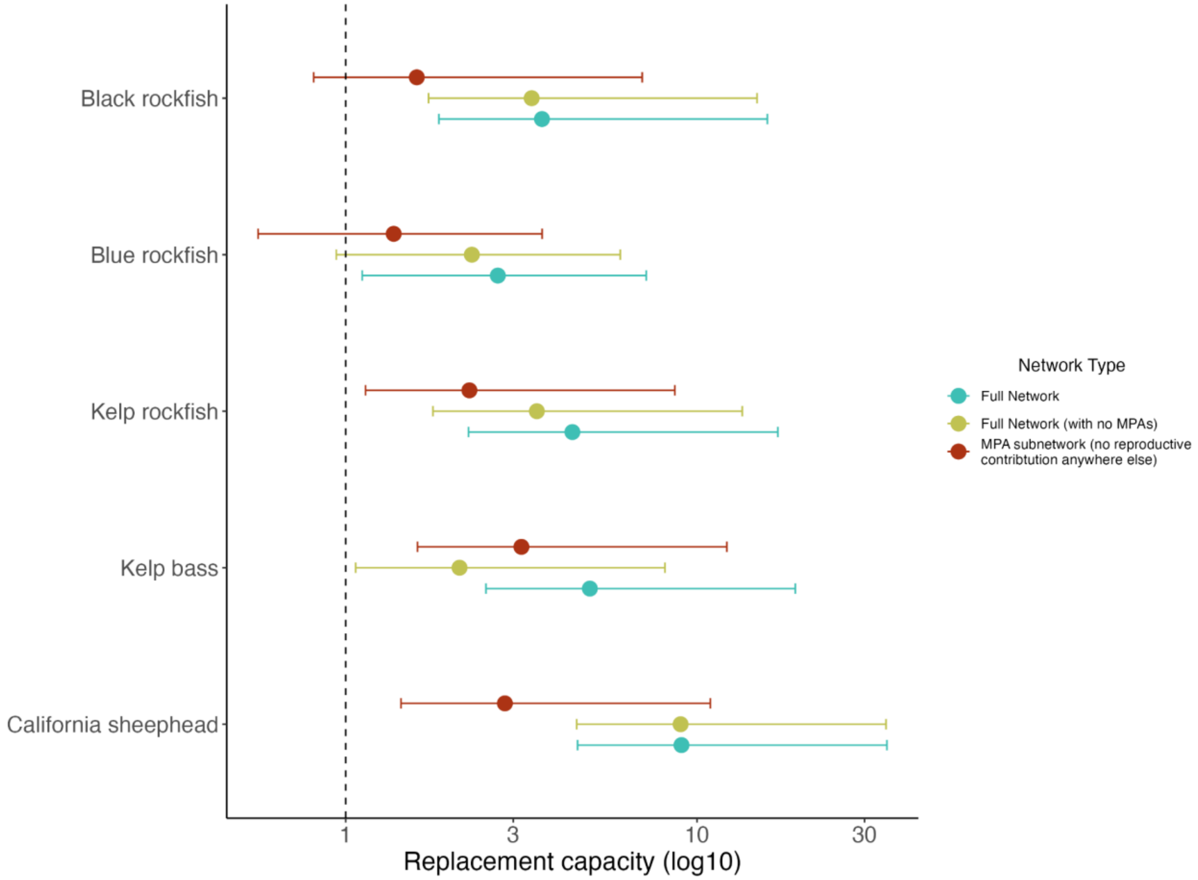
Results

What are the population consequences of ecological connectivity across the network?

Q1a: What is the replacement capacity of the full coastal network (i.e., entire metapopulations) and how does it vary across the 5 species?

We found that all species had persistent metapopulations, with replacement capacity for all species being above one (blue points in **Figure 2**). California Sheephead had the highest replacement capacity, followed by Kelp Bass, Kelp Rockfish, Black Rockfish and lastly Blue Rockfish. For all species there is substantial variation in the metric of replacement capacity based on the steepness parameter suggesting high importance of this parameter in understanding metapopulation persistence.

Figure 2. Replacement capacity across varying network types: Full network (MPAs and fished areas), Full network (no MPAs - all areas are fished), and the MPA sub-network (Only the MPAs, no reproductive contribution from fished areas), by the five species: Black Rockfish, Blue Rockfish, Kelp Rockfish, Kelp Bass, California Sheephead. If the point lies to the right of the dashed line (1), the metapopulation is persistent. The error bars represent the total variation in the steepness parameter, h.



Q1b: What is the replacement capacity of the MPAs portion of the network alone?

We found that when evaluating replacement capacity across only the MPA sub-network that all species had persistent metapopulations with Kelp Bass having the highest replacement capacity followed by California Sheephead, Kelp Rockfish, Black Rockfish and finally Blue Rockfish. When the metric was calculated using the lower-end of the steepness parameter, h, both Blue and Black Rockfish's metapopulation across the MPA sub-network were not persistent. To assess the role of connections between MPAs and non-MPAs we compared the magnitude of change in replacement capacity between the full network and the MPA sub-network and found that the presences of non-MPA and MPA connections substantially enhanced replacement capacity for all species (**Figure 2** comparing blue and red points; **Table 2**). California Sheephead had the highest increase in replacement capacity, 213%, when connections between non-MPA and MPAs were considered. Black Rockfish had a 127% increase, with Blue Rockfish and Kelp Rockfish had increases of 98% and 96%, respectively. Kelp Bass had the lowest impact but still a substantial 57% increase in replacement capacity when connections between non-MPA and MPAs were considered.

Table 2. The percent change in metapopulation replacement capacity for all 5 species. The effect of MPAs on the full network is the percentage change in replacement capacity from the full network with MPAs and the full network without MPAs.

	The percent change on metapopulation replacement capacity				
Objective	**California sheephead**	**Kelp bass**	**Kelp rockfish**	**Blue rockfish**	**Black rockfish**
Effect of MPAs on the full network	+ 1%	+ 135%	+ 26%	+ 19%	+ 7%

Q1c: What would the replacement capacity of the full coastal network be in the absence of MPAs?

We found that when evaluating replacement capacity of the full network with no MPAs that all species had persistent metapopulations with California Sheephead having the highest replacement capacity followed by Black Rockfish, Kelp Rockfish, Kelp Bass and finally Blue Rockfish. When the metric was calculated using the lowest-end of the steepness parameter, h, Blue Rockfish's metapopulation was not persistent. To assess the role of the MPAs on the network we compared the magnitude of change in replacement capacity between the full network with MPAs and the full network without MPAs and found that the role of MPAs enhanced replacement capacity for all species but at varying magnitudes (**Figure 2** comparing blue and yellow points; **Table 2** first row). Kelp Bass showed the largest difference, in that the presence of MPAs enhanced replacement capacity by 135%. Kelp Rockfish had the second highest enhancement with MPAs increasing replacement capacity by 26%, while Blue Rockfish increased by 19%. Black Rockfish and California Sheephead had much smaller increases in replacement capacity with the presence of MPAs with a 7% and 1% increase respectively.

Q1d: Which MPAs contribute more to the effectiveness of the California ecological network?

Examining the two metrics of site importance to the effectiveness of the network, we were able to identify (1) the top ten important sites for each species **(Table 3-7)**, (2) general trends for which regions displayed the highest site values across the two metrics within a species **(Table 8-9) and** (3) site designation differences (whether the site is a SMR, SMCA, a special closure or a non-MPA; **Table 10-11**). The full list of sites for both relative realized export and relative patch importance values for each species can be found in Table S3 to S7. Additionally, we have identified for each species the top ten MPAs for each site value metric (**Table S2**).

For California Sheephead, the top ten sites for both metrics of realized export and patch importance were almost exclusively south coast mainland sites with the exception of one Channel Island location for the realized export metric on West San Clemente Channel Island (**Table 3 and Table 8-9**). Most high leverage sites were not actually MPAs for California Sheephead with only one SMCA (Swami's) and one SMR (South La Jolla; **Table 10-11**, **Figure S12-13**). Kelp Bass had slightly more representation in the Channel Islands but still a majority of the high valued sites were found across the south coast mainland. Realized export had all top sites as MPAs while patch importance had only 30% MPAs with the others being non-MPAs (**Figure S14**). Across all high leverage sites about ⅓ were SMCAs, ⅓ were SMRs and ⅓ were non-MPAs all found north of San Diego.

The high-valued sites for Kelp Rockfish are almost exclusively found in the south coast Channel Islands, with two MPAs: Point Lobos SMR and Point Buchon SMR found in the central coast for realized export (**Table 4 and Table 8-9**). A majority of the sites for realized export were SMRs with one SMCAs: Painted Cave, one special closure: San Miguel Island and two non-MPAs (**Table 10**, **Figure S10**). For patch importance, 50% of sites were non-MPAs, 40% were SMCAs and 1 SMR with all but one SMCA found in the central Channel Islands (Santa Barbara, Catalina and San Clemente Islands; **Table 11, Figure S11**)).

Blue and Black Rockfish showed a regional division based on the metric types. For realized export, most top sites for Blue Rockfish were found in the central and north coast (80%) while 2 were in the south coast, Channel Islands **(Table 6 and Table 8, Figure S8**). Black Rockfish had all but one site on the north coast with one SMCA being in the central coast (**Table 7 and Table 8**, **Figure S6**). For patch importance, however, all top sites for both blue and black Rockfish were found in the south coast Channel Islands (**Table 9**, **Figure S7; S9**). For site designation, across both metrics, around 50% of the top sites for both blue and black Rockfish were SMR MPAs (**Table**

10-11). Blue Rockfish had 2 SMCAs and one special closure while black Rockfish had 4 SMCAs. Patch importance had slightly more non-MPAs for both species and for realized export had 3 and 1 non-MPAs for blue and black Rockfish respectively.

Table 3. The ten highest valued sites (considering both MPAs and non-MPAs) sorted highest to lowest in the two metrics: realized export and patch importance for **California Sheephead**. SMR is a MPA which is a State Marine Reserve and SMCA is an MPA that is a State Marine conservation area. The non-MPAs have the ROMS cell number and the closest city or general landmark in parentheses (see **Figure S12-S13** for the associated map of these top sites).

Realized Export	Patch Importance
111 (Point Vincente)	89 (Camp Pendleton)
120 (Malibu)	83 (Encinitas)
78 (San Diego)	84 (Carlsbad)
75 (San Diego)	Swami's SMCA
74 (San Diego)	88 (Camp Pendleton)
South La Jolla SMR	85 (Carlsbad)
Swami's SMCA	90 (Camp Pendleton)
108 (Point Vincente)	82 (Encinitas)
76 (San Diego)	92 (Camp Pendleton)
550 (W San Clemente Channel Island)	86 (Oceanside)

Table 4. The ten highest valued sites (considering both MPAs and non-MPAs) sorted highest to lowest in the two metrics: realized export and patch importance for **Kelp Bass**. SMR is a MPA which is a State Marine Reserve and SMCA is an MPA that is a State Marine conservation area. The non-MPAs have the ROMS cell number and the closest city or general landmark in parentheses (see **Figure S14** for the associated map of these top sites).

Realized Export	Patch Importance
South La Jolla SMR	San Diego-Scripps Coastal SMCA
Swami's SMCA	Swami's SMCA
Crystal Cove SMCA	82 (Encinitas)
Carrington Point SMR	Matlahuayl SMR
Cabrillo SMR	85 (Carlsbad)
Abalone Cove SMCA	South La Jolla SMR
Laguna Beach SMR	88 (Camp Pendleton)
Laguna Beach SMCA	89 (Camp Pendleton)
Point Vicente SMCA	86 (Oceanside)
Skunk Point SMR	83 (Encinitas)

Table 5. The ten highest valued sites (considering both MPAs and non-MPAs) sorted highest to lowest in the two metrics: realized export and patch importance for **Kelp Rockfish**. SMR is a MPA which is a State Marine Reserve and SMCA is an MPA that is a State Marine conservation area. The non-MPAs have the ROMS cell number and the closest city or general landmark in parentheses (see **Figure S10-S11** for the associated map of these top sites).

Realized Export	Patch Importance
Carrington Point SMR	Painted Cave SMCA
Painted Cave SMCA	Santa Barbara Island SMR
Harris Point SMR	556 (SE San Clemente Channel Island)
South Point SMR	521 (NE Santa Barbara Channel Island)
San Miguel Island Special Closure	Blue Cavern Onshore SMCA
495 (W Santa Cruz Channel Island)	533 (SE Catalina Channel Island)
489 (NW San Miguel Channel Island)	Farnsworth Onshore SMCA
Point Buchon SMR	Arrow Point to Lion Head Point SMCA
Skunk Point SMR	530 (NW Catalina Channel Island)
Point Lobos SMR	555 (S San Clemente Channel Island)

Table 6. The ten highest valued sites (considering both MPAs and non-MPAs) sorted highest to lowest in the two metrics: realized export and patch importance for **Blue Rockfish**. SMR is a MPA which is a State Marine Reserve and SMCA is an MPA that is a State Marine conservation area. The non-MPAs have the ROMS cell number and the closest city or general landmark in parentheses (see **Figure S8-S9** for the associated map of these top sites).

Realized Export	Patch Importance
Montara SMR	Painted Cave SMCA
Asilomar SMR	505 (NW Santa Cruz Channel Island)
Carmel Pinnacles SMR	Richardson Rock SMR
Point Lobos SMR	523 (SW Santa Barbara Channel Island)
Pillar Point SMCA	530 (NW Catalina Channel Island)
Point Sur SMR	San Miguel Island Special Closure
218 (17-mile Dr. Monterey Peninsula)	Harris Point SMR
488 (NW San Miguel Channel Island)	Judith Rock SMR
Bodega Head SMR	518 (S Anacapa Channel Island)
489 (NW San Miguel Channel Island)	Carrington Point SMR

Table 7. The ten highest valued sites (considering both MPAs and non-MPAs) sorted highest to lowest in the two metrics: realized export and patch importance for **Black Rockfish**. SMR is a MPA which is a State Marine Reserve and SMCA is an MPA that is a State Marine conservation area. The non-MPAs have the ROMS cell number and the closest city or general landmark in parentheses (see **Figure S6-S7** for the associated map of these top sites).

Realized Export	Patch Importance
Bodega Head SMR	Painted Cave SMCA
Bodega Head SMCA	505 (NW Santa Cruz Channel Island)
Point Reyes SMR	Richardson Rock SMR
Saunders Reef SMCA	488 (NW San Miguel Channel Island)
Point Arena SMR	495 (W Santa Cruz Channel Island)
Stewarts Point SMR	Harris Point SMR
MacKerricher SMCA	492 (SW San Miguel Channel Island)
256 (Bolinas)	489 (NW San Miguel Channel Island)
Sea Lion Gulch SMR	506 (NNW Santa Cruz Channel Island)
South Cape Mendocino SMR	Carrington Point SMR

Table 8. The proportion of the top ten relative **realized export** sites for all four focal fish species based on the region the site is found in California (North Coast, Central Coast, Southern coast Channel Islands, Southern coast Mainland).

	California Sheephead	**Kelp Bass**	**Kelp Rockfish**	**Blue Rockfish**	**Black Rockfish**
North Coast	0%	0%	0%	10%	90%
Central Coast	0%	0%	20%	70%	10%
South Coast Channel Islands	10%	30%	80%	20%	0%
South Coast Mainland	90%	70%	0%	0%	0%

Table 9. The proportion of the top ten relative **patch importance** sites for all four focal fish species based on the region the site is found in California (North Coast, Central Coast, Southern coast Channel Islands, Southern coast Mainland).

	California Sheephead	Kelp Bass	Kelp Rockfish	Blue Rockfish	Black Rockfish
North Coast	0%	0%	0%	0%	0%
Central Coast	0%	0%	0%	0%	0%
South Coast Channel Islands	0%	0%	100%	100%	100%
South Coast Mainland	100%	100%	0%	0%	0%

Table 10. The proportion of the top ten relative **realized export** sites for all four focal fish species based on the site's designation (State Marine Reserve, State Marine Conservation Area, Special Closure or non-MPA).

	California Sheephead	Kelp Bass	Kelp Rockfish	Blue Rockfish	Black Rockfish
State Marine Reserve	10%	50%	60%	60%	60%
State Marine Conservation Area	10%	50%	10%	10%	30%
Special Closure	0%	0%	10%	0%	0%
Non-MPA	80%	0%	20%	30%	10%

Table 11. The proportion of the top ten relative **patch Importance** sites for all four focal fish species based on the site's designation (State Marine Reserve, State Marine Conservation Area, Special Closure or non-MPA).

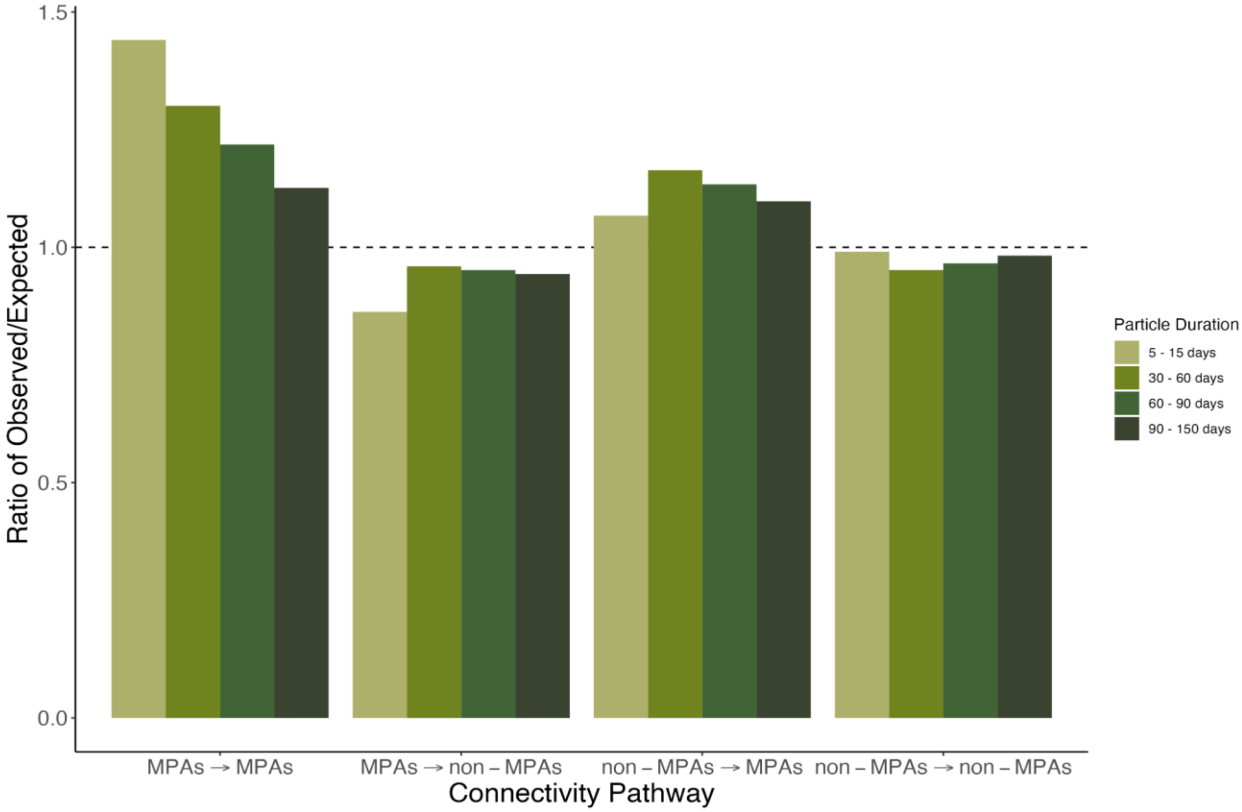
	California Sheephead	Kelp Bass	Kelp Rockfish	Blue Rockfish	Black Rockfish
State Marine Reserve	0%	20%	10%	40%	30%
State Marine Conservation Area	10%	20%	40%	10%	10%
Special Closure	0%	0%	0%	10%	0%
Non-MPA	90%	60%	50%	40%	60%

How does particle transport contribute to environmental connectivity across the network?

Q2a: How does environmental connectivity vary across both transport duration and connectivity pathways within shallow rocky reef and kelp forest habitats?

We found that particle transport contribution across shallow rocky reef and kelp forest habitats differed across the 4 connectivity pathways (Figure 3). Pathways of particle contribution into MPAs (MPAs into other MPAs and non-MPA into MPAs) had higher levels of particle contribution than expected based on habitat area alone. While the pathways of particle contribution into non-MPAs (MPAs into non-MPAs or non-MPAs into other non-MPAs) had lower contributions than expected based on habitat area alone. There wasn't a strong effect of PLD for whether we'd expect more or less contribution based on habitat area across all connectivity pathways (i.e., The bars were always found either all above or all below the 1 line across all PLDs within each pathway), however it looks like there is a pattern for decreasing contribution from MPAs into other MPAs with increasing PLD.

Figure 3. The ratio of proportional observed to expected shallow rocky reef and kelp forest habitat contribution estimates of transport across the four connectivity pathways, while controlling for differences in habitat area. Each colored bar represents the pelagic larval duration of the simulation. If the value is greater than 1, there is more particle transport than expected by habitat area alone.



Q2b: How does environmental connectivity vary across both transport duration and connectivity pathways within other coastal and subtidal habitats found within the California MPA network?

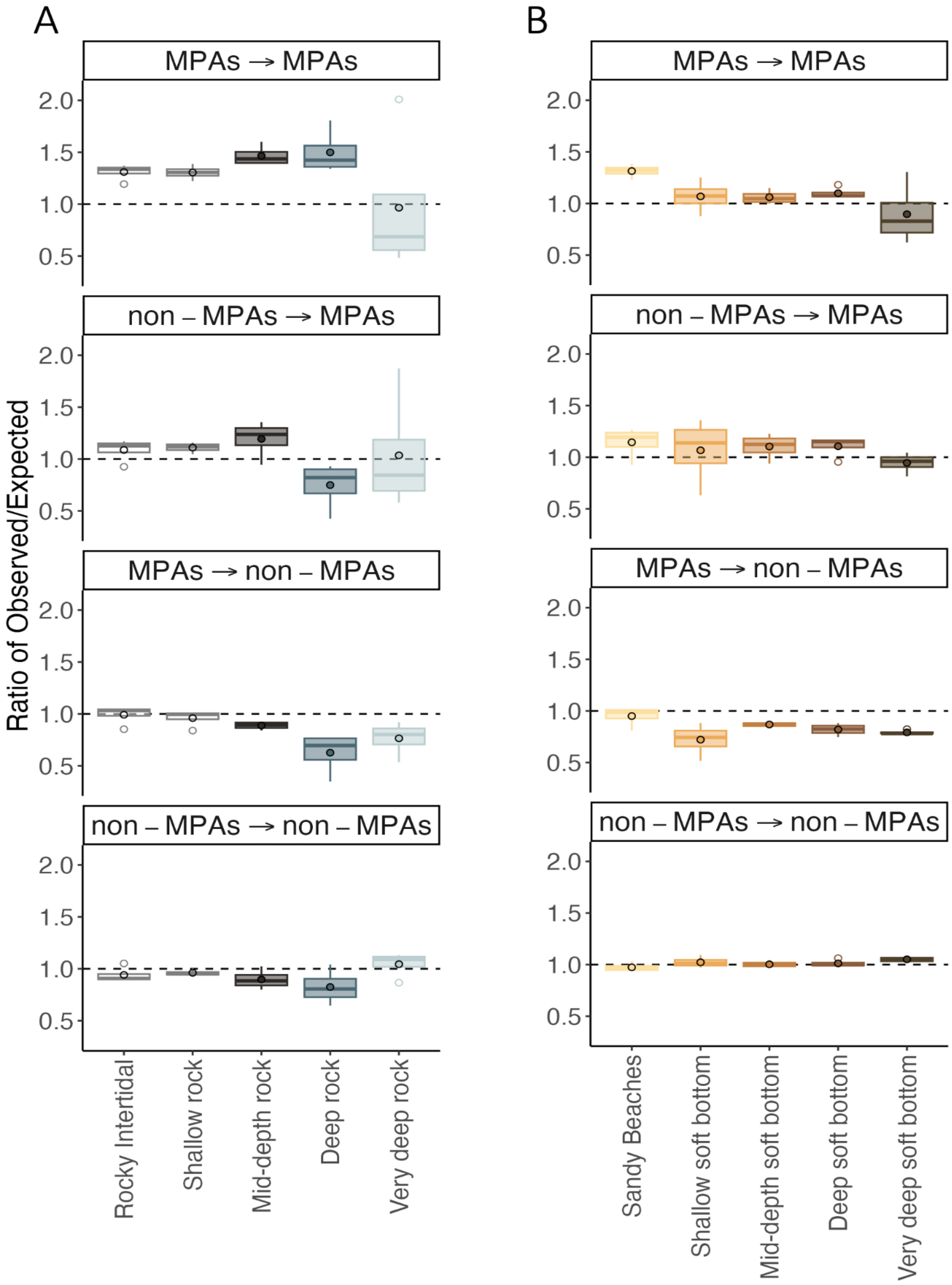
For both rocky intertidal (Figure 4a) and sandy beaches (Figure 4b), we found the contribution of transport into MPAs (from both other MPAs and non-MPAs) to be higher than expected based on area for all transport durations except 5-15 days from non-MPAs (Figure S15). The contribution of transport into non-MPAs had about the same amount or slightly less than expected by area from MPAs and lower contribution of transport than expected by area from other non-MPAs (besides the 5-15 day duration where we saw the opposite trend).

For subtidal shallow, mid-depth and deep rock habitats we found contribution of particle transport into MPAs from other MPAs to be higher than expected based on area across all particle durations (Figure 4a). Similarly, shallow and mid-depth rock had higher contributions of particle transport into MPAs from non-MPAs than expected by habitat area (except for the mid-depth rock particle duration of 5-15 days; Figure S16), while the transport of particles from non-MPAs into MPAs at deep rock was less than expected by habitat area. Very deep rock also had higher contributions of transport into MPAs (from both other MPAs and non-MPAs), but only for the particle duration of 5-15 days. For all subtidal rock habitats, we found the contribution of particle transport into non-MPAs (from both other MPAs and non-MPAs) to be less than expected based on habitat area (except for non-MPA into other non-MPA for very deep rock habitat).

Subtidal shallow, mid-depth and deep soft bottom habitats also had higher contributions of particle transport into MPAs (from both other MPAs and non-MPAs) than predicted by habitat area alone (Figure 4b; besides 30-60 days of particle duration from MPAs in shallow soft bottom and 5-15 days from non-MPAs in shallow, mid-depth and deep soft bottom habitats, Figure S16). The very deep soft bottom habitat had lower contributions of particle transport into MPAS (from both other MPAs and non-MPAs) than predicted by habitat area (with the exception of the 5-15 day particle duration for MPA into MPAs). Across all soft bottom habitats, particle transport into non-MPAs from MPAs was lower than expected based on habitat area and transport to non-MPAs from other non-MPAs were all around what is expected based on habitat area.

Figure 4. The ratio of proportional observed to expected contribution of transport across rocky and soft bottom habitats based on habitat area. (A) The blue-gray color palette signifies rocky habitats, while (B) the brown color palette signifies soft bottom habitats. If a value is greater than 1 (above the horizontal dashed line), there is more

particle transport than expected by habitat area alone. The filled point signifies the mean ratio across the 4 particle durations for each treatment. The centerline of the boxplot is the median, lower and upper lines indicate the 25% and 75% quantiles of the distribution, and the unfilled points indicate outliers.


A
B
MPAs → MPAs
non – MPAs → MPAs
MPAs → non – MPAs
non – MPAs → non – MPAs
Ratio of Observed/Expected
2.0
1.5
1.0
0.5
Rocky Intertidal
Shallow rock
Mid-depth rock
Deep rock
Very deep rock
Sandy Beaches
Shallow soft bottom
Mid-depth soft bottom
Deep soft bottom
Very deep soft bottom

Discussion

One of the main goals from the Marine Life Protection Act (MLPA) is to ensure that the state's MPAs are designed and managed, to the extent possible, as a network.

In this report we strived to answer this question via two ways: through (1) **ecological connectivity** as the dynamics of species metapopulations interacting with ocean currents and spatially heterogeneous fishing pressure across the network, and (2) **environmental connectivity** as the way particles are transported via ocean currents to and from sites which share common habitats. Most broadly, we can say that for both ecological and environmental connectivity *we found that the California MPAs are in fact working as an effective network.* We found that all 5 fish species had persistent metapopulations with varying strengths of replacement capacity. For environmental connectivity we found higher than predicted particle transport into MPAs based on the habitat area. Lastly, we were able to identify the highest leverage sites, specific to connectivity and found differences across species, region and site designation. From an adaptive management lens, these metrics can help us understand which MPA and non-MPAs are most critical in supporting connectivity across the network and potentially highlight areas to sustain or enhance protection and management.

In the planning stages of the California MPA network, using ocean circulation models (White et al. 2013), there was a focused effort to site MPAs in areas which would enhance connections between other MPAs. We found when examining metapopulation persistence across the sub-network of only MPAs (excluding reproductive contribution from anywhere else besides MPAs), that every species had persistent metapopulations (besides blue and black Rockfish at some of the lower levels of the steepness parameter). Persistence could emerge via: (1) high larval retention at the local scale resulting in a collection of individual self persistent MPAs or (2) the geographic placement of MPAs interacting with ocean currents to create a network which are connected via dispersal making this sub-network persistent across the metapopulation. As we found no self-persistence in any individual/single MPA for any species analyzed, we conclude that the spatial configuration of MPAs leading to high connectivity amongst them is supporting a persistent metapopulation. In our models, the total MPA area makes up 15.5 - 18% (depending on the species' range) of the total potential habitat in the California model domain. This speaks to the success of the planning process, with considering less than 20% of the spatial coverage of the California coastline, all fish metapopulations remained persistent.

We found for 3 of the 5 species, the effect of MPAs via the cessation of fishing, considerably enhanced replacement capacity (California Sheephead and Black Rockfish had positive but incremental increases in replacement capacity). This was particularly strong for Kelp Bass which experienced a 135% increase in replacement capacity when MPAs were added into the network. Kelp and Blue Rockfish also had moderate increases of 26% and 19% respectively. This suggests that the protection MPAs provide for these three species substantially enhance biomass and larval production, creating vital source populations which permeate across their metapopulation networks. Conversely, there was little effect of replacement capacity of black Rockfish in response to the MPA effect. This can be explained by the areas where black Rockfish are in highest abundance (i.e., the north coast) have reduced fishing pressure (represented in our model as increased distances from ports and decreased number of trips) relative to other regions within California like the southern region. As the MPAs that black Rockfish most inhabit experience lower fishing pressure, when the cessation of fishing is removed this results in smaller changes in biomass and larval production thus replacement capacity across the metapopulation. California Sheephead also did not have a large change in replacement capacity in our models. This is a result of the enhanced biomass occurring with the cessation of fishing in MPAs only increases male's abundance/biomass and not female's which leads to no enhancement of larval production in MPAs. If we were to update the model to consider other mechanisms of female to male transition, we may see more of an MPA effect. For example, if fishing (which targets the removal of big males) changes the local population’s sex ratio and decreases the size at which female Sheephead transition, non-MPA females may have even less time at maturity where they are fecund and less overall reproductive output, relative to MPAs where the transition would be at a larger size due to the preservation of large males.

Using metrics of realized export and patch value we were able to identify high leverage sites for each fish species, account for differences across site designation and explain regional mechanisms of connectivity. We saw 14% more SMRs relative to SMCAs across the high valued sites for these five species, however, SMCAs still made up 20% of the total top sites. All of these SMCAs were areas of no-take for these species (although when only considering MPAs (Table S2) Dana Point was a high leverage MPA for California Sheephead and Kelp Bass even though take of finfish is allowed here). Understanding which SMRs and SMCAs are critical for connectivity across these metapopulations can help guide which locations to prioritize continual management and protection. Although MPAs made up a majority of high leverage sites for connectivity across these 5 species’ metapopulations, there were a considerable number of non-MPA regions which came out as important sites. California Sheephead in particular had a majority of its high valued sites in non-MPAs. We believe this is again a product of an assumption in our model where the cessation of fishing in MPAs increases male biomass but not female (as they transitioned to male once they reach a standard size). As MPAs did not show a substantial increase in larval production relative to non-MPAs, these two metrics were most likely lower than they actually should be for MPAs. However, we can still use information around the high values of areas which are not MPAs as possible sites for future protection, specific to enhancing connectivity. On the south coast mainland, many of the non-MPA ROMS cells which parallel the coastline of Camp Pendleton and beach communities of Encinitas, Carlsbad and Oceanside came out as high leverage sites for both California Sheephead and Kelp Bass. For the Northern Channel Islands ROMS cell 489 (the region between Harris Rock and Richardson rock SMRs on the northwest of San Miguel Channel Island) came out as important for blue, black and kelp Rockfish, while ROMS cell 495 (the region on the northwest tip of Santa Cruz Channel Island) was high valued for both black and kelp Rockfish. Lastly, ROMS cell 530 which is on the northwest region of Catalina Channel Island was found to be important for kelp and blue Rockfish.

Differences between the two site value metrics may highlight the regional mechanisms for connectivity across the coastline. Realized export displays how much larvae successfully transport to a neighboring site within the network while patch importance considers the intersection of reproductive capacity with the number of connections a site makes to other sites. We see a regional partition amongst the metrics in both blue and black Rockfish, where their range spans the north/central and south coast. A majority of the high leverage sites for these two species were split with high realized export sites in the north and central coasts and high patch importance in the south coast, Channel Islands. The north and central coast depict more of a linear network along the coastline where connections between sites are driven by high pulses of larval recruitment from sites found up- or down-coast from them. For both blue and black Rockfish, their biomass is largest in these areas, where these sub-populations are larval production powerhouses for the metapopulation. So even if some larvae are transported offshore (due to the less connected nature of a linear network) the high numbers of larvae produced at these sites are able to still successfully recruit to neighboring sites. In the south coast blue and black Rockfish have relatively lower biomass compared to the central and north coast regions. However, the connected nature of the network across the Channel Islands and mainland via currents and eddies allows for a higher success of (the potentially less) larvae to make it to another site and more than one site for that matter. This is represented in the number of high value sites of patch importance for blue and black Rockfish in the south coast region.

When calculating particle transport across the coastline for 11 coastal and subtidal habitats, we found transport from MPAs to other MPAs to be higher than expected based on habitat area, with this being most pronounced in the rocky substrate habitats. These results are a product of the strategic design and placement of the MPAs in relation to ocean currents. This again highlights the achievements of the MLPA science advisory team in siting MPAs in areas where they are in fact more connected to other MPAs. This level of connectedness allows for MPAs to be smaller in size but also help buffer the metapopulation from experiencing drastic collapse from a disturbance via rescue effects. When examining environmental connectivity across other pathways, we found a unidirectional flow of increased particle transport from non-MPAs into MPAs but not from MPAs into no-MPAs. A central design goal for the California MPA network was based on centering transport of one MPA to another. As a consequence of this, realized transport of MPAs to non-MPAs is lower than expected when controlling for habitat area. Although non-MPAs have less connectivity between other non-MPAs or transport from MPAs, the expansive habitat area that they contain counteracts the lower level of transport.

We did not find obvious trends between PLD and our metrics of connectivity. For environmental connectivity, a majority of the time PLD did not change whether the level of particle transport into a specific habitat was greater or less than expected based on the area of said habitat. There was a decreasing trend of particle transport with increasing PLD in the rocky reef habitat of MPAs into other MPAs. Additionally for ecological connectivity, we found no relationship between the length of PLD for a species and replacement capacity. Two species (Blue and Black Rockfish) with the longest PLDs did have the lower replacement capacity values but this trend did not hold with decreasing PLD. The lack of an apparent relationship demonstrates that understanding realized connectivity for a population is more complex than the species PLD, as other studies have found (Weersing and Toonen 2009). This may be a product of geography or other varying life history factors interacting with PLD making it difficult to discern any relationships. Here we know species differed in the mechanism of connectivity (i.e., value of realized export or patch importance) based on the region, where in the north and central coast the network is more linear than the southern region. This can drastically change the distance of transport while dispersing, making PLD not a good predictor for dispersal distance. Furthermore, it’s hard to make this comparison across these species as they differ in their geographic distributions, habitat associations and seasonality of spawning. Currently, one limitation of our model for calculating ocean connectivity is that there is no seasonal solution to the ROMS model. However, species spawn at varying times of the year, and the seasonal dynamics of when propagules subside in the water column along with variation in upwelling and temperature changes throughout the year can have varying effects the impact currents have on their transport. This is something we plan to update in future models. Lastly, the particles in the ROMS model are strictly passive and do not incorporate any simulated behavior (e.g., diel or ontogenetic changes in depth or swimming behavior). We fully recognize the importance of this shortcoming, but it is a necessary first approximation. Such non-passive behaviors are taxonomically specific and can be applied in the future for particular species of interest as appropriate data become available (Drake et al. 2013).

Future work

We have a series of suggestions for future work that would lead to even greater utility of MPA network connectivity modeling. These largely depend on further development of the ROMS model used to inform the dispersal patterns of propagules:

1) Expand the ROMS solutions to years with atypical oceanographic features. All the oceanographic transport modeling was for years with typical oceanographic features (1999-2012). This means that the larval transport modeling was representative of normal years but potentially not for years that had, for

example, ENSO events or marine heatwaves. Consequently, the patterns of connectivity identified in this study may not hold for atypical years. This is problematic because, the greatest perturbation to marine communities that we have seen over the course of the MPA monitoring occurred during the 2014-2016 marine heatwave, which was not part of the ROMS model and our analyses.

Updating the models to 2023 would allow determination of the degree of dissimilarity between the connectivity patterns of the current model (for the years 1999-2012) and the heatwave years and provide insight into how such differences could degree the MPA networking properties and the stability they provide. It would also allow a way to assess adaptive management of the network by understanding the importance of connectivity during periods of environmental stress.

2) *Tailor analyses to capture the seasonal differences in reproduction.* Species differ in the particular seasons that they release their young (i.e. spawn). Current patterns vary with seasons, including coastal upwelling, which leads to differences in dispersal patterns among species depending on when they release young. In the current model, differences in species habitat associations and planktonic larval durations were used as proxies for species. Spawning periods were not formally part of the models. For the many species for which timing of spawning is available, much better estimates of connectivity and the emergent properties resulting from the estimates (e.g., stability of populations) could be made if seasonal resolution was incorporated into the analyses.
3) *Evaluate the relationships between local oceanographic processes and MPA connectivity metrics.* We did not explore the drivers of variation in MPA connectivity metrics, such as local differences in exposure to coastal upwelling. Exposure to oceanographic processes such as coastal eddies and coastal

upwelling are known to drive variation in larval advection and retention (e.g., Ebert and Russel XXXX, Woodson et al XXXX). Thus, examining the relationships between these features and connectivity metrics would advance our understanding of how these relationships influence overall network connectivity and the importance of MPAs to the persistence of species metapopulations.

These local features such as coastal upwelling influence the relative exposure of species to multiple environmental stressors (increased temperature, reduced dissolved oxygen and pH) and recent analyses document the regional variation of MPA exposure to multiple stressors across the California network (Hamilton et al 2023). Knowledge of how this variable exposure among MPAs and its consequences for species performance (e.g., Willis-Norton et al 20XX) contribute to patterns of connectivity and population persistence will also bolster our understanding of network performance. Moreover, how these patterns of exposure and connectivity will change with ongoing climate change and how they will interact with changing patterns of fishing pressure will inform the adaptive management of the network and fisheries.

References

Baetscher, D. S., E. C. Anderson, E. A. Gilbert-Horvath, D. P. Malone, E. T. Saarman, M. H. Carr, and J. C. Garza. 2019. Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast. Molecular Ecology 28:1611–1623.

Botsford, L. W., J. W. White, M. H. Carr, and J. E. Caselle. 2014. Marine Protected Area Networks in California, USA. Pages 205–251 Advances in Marine Biology. Elsevier.

Botsford, L. W., J. W. White, M.-A. Coffroth, C. B. Paris, S. Planes, T. L. Shearer, S. R. Thorrold, and G. P. Jones. 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. Coral reefs 28:327–337.

Botsford, L. W., J. W. White, and A. Hastings. 2019. Population dynamics for conservation. Oxford University Press, USA.

Burgess, S. C., K. J. Nickols, C. D. Griesemer, L. A. K. Barnett, A. G. Dedrick, E. V. Satterthwaite, L. Yamane, S. G. Morgan, J. W. White, and L. W. Botsford. 2014. Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. Ecological Applications 24:257–270.

Carr, M. H., S. P. Robinson, C. Wahle, G. Davis, S. Kroll, S. Murray, E. J. Schumacker, and M. Williams. 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. Aquatic Conservation: Marine and Freshwater Ecosystems 27:6–29.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of Connectivity in Marine Populations. Science 311:522–527.

Cowen, R. K., and S. Sponaugle. 2009. Larval Dispersal and Marine Population Connectivity. Annual Review of Marine Science 1:443–466.

Dedrick, A. G., K. A. Catalano, M. R. Stuart, J. W. White, H. R. Montes, and M. L. Pinsky. 2021. Persistence of a reef fish metapopulation via network connectivity: theory and data. Ecology Letters 24:1121–1132.

Drake, P. T., C. A. Edwards, S. G. Morgan, and E. P. Dever. 2013. Influence of larval behavior on transport and population connectivity in a realistic simulation of the California Current System. Journal of Marine Research 71:317–350.

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-Specific Sensitivity: Applying a New Structured Population Model. Ecology 81:694–708.

Ellner, S. P., D. Z. Childs, and M. Rees. 2016. Data-driven modelling of structured populations. A practical guide to the Integral Projection Model. Cham: Springer.

Garavelli, L., J. W. White, I. Chollett, and L. M. Chérubin. 2018. Population models reveal unexpected patterns of local persistence despite widespread larval dispersal in a highly exploited species. Conservation Letters 11:e12567.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41.

Harrison, H. B., M. Bode, D. H. Williamson, M. L. Berumen, and G. P. Jones. 2020. A connectivity portfolio effect stabilizes marine reserve performance. Proceedings of the National Academy of Sciences 117:25595–25600.

Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences 103:6067–6072.

Hilty, J., G. Worboys, A. Keeley, S. Woodley, B. Lausche, H. Locke, M. Carr, I. Pulsford, J. Pittock, J. W. White, D. Theobald, J. Levine, M. Reuling, J. Watson, R. Ament, and G. Tabor. 2020. Guidelines for conserving connectivity through ecological networks and corridors.

James, M. K., P. R. Armsworth, L. B. Mason, and L. Bode. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. Proceedings of the Royal Society of London. Series B: Biological Sciences 269:2079–2086.

Kinlan, B. P., and S. D. Gaines. 2003. Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. Ecology 84:2007–2020.

Kirlin, J., M. Caldwell, M. Gleason, M. Weber, J. Ugoretz, E. Fox, and M. Miller-Henson. 2013. California's Marine Life Protection Act Initiative: Supporting implementation of legislation establishing a statewide network of marine protected areas. Ocean & Coastal Management 74:3–13.

Kritzer, J. P., and P. F. Sale. 2010. Marine Metapopulations. Elsevier.

Ovaskainen, O., and I. Hanski. 2001. Spatially Structured Metapopulation Models: Global and Local Assessment of Metapopulation Capacity. Theoretical Population Biology 60:281–302.

Saarman, E., M. Gleason, J. Ugoretz, S. Airamé, M. Carr, E. Fox, A. Frimodig, T. Mason, and J. Vasques. 2013. The role of science in supporting marine protected area network planning and design in California. Ocean & Coastal Management 74:45–56.

Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:159–169.

Walters, C. 1996. Estimation of historical stock sizes and recruitment anomalies from relative abundance time series. https://www.infona.pl/resource/bwmeta1.element.elsevier-2fd6c6a0-ee9d-3481-b37f-fdd33f8ce2d8.

Watson, J. R., C. G. Hays, P. T. Raimondi, S. Mitarai, C. Dong, J. C. McWilliams, C. A. Blanchette, J. E. Caselle, and D. A. Siegel. 2011. Currents connecting communities: nearshore community similarity and ocean circulation. Ecology 92:1193–1200.

Weersing, K., and R. J. Toonen. 2009. Population genetics, larval dispersal, and connectivity in marine systems. Marine Ecology Progress Series 393:1–12.

White, J. W. 2010. Adapting the steepness parameter from stock–recruit curves for use in spatially explicit models. Fisheries Research 102:330–334.

White, J. W., L. W. Botsford, A. Hastings, M. L. Baskett, D. M. Kaplan, and L. A. K. Barnett. 2013. Transient responses of fished populations to marine reserve establishment: Transient dynamics in marine reserves. Conservation Letters 6:180–191.

White, J. W., L. W. Botsford, A. Hastings, and J. L. Largier. 2010. Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. Marine Ecology Progress Series 398:49–67.

White, J. W., M. H. Carr, J. E. Caselle, L. Washburn, C. B. Woodson, S. R. Palumbi, P. M. Carlson, R. R. Warner, B. A. Menge, and J. A. Barth. 2019. Connectivity, dispersal, and recruitment. Oceanography 32:50–59.

White, J. W., K. J. Nickols, D. Malone, M. H. Carr, R. M. Starr, F. Cordoleani, M. L. Baskett, A. Hastings, and L. W. Botsford. 2016. Fitting state-space integral projection models to size-structured time series data to estimate unknown parameters. Ecological Applications 26:2677–2694.

White, J.W., Spiecker, B.J., Yeager, M. E,. Caselle, J.E. *Marine Protected Areas and Temperate Reef Fishes*: Allen, L. G., Pondella, D. J. and Horn, M.H. Second Eds. In Press. *The ecology of marine fishes: California and adjacent waters*. Univ of California Press.

Yaffee, S. L. 2020. Beyond Polarization: Public Process and the Unlikely Story of California’s Marine Protected Areas. Island Press.

Appendices

Extended Methods

Larval connectivity

Larvae spawn at each local population in each year, disperse according to their larval connectivity and enter the benthic population in destination cells as new recruits.

We modeled larval connectivity using Regional Ocean Model System (ROMS) particle tracking which simulates larval dispersal in three spatial dimensions (through the movement of X, Y, Z vectors) and one temporal dimension (time step = hourly). Every particle's location can be evaluated at each timestep, and we used this feature to calculate a fish's larval dispersal, letting the model run for an equivalent time of the species known pelagic larval duration (PLD). This simulated dispersal is based on an average solution across 15 years (1999-2013) and the range spans from 100km south of CA into Baja California, Mexico and north up through Oregon, although for this project we focused on only California's range. Approximately 88000 "larvae" particles are released across 557 ROMS cells (365 cells in California). Solutions were run at eight "lengths of time" to simulate differing PLDs of each fish species' life history: 5, 10, 15, 30, 60, 90, 120, 150, and 180 days. If species exhibit a range of PLDs, then we took an elemental average of the corresponding connectivity matrix solutions (e.g., California Sheephead's PLD is 37-78 days, so we used the average of 30, 60 and 90 PLD ROMS solutions).

Larvae move hourly, but with daily averaged currents (i.e. every hour we interpolate the daily average currents from the ROMS model in space and time to find the current at each particle location, then we move each particle with its appropriate current velocity). Landward of the 500 m depth isobath, larvae are also given a random kick simulating tidal currents of 5 cm/s. This kick is also given every hour in addition to the daily-averaged motion. Settlement only occurs within 10% of PLD (e.g for PLD of 30 days: 27-33 days). The ROMS output can be considered a measure of connectivity among cells (locations) but should not be considered – on its own – an estimate of one cell's contribution of larvae (propagules) to other cells. This is because cells in ROMS grids are only characterized by oceanographic forcing and spatial dimensions (and vertical layers), and we simulated the release of the same number of particles from each cell. To estimate the actual settlement of a species, propagule production for donor cells and amount of suitable habitat for receiving cells must be incorporated. To do this, we built Species Distribution Models (SDMs) to quantify the maximum carrying capacity of each species in each ROM cell.

Species Habitat Associations

We constructed a SDM for each of the 5 fish species to calculate the maximum carrying capacity of fish biomass each ROMS cell contains. To quantify the associations of habitat with shallow subtidal rocky reef fish species, we used underwater SCUBA surveys from the Partnership for Interdisciplinary Studies of the Coastal Oceans (PISCO; https://www.piscoweb.org/) and Reef Check California (RCCA; https://www.reefcheck.org/country/usa-california/) across their long-term monitoring sites (1999-2022) paired with suite of environmental variables. PISCO is an academic consortium that conducts research to advance understanding of the coastal ocean within the California Current Large Marine Ecosystem and inform management and policy. Reef Check is a non-profit organization leading citizen scientists* to promote stewardship of sustainable reef communities worldwide. We first assembled predictor and response variables across all PISCO and RCCA survey locations. For our models, we calculated the response variable for each SDM as the 75% quantile of biomass density of each species through all survey years at each survey location. Due to misaligned sampling PISCO and RCCA surveys (RCCA only samples a bottom transect for fish which PISCO samples bottom and mid-water transects) we compared spatially paired survey locations where both RCCA and MLPA sample and determined that RCCA are possibly missing some individuals of Blue Rockfish and Kelp Rockfish, so we only used PISCO survey data for those species. The biomass density for all other species were comparable across the paired sites therefore we concluded that those species were appropriately captured in the bottom transect so both RCCA and PISCO surveys were used for all remaining species. For the predictor variables, we chose environmental variables which would ecologically explain fish presence and/or abundance across California. These variables can be grouped into substrate, abiotic, and biotic variables.

For substrate analysis, we used the same bathymetry data as mentioned above in the above habitat estimates section and used a variety of spatial analytical tools in ArcGIS10 to calculate 4 substrate descriptors: depth (meters), vector ruggedness metric (vrm, or rugosity), slope, and the proportional amount of rock to sand present within each pixel. The spatial resolution of each pixel was aggregated to 900 m^2 and the spatial extent of these rasters extended from coastline to 30m in depth which encompasses the depth range of shallow rocky subtidal SCUBA surveys done by RCCA and PISCO.

The abiotic variables that were collected for the SDMs consisted of sea surface temperature, metrics of upwelling (e.g., BEUTI and CUTI; Jacox et al. 2018) and wave metrics (e.g., orbital wave velocity and wave height). Through examining correlations among these predictors, we concluded in exclusively using sea surface temperature (SST). Temperature data and the derived products were produced from the Daily Global 5km Satellite Sea Surface Temperature Dataset through the NOAA Coral Reef Watch (https://coralreefwatch.noaa.gov/product/5km/index_5km_sst.php). The derived product was the mean monthly SST calculated from daily values for each month then the monthly mean SST is calculated across the 12 months for each year.

We further aggregated SST through time as the mean, 25% or 95% quantile across all survey years.

Biotic predictors consisted of two metrics of kelp abundance: kelp canopy biomass and kelp canopy cover. For kelp biomass we used Landsat satellite imagery data downloaded via kelpwatch.org (Bell et al., 2023). This data calculates biomass via a model which converts satellite imagery of kelp cover to biomass once a quarter every year. At each 900m^2 pixel, we calculated the maximum biomass per year and then averaged kelp biomass across survey years. For kelp canopy cover we used a temporal maximum composite across 1989,1999, 2002-2006, 2008, 2009 and 2013-2016 shapefile of kelp cover (presence) recorded from California Department of Fish and Wildlife (CDFW) flyover data. So, this variable can be thought of as the maximum potential for kelp cover.

To make correlations between fish biomass density across the long-term monitoring sites to the spatial explicit environmental predictors we drew polygon shapefiles around each PISCO or RCCA survey location. Although they varied in shape and size (average size: 90,000 m^2) we believe the spatial scale is appropriate for the range of habitat a fish might use on average (Freiwald, 2012). Using these polygons, we extracted environmental data for each raster variable allowing us to associate the predictor data to the response data. For the kelp cover (which was a shapefile) and the amount of rock (which was a binary raster of rock and sand) we calculated the proportional cover or rock within every survey polygon (summing each pixel within a polygon that has rock or kelp presence and dividing it by the total number of pixels in a polygon). Lastly, we explored correlations among predictor variables via correlation plots and principal component analysis and VIF tests. With eliminating predictors that were highly correlated we came to these final predictors for model fitting: Depth (mean and standard deviation), VRM (mean and standard deviation), Slope (mean and standard deviation), proportion of rock (mean and sd), Mean SST, 95% SST, 25% SST, Mean kelp biomass (Landsat) and Proportion of kelp cover (CDFW flyover).

Using the fish biomass density data from the PISCO and RCCA surveys alongside extracted predictor variables at those survey sites, we fit models to best explain patterns of fish presence and density across the 231 survey sites. We adopted a hurdle model approach which combines two model types. The first is a logistic regression which predicts whether a fish is present or absent at a given location. This sets the spatial distribution of the fish but also accounts for zero-inflated data. The second model is a generalized additive model (GAM) which predicts the biomass density of a fish at a given location. For GAMs all fish species were log transformed to meet assumptions of normality. This model is used to quantify the total biomass density within the distribution set by the logistic model. We fit models using a K-fold cross validation method approach, splitting data into a train (80%) and test (20%). Using a Kolmogorov-Sminov test we made sure the train and test datasets were evenly distributed across latitude.

For our logistic models, we used the ‘bestglm’ function in R with the training dataset which compares all predictors and outputs the top models. We then took the top models which had a delta AIC ≤ 2 and ran a 5-fold cross validation – taking the average AIC for each model to determine the best fit model. Lastly, we tested the best fitting model on the 20% test dataset, comparing the predicted with the observed fish presence to examine how well the models fit via a linear model and visual comparisons on a map of California. For the GAMs we used the ‘FSSgam’ function in on the same train dataset and compared all predictors and outputs the top models. We took the top models which had a delta AIC >= 2 and ran a 5-fold cross validation – taking the average AIC for each model to determine the best fit GAM. Finally, we tested the best fitting GAM on the 20% test dataset, comparing the predicted with the observed fish biomass to examine how well the models fit via a linear model and visual comparisons on a map of California.

To predict the fish biomass density, we used the 'predict' function in the [raster] R package using the best logistic and GAM models. To spatially standardize the predictor variables to the survey data we aggregated all predictor data to the average size of a MLPA/RCCA site – 90 km^2. Once all predictors were rasterized and standardized into the same spatial scale, we stacked all variables. Each 300m x 300m pixel has a value for all 13 predictor variables. We then used the raster stack to predict biomass density of each fish using best fit models. To calculate total fish biomass in a given ROMS cell we first converted total biomass from biomass density at the pixel scale. We calculated the amount of rock in each pixel as we are assuming that fish only occupy rock in a pixel as the surveys which these models are based on are in rocky reefs. We then divided the total area of rock by 60m^2 to quantify the number of 'transects' that exist in a pixel and multiple predicted biomass density by the number of transects that exist in each pixel. Lastly, we summed the total biomass across all pixels within a ROMS cell to get total biomass per fish species. This total biomass is divided by the biomass per recruit for each species to quantify a threshold of recruits a ROMS cell can occupy. This is explained more below in *Demographic data*.

Spatial Fishing Effort

To test the effect of MPAs in our model we must consider spatial patterns of fishing. For cells in the model which are considered an MPA, fishing mortality is simply set to 0. For all other cells, we quantified spatial variation in fishing mortality through constructing a dynamic spatial explicit fishing fleet model. We used fishing effort information via aggregate data from the CDFW logbooks which were spatially overlapping with our rocky reef rasters (suggesting they are fishing in or along shallow rocky reefs) and removed trips which reported as targeting offshore/pelagic species:

striped bass, sturgeon, tuna and misc. offshore. At each (10’ x 10’) spatial block we calculated effort based on two predictors: (1) The distance from each major fishing port and the overall effort (# of trips) from CDFW logbooks that went to that pixel (Figure 1). We used the mean F from stock assessments (Table 1) and spatially distributed this effort across the coastline. At each timestep, fishing mortality was calculated via the CPUE at the previous timestep.

Demographic data

In addition to parameterizing the model with information on larval connectivity, habitat associations and fishing, we collected other demographic information needed for the IPCM. See Table 1 the parameterization for demographic metrics. To model growth at benthic life stages, we used a size dependent Von Bertalanffy growth function. Survival was calculated as the sum of natural and fishing mortality, where MPAs had only natural mortality (fishing mortality = 0). To quantify total larval production across population structure, we calculated fecundity using a fecundity-length relationship which combines size at maturity with species-specific constants. We constructed a Beverton-Holt density dependent model to quantify recruitment from larval to benthic stages. This model sets the relationship between the number of settlers coming into a cell and the number of recruits surviving to benthic stages. Settlers are calculated as the product of total larval production and the connectivity from each other cell. The survival parameter, a, which accounts for mortality in spatial explicit models (i.e., the product of larval survivorship, retention and density independent settlement), can be calculated from the steepness parameter ‘h’ in the stock assessment which is the number of recruits when the unfished population reaches 20% of its stock. Using steepness we can calculate the slope of the stock recruitment function at zero as, (1-h)/4h. To account for space we multiply the slope, a, by the dominant eigenvalue of the connectivity matrix. The term which sets the carrying capacity (or the maximum number of recruits a cell can contain) in the Beverton-Holt function, b, is calculated as the ratio of predicted biomass (from the SDM) to the biomass per recruit. This gives us the total number of recruits that can settle into each ROMS cell based on habitat quality (via the SDM).

Site Value Metrics

The two metrics we used in this report are **realized export** and **patch importance**. Realized export can be defined as the total contribution of larval export from a patch to its neighbors. Specifically calculated as the sum of column *i* of the connectivity matrix **C**, the total per capita export of larvae from patch *i* to all other patches and to itself.

$E_i = \sum_{j=1}^{n} \square = c_{ij}.$

In theory a patch could be dependent entirely on import from elsewhere but act as a stepping-stone connecting disjunct regions of the metapopulation; such a patch would have low c_{ii} but high E_i. Versions of this metric have been proposed by Figueira and Crowder (2006; their model included adult mortality but the expressions are otherwise equivalent) and Runge et al. (2006; their value is equivalent to E_i multiplied by the equilibrium population density in patch *i*).

The second metric, patch importance relies on the level of connectedness in combination with the reproductive capacity via the population size structure at a given patch. This metric uses eigenvector centrality which has been used as a measure of contribution in a variety of contexts. In a structured population model, element v_i of **v** is the reproductive capacity of the i^{th} age class (Caswell 2001). Several recent papers have proposed using centrality as a measure of patch contribution in marine metapopulations (Nilsson Jacobi and Jonnson 2011, Watson et al. 2011). The eigenvector **v** is also widely used as a measure of centrality in the graph-theoretic analysis of social networks (Bonacich 1972, Borgatti 2005) and underpins Google's PageRank algorithm (Brin and Page 1998). Other graph-theoretic measures of centrality are available (see Zamborian and Mason et al. 2017), such as betweenness centrality, which is a measure of the number of connectivity pathways passing through a patch (or node, in graph terminology), weighted by the strength of those pathways (Borgatti and Everett 2005, Borgatti et al. 2009). Bode et al. (2009) proposed using betweenness centrality as a measure of metapopulation patch value. However, calculating betweenness centrality becomes computationally prohibitive for large numbers of patches using traditional algorithms (Yang and Chen 2011), such as in large marine metapopulations. So we focus on eigenvector centrality, which is computationally trivial.

Results

Table S1. The top SDM models for each species. For each species we ran a hurdle model approach, where the logistic regression model sets the distribution for the species (with predicting presence/absence) and the generalized additive model (GAM) is used to predict the biomass density of each species. The predictors are and the GAMs r-squared and deviance explained given for each model.

Species	Model type	Model	r^2	Deviance explained
Black Rockfish (Sebastes melanops)	Logistic	Mean depth + Mean minimum sea surface temperature		
Black Rockfish (Sebastes melanops)	GAM	s(Mean kelp biomass, k =5) + s(Mean minimum sea surface temperature, k = 6) + s(Mean VRM(log10), k = 5) + s(Standard deviation of proportion of rock, k = 5)	0.774	79%
Blue Rockfish	Logistic	Standard deviation depth + Mean proportion of rock + Mean minimum sea surface temperature		

(Sebastes mystinus)				
Blue Rockfish (Sebastes mystinus)	GAM	s(Proportional kelp cover, k =5) + s(Mean minimum sea surface temperature, k = 5) + s(Standard deviation of VRM(log10), k = 5) + s(Standard deviation of proportion of rock, k = 5)	0.811	82.3%
Kelp Rockfish (Sebastes atrovirens)	Logistic	Mean depth + Mean minimum sea surface temperature + Mean kelp biomass		
Kelp Rockfish (Sebastes atrovirens)	GAM	s(Mean kelp biomass, k =5) + s(Mean minimum sea surface temperature, k = 6) + s(Mean depth, k = 5) + s(Mean slope, k = 5) + s(Mean of proportion of rock, k = 5)	0.819	84.1%
California Sheephead (Bodianus pulcher)	Logistic	Mean depth + Mean slope + Mean average sea surface temperature + Standard deviation of proportion of rock		

California Sheephead (Bodianus pulcher)	GAM	s(Mean kelp biomass, k =5) + s(Mean average sea surface temperature, k = 6) + s(Mean slope, k = 5) + s(Mean depth, k = 5) + s(Standard deviation of proportion of rock, k = 5)	0.69	70.8%
Kelp Bass (Paralabrax clathratus)	Logistic	Standard deviation of slope + Mean slope + Mean minimum sea surface temperature		
Kelp Bass (Paralabrax clathratus)	GAM	s(Proportional kelp cover, k =5) + s(Mean minimum sea surface temperature, k = 5) + s(Mean depth, k = 5)	0.909	91.2%

Figure S1. The map of total biomass of Black Rockfish calculated as the summed biomass that was predicted from the SDMs.

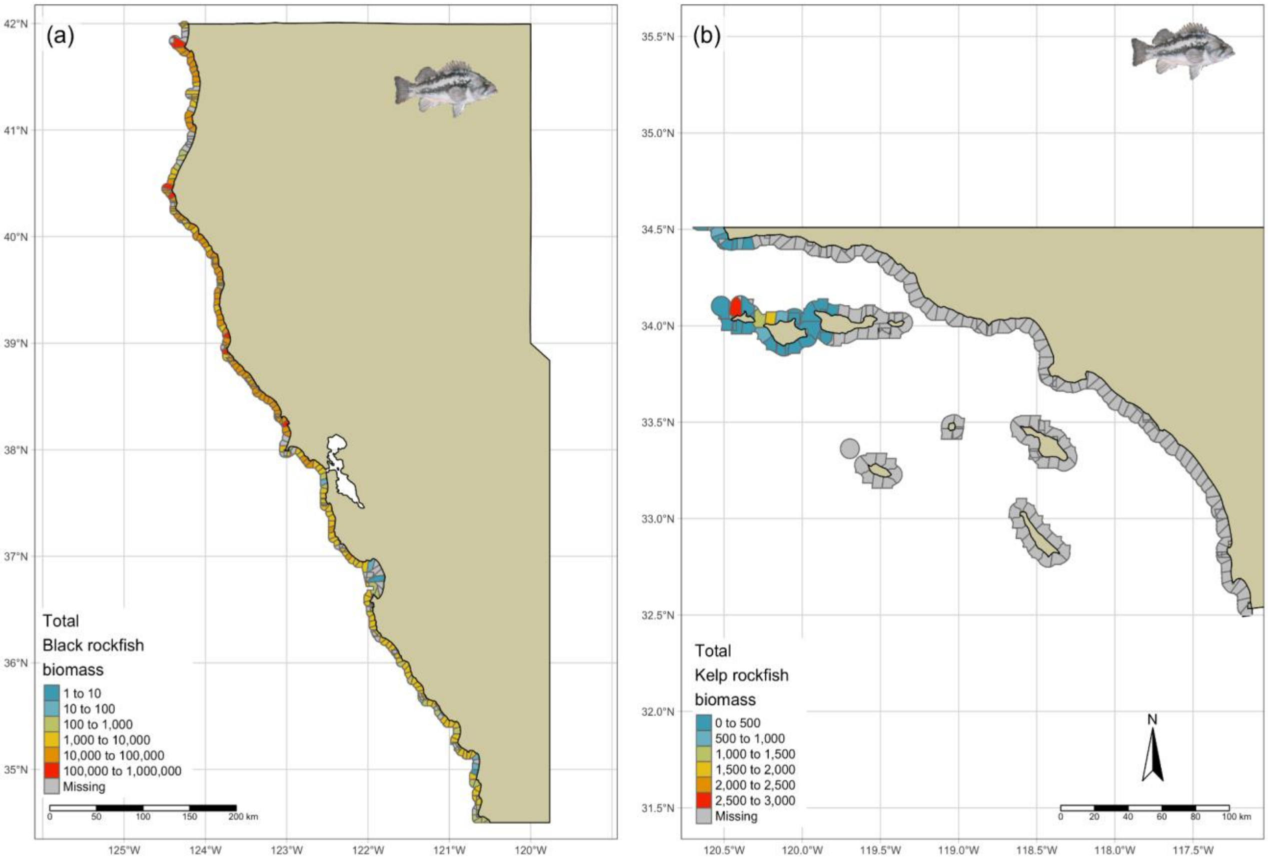


Figure S2. The map of total biomass of Blue Rockfish calculated as the summed biomass that was predicted from the SDMs.

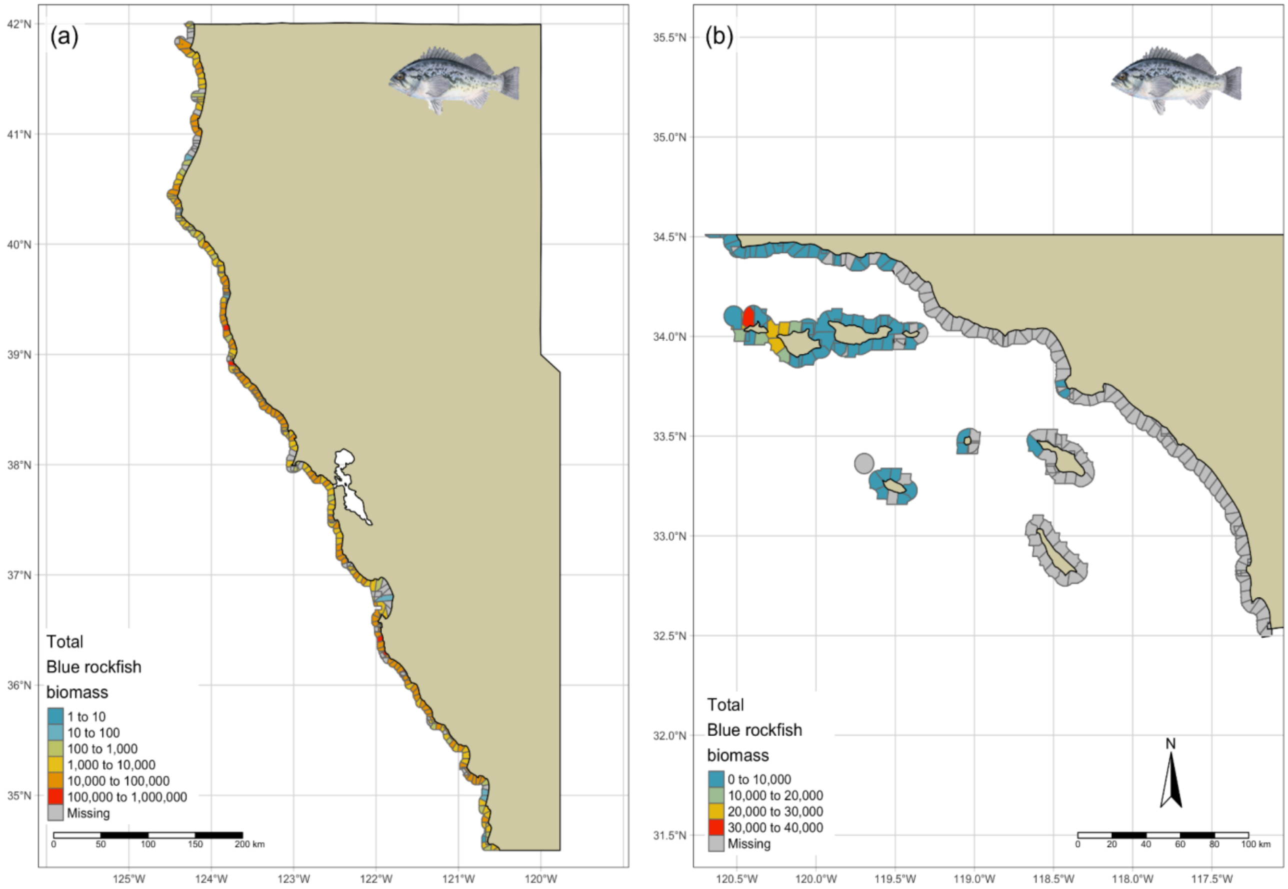


Figure S3. The map of total biomass of Kelp Rockfish calculated as the summed biomass that was predicted from the SDMs.

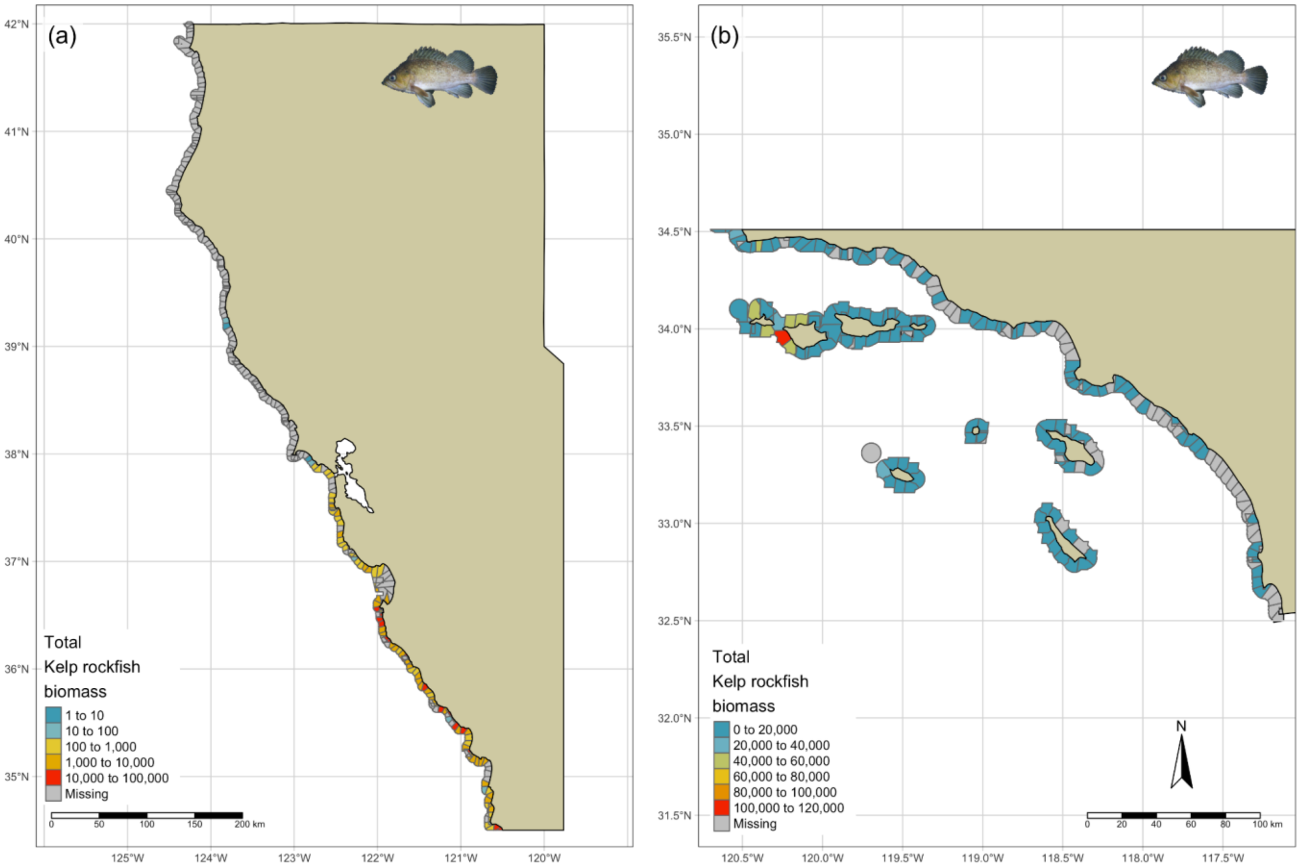


Figure S4. The map of total biomass of Kelp Bass calculated as the summed biomass that was predicted from the SDMs.

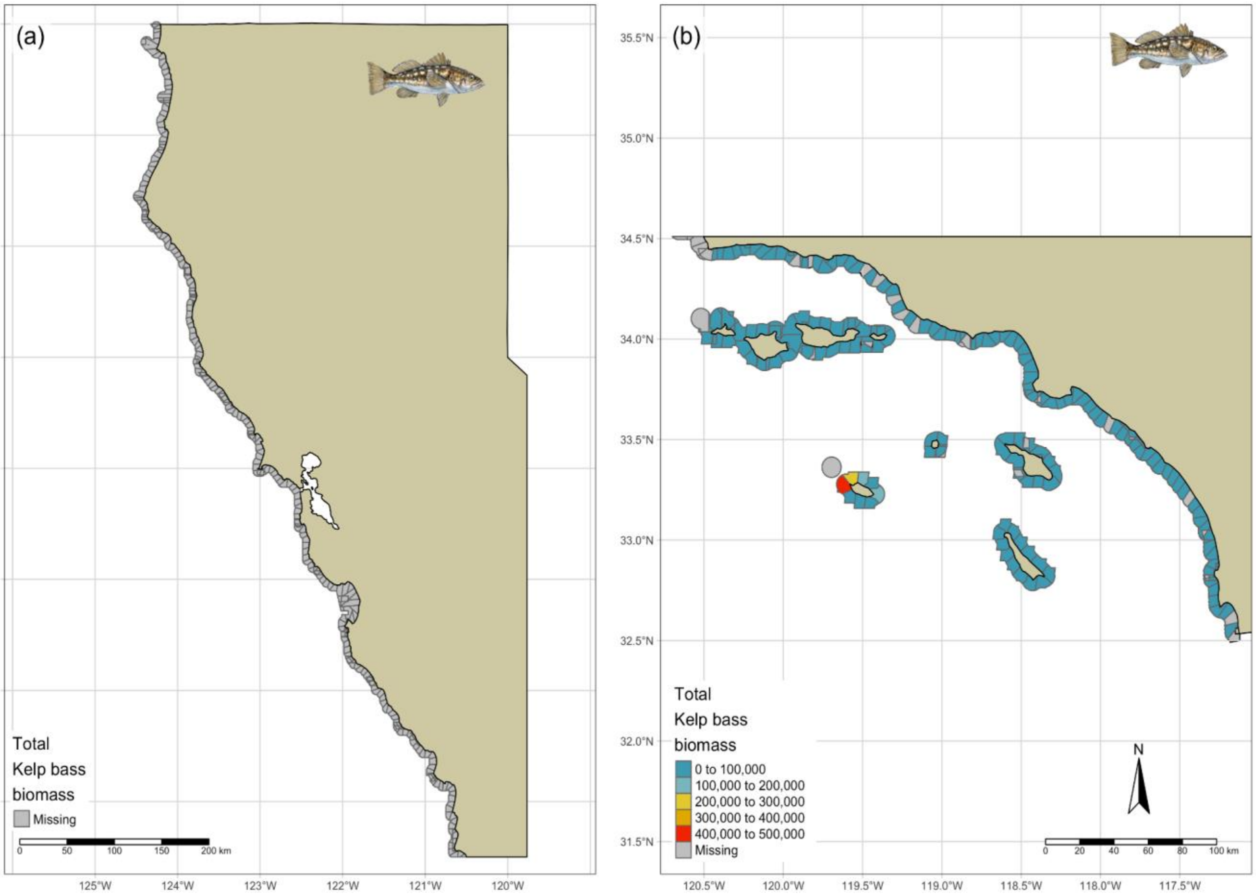


Figure S5. The map of total biomass of California Sheephead calculated as the summed biomass that was predicted from the SDMs.

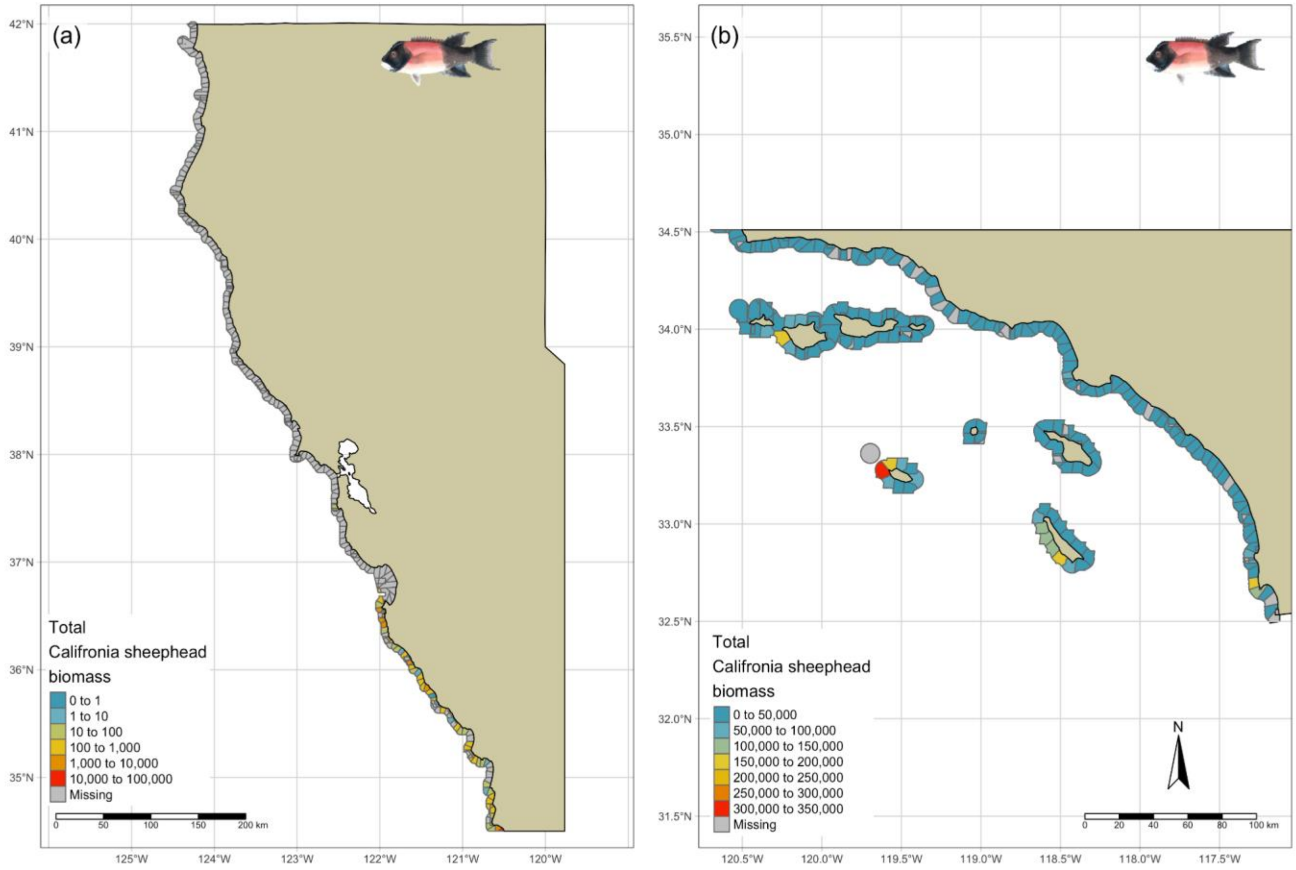


Table S2. The ten highest MPA values sorted highest to lowest in the two metrics: realized export and patch important for all four focal fish species. Color of the box indicates the region: dark blue = Southern coast, Mainland; light blue = Southern coast, Channel Islands; orange = Central coast; green = North coast. Solid colored boxes indicate the MPA was a SMR, diagonal hatched colored boxes indicate the MPA was a SMCA and gridded colored boxes indicate the MPA is a special closure. The only difference between this table and Table 3-11 is here we filtered for only MPAs and sorted for the top ten.

California Sheephead		Kelp Bass		Kelp Rockfish		Blue Rockfish		Black Rockfish	
Realized Export	Patch Importance	Realized Export	Patch Importance	Realized Export	Patch Importance	Realized Export	Patch Importance	Realized Export	Patch Importance
South La Jolla SMR	Swami's SMCA	South La Jolla SMR	San Diego-Scripps Coastal SMCA	Carrington Point SMR	Painted Cave SMCA	Montara SMR	Painted Cave SMCA	Bodega Head SMR	Painted Cave SMCA
Swami's SMCA	San Diego-Scripps Coastal SMCA	Swami's SMCA	Swami's SMCA	Painted Cave SMCA	Santa Barbara Island SMR	Asilomar SMR	Richardson Rock SMR	Bodega Head SMCA	Richardson Rock SMR
Point Vicente SMCA	Matlahuayl SMR	Crystal Cove SMCA	Matlahuayl SMR	Harris Point SMR	Blue Cavern Onshore SMCA	Carmel Pinnacles SMR	San Miguel Island Special Closure	Point Reyes SMR	Harris Point SMR
Crystal Cove SMCA	South La Jolla SMR	Carrington Point SMR	South La Jolla SMR	South Point SMR	Farnsworth Onshore SMCA	Point Lobos SMR	Harris Point SMR	Saunders Reef SMCA	Carrington Point SMR
Dana Point SMCA	Dana Point SMCA	Cabrillo SMR	Laguna Beach SMCA	San Miguel Island Special Closure	Arrow Point to Lion Head Point SMCA	Pillar Point SMCA	Judith Rock SMR	Point Arena SMR	Asilomar SMR
Arrow Point to Lion Head Point SMCA	Laguna Beach SMCA	Abalone Cove SMCA	Cabrillo SMR	Point Buchon SMR	Carrington Point SMR	Point Sur SMR	Carrington Point SMR	Stewarts Point SMR	Point Reyes SMCA
Naples SMCA	Laguna Beach SMR	Laguna Beach SMR	Laguna Beach SMR	Skunk Point SMR	Richardson Rock SMR	Bodega Head SMR	Anacapa Island Special Closure	MacKerricher SMCA	Pillar Point SMCA
Carrington Point SMR	Crystal Cove SMCA	Point Vicente SMCA	Crystal Cove SMCA	Point Lobos SMR	South La Jolla SMR	Piedras Blancas SMR	Scorpion SMR	Sea Lion Gulch SMR	South Point SMR
Abalone Cove SMCA	Cabrillo SMR	Laguna Beach SMCA	Dana Point SMCA	Point Sur SMR	Swami's SMCA	Bodega Head SMCA	South Point SMR	South Cape Mendocino SMR	Montara SMR
Skunk Point SMR	Point Vicente SMCA	Skunk Point SMR	Abalone Cove SMCA	Asilomar SMR	Anacapa Island Special Closure	Point Cabrillo SMR	Skunk Point SMR	Russian River SMCA	Carmel Pinnacles SMR

Figure S6. The map of relative **realized export** for black Rockfish. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

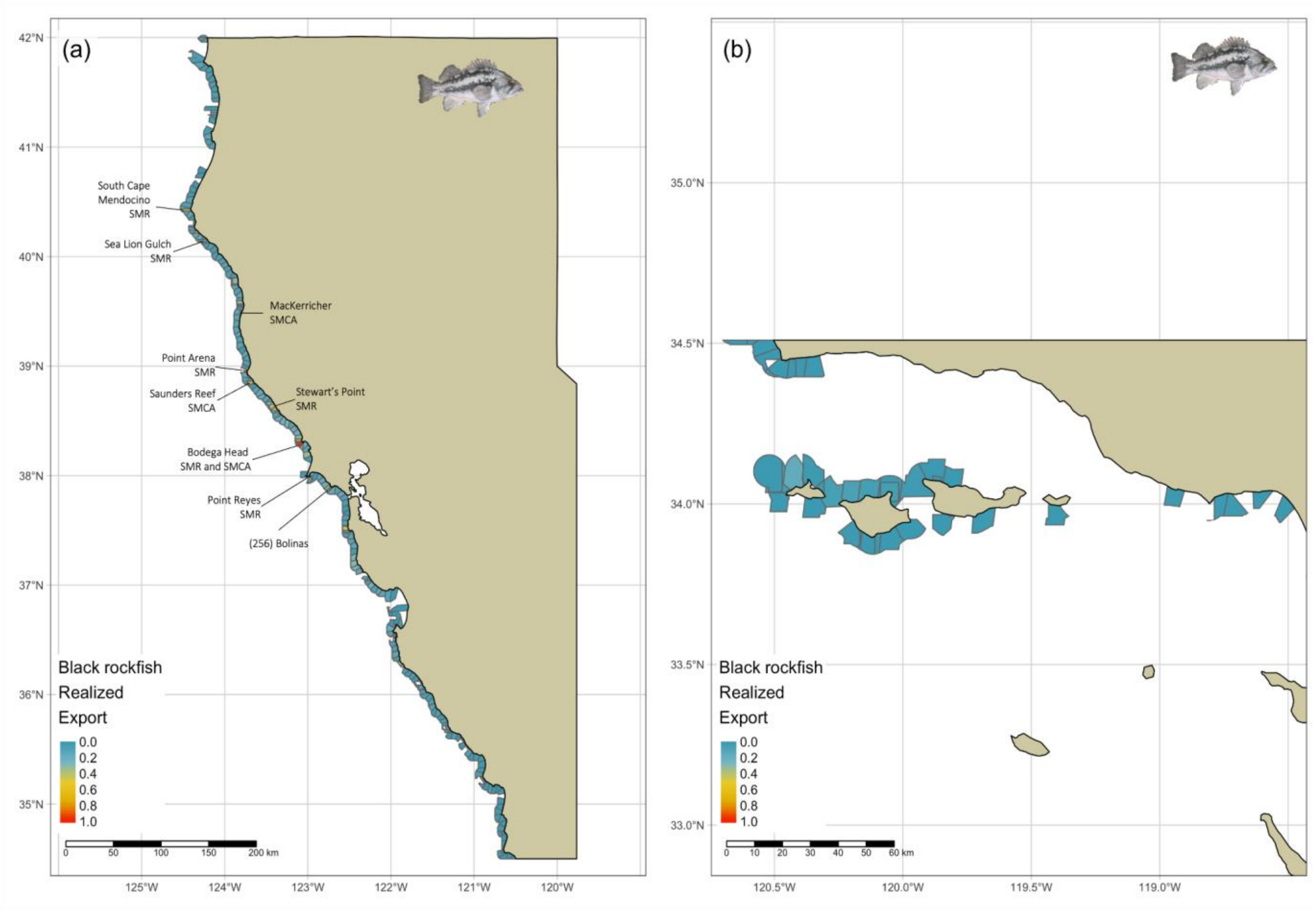


Figure S7. The map of relative **patch importance** for black Rockfish. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

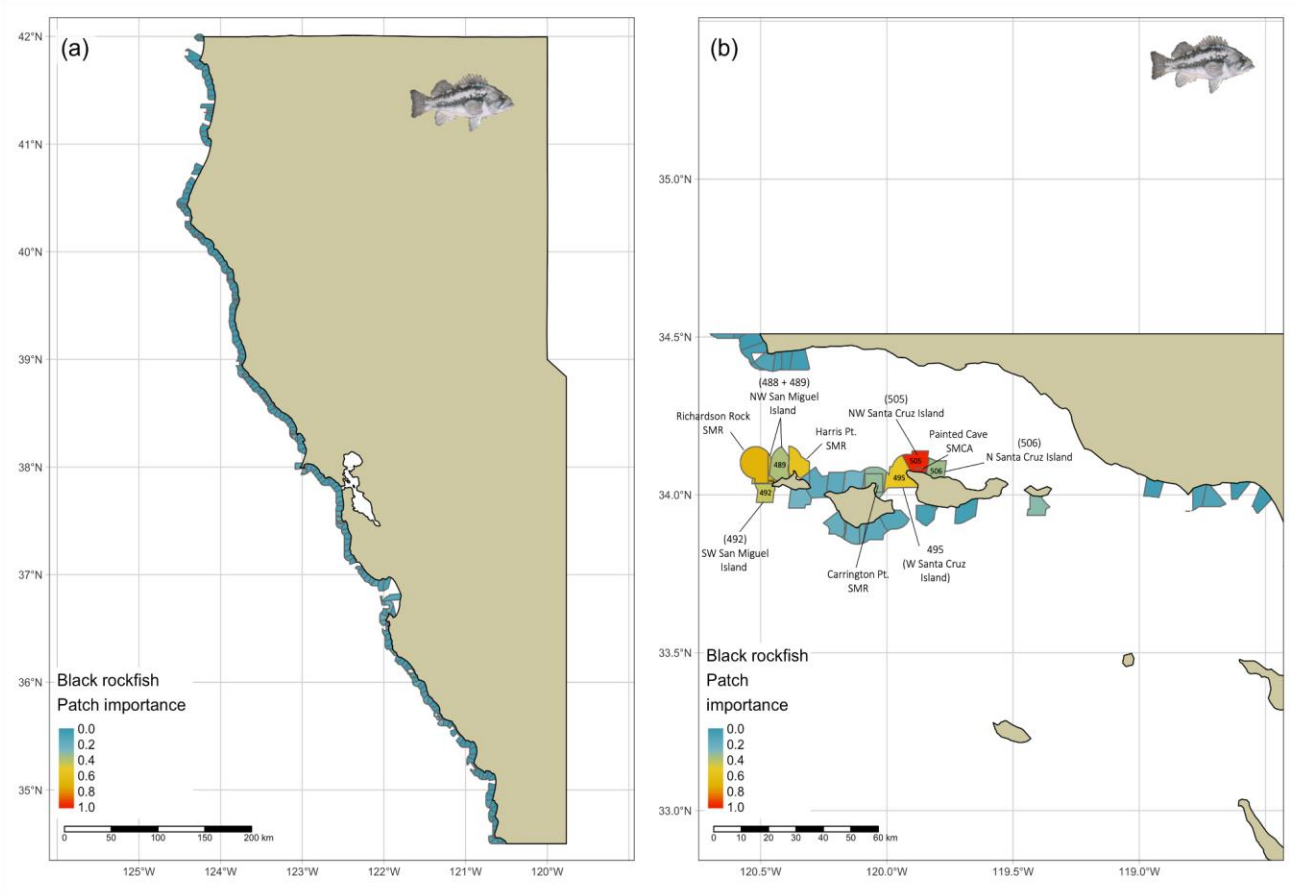


Figure S8. The map of relative **realized export** for blue Rockfish. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

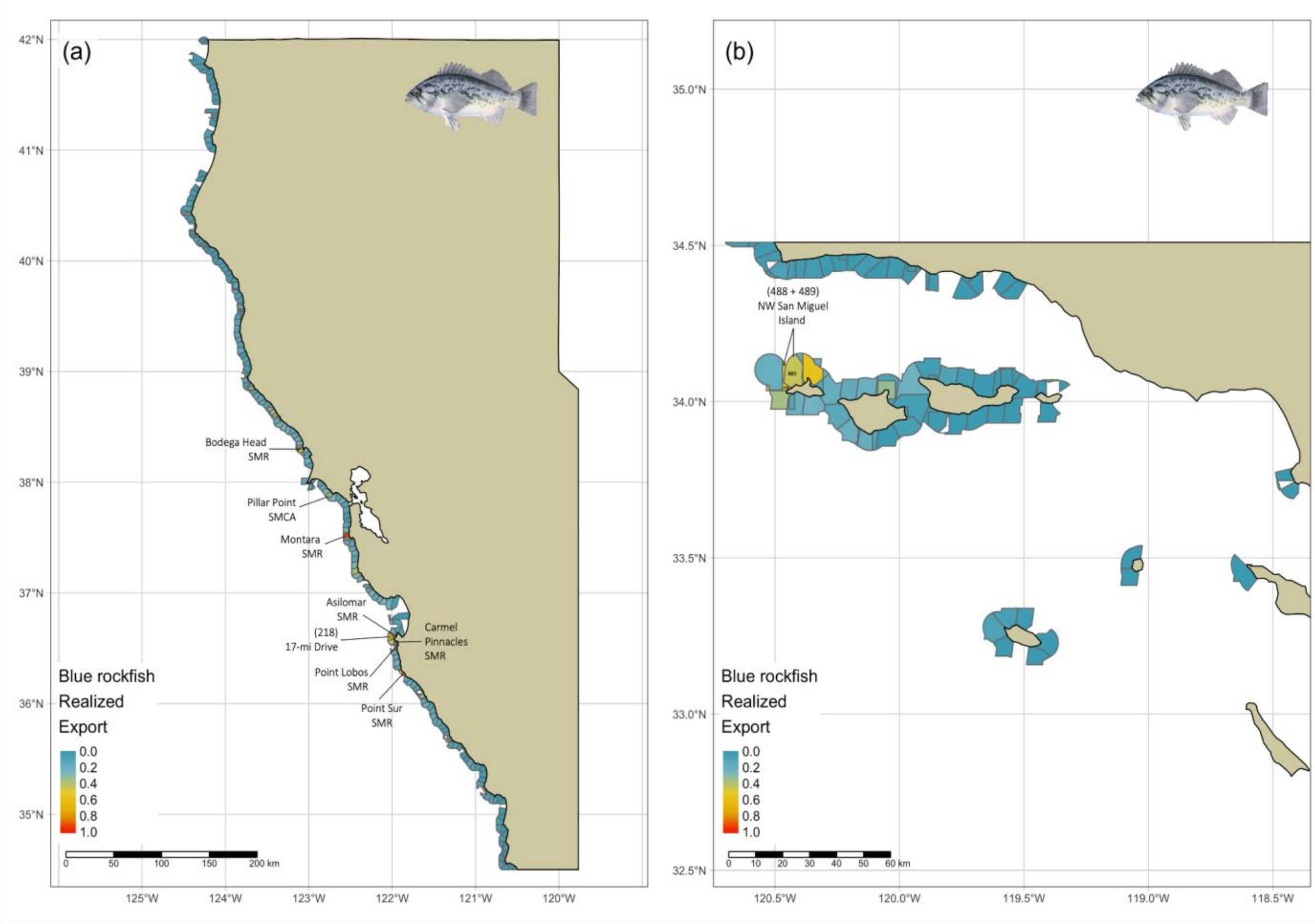


Figure S9. The map of relative **patch importance** for blue Rockfish. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

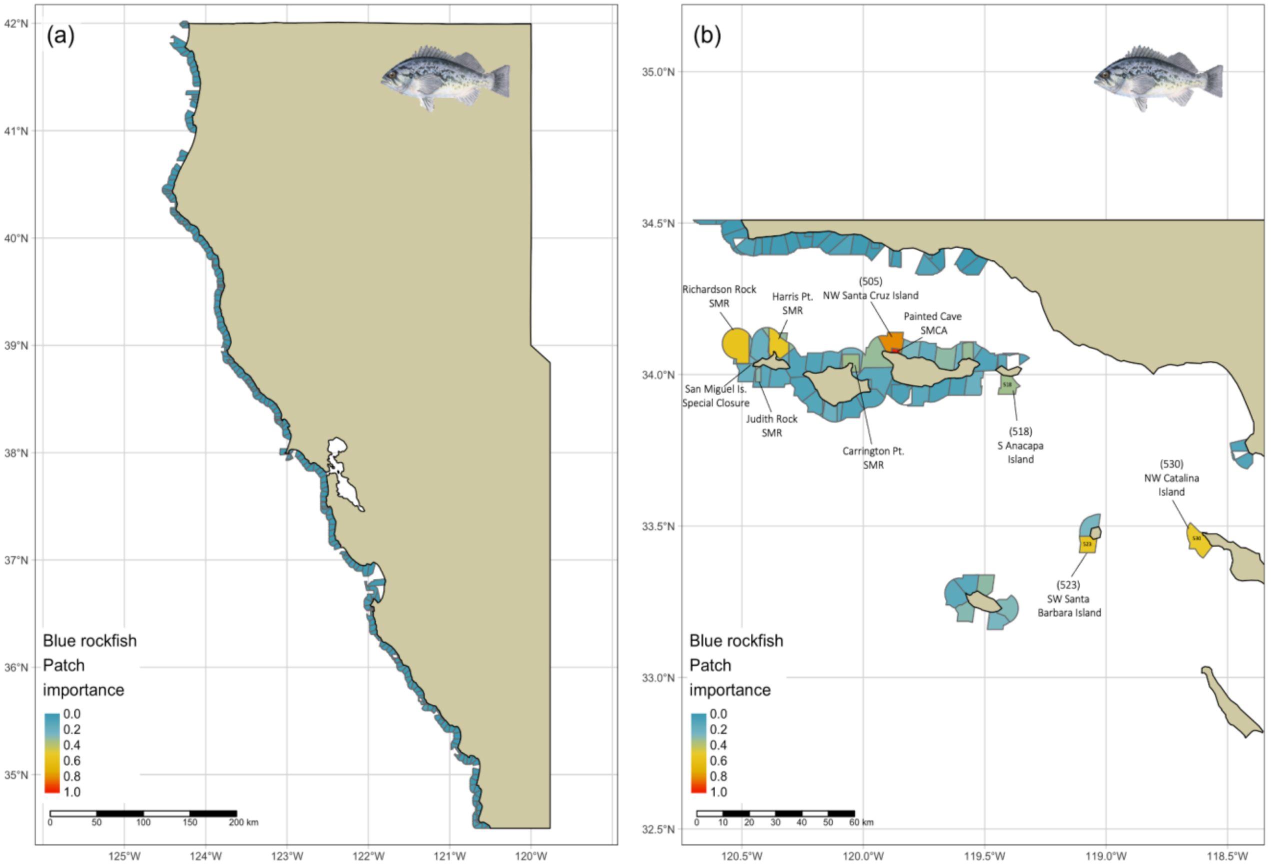


Figure S10. The map of relative **realized export** for kelp Rockfish. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

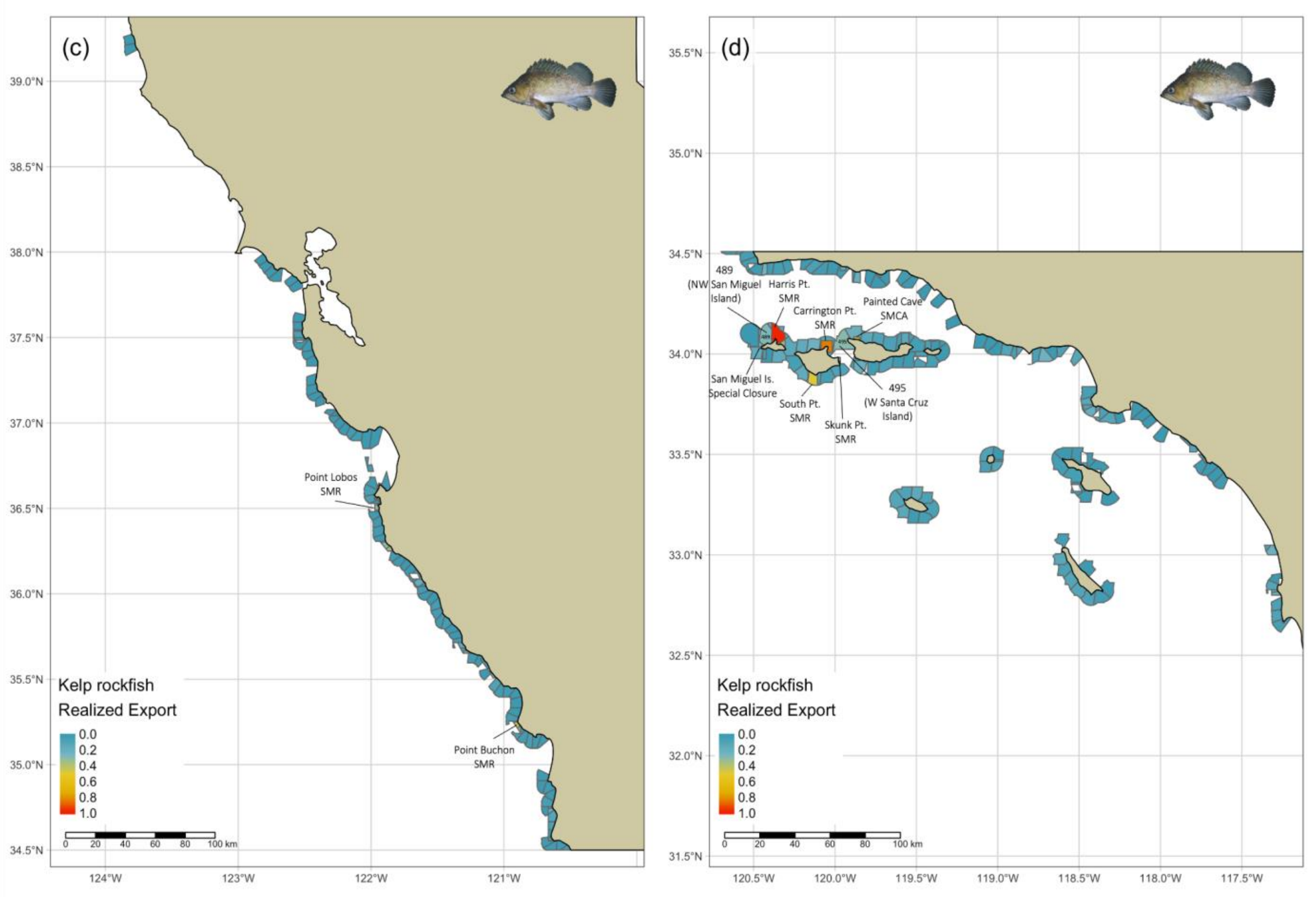


Figure S11. The map of relative **patch importance** for kelp Rockfish. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

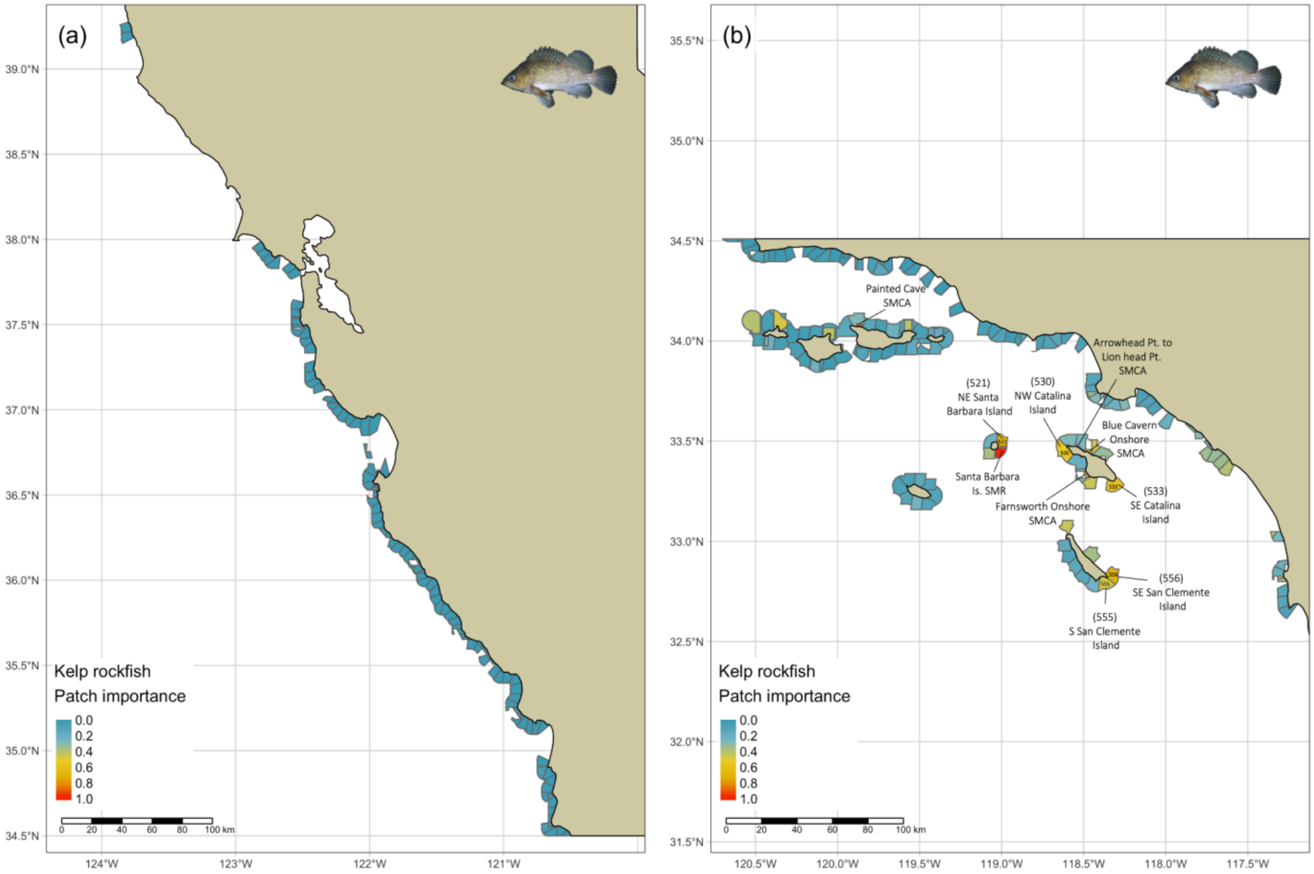


Figure S12. The map of relative **realized export** for California Sheephead. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

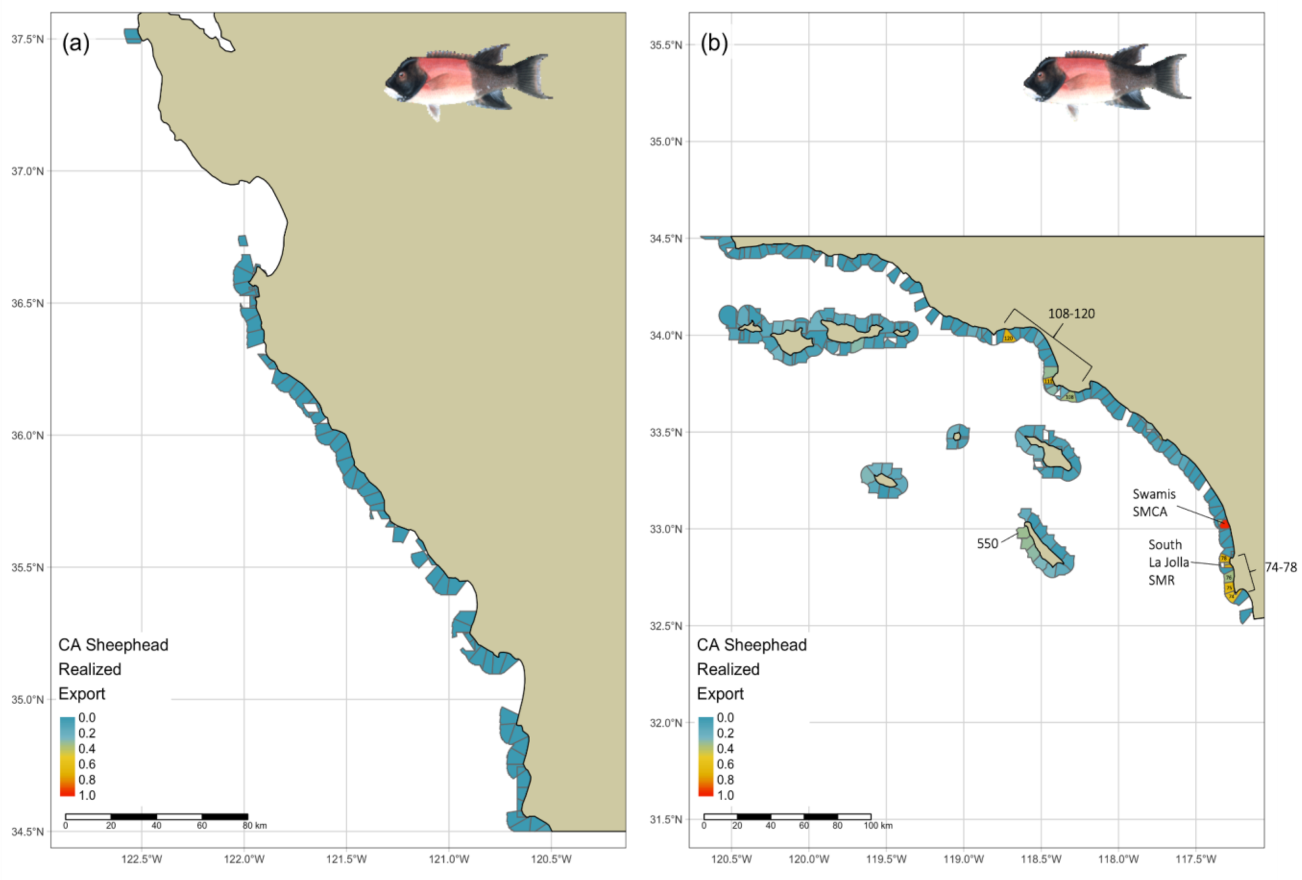


Figure S13. The map of relative **patch importance** for California Sheephead. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

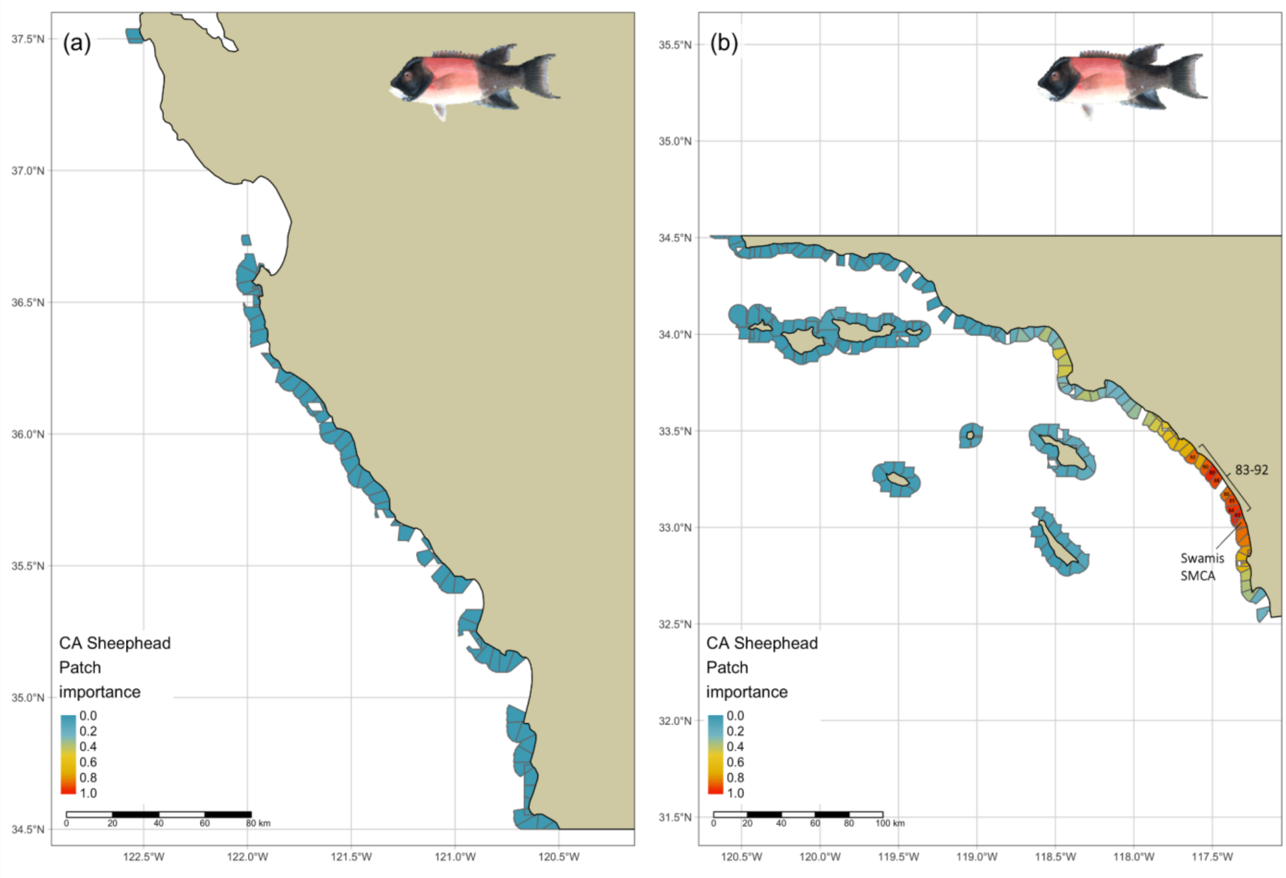


Figure S14. The map of relative **patch importance** (a) and **realized export** (b) for Kelp Bass. The top 10 locations (ROMS cells) are labeled. If location is not a MPA, the label is the ROMS cell number in parentheses with the closest landmark.

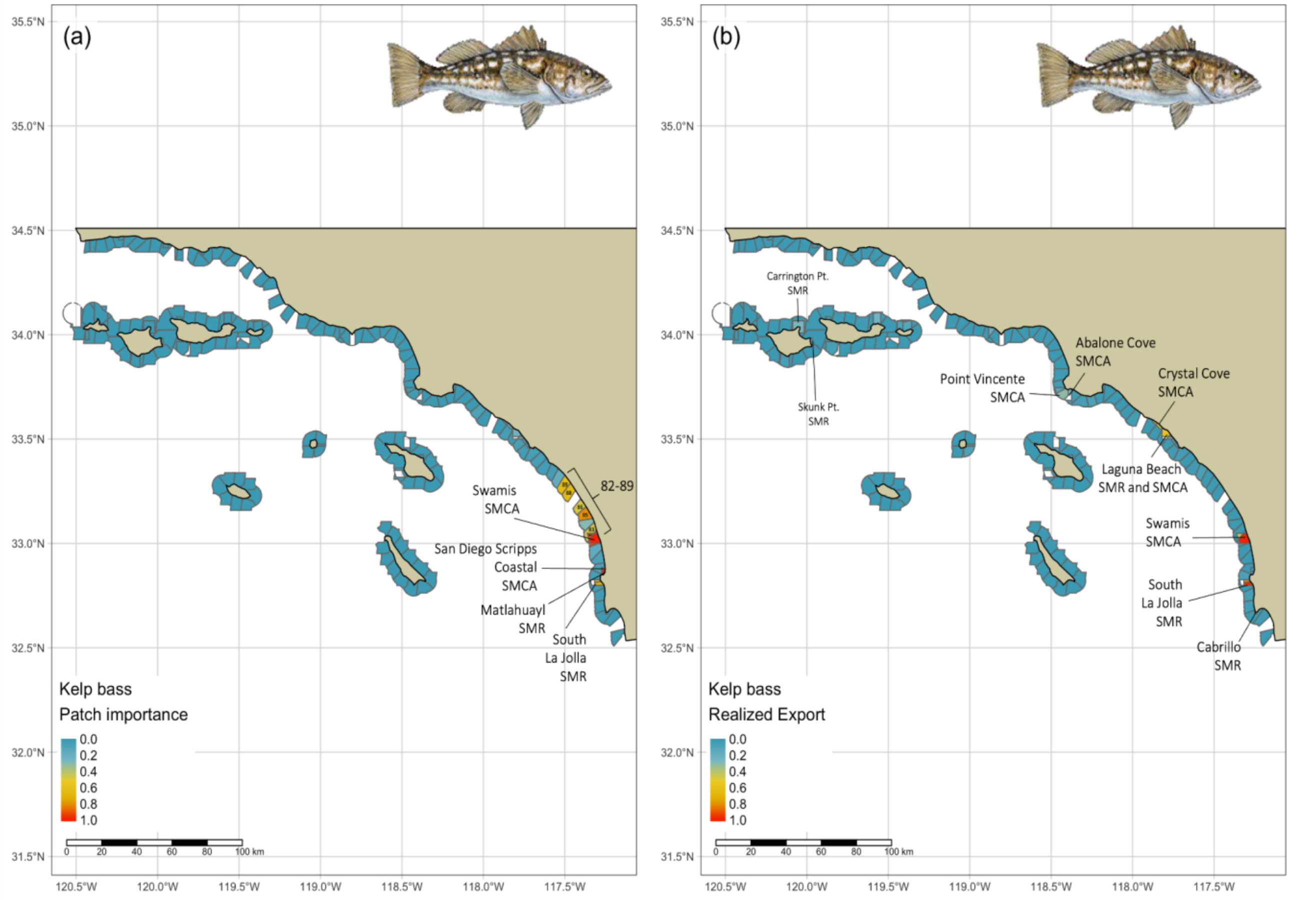


Figure S15. The ratio of proportional observed to expected contribution estimates of transport across the 2 coastal habitats, while controlling for differences in habitat area. The blue-gray color palette signifies rocky habitats, while the brown color palette signifies soft bottom habitats. Each colored bar represents the particle duration of the simulation. If the value is greater than 1 (horizontal dashed line), there is more particle transport than expected by habitat area alone.

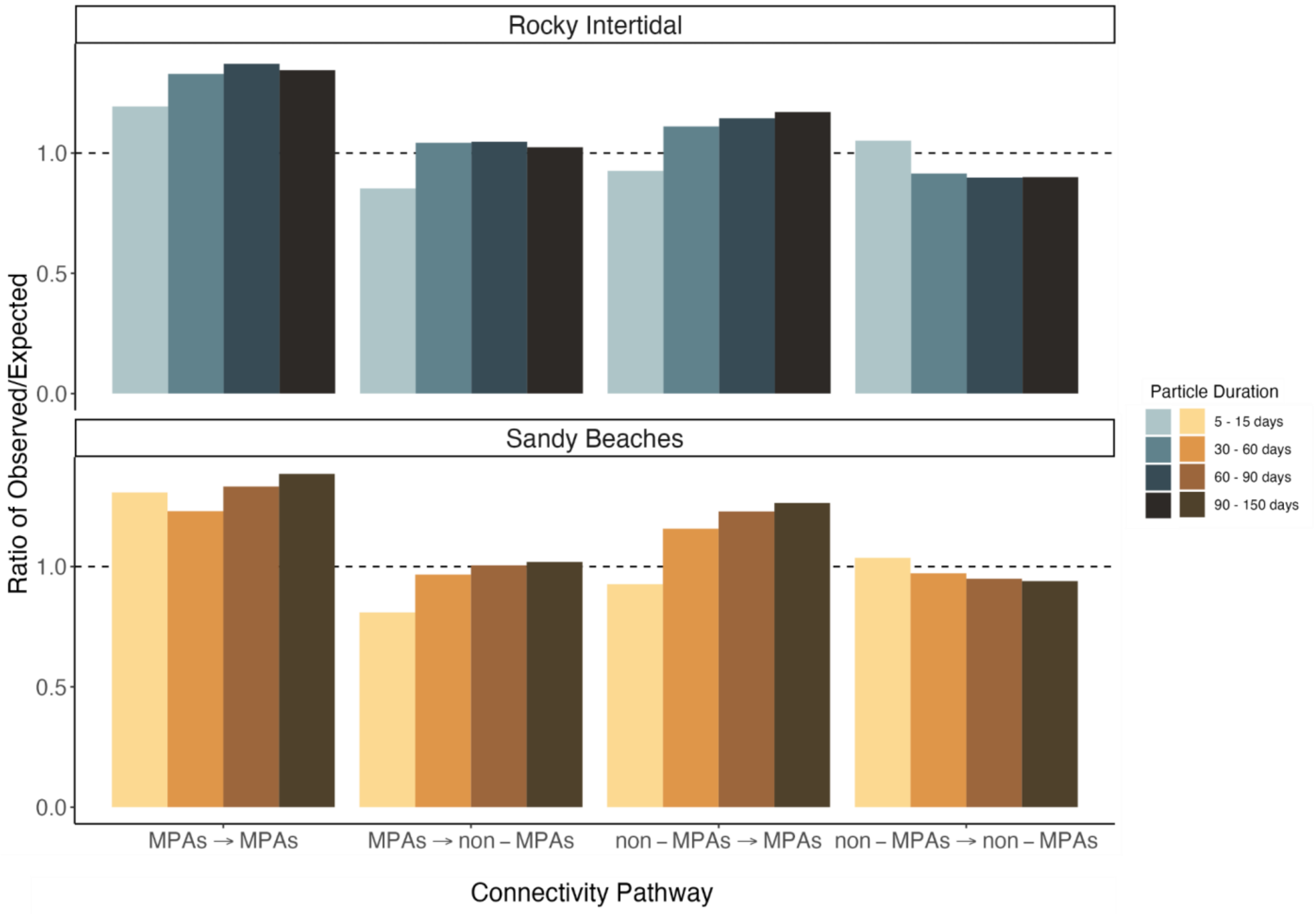


Figure S16. The ratio of proportional observed to expected contribution estimates of transport across the subtidal habitats, while controlling for differences in habitat area. The blue-gray color palette signifies rocky habitats, while the brown color palette signifies soft bottom habitats. Each colored bar represents the particle duration of the simulation. If the value is greater than 1 (horizontal dashed line), there is more particle transport than expected by habitat area alone.

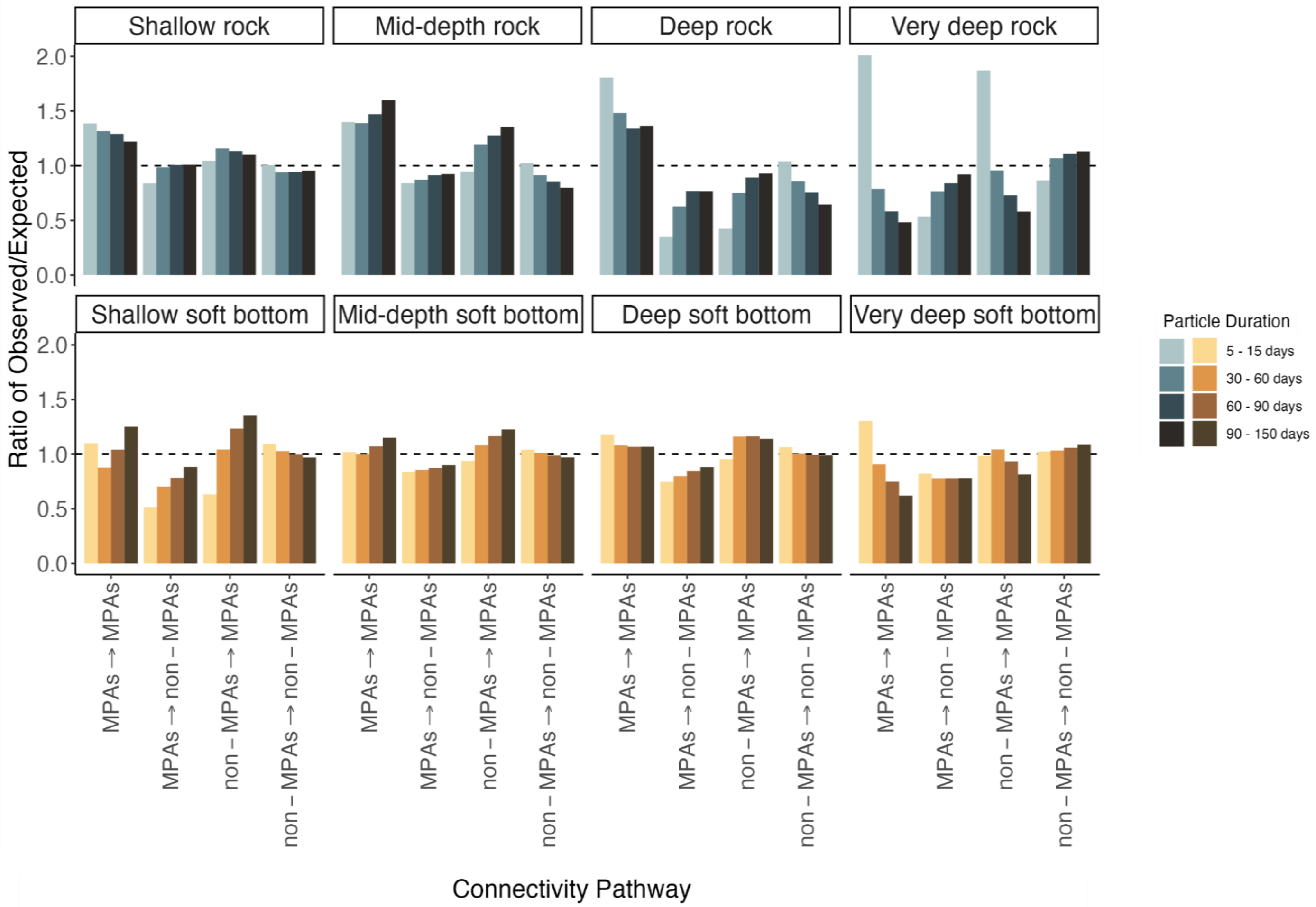


Table S3. The relative MPA value scores for the California Sheephead across all MPAs.

MPA Name	Region	Realized Export (relative)	Patch Importance (relative)
Cabrillo SMR	South coast mainland	0.067	0.418
South La Jolla SMR	South coast mainland	0.750	0.738
Matlahuayl SMR	South coast mainland	0.018	0.802
San Diego-Scripps Coastal SMCA	South coast mainland	0.003	0.824
Swami's SMCA	South coast mainland	0.671	0.922
Laguna Beach SMCA	South coast mainland	0.069	0.593
Laguna Beach SMR	South coast mainland	0.137	0.523

Crystal Cove SMCA	South coast mainland	0.252	0.438
Abalone Cove SMCA	South coast mainland	0.159	0.247
Point Vicente SMCA	South coast mainland	0.281	0.281
Point Dume SMCA	South coast mainland	0.074	0.092
Campus Point SMCA	South coast mainland	0.052	0.017
Naples SMCA	South coast mainland	0.185	0.012
Point Conception SMR	South coast mainland	0.011	0.011
Richardson Rock SMR	South coast Channel Island	0.001	0.035
San Miguel Island Special Closure	South coast Channel Island	0.072	0.030

Judith Rock SMR	South coast Channel Island	0.024	0.025
Harris Point SMR	South coast Channel Island	0.015	0.036
Carrington Point SMR	South coast Channel Island	0.173	0.066
Skunk Point SMR	South coast Channel Island	0.154	0.044
South Point SMR	South coast Channel Island	0.086	0.025
Painted Cave SMCA	South coast Channel Island	0.076	0.136
Gull Island SMR	South coast Channel Island	0.140	0.017
Anacapa Island SMCA	South coast Channel Island	0.086	0.036

Scorpion SMR	South coast Channel Island	0.061	0.056
Anacapa Island SMR	South coast Channel Island	0.043	0.054
Anacapa Island Special Closure	South coast Channel Island	0.043	0.053
Santa Barbara Island SMR	South coast Channel Island	0.074	0.090
Arrow Point to Lion Head Point SMCA	South coast Channel Island	0.212	0.154
Blue Cavern Onshore SMCA	South coast Channel Island	0.101	0.185
Long Point SMR	South coast Channel Island	0.040	0.185
Farnsworth Onshore SMCA	South coast Channel Island	0.043	0.101

Casino Point SMCA	South coast Channel Island	0.006	0.195
Lover's Cove SMCA	South coast Channel Island	0.002	0.195
Vandenberg SMR	Central coast	0.000	0.006
Point Buchon SMR	Central coast	0.002	0.003
White Rock SMCA	Central coast	0.003	0.002
Piedras Blancas SMR	Central coast	0.000	0.002
Big Creek SMR	Central coast	0.003	0.001
Point Sur SMR	Central coast	0.004	0.000
Point Lobos SMR	Central coast	0.001	0.000
Carmel Pinnacles SMR	Central coast	0.000	0.000

Asilomar SMR	Central coast	0.000	0.000
Lovers Point - Julia Platt SMR	Central coast	0.000	0.000
Montara SMR	Central coast	0.000	0.000
Pillar Point SMCA	Central coast	0.000	0.000

Table S4. The relative MPA value scores for the Kelp Bass across all MPAs.

MPA Name	Region	Realized Export (relative)	Patch Importance (relative)
Cabrillo SMR	South coast mainland	0.292	0.312
South La Jolla SMR	South coast mainland	1.000	0.742
Matlahuayl SMR	South coast mainland	0.098	0.887
San Diego-Scripps Coastal SMCA	South coast mainland	0.032	1.000
Swami's SMCA	South coast mainland	0.718	0.995
Laguna Beach SMCA	South coast mainland	0.243	0.357
Laguna Beach SMR	South coast mainland	0.279	0.303
Crystal Cove SMCA	South coast mainland	0.532	0.226

Abalone Cove SMCA	South coast mainland	0.287	0.047
Point Vicente SMCA	South coast mainland	0.245	0.045
Point Dume SMCA	South coast mainland	0.117	0.008
Campus Point SMCA	South coast mainland	0.011	0.000
Naples SMCA	South coast mainland	0.034	0.000
Point Conception SMR	South coast mainland	0.000	0.000
San Miguel Island Special Closure	South coast Channel Island	0.054	0.000
Judith Rock SMR	South coast Channel Island	0.035	0.000
Harris Point SMR	South coast Channel Island	0.007	0.000

Carrington Point SMR	South coast Channel Island	0.293	0.000
Skunk Point SMR	South coast Channel Island	0.220	0.000
South Point SMR	South coast Channel Island	0.052	0.000
Painted Cave SMCA	South coast Channel Island	0.123	0.001
Gull Island SMR	South coast Channel Island	0.066	0.000
Anacapa Island SMCA	South coast Channel Island	0.112	0.001
Scorpion SMR	South coast Channel Island	0.165	0.001
Anacapa Island SMR	South coast Channel Island	0.128	0.002

Anacapa Island Special Closure	South coast Channel Island	0.088	0.002
Santa Barbara Island SMR	South coast Channel Island	0.090	0.003
Arrow Point to Lion Head Point SMCA	South coast Channel Island	0.154	0.014
Blue Cavern Onshore SMCA	South coast Channel Island	0.115	0.018
Long Point SMR	South coast Channel Island	0.038	0.019
Farnsworth Onshore SMCA	South coast Channel Island	0.043	0.006
Casino Point SMCA	South coast Channel Island	0.005	0.020
Lover's Cove SMCA	South coast Channel Island	0.003	0.020

Table S5. The relative MPA value scores for the Kelp Rockfish across all MPAs.

MPA Name	Region	Realized Export (relative)	Patch Importance (relative)
Cabrillo SMR	South coast mainland	0.058	0.279
South La Jolla SMR	South coast mainland	0.118	0.351
Swami's SMCA	South coast mainland	0.083	0.315
Laguna Beach SMR	South coast mainland	0.119	0.263
Crystal Cove SMCA	South coast mainland	0.101	0.271
Abalone Cove SMCA	South coast mainland	0.156	0.263
Point Vicente SMCA	South coast mainland	0.177	0.293
Point Dume SMCA	South coast mainland	0.088	0.078

Campus Point SMCA	South coast mainland	0.055	0.094
Naples SMCA	South coast mainland	0.083	0.047
Point Conception SMR	South coast mainland	0.100	0.076
Richardson Rock SMR	South coast Channel Island	0.064	0.399
San Miguel Island Special Closure	South coast Channel Island	0.254	0.320
Judith Rock SMR	South coast Channel Island	0.156	0.280
Harris Point SMR	South coast Channel Island	0.344	0.330
Carrington Point SMR	South coast Channel Island	0.424	0.418

Skunk Point SMR	South coast Channel Island	0.215	0.260
South Point SMR	South coast Channel Island	0.193	0.220
Painted Cave SMCA	South coast Channel Island	1.000	1.000
Gull Island SMR	South coast Channel Island	0.085	0.095
Anacapa Island SMCA	South coast Channel Island	0.144	0.169
Scorpion SMR	South coast Channel Island	0.190	0.279
Anacapa Island SMR	South coast Channel Island	0.127	0.277
Anacapa Island Special Closure	South coast Channel Island	0.149	0.304

Santa Barbara Island SMR	South coast Channel Island	0.194	0.826
Arrow Point to Lion Head Point SMCA	South coast Channel Island	0.145	0.476
Blue Cavern Onshore SMCA	South coast Channel Island	0.187	0.530
Farnsworth Onshore SMCA	South coast Channel Island	0.080	0.503
Vandenberg SMR	Central coast	0.067	0.044
Point Buchon SMR	Central coast	0.150	0.050
White Rock SMCA	Central coast	0.096	0.027
Piedras Blancas SMR	Central coast	0.123	0.039
Big Creek SMR	Central coast	0.066	0.018

Point Sur SMR	Central coast	0.091	0.017
Point Lobos SMR	Central coast	0.109	0.014
Carmel Pinnacles SMR	Central coast	0.077	0.014
Asilomar SMR	Central coast	0.196	0.021
Lovers Point - Julia Platt SMR	Central coast	0.090	0.009
Pillar Point SMCA	Central coast	0.043	0.006
Montara SMR	Central coast	0.048	0.006

Table S6. The relative MPA value scores for the Blue Rockfish across all MPAs.

MPA Name	Region	Realized Export (relative)	Patch Importance (relative)
Point Vicente SMCA	South coast mainland	0.005	0.103
Campus Point SMCA	South coast mainland	0.028	0.079
Naples SMCA	South coast mainland	0.073	0.033
Point Conception SMR	South coast mainland	0.090	0.079
Richardson Rock SMR	South coast Channel Island	0.271	0.567
San Miguel Island Special Closure	South coast Channel Island	0.470	0.436
Judith Rock SMR	South coast Channel Island	0.490	0.356

Harris Point SMR	South coast Channel Island	0.355	0.393
Carrington Point SMR	South coast Channel Island	0.456	0.346
Skunk Point SMR	South coast Channel Island	0.047	0.192
South Point SMR	South coast Channel Island	0.167	0.208
Painted Cave SMCA	South coast Channel Island	0.056	1.000
Gull Island SMR	South coast Channel Island	0.050	0.074
Anacapa Island SMCA	South coast Channel Island	0.008	0.141
Scorpion SMR	South coast Channel Island	0.023	0.214

Anacapa Island Special Closure	South coast Channel Island	0.006	0.275
Vandenberg SMR	Central coast	0.079	0.043
Point Buchon SMR	Central coast	0.424	0.081
White Rock SMCA	Central coast	0.294	0.050
Piedras Blancas SMR	Central coast	0.577	0.083
Piedras Blancas SMCA	Central coast	0.279	0.109
Big Creek SMR	Central coast	0.395	0.045
Point Sur SMR	Central coast	0.813	0.068
Point Lobos SMR	Central coast	0.893	0.061
Carmel Pinnacles SMR	Central coast	0.898	0.086

Asilomar SMR	Central coast	0.971	0.120
Lovers Point - Julia Platt SMR	Central coast	0.377	0.036
Natural Bridges SMR	Central coast	0.131	0.061
Año Nuevo SMR	Central coast	0.213	0.037
Pillar Point SMCA	Central coast	0.846	0.068
Montara SMR	Central coast	1.000	0.063
Egg (Devil's Slide) Rock to Devil's Slide Special Closure	Central coast	0.105	0.057
Double Point/Stormy Stack Rock Special Closure	Central coast	0.213	0.038
Point Resistance Rock Special Closure	Central coast	0.032	0.022

Point Reyes SMCA	Central coast	0.132	0.077
Point Reyes SMR	Central coast	0.442	0.055
Bodega Head SMCA	North coast	0.556	0.046
Bodega Head SMR	North coast	0.606	0.053
Russian River SMCA	North coast	0.287	0.024
Stewarts Point SMR	North coast	0.522	0.027
Del Mar Landing SMR	North coast	0.259	0.033
Saunders Reef SMCA	North coast	0.511	0.021
Point Arena SMR	North coast	0.464	0.020
Van Damme SMCA	North coast	0.222	0.015

Point Cabrillo SMR	North coast	0.526	0.023
MacKerricher SMCA	North coast	0.368	0.021
Ten Mile Beach SMCA	North coast	0.018	0.009
Ten Mile SMR	North coast	0.229	0.010
Rockport Rocks Special Closure	North coast	0.020	0.016
Vizcaino Rock Special Closure	North coast	0.107	0.016
Double Cone Rock SMCA	North coast	0.160	0.012
Big Flat SMCA	North coast	0.049	0.009
Sea Lion Gulch SMR	North coast	0.144	0.014
Steamboat Rock Special Closure	North coast	0.022	0.005

South Cape Mendocino SMR	North coast	0.229	0.008
Sugarloaf Island Special Closure	North coast	0.077	0.011
Reading Rock SMCA	North coast	0.099	0.002
False Klamath Rock Special Closure	North coast	0.034	0.002
Castle Rock Special Closure	North coast	0.048	0.003
Southwest Seal Rock Special Closure	North coast	0.029	0.002
Pyramid Point SMCA	North coast	0.041	0.001

Table S7. The relative MPA value scores for the Black Rockfish across all MPAs.

MPA Name	Region	Realized Export (relative)	Patch Importance (relative)
Gull Island SMR	South coast mainland	0.000	0.064
Painted Cave SMCA	South coast mainland	0.000	1.000
South Point SMR	South coast mainland	0.004	0.187
Carrington Point SMR	South coast mainland	0.068	0.322
Harris Point SMR	South coast Channel Island	0.019	0.442
Richardson Rock SMR	South coast Channel Island	0.022	0.694
Point Conception SMR	South coast mainland	0.008	0.074

Vandenberg SMR	Central coast	0.016	0.042
Point Buchon SMR	Central coast	0.096	0.105
White Rock SMCA	Central coast	0.100	0.066
Cambria SMCA	Central coast	0.037	0.021
Piedras Blancas SMR	Central coast	0.192	0.117
Piedras Blancas SMCA	Central coast	0.048	0.158
Big Creek SMR	Central coast	0.103	0.070
Point Sur SMR	Central coast	0.293	0.121
Point Lobos SMR	Central coast	0.222	0.116
Carmel Bay SMCA	Central coast	0.073	0.106

Carmel Pinnacles SMR	Central coast	0.080	0.160
Asilomar SMR	Central coast	0.137	0.231
Pacific Grove Marine Gardens SMCA	Central coast	0.062	0.101
Edward F. Ricketts SMCA	Central coast	0.025	0.065
Lovers Point - Julia Platt SMR	Central coast	0.016	0.076
Greyhound Rock SMCA	Central coast	0.188	0.042
Año Nuevo SMR	Central coast	0.065	0.087
Pillar Point SMCA	Central coast	0.275	0.186
Montara SMR	Central coast	0.379	0.170
Egg (Devil's Slide) Rock to Devil's Slide Special Closure	Central coast	0.024	0.154

Duxbury Reef SMCA	Central coast	0.152	0.052
Double Point/Stormy Stack Rock Special Closure	Central coast	0.101	0.104
Point Resistance Rock Special Closure	Central coast	0.332	0.062
Point Reyes SMCA	Central coast	0.124	0.204
Point Reyes SMR	Central coast	0.593	0.121
Bodega Head SMCA	North coast	0.821	0.128
Bodega Head SMR	North coast	1.000	0.149
Russian River SMCA	North coast	0.413	0.064
Salt Point SMCA	North coast	0.113	0.033
Stewarts Point SMCA	North coast	0.131	0.018

Stewarts Point SMR	North coast	0.470	0.068
Del Mar Landing SMR	North coast	0.350	0.082
Saunders Reef SMCA	North coast	0.497	0.054
Sea Lion Cove SMCA	North coast	0.113	0.016
Point Arena SMR	North coast	0.475	0.054
Van Damme SMCA	North coast	0.069	0.042
Point Cabrillo SMR	North coast	0.305	0.067
MacKerricher SMCA	North coast	0.474	0.059
Ten Mile Beach SMCA	North coast	0.027	0.028
Ten Mile SMR	North coast	0.301	0.032

Rockport Rocks Special Closure	North coast	0.043	0.046
Vizcaino Rock Special Closure	North coast	0.187	0.046
Double Cone Rock SMCA	North coast	0.305	0.036
Big Flat SMCA	North coast	0.200	0.024
Sea Lion Gulch SMR	North coast	0.436	0.043
Steamboat Rock Special Closure	North coast	0.065	0.015
South Cape Mendocino SMR	North coast	0.429	0.024
Sugarloaf Island Special Closure	North coast	0.177	0.033
Reading Rock SMCA	North coast	0.178	0.008

False Klamath Rock Special Closure	North coast	0.064	0.008
Castle Rock Special Closure	North coast	0.095	0.012
Southwest Seal Rock Special Closure	North coast	0.038	0.006
Pyramid Point SMCA	North coast	0.141	0.004