Towards transboundary networks of climate-smart marine reserves in the Southern California Bight

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Abstract

Climate-smart conservation addresses the vulnerability of biodiversity to climate change impacts but may require transboundary considerations. Here, we adapt and refine 16 biophysical guidelines for climate-smart marine reserves for the transboundary California Bight ecoregion. We link several climate-adaptation strategies (e.g., maintaining connectivity, representing climate refugia, and forecasting effectiveness of protection) by focusing on kelp forests and associated species. We quantify transboundary larval connectivity along ~800 km of coast and find that the number of connections and the average density of larvae dispersing through the network under future climate scenarios could decrease by ~50%, highlighting the need to protect critical steppingstone nodes. We also find that although focal species will generally recover with 30% protection, marine heatwaves could hinder subsequent recovery in the following 50 years, suggesting that protecting climate refugia and expanding the coverage of marine reserves is a priority. Together, these findings provide a first comprehensive framework for integrating climate resilience for networks of marine reserves and highlight the need for a coordinated approach in the California Bight ecoregion.

Introduction

Marine reserves can rebuild the biomass of overfished species[1], conserve biodiversity[2], and enhance the resilience and adaptive capacity of ecosystems to climate impacts[3-7]. However, delivering large-scale benefits requires networks of marine reserves that are functionally interconnected, and are large enough to protect the underlying biophysical processes that maintain species distribution and composition[8]. A rich literature exists on biophysical guidelines for designing networks of marine reserves for fisheries, conservation, and climate-adaptation objectives[9-12], but most are limited to analysis within country or state boundaries. By contrast, ecoregion-scale planning efforts may span thousands of kilometres and, in many cases, cross multiple national or international jurisdictions[13,14]. Consequently, before designing networks of transboundary marine reserves, planners need to develop shared biophysical guidelines and comprehensive spatial analyses across borders[15].

Climate change is one of the main threats to marine ecosystems[16] that could be partially addressed by large-scale, coordinated, climate-smart networks of marine reserves[11,17,18]. Although marine reserves cannot directly abate climate-change threats, they can indirectly

136 mitigate climate-change impacts by promoting ecological resilience[3-5,19]. Climate-smart
137 conservation is a multiple-step approach that addresses the vulnerability of species and
138 ecosystems to changes in climate and ocean chemistry, and supports resilience of populations
139 and ecosystems[17]. Climate-adaptation strategies include protecting areas that act as climate
140 refugia[11,18,20], maintain ecological connectivity to ensure metapopulation persistence[21],
141 facilitate species' range shifts, and recover important species for ecosystem functioning (e.g.,
142 predators)[22]. Complementary strategies include supporting ecosystem resilience by addressing
143 threats not directly abated by marine reserves[11] (e.g., pollution and other impacts) and
144 protecting and restoring habitats that could mitigate some of the effects of climate change (e.g.,
145 through carbon sequestration). Because global conservation targets aim to protect 30% of
146 marine habitats by 2030[23,24] while adapting to climate change, there is a need to integrate
147 multiple adaptation strategies for designing networks of climate-smart reserves.

148

149 Given the highly dynamic nature of the oceans, biophysical modelling of larval dispersal is an
150 essential tool to inform transboundary conservation[25,26]. However, these models should
151 consider the implications of climate change on larval dynamics, such as changes in dispersal
152 distances and the availability of suitable habitats for settlement[21,27]. These considerations are
153 essential because transboundary dispersal may be critical for metapopulation persistence.
154 Notably, certain areas may be less impacted by climate change and act as climate refugia[28],
155 providing food, shelter, and habitat, despite future changes. Identifying climate refugia at large
156 spatial scales can be challenging, requiring the use of ecosystem attributes (resistance,
157 resilience, persistence[29]) or environmental proxies (e.g., micro climates)[30]. If we map these
158 areas, we can prioritize their protection and assess changes in larval connectivity for future
159 scenarios. Climate change may undermine the effectiveness of transboundary networks of
160 marine reserves to facilitate recovery of exploited species. Thus, it is a priority to assess
161 whether proposed protection targets[23,24] will facilitate recovery of overexploited species in the
162 future and whether increased protection or alternative strategies will be necessary to ensure
163 their recovery.

164

165 The Southern California Bight ecoregion (henceforth "California Bight") in the northwest
166 Pacific Ocean ─ shared between the state of California, USA, and the Peninsula of Baja
167 California, Mexico ─ has a long history of research cooperation and binational environmental
168 agreements[31,32]. It is considered a marine climate-change "hotspot" – rapidly warming ocean
169 regions that are natural laboratories for evaluating climate adaptation options[33]. Recent marine

170   heatwaves[34-37] and prolonged hypoxic events[3] exemplify the impacts of climate variability and

171   environmental extremes on species, ecosystems, and coastal economies of this region.

172   Documentation of these changes includes mass mortality events and range shifts of

173   economically or ecologically important species[3,34,37-39]. This threatens the conservation and

174   economic sustainability outcomes that both countries seek to deliver through marine zoning.

175

176   In 2012, California implemented a network of marine protected areas covering 16% of state

177   waters, with more than half being fully protected marine reserves. This network was based on

178   stakeholder input and biophysical guidelines to ensure ecological connectivity, habitat

179   representation and replication, while balancing users' needs[40]. However, the establishment of

180   marine protected areas did not include climate-adaptation objectives[41]. Moreover, the network

181   did not consider the transboundary nature of the region, where many species move across the

182   USA-Mexico border through larval dispersal and adult movement.

183

184   By contrast, although Baja California has extensive coastal areas protected, there is a lack of

185   an integrated network of marine reserves, with less than 1% of the coastal waters fully

186   protected[20,42]. In this region, coastal resource management is based on territorial user rights

187   granted to fishing cooperatives and independent permit holders, with successful local cases of

188   community-based marine reserves sparking other cooperatives' interest[42]. Additional

189   community-led marine reserves are awaiting government approval, while environmental

190   NGOs, scientists, fishing cooperatives, and governmental agencies are promoting a region-

191   wide marine spatial planning process[42].

192

193   Here, we first adapt and refine 16 biophysical guidelines for climate-smart, transboundary

194   marine reserve design for the California Bight ecoregion ─ spanning over eight degrees of

195   latitude. We used kelp forest ecosystems (dominated by giant kelp, *Macrocystis pyrifera*) and

196   focal species of fishes and invertebrates of commercial and ecological importance to identify,

197   analyze, and map areas that integrate and meet the proposed climate-smart guidelines. Then

198   we explore the magnitude and importance of transboundary connectivity in the region and ask

199   whether binational connections will be lost under future climate scenarios. We also ask whether

200   sea surface temperature variability can be used as a proxy for climate refugia and whether

201   marine heatwaves in the following 50 years will undermine the effectiveness of marine reserves

202   for facilitating recovery of vulnerable species in the California Bight. Our research can inform

203 the delivery of networks of climate-smart marine reserves by 2030 in the California Bight and
204 other regions.

205

206 **Methods**

207

208 **Study area**

209

210 The California Bight ecoregion is located in the southern California Current System in the
211 northeast Pacific Ocean and spans the USA-Mexico international border, from Point
212 Conception, California, USA, in the north to Punta Abreojos, Baja California Sur, Mexico, in
213 the south[43]. This highly productive ecoregion is in a transitional zone between the southward-
214 flowing, cold, nutrient-rich California Current and the northward-flowing, warm, nutrient-
215 depleted Davidson Current[44]. This transboundary ecoregion is characterized by strong
216 latitudinal gradients in environmental conditions and oceanographic features that support a
217 diverse assemblage of species and habitats[45]. We divided the California Bight into four sub-
218 regions: southern California, northern and central Baja California, and Guadalupe Island. These
219 four sub-regions represent geographic borders (the USA-Mexico border) and distinct
220 biogeographic areas where species composition varies because of environmental conditions[46].

221

222 **Developing and integrating biophysical guidelines**

223

224 We developed biophysical guidelines (Table 1) for designing transboundary networks of
225 climate-smart marine reserves for biodiversity conservation, fisheries replenishment, and
226 climate-adaptation objectives in the California Bight. We compiled, adapted, and refined the
227 guidelines using criteria developed for California, Mexico, and other regions[9,10,40,47]. Our work
228 does not provide an extensive review of the proposed guidelines or their ecological rationale,
229 as this has been addressed in previous work[9,10]. Instead, we summarise our findings in the
230 context of transboundary and climate-smart spatial planning.

231

232 Our work builds on a workshop held in 2017, which developed biophysical design guidelines
233 for the Pacific region of Baja California[42]. Following this first workshop, five working groups
234 comprising researchers from Mexico, the USA and Australia, fishing cooperatives,
235 governmental agencies, and non-profit organizations in Mexico and the USA further developed
236 the principles and their application to the California Bight (Table 1). Finally, following a

237   second workshop held in 2019, we conducted spatial analysis and developed maps that
238   integrate and meet some of the proposed guidelines for the California Bight, focussing on giant
239   kelp (*M. pyrifera*) forests (henceforth "giant kelp") and six focal species of commercial and
240   ecological importance associated with giant kelp. Focal species included California Sheephead
241   (*Semicossyphus pulcher*), sea basses (*Paralabrax clathratus* and *P. nebulifer*), whitefish
242   (*Caulolatilus princeps*), spiny lobster (*Panulirus interruptus*), abalone (*Haliotis* spp.), sea
243   urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*), and sea cucumbers
244   (*Apostichopus* spp. And *Parastichopus* spp.). We did not always use the same focal species
245   among principles and analysis (see, Supplementary Table 1) because of differences in the
246   availability of data, and in some cases, we used data from multiple taxa as composite focal
247   species.

248

249   The proposed transboundary climate-smart guidelines fall into five major categories: (1) habitat
250   representation and replication; (2) protecting critical and unique areas; (3) incorporating
251   connectivity; (4) allowing time for recovery; and (5) minimizing and avoiding threats (Fig. 1).
252   Marine habitats are broad indicators of the distribution of biodiversity[48], which are relatively
253   easy to map, and if adequately represented (e.g., protect enough of each habitat) can effectively
254   protect biodiversity and replenish overfished populations[9,10]. Moreover, each habitat should be
255   replicated in the network in case a large-scale disturbance impacts part of the system[49]. It is
256   also important to represent and replicate habitats or areas more resistant and resilient to climate
257   stressors (climate refugia), which can replenish impacted populations and habitats[9,10].

258

259   To facilitate recovery of focal species populations, the network should also protect areas critical
260   for their life cycles, such as those required for spawning, nesting, or breeding[9,10]. Notably,
261   because most marine species are structured as metapopulations, connected through movements
262   of adults, juveniles, or larval dispersal, ensuring the metapopulation persistence of focal species
263   requires incorporating ecological connectivity[9,10,47,50]. It is also crucial to consider changes in
264   ocean conditions that could modify patterns of larval dispersal and recruitment and precipitate
265   range shifts among species. Determining how much time overexploited species need to recover
266   is essential to assessing the network's effectiveness, especially if this is done while evaluating
267   the projected impacts of climate change for vulnerable species. Finally, we need to consider
268   threats that marine reserves can abate, versus those that reserves cannot abate, therefore
269   requiring alternative strategies to support ecosystem resilience[19,51].

270

271 **Binational habitat mapping**

272

273 We mapped the distribution of intertidal, estuarine, subtidal, and deep-sea habitats in the

274 territorial seas (within 12 nautical miles of the coast) of the California Bight (Supplementary

275 Table 2 and 3). We extracted depth contours (30, 100, and 200 m) from the General

276 Bathymetric Chart of the Oceans[52] and the California Department of Fish and Wildlife (CDFW,

277 2010 version) using ESRI ArcGIS Pro v10.8. We then used these contours to classify subtidal

278 habitats based on depth categories (0-30, 30-100, 100-200, over 200 m). We obtained intertidal,

279 estuarine and subtidal habitat polygons for southern California (CDFW, 2010 version) and

280 northern Baja California from published work[53]. There was no available coastline or habitat

281 mapping in the sub-regions of central Baja California and Guadalupe Island. We followed

282 Arafeh-Dalmau, et al. [53] and digitized the coastline and mapped intertidal and subtidal habitats

283 by visualizing Google Earth historical images.

284

285 We then combined existing maps of giant kelp distribution for California (CDFW, 2010

286 version) and Baja California[53] with a 35-year satellite time series that maps the distribution and

287 persistence of giant kelp at 30-m^2 grid resolution, and classifies giant kelp persistence into three

288 classes (high, mid, and low). For more details see Arafeh-Dalmau, et al. [20]. Highly persistent

289 giant kelp can be a good proxy for climate refugia because they have endured through time

290 despite multiple cycles of marine climate oscillations[20]. We classified giant kelp polygons that

291 did not overlap with persistence maps as having low persistence. We also collected information

292 and mapped the distribution of tidal flats in southern California[54] and eelgrass (*Zostera marina*)

293 for northern and central Baja California from existing information (Pronatura Noroeste A.C.)

294 and *in situ* presence-absence surveys combined with low-altitude drone imagery (for more

295 details, see Supplementary Table 3). Finally, we catalogued geomorphic features data[55] to map

296 submarine canyons.

297

298 **Vulnerability of habitats and focal species to human threats**

299

300 We conducted an expert-knowledge survey to quantify the vulnerability of six marine habitat

301 types (estuaries, rocky intertidal, seagrass, kelp forest/rocky reefs, deep sea and pelagic) to

302 eight major threats (marine heatwaves, ocean acidification, hypoxia, sea-level rise, storms,

303 resource extraction, pollution, and physical habitat destruction) for the California Bight. The

304 survey allowed experts to score the vulnerability of each habitat to each threat. Options

305   included no threat, low, moderate, and high threat (coded 0, 1, 2, and 3, respectively; for more

306   details see Supplementary Methods).

307

308   We complemented and expanded the expert-knowledge survey through a review of published

309   studies for the California Bight that empirically examined the vulnerability and recovery rate

310   of five focal species (California Sheephead, lobster, abalone, sea urchin, giant kelp;

311   Supplementary Table 1) following marine heatwaves, hypoxia, and ocean acidification. We

312   scored vulnerability to climate stressors that a species experiences as high for lethal effects,

313   medium for extensive sublethal effects, and low for limited sublethal effects. We scored a

314   species recovery rate from climatic stresses as rapid (< 1 year), moderate (2-5 years), or slow

315   (> 5 years) (for more details, see Supplementary Methods).

316

317   **Sea surface temperature variability as a proxy for climate refugia**

318

319   To identify potential climate refugia, we used two proxies: temperature variability[30] and giant

320   kelp persistence[20]. We analyzed patterns in their spatial variation and their correlation across a

321   1-km^2 grid in the California Bight. We conducted this analysis to ascertain whether sea surface

322   temperature variability is a comprehensive proxy of climate refugia for each sub-region in the

323   California Bight. We obtained 17 years (2003-2019) of daily SST data from the Aqua-MODIS

324   satellite at 1-km^2 grid resolution, accessed through the NOAA-ERDDAP data repository

325   (https://coastwatch.pfeg.noaa.gov/erddap/index.html). We estimated an annual cycle using a

326   30-day weighted moving average smoothing window for each year to create an annual

327   climatology. We then used these annual cycles to estimate SST variability by computing the

328   variance relative to the moving mean of the annual cycle (see Supplementary Fig. 1, for

329   example). This SST variability metric represents high-frequency (24-h or faster) temperature

330   variability. We then computed the mean SST variance across the 1-km^2 grid to evaluate the

331   accuracy of our model for SST variability with *in situ* sensors (a series of MiniDOT

332   temperature/dissolved-oxygen sensors [PME Inc.] across Baja California[56]) and compared

333   variability at sub-daily intervals. We then computed the mean giant kelp persistence[20] over the

334   same 1-km^2 grid cells. We examined the correlation (linear least-squares regression) between

335   these datasets for each sub-region, excluding Guadalupe Island, which does not have giant kelp.

336

337   **Transboundary movement of juveniles and adults into critical areas**

338

339   To assess transboundary connectivity, we reviewed and mapped the transboundary movements

340   of sharks, bony fishes, seabirds, marine mammals, and sea turtles between southern California

341   and the three sub-regions in Baja California. We reviewed data from published papers and

342   public databases (e.g., Tagging of Pacific Predators (TOPP) animal tracking dataset) for the

343   period 1999-2019 using a combination of keywords: (1) movement or migration, (2) adults or

344   juvenile, and (3) shark, bony fish, sea bird, marine mammals, or sea turtles. Because most

345   studies tagged animals in USA waters, we considered connectivity only for organisms released

346   in USA waters that moved into Mexican juvenile or adult habitats (e.g., spawning, breeding,

347   nursery, resting, or foraging habitats). We aggregated the number of tagged studies that

348   released organisms in southern California that were subsequently recorded in the three sub-

349   regions in Baja California into 0.25° grid cells. Grid cells with high numbers of tagged animals

350   recorded in Baja California were identified as essential areas for juvenile and adult

351   transboundary connectivity.

352

353   **Transboundary larval dispersal model and impact of climate change**

354

355   To further explore transboundary connectivity, we implemented the AGRIF version of the

356   Regional Ocean Modelling System (ROMS; for more details, see Supplementary Methods,

357   Supplementary Fig. 2) to simulate passive spores and larval dispersal (henceforth "larval

358   dispersal") for four focal species (California Sheephead, abalone, sea urchin and giant kelp;

359   Supplementary Table 1) in the California Bight. We obtained information about spawning time

360   and planktonic larval duration (PLD) from the literature (Supplementary Table 4), and for

361   simplicity rounded to the nearest week when PLD exceeded 7 days.

362

363   To measure larval connectivity, we divided the coast into 54 polygons, each covering 20 km

364   of latitude and limited by the 200 m isobath (Supplementary Fig. 3). This isobath represents

365   the edge of the continental shelf that is a limit for coastal environments, where most fishing

366   takes place[43]. In the centroid of each polygon, we released 1,000 virtual larvae at the start of

367   each month of the year and followed their trajectories hourly for 60 days (2 months). We

368   imported hourly coordinates for each modelled particle into MATLAB (Mathworks). We

369   identified the intersection between particles and each polygon at the end of the PLD with a

370   selection-by-location function. We generated connectivity matrices reflecting the proportion of

371   larvae that settled in each polygon relative to the total number of larvae released at each site.

372   We averaged matrices for the larval release dates within each month during each species'

373   spawning season. We calculated local retention as the proportion of larvae released within a
374   polygon remaining within the natal area at the end of the PLD for each species. We explored
375   connectivity matrices for each season using graph theory and a spatial network approach using
376   the software GEPHI[57], where nodes represent larval release sites and links represent directional
377   larval dispersal probabilities. We estimated network density to compare changes in
378   cohesiveness or saturation that relate to functional attributes, such as resilience[58]. We defined
379   density as the number of links observed divided by the maximum number of possible links[58],
380   representing the probability that any given tie between two random nodes is present[59].

381

382   We simulated two contrasting scenarios to investigate the potential effect of climate change on
383   larval connectivity due to reduction of PLD with increased temperatures and the reduction of
384   recruitment habitat due to climate change, since both could significantly alter metapopulation
385   dynamics[21,27]. In the first or "Current" scenario, we downscaled the larval connectivity matrices
386   to the polygon unit (following the approach described by Alvarez-Romero, et al. [21]) based on
387   two factors: probability of connections between two polygons according to the connectivity
388   matrix based on the PLD reported for each species in the literature, and the total area with giant
389   kelp found within each polygon. The second or "Future" scenario employed shortened
390   connectivity matrices due to warming and consequent restriction of giant kelp to highly
391   persistent habitats, defined as potential climate refugia[20]. We calculated the reduction in PLD
392   in fish and invertebrates following a 3°C increment in SST using previously described
393   methods[21,60] (Supplementary Table 4). This increase in temperature is extreme, yet not unlikely
394   for the end of the 21st century under the highest IPCC Shared Socio-Economic Pathway (SSP5-
395   8.5)[61].

396

397   **Simulating recovery time for focal species**

398

399   To project the expected effectiveness of transboundary marine reserve networks for recovery
400   of exploited populations, in the absence of climate-change impacts, we simulated the effect of
401   marine reserves on six focal species within the region (sea bass, whitefish, lobster, abalone, sea
402   cucumber and sea urchin; Supplementary Table 1) using a deterministic, discrete-time logistic
403   growth model with spatially implicit reserve and fishing zones:

404

405    $$X_{t+1} = X_t + \left(rX_t \left(1 - \frac{X_t}{K} \right) \right) - ((1-R)X_t F_{MSY}),$$

406

407 where X_t represents biomass at time t, r is the intrinsic growth rate, and K is the carrying

408 capacity. The last term represents harvesting of biomass outside the reserve, where the $(1 - R)$

409 parameterization corresponds to the portion of biomass outside the reserve. We test three

410 different scenarios of reserve coverage: $R = (10\%, 30\%, 100\%)$. The first two scenarios are

411 representative of commonly cited protection targets, while the third scenario provides an upper

412 bound of maximum attainable protection. We estimated population parameters and fishing

413 mortality (F_{MSY}) by applying a catch-only data-limited stock assessment method[62] to catch data

414 from 2000-2015 in Baja California, from Comisión Nacional de Acuacultura y Pesca

415 (CONAPESCA) (Supplementary Table 5, Supplementary Fig. 4). We ran all simulations for

416 50 years, with initial biomass set at 20% of carrying capacity and fishing mortality outside the

417 reserve held constant at F_{MSY}. We considered a population "recovered" when the population

418 size was within 90% of the theoretical equilibrium size ($\bar{X}$):

419

420 $$\bar{X} = \frac{K[r - (1-R)F_{msy}]}{r}.$$

421

422 **Considering the impact of marine heatwaves on focal species biomass and recovery**

423

424 For a subset of focal species of invertebrates with limited movement (abalone, sea cucumber

425 and sea urchin; Supplementary Table 1, 6) vulnerable to marine heatwaves, we explored

426 recovery for three climate-change scenarios by running a stochastic version of the model. We

427 simulated the impact on the biomass of species based on the probability of a year experiencing

428 marine heatwaves with a cumulative intensity at least as strong as those that impacted the

429 California Bight in 2014-2015[34,36-38]. We used 17 years of giant kelp forest community data

430 (1999-2015), which integrate four different monitoring programs for the California Bight[37], to

431 model the rate of change of the density of the focal species following the 2014-2015 extreme

432 marine heatwaves (henceforth "marine heatwaves"). We excluded monitoring data north of

433 latitude 33.8°N and west of longitude 118.7°W because this area is subject to colder average

434 temperatures, forms a separate sub-bioregion[63], and giant kelp forest communities there are

435 less impacted by marine heatwaves[64] (for more details, see Supplementary Methods).

436

437 We used 0.25° grid cell Optimum Interpolation Sea Surface Temperature data set[65] to estimate

438 the average annual cumulative intensities registered in 2014-2015 marine heatwaves, based on

439   the climatology for 1983-2012. Then we estimated projected marine heatwaves for the 2020-

440   2100 period for three climate scenarios generated under each of three SPPs[66] — SSP1-2.6,

441   SSP2-4.5, SSP5-8.5 — from a multi-model ensemble mean derived from 11 Earth-System

442   models from the Coupled Model Intercomparison Project Phase 6 (for more details see

443   Supplementary Methods).

444

445   We derived the probability of a marine heatwave year using a generalized linear model with a

446   binomial link function, fitted to marine heatwave years for the three climate scenarios. Then

447   we used the empirically derived density change effect of a marine heatwave on abalone, sea

448   urchins, and sea cucumber to yield the model:

449

450    $X_{t+1} = (1 - \delta\Phi_t) X_t + \left(rX_t \left(1 - \frac{X_t}{K}\right)\right) - ((1 - R)X_t F_{MSY}),$

451

452   where $\delta \in [0, 1]$ represents the density-reducing effect of the MHW, and $\Phi_t = 1$ if the year t

453   has a MHW and $\Phi_t = 0$, otherwise. We ran 10,000 independent simulations of this model for

454   each of the three species and three climate scenarios. All data analyses and simulations were

455   conducted in R 4.0.4[67].

456

457   **Mapping threats**

458

459   We mapped climate and land-based threats that marine reserves cannot directly abate but can

460   build resilience to (henceforth "threats") at a 1-km^2 grid resolution in the California Bight using

461   the most comprehensive dataset available for the cumulative human impact (see Halpern, et

462   al. [68]). We classified those cells with high cumulative impacts (top 10%) for each sub-region

463   as "highly threatened".

464

465   For each of the three sub-regions in Baja California, we mapped two extractive activities that

466   marine reserves can directly abate: small-scale commercial fishing and recreational fishing

467   (henceforth "fishing"). We prioritized the analysis for these regions because they have less

468   spatial information available. We mapped the total catch of small-scale fisheries (tonnes) at

469   one-hectare grid resolution (Supplementary Table 7) inside authorized fishing polygons using

470   19 years (2000-2018) of catch information referenced to each fishing cooperative and

471   individual permit holder (hereafter "concessions") from CONAPESCA. Each fishery has a

472 designated concession where cooperatives can extract specific resources (for more details see

473 Supplementary Methods). Then, we estimated the probability of recreational fishing sites or

474 banks in a 100-m^2 grid resolution based on georeferenced commercial and non-commercial

475 sport fishing maps (e.g., FISH.n.MAP CO., Baja California North, Sportfishing Atlas Baja

476 California Edition) for the three sub-regions in Baja California (for more details see

477 Supplementary Methods).

478

479 **Results**

480

481 We provide 16 biophysical guidelines for designing transboundary networks of climate-smart

482 marine reserves adapted for the California Bight and recommendations for their application

483 (Table 1). The guidelines provide recommendations for habitat representation and replication

484 (Supplementary Table 8), protecting critical and unique areas, incorporating connectivity,

485 allowing time for recovery, and minimizing or avoiding local threats. Instead of addressing

486 measures for adapting to changes in climate and ocean chemistry separately[9,10], we integrate

487 climate-adaptation strategies within each of the other principles, to achieve a climate-smart

488 network.

489

490 **Habitat mapping**

491

492 We produced maps of the distribution of 31 coastal and island habitats from intertidal to deep-

493 sea habitats for the four sub-regions (Fig. 2, Supplementary Table 3). Although southern

494 California covers fewer degrees of latitude than northern and central Baja California, it

495 represents almost half (~46%) of the area of the California Bight. We mapped rocky intertidal

496 and sandy beaches for ~2700 km of coastal and island coastline. Our habitat mapping includes

497 biogenic habitats such as eelgrass and surfgrass (*Phyllospadix* spp.) and different levels of giant

498 kelp persistence. We also mapped subtidal sandy and rocky habitats at different depths and

499 submarine canyons in all regions. We found no seamounts, guyots or other geomorphic features

500 of importance for biodiversity in the territorial sea of the California Bight. We could not map

501 surfgrass and rocky habitats deeper than 30 m for the three regions in Baja California. Finally,

502 we found no giant kelp or estuarine habitats in Guadalupe Island.

503

504 **Vulnerability of habitats and focal species to human threats**

505

506   We received 55 responses to our expert-knowledge survey. Respondents ranked estuaries and

507   rocky intertidal habitats as the most threatened habitats, whereas pelagic and deep-sea habitats

508   ranked as the least threatened (Fig. 3a). Across habitats, marine heatwaves and resource

509   extraction were identified as the most serious threats, while storm events and sea-level rise

510   were the least threatening (Fig. 3b). Moreover, although the respondents ranked warming as

511   the most threatening stressor, non-climate related threats, on average, scored higher (2.23 $\pm$

512   0.17) than climate threats (1.94 $\pm$ 0.18).

513

514   Our risk assessment indicated that mobile species, such as California Sheephead and lobsters,

515   are least vulnerable and recover fastest because they are least sensitive to acute climate

516   stressors. In contrast, sessile species like giant kelp, or species with limited mobility, such as

517   abalone and sea urchins, exhibit high and intermediate vulnerability to at least one climate

518   stressor (Fig 3c). The recovery from climate stressors is intermediate for giant kelp, but slower

519   for abalone and sea urchins. The combination of higher vulnerability and slow recovery renders

520   these sessile or limited mobility benthic invertebrates most vulnerable to climate stressors (see

521   Supplementary Results for detailed justification).

522

523   **Sea surface temperature variability as a proxy for climate refugia**

524

525   Analysis of remote sensing SST and giant kelp canopy data revealed that high kelp persistence

526   coincides with low temperature variability in southern California (p = 0.042), has no relation

527   with temperature variability in northern Baja California (p = 0.745), and correlates with high

528   temperature variability in central Baja California (p = 0.007) (Fig. 4). We also found that SST

529   variability performs well compared to the observed high frequency bottom temperature

530   variance (R^2 = 0.87; Supplementary Fig. 5). Even when we excluded an outlier site (Punta

531   Prieta) which has the highest temperature variability of all sites, we found a correlation

532   coefficient R^2 > 0.6. Our results suggest that in the absence of other metrics, SST variability

533   may identify potential refugia for giant kelp and possibly kelp-associated species in the

534   southern portion of the region (central Baja California).

535

536   **Transboundary movement of juveniles and adults**

537

538   We found movement data for juvenile and adult individuals for seven shark, three bony fish,

539   four seabird, four marine mammal, and one sea turtle species (Supplementary Table 9). Focal

540 species are relatively large and migratory, with reported connectivity distances ranging from

541 hundreds (e.g., white seabass, yellowtail) to thousands of kilometers (e.g., white sharks, blue

542 whales; Supplementary Table 9) and temporal scales of two weeks (e.g., bottlenose dolphin,

543 Black-vented shearwater) to over two years (white seabass). Greater connectivity was reported

544 in northern Baja California, from north of Ensenada (31.8°N) and near the USA/Mexico border,

545 followed by Punta Colonet (30.9°N), and areas in central Baja California, with important

546 locations near the southern limit of the California Bight in Bahía Asunción (27.1°N). We also

547 found areas of high connectivity between southern California and Guadalupe Island (Fig. 5).

548

549 Tagging studies highlight transboundary nursery and foraging areas for white sharks in near-

550 shore regions of central Baja California (Supplementary Table 9) and spawning areas for

551 California Scorpionfish and Vermilion Rockfish in the USA-Mexico border. Breeding areas

552 are also reported for Laysan albatross in Guadalupe Island, post-breeding dispersal areas for

553 black-footed albatross offshore of San Quintín (30.5°N), in northern Baja California, and

554 habitat use for the red knot in Guerrero Negro and Ojo de Liebre Lagoons (27.7°N) in central

555 Baja California. In general, most studies did not report specific transboundary feeding,

556 spawning, or foraging locations for most species, but rather broad general distributions along

557 the California Bight (Supplementary Table 9).

558

559 **Transboundary larval dispersal model**

560

561 Results of the larval dispersal models reveal that the California Current transports larvae

562 southward throughout the year from California to Baja California, while a coastal undercurrent

563 also transports larvae northward from Mexico towards California during summer and winter

564 (Supplementary Movie 1). In the Current scenario, we observed transboundary larval

565 connectivity along a stretch of coast covering ~800 km, where larvae from Mexico travel ~400

566 km north, reaching Point Conception (34.5°N) at the northern limit of the California Bight,

567 while larvae from the USA travel ~400 km south to El Rosario (29.8°N) in northern Baja

568 California (Fig. 6a).

569

570 The strength of larval connectivity is a function of the geographic distance between sites, which

571 generally decreases as the distance between sites increases. Connectivity patterns are strongly

572 influenced by the life history of species, including planktonic larval duration (PLD) and

573 spawning time. For example, propagules of the giant kelp (with a PLD of a few days to hours)

574   move almost exclusively between adjacent sites on scales of < 25-50 km throughout the year,

575   while larval dispersal of abalone (PLD = 7 days) occurs between sites 25-100 km apart, year-

576   round. For these species, we found high levels of local larval retention (45% and 25% on

577   average, respectively) compared to species with longer PLDs (average $\leq$ 7%). For all species,

578   connections extend from southern California to central Baja California, but we found some

579   isolated sites (with null probabilities of connectivity to other sites) for short PLD, such as in

580   the offshore islands in southern California (henceforth "Channel Islands") and areas in central

581   Baja California.

582

583   In contrast, larvae of the California Sheephead (PLD = 42 days) can travel 75-500 km during

584   the fall, and larvae of sea urchins (PLD = 56 days) can be transported 100-700 km during winter

585   (Fig. 6a). Thus, transboundary connectivity is more important for species with longer PLD.

586   The importance of transboundary connections varied by commercial species and country. For

587   example, for sea urchin, 16% of all the larvae that settled within each country originated from

588   the other country. On the other hand, for California Sheephead, 20% of all larvae in the USA

589   came from Mexico and only 3% in Mexico from the USA. Although transboundary

590   connectivity is more important for species with longer PLD in any single generation, long-term

591   resilience over multiple generations depends on sites across the border that are tens to hundreds

592   of kilometers away, even for species with short PLD.

593

594   Climate change is predicted to cause a significant decline in the number and strength of

595   connections for all species. In the Future scenario, which considers the effects of climate

596   change, the number of connections present and consequently the average density of larvae

597   dispersing in the network decreased by half (range from -24% on giant kelp to -63% on

598   abalone), the average probability of the connections reduced by an order of magnitude (range

599   from -90.7% in California Sheephead to -96.0% in giant kelp), while local retention improved

600   for all species except giant kelp (Supplementary Table 4). We found that binational connections

601   were significantly reduced (61% and 52% lost for California Sheephead and sea urchins,

602   respectively) or completely lost (giant kelp and abalone) either because larvae cannot reach as

603   far or because stepping-stone connections disappeared due to the loss of giant kelp with low

604   and intermediate persistence. For sea urchin and California Sheephead, the number of larvae

605   crossing the border dropped to $\leq$ 3%. For species with short PLD, some sites become

606   completely disconnected, forming independent sub-networks, or sites become only loosely

607   connected through a few key sites, especially around the Channel Islands and in northern and

608 central Baja California (Fig. 6b). Importantly, the Future scenario identified some sites (e.g.,

609 around the northern Channel Islands and Vizcaino Bay in latitudes 28-29°N) that may be

610 crucial to avoid the collapse of connectivity in the region and should be prioritized for

611 protection from additional impacts.

612

613 **Time for recovery of focal species and reserve coverage**

614

615 The deterministic recovery model revealed that, overall, increased protection results in faster

616 recovery and higher equilibrium biomasses. For all protection levels in the region (i.e., 10, 30,

617 and 100%), sea cucumber showed the fastest recovery from fishing, at less than 10 years (Fig.

618 7a). Abalone and lobster showed the slowest rates of recovery, requiring between 31 and 47

619 years. Importantly, our results show that protecting 10, 20, or even 30% of abalone populations

620 is not enough to allow recovery (Fig. 7b), highlighting that increasing reserve coverage and

621 combining with other management actions is needed to facilitate population recoveries for

622 slow-growing populations such as abalone. All fish and sea urchin species showed an

623 intermediate recovery, requiring 15-20 years, regardless of reserve coverage. All populations

624 reach recovery status fastest under a 100% protection, followed by 30% and then 10% (Fig.

625 7b).

626

627 **Considering impacts of marine heatwaves on focal species recovery**

628

629 We found an average cumulative marine heatwave intensity for 2014 and 2015 of 465.6 °C

630 days and 684.5 °C days, respectively, for the nine pixels with monitoring data. When modelling

631 future marine heatwaves, we found that by 2100 the probability of any given year experiencing

632 a marine heatwave of this magnitude will be 0.46, 0.88, and 0.99 for scenarios SSP1-2.6, SSP2-

633 4.5 and SSP5-8.5, respectively (Fig. 8). Importantly, if greenhouse gas emissions are not

634 mitigated, the California Bight could be in a permanently extreme marine heatwave within the

635 next 50 years (Fig. 8).

636

637 In linear models of yearly density change, we found significant differences between years with

638 (2014-2015) and without (1999-2013) marine heatwaves for abalone, sea urchin, and sea

639 cucumber (Supplementary Table 10; $p < 0.01$). Simulated yearly density of abalone, sea urchin,

640 and sea cucumber species decreased during marine heatwaves (2014-2015) by 59.1%, 67.3%,

641 and 72.4%, respectively.

642

643 When accounting for potential impacts due to marine heatwaves for vulnerable species, we

644 found that no species reaches recovery status under any combination of emission scenario and

645 reserve coverage, with abalone being particularly vulnerable (Fig. 7a). While not reaching

646 equilibrium, sea cucumbers show the largest population sizes across climate and protection

647 scenarios, but there was great uncertainty about those changes. Our simulations suggest that

648 even rapidly growing species such as sea cucumber may not reach equilibrium biomass within

649 the next 50 years even under 100% protection (Fig. 7a).

650

651 **Mapping threats**

652

653 We found highly threatened areas that require management to support resilience, mainly near

654 cities in southern California and northern Baja California (e.g., Los Angeles, San Diego,

655 Tijuana, and Ensenada; Fig. 9a). However, in central Baja California and Guadalupe Island,

656 we found highly threatened areas also in remote offshore sites. Both regions are isolated and

657 scarcely populated, with Guadalupe Island located ~250 km from the mainland of Baja

658 California Peninsula. We also found an overlap of highly threatened areas with areas of high

659 fishing pressure in northern Baja California but also in less populated areas further south at San

660 Quintín (mainly recreational fishing) and El Rosario (primarily commercial fishing) (Fig. 9b-

661 c). On the other hand, fishing pressure in central Baja California was lower and mainly

662 concentrated near Punta Eugenia and Bahía Tortugas for commercial fishing and south of

663 Cedros Island for recreational fishing. Sea urchin and sea cucumber are the most important

664 commercial fishing catch in northern Baja California, lobster and abalone in central Baja

665 California, and abalone in Isla Guadalupe (Supplementary Table 7).

666

667 **Discussion**

668

669 Our results show that although southern California occupies ~25% of the California Bight

670 extension, spanning the USA-Mexico border, it contains almost half of the marine habitats and

671 supports strong ecological connections with northern Baja California. This transboundary

672 connectivity is already significant for populations with long planktonic larval duration (PLD)

673 and highly mobile adults and juveniles, and is likely to become more important as species shift

674 their distributions in response to changing environmental conditions. Given that many

675 populations of ecologically and commercially important species depend on both countries, it is

676 essential to protect important transboundary areas for migratory species and larval dispersal to
677 recover and maintain populations, communities, and genetic flows[10,69] and benefit both
678 conservation and fisheries[47,50,70,71].

679

680 Under a future climate scenario, we found that many areas in the California Bight become
681 isolated and binational connections will diminish or be lost, especially for species with short
682 PLD. However, local retention improves for most species, suggesting that establishing large
683 marine reserves in areas that will become more isolated is critical to maintaining self-
684 replenishment and supporting local populations[61,72]. Like other studies[21,27], we found that the
685 strength of connections weakens, the overall larval recruitment decreases, and that some nodes
686 for species with short PLD may become disconnected. Under this future climate scenario,
687 networks of marine reserves will need to prioritize the protection of key stepping-stone nodes
688 to avoid the collapse and fragmentation of larval dispersal in the region. If not adequately
689 protected from fishing, depleted populations' limited supply of larvae could lead to genetic
690 bottlenecks[73] and local population collapse[74], with economic implications.

691

692 Our results indicate that SST variability is a good proxy for climate refugia, particularly for
693 central Baja California. Areas with high-frequency daily variability in ocean conditions (24
694 hours or less) can provide refuge[30,75,76], similarly to deeper nearby habitats where vulnerable
695 sessile species can survive adverse conditions and mobile species can retreat[77,78]. The observed
696 lack of relationship between SST variability and giant kelp persistence in southern California
697 and northern Baja California may imply that giant kelp there are less limited by nutrient
698 availability and temperature extremes than giant kelp near their southern distribution limit in
699 central Baja California[79]. Therefore, it is a research priority to assess whether highly persistent
700 giant kelp provide refuge for vulnerable species to climate impacts.

701

702 The probability that the California Bight will be subject to similar marine heatwaves as extreme
703 as those in 2014-2015 in the following decades is high, and it becomes more likely every year
704 while carbon emissions continue to rise, consistent with global analysis[80]. Even if carbon
705 emissions can be reduced in the next decades, the California Bight will most likely face new
706 extreme events. Along with marine heatwaves, resource extractions are the main threats in the
707 region, which can have interactive and cumulative effects and degrade the resilience of marine
708 ecosystems[81]. Notably, when we include the potential impacts of future marine heatwaves on

709   the recovery of vulnerable species (sessile or limited mobility), our modelling results suggest

710   that even with high levels of protection, these species of commercial and ecological importance

711   will not fully recover in subsequent decades. Results from the expert-opinion survey and

712   literature review corroborate the notion that species with limited movement and with slow

713   recovery (e.g., abalone) are more vulnerable than mobile, fast-recovering species. Protecting

714   climate refugia from extractive activities might be the best available climate-adaptation

715   strategy[11] to buffer the impacts of future marine heatwaves on vulnerable species.

716

717   Coordinated conservation efforts for entire ecoregions will support climate-smart designs for

718   biodiversity conservation and fisheries management to a greater degree than networks

719   developed separately by each nation[50,71,82,83]. We linked climate-smart strategies[11,17] (e.g.,

720   assessing climate impacts and vulnerabilities, representing climate refugia, incorporating

721   connectivity, forecasting effectiveness of protection) using kelp forest ecosystems and

722   associated focal species considering future threats from climate change. Notably, the climate-

723   smart focus of our work addresses the growing need to meet post-2020 conservation targets

724   and protect 30% of the oceans by 2030 while adapting to climate change[23,24].

725

726   We developed biophysical guidelines to ensure that a transboundary network of marine

727   reserves in the California Bight would complement the existing network in California[63], by

728   adapting and refining existing best practice guidelines from California, Mexico, and other

729   regions[9,10,40]. Setting representation targets at 30% of the distribution of each habitat in each

730   biogeographic sub-region will protect ecological communities and processes in the California

731   Bight[9,10,22] and support adequate recovery for a range of focal species[84]. However, we found

732   certain habitats (e.g., seagrass, giant kelp forests) to be more vulnerable to threats and may

733   require higher levels of protection[49]. Habitat representation targets can be adjusted if robust

734   fisheries measures are in place[9,10], but will need to consider the between-country differences

735   in catch and management policies[53,85].

736

737   Many focal migratory species in the California Bight can move for hundreds to thousands of

738   kilometres[85]. Protecting these species requires a combination of marine reserves and other

739   management tools, such as gear restrictions, catch quotas, seasonal bans, or species moratoria,

740   among other measures[9,70]. Although marine reserves cannot fully protect species with long-

741   distance (>10s km) movements that migrate outside their borders, they can protect areas critical

742   for their life history (e.g., nursery, foraging, spawning)[9,10,70]. For these actions to effectively be

743   in place, protecting critical areas across the border will require increased investment in

744   international cooperation and governance[86]. Moreover, we found little information about

745   critical transboundary sites, highlighting the need to develop research programs and

746   collaborations to generate this information. Notably, setting adequate protection and

747   management strategies will also require a better understanding of the populations of focal

748   migratory species within and across borders in the California Bight[85].

749

750   Our findings that transboundary connectivity is more important for species with longer PLD

751   agree with empirical data on the genetic structure of these species. For example, studies found

752   strong genetic differentiation for neutral genetic markers for species with short dispersal

753   distances, such as giant kelp[87] and pink abalone[73], between southern California and populations

754   from Baja California. In contrast, studies found lack of genetic structure for California

755   Sheephead between California and Baja California[88] and purple and red sea urchin from

756   Washington to southern California[89,90]. To meet international commitments[24], fully protected

757   areas will need expansion in California (currently ~10%) and in Baja California (currently <

758   1%). This provides an opportunity for both regions to coordinate efforts and maximize

759   conservation and fisheries benefits based on biophysical principles and modelling of larval

760   dispersal.

761

762   We recommend establishing marine reserves in areas where threats can be managed effectively

763   within reserves in the California Bight. Areas with high cumulative impacts (e.g., coastal

764   development, pollution, runoffs) are likely degrading ecosystem health, fisheries productivity,

765   and resilience to climate change (reviewed by Green, et al. [9]), preventing marine reserves from

766   producing the expected benefits[9,10]. However, these are general recommendations since

767   reducing overfishing inside marine reserves, combined with restoration actions and other

768   management strategies that directly address those threats, can build resilience[3,5,7] to threats not

769   directly managed by marine reserves and contribute to the recovery of degraded areas.

770   Therefore, the decision to protect or restore highly threatened areas requires cost-benefit

771   analysis on a site-specific basis[91] and other considerations such as ecological connectivity.

772

773   Prior to our effort, there were no comprehensive high-resolution maps of small-scale fisheries

774   catch in the Peninsula of Baja California, limiting our capacity to conduct cost-effective marine

775   spatial planning. Although information on recreational fishing existed[53], we updated and

776   extended the mapping to cover the three sub-regions in Baja California. These maps, combined
777   with existing data from socioeconomic activities from California, provides the unique
778   opportunity to guide marine spatial planning and identify priority areas for conservation that
779   meet our biophysical design principles while minimizing the potential conflict from
780   implementation to stakeholders' activities[48].

781

782   We note that our findings are subject to some caveats. We simulated passive larval dispersal
783   and did not consider other biological traits (e.g., larval mortality, behavior, and settlement
784   competency)[92]. However, we did tailor our model to the availability of giant kelp. Successful
785   recruitment of larvae is linked to the quality and suitability of available habitats[22,93,94].
786   Although our climate scenario is a realistic expectation if carbon emissions are not mitigated
787   in the 21st century[61] (decrease in PLD following a 3°C warming tailored to the availability of
788   only highly persistent giant kelp habitat), it is an extreme scenario. Thus, if our model was to
789   be used for identifying climate-smart networks of marine reserves, we recommend adjusting
790   the model to consider multiple emission scenarios (e.g., SSP1-2.6, SSP2-4.5, SSP5-8.5) based
791   on projected multi-model ensemble means for the California Bight.

792

793   While it is currently unfeasible to obtain information for all habitats and species in a region,
794   we chose giant kelp forests because of existing information on their persistence[20] and the
795   availability of long-term information for associated focal species[37]. Also, kelp forests are
796   threatened by marine heatwaves globally[35,95], acting as early indicators of climate-change
797   impacts to other ecosystems. However, as more information becomes available, similar
798   assessments for other vulnerable ecosystems, such estuaries, and rocky intertidal habitats
799   should be conducted. Although our analysis found no positive correlation between SST
800   variability and persistence of giant kelp forests for southern California and northern Baja
801   California, SST variability may still be a good proxy for climate refugia for these regions, but
802   anthropogenic activities may be eroding the persistence of giant kelp forests and masking the
803   potential relationship. For example, many of the kelp forests in mainland southern California
804   and northern Baja California experience high human impacts (e.g., run-offs, overfishing), while
805   central Baja California is sparsely populated and less impacted. Also, our analysis compared
806   SST variability with giant kelp persistence, and we did not include other species vulnerable to
807   climate change such as sessile invertebrates. Therefore, it is a research priority to understand
808   the drivers and synergies controlling species and habitat resilience to extreme events.

809

810   We also acknowledge caveats in our recovery model which did not include the potential benefit

811   of larval dispersal from climate refugia, where populations may be less impacted by marine

812   heatwaves. Also, we simulated the loss of biomass based on empirical data of the impacts of

813   the 2014-2015 marine heatwaves from giant kelp forest monitoring surveys[37] at shallow depths

814   (typically less than 15 m). Thus, our results need to be taken with due care, as some deeper

815   populations of invertebrate and sessile (or limited mobility) species might be less impacted[77,78],

816   survive, and support the replenishment of nearby affected areas. Finally, we used catch-only

817   methods to estimate population parameters and fishing mortality. Recent work has shown that

818   these methods may produce biased estimates[96], however our parameter estimates are similar to

819   those reported in other studies[97]. Regardless of the potential limitations, our results are

820   consistent with other work that suggest the need to increase the coverage of marine reserves to

821   rebuild marine life, including protection of climate-refugia[5,98-100]. Notably, other management

822   actions such as fishing moratoria, catch quotas, and repopulation of vulnerable species will be

823   needed to complement marine reserves.

824

825   Fully protecting 30%[24] of the California Bight by 2030 will require national and transboundary

826   policies and political will. Importantly, there is a need to integrate biophysical guidelines with

827   socio-economic and governance principles to produce effective, equitable and robust policies

828   and practices[42,101] while considering cultural and management differences across the border.

829   Unfortunately, despite the scientific capacity and established collaboration among institutions

830   and research groups between the USA and Mexico[31], existing political cooperation matches

831   neither the level of ecological connectivity observed[85], nor the needs identified under current

832   and projected climate impacts. Urgent, coordinated binational action needs to be taken to

833   preserve fisheries and conserve biodiversity in the region. It is a grand challenge, given the

834   strong asymmetries in economic wellbeing, governance, implementation capacity, resources,

835   and language, among other barriers.

836

837   Marine reserves in Baja California will require co-management that includes local fishing

838   cooperatives, complemented with other effective management strategies[42]. Some well-

839   managed fishing concessions may need less protection, and in some cases, coordination with

840   improved management and restoration actions may achieve biodiversity, fisheries, and climate-

841   adaptation objectives. On the other hand, California has the legislative infrastructure for

842   expanding its existing network of marine reserves and the experience in marine spatial planning

843   to create synergies across the border. This collaborative and socio-ecological setting creates a

844   unique opportunity for the California Bight to implement transboundary and climate-smart

845   marine spatial planning and influence marine conservation worldwide.

846

847   Here, we provide a case study that links biophysical design principles for transboundary

848   climate-smart networks of marine reserves. Our analysis suggests that achieving climate-smart

849   status requires integrating multiple adaptation strategies such as protecting climate refugia and

850   considering the implications of climate change for ecological connectivity and protection

851   efficiency. Given that many marine ecoregions worldwide are shared by nations[43], our

852   biophysical guidelines and recommendations can inform other regions' aspirations to achieve

853   post-2020[23,24] protection targets. These regions will need to develop biophysical dispersal

854   models to understand patterns of connectivity, identify potential climate refugia and levels of

855   protection needed to maximize biodiversity, fisheries, and climate adaptation outcomes.

856   Notably, to design climate-smart networks of marine reserves, they will need to coordinate

857   research programs and policies while considering cultural, governance, and management

858   differences across borders.

859

860   **Acknowledgements**

861

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876

877 **Table 1.** Biophysical guidelines and transboundary and climate-smart considerations for the

878 design of networks of marine reserves in the Southern California Bight, compiled, adapted, and

879 refined from California, Mexico, and other regions[9,10,40].

880

Biophysical guidelines	Transboundary and climate-smart considerations for application
Habitat representation and replication	
1. Represent at least 30% of each habitat type in each biogeographic sub-region. Habitat representation targets should consider habitat rarity and vulnerability, and fishing pressure and management outside reserves	Habitat types include intertidal, subtidal, biogenic (e.g., kelp forests, seagrass beds), and deep-sea habitats. The four biogeographic sub-regions include southern California, northern Baja California, central Baja California, and Guadalupe Island[46]. Ensure representing the variation in biodiversity across geographic gradients. Consider higher levels of protection for vulnerable habitats (e.g., rocky intertidal, estuaries), rare habitats (e.g., eelgrass beds, island habitats), and overfished or poorly managed habitats[9,10] for each sub-region. Consider differences in fisheries management across borders[85].
2. Represent at least three examples of each habitat type in widely separated reserves to reduce the chance that they will all be impacted by a large-scale disturbance	Replicate habitats should meet a minimum size required to encompass 90% of the biodiversity associated with each habitat[40] (Supplementary Table 6).
3. Represent and replicate climate-refugia habitats in each biogeographic sub-region	Adjust and increase representation targets for each biogeographic sub-region to protect highly persistent giant kelp[20]. Represent deeper habitats used by vulnerable species (i.e., sessile species) or areas with high temperature variability as these populations might support recovery of nearby populations after an extreme event[30,77,78].
4. Represent habitats used by focal species for ecosystem resilience	Represent habitat attributes (e.g., steepness, rugosity) known to favour the biomass recovery of species[102] that enhance the resilience of ecosystems to adapt to climate change[103]. Examples include predatory species that stabilize sea urchin populations, allowing giant kelp to persist[7,103].
Protect critical and unique areas	
5. Protect critical areas in the life history of focal species in marine reserves	Critical areas include spawning, nesting, or breeding areas, nursery habitats (e.g., estuaries and seagrass beds), resting and feeding areas[9,10]. If necessary, combine protection with other measures such as temporal fisheries closures during spawning season or regulations to protect migratory species like cetaceans and large sharks. Coordinate binational protection and other measures when focal migratory species use transboundary critical and unique areas, particularly near the USA/Mexico border where there is higher transboundary movement.
6. Protect areas with special and unique biodiversity in marine reserves	Protect special and unique features including areas with remaining populations of rare species, protected species, unique habitats, healthy habitats, high species richness, and endemic species[9,10].
Incorporate connectivity	
7. Consider movement patterns of adult and juvenile organisms when determining the size of marine reserves. They should be more than twice the size of the home range of species and consider other management tools for species with long-distance movements (>10 km).	Base the size for protection on the habitats that species use, rather than the overall size of the marine reserve[9,10,70]. Ensure marine reserves extend from intertidal (minimum linear extension of 5 km) to deeper habitats (will vary depending on the slope)[40]. Species movement can vary from short distances of 100 m for abalone to long distances of 100 to 1000 km for sharks and tuna species[9,10,40].
8. Consider larval dispersal to replenish populations within marine reserves and in adjacent areas, enhance metapopulation persistence, and support fisheries in adjacent areas.	There is strong transboundary connectivity in the region with larval dispersal patterns driven by seasonal north-south currents, which reverse twice a year. Marine reserves should be separated by no more than 25-100 km to ensure connectivity of species with short dispersal distances (e.g., abalone).

9. Consider large marine reserves for isolated areas to support larval self-replenishment	Species with short dispersal distances require binational coordination near the USA/Mexico border, whereas species with long dispersal distances (e.g., lobster), require coordination for the entire region. Consider larger self-sustained marine reserves[72] when an area is isolated. Isolation can be a function of distance to nearby suitable habitat or short planktonic larval duration for certain focal species, like abalone and giant kelp. There are isolated areas in the entire region, especially in central Baja California from 28-29°N.
10. Consider changes in larval duration and habitat availability due to changes in climate and ocean chemistry.	
11. Facilitate range shifts of species driven by climate change	Simulations suggest that a decrease in planktonic larval duration and giant kelp availability due to climate change will weaken the number and geographic scale connections, decreasing transboundary connectivity and increasing isolation. The Channel Islands and areas in central Baja California are expected to become more isolated. Distribute reserves across geographic, latitudinal and depth gradients to facilitate the latitudinal and depth shifts of species in response to climate change.

Allow time for recovery

12. Establish marine reserves for the long-term (>25 years), preferably permanently, to allow populations of focal species to recover and replenish adjacent areas and maintain ecosystem functioning and resilience	Populations of focal species recover at different rates in marine reserves and adjacent areas in the California Bight[96]. Populations of some focal species, such as sea-cucumber, are likely to recover within a decade, while others, like abalone, will take over 40 years of protection. When possible, establish permanent marine reserves to allow full population recovery and maximum biomass export to adjacent areas. Establish permanent marine reserves near the USA/Mexico border where there is strong transboundary connectivity to maximize national conservation efforts.
13. Short-term or seasonal closures should be used in addition to, rather than instead of, permanent marine reserves.	Short term (<5-10 years) closures have limited benefits for enhancing fisheries, conserving biodiversity, or building ecosystem resilience. The exception is seasonal closures that can be used to protect critical areas (e.g., spawning or nursery areas), which can be very important to protect or restore populations of focal fisheries species.
14. Establish permanent and increase the coverage of marine reserves when the objective is to protect focal species that are sensitive to marine heatwaves	Some species that are vulnerable to marine heatwaves (sessile or low-mobility species) will likely not reach exploited equilibrium in the next 50 years (at least for shallow populations), which could be achieved only by permanent reserves and increase the area of protection. This is particularly important in Baja California, where average temperatures are higher.

Minimize and avoid local threats

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15. Establish marine reserves in areas with lower levels of cumulative threats for each biogeographic region	Consider the cumulative effects of multiple threats in each location and distinguish among threats that marine reserves cannot directly abate[51] ─ but can build resilience to[19] ─ and threats marine reserves can directly abate. Threats not directly abated by marine reserves include climate and land-based stressors. While in southern California and northern Baja California areas with higher threats are mostly located near urban areas, in central Baja California and Guadalupe Island they are mostly found off the coast.
16. Preferably, establish marine reserves in areas where threats can be managed effectively within reserves	Threats directly abated by marine reserves are those related to extractive uses, such as commercial and recreational fishing and aquaculture activities.

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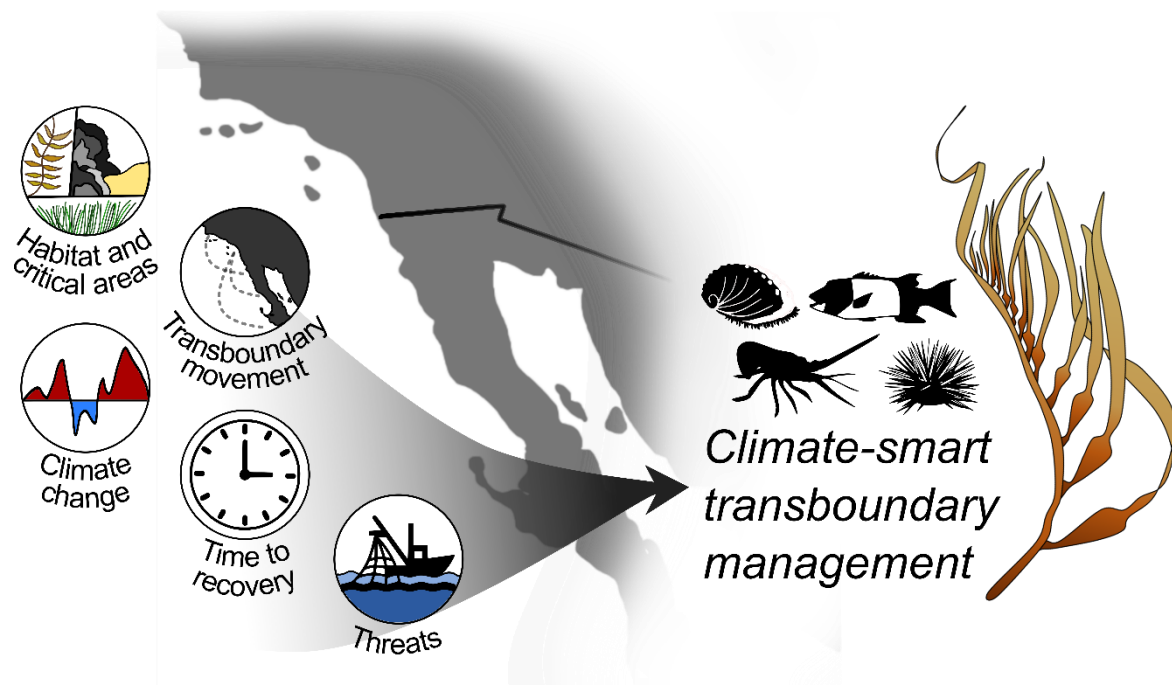
Fig. 1 Graphical framework. Represents the biophysical principles used to develop spatial maps and analyses based on giant kelp forest ecosystems and associated species for transboundary networks of climate-smart marine reserves in the California Bight.
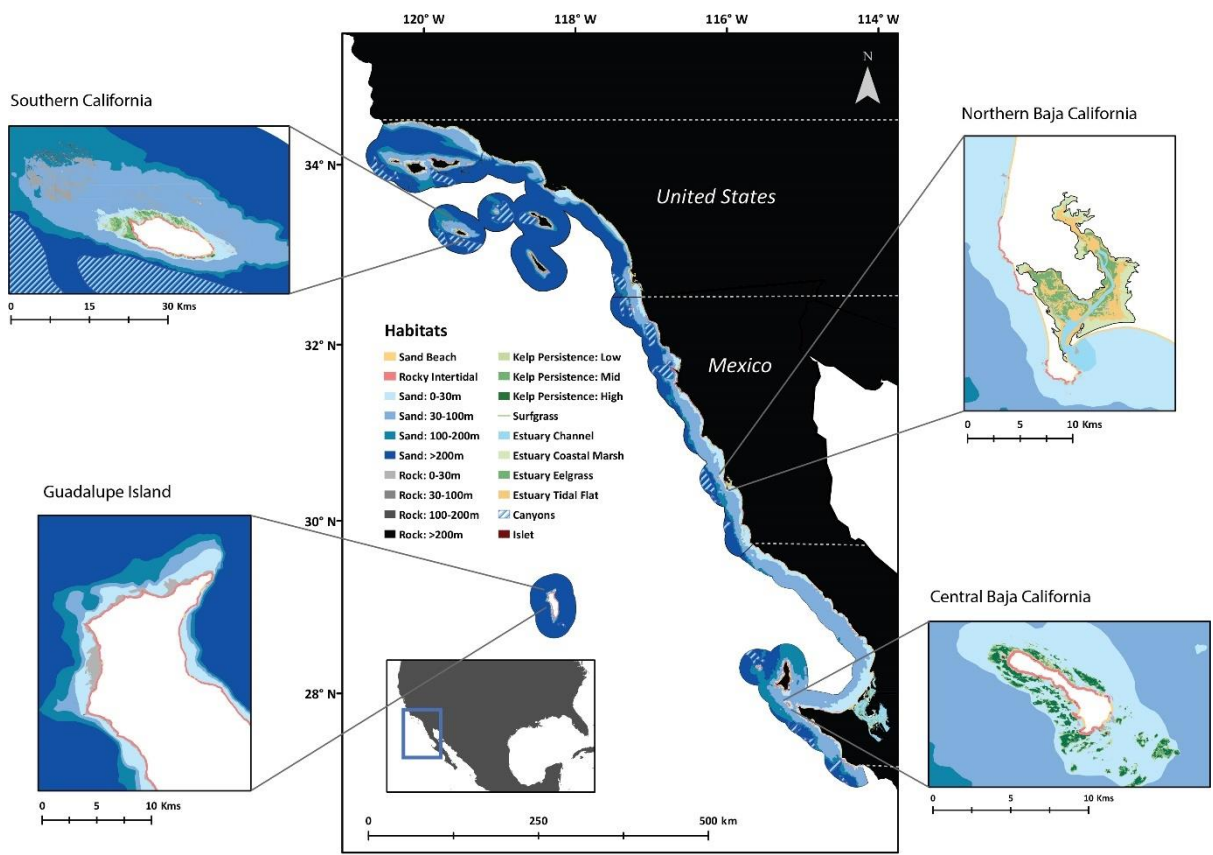
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Fig. 2 Distribution of marine habitats for the Southern California Bight. Inserts represent examples of intertidal, subtidal, estuary, and deep-sea habitats for each sub region. Southern California for San Nicolas Island with giant kelp forests, subtidal shallow and deeper habitats, northern Baja California for San Quintin Estuary, central Baja California for Isla Natividad intertidal and shallow habitats, and for Guadalupe Island intertidal and subtidal habitats at different depths. Dashed white lines represent the limits of each sub-region.
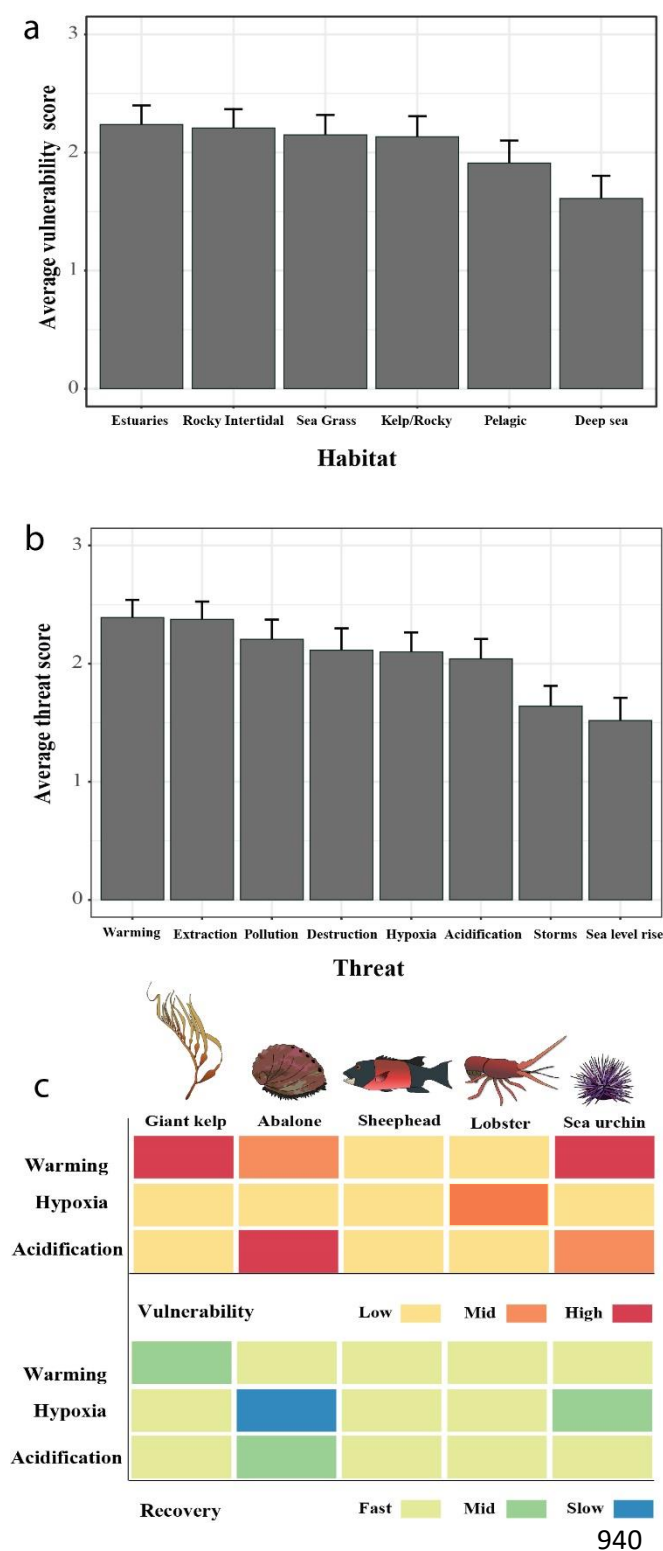
Fig 3. Vulnerability of habitats and focal species to human threats. Average score ($\pm$ 95% confidence interval) for **a** vulnerability of marine habitats to human threats and **b** threat of individual stressors across marine ecosystems based on expert opinion surveys. **c** Ranking of focal species vulnerability to climate threats and their recovery rates based on scientific literature. Images credit: Katherine E. Dale.

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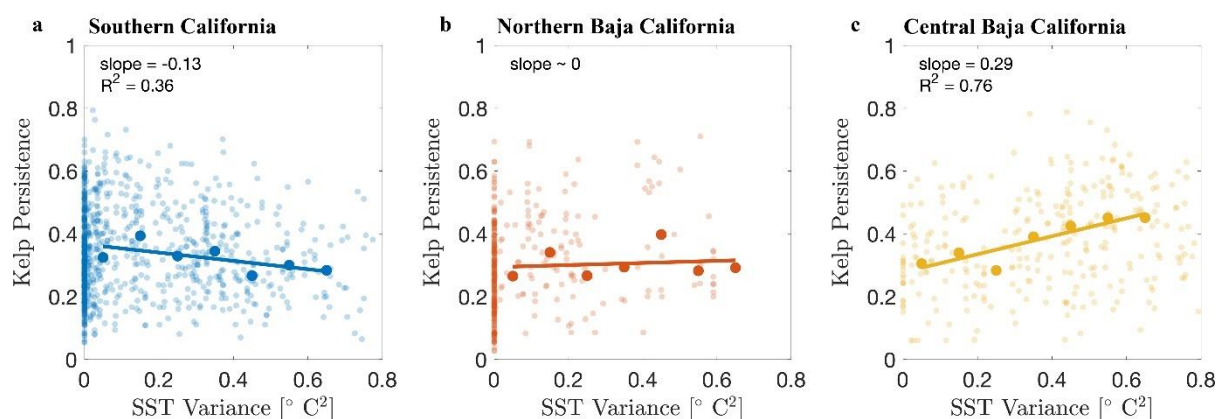
948 **Fig 4. Sea surface temperature variability as a proxy for climate-change refugia.**
949 Relationship between giant kelp persistence and SST variability for **a** southern California, **b**
950 northern Baja California, and **c** central Baja California. Raw data (light circles), binned-
951 averaged values (large circles), and best fit to bin-averaged data (line) are shown.

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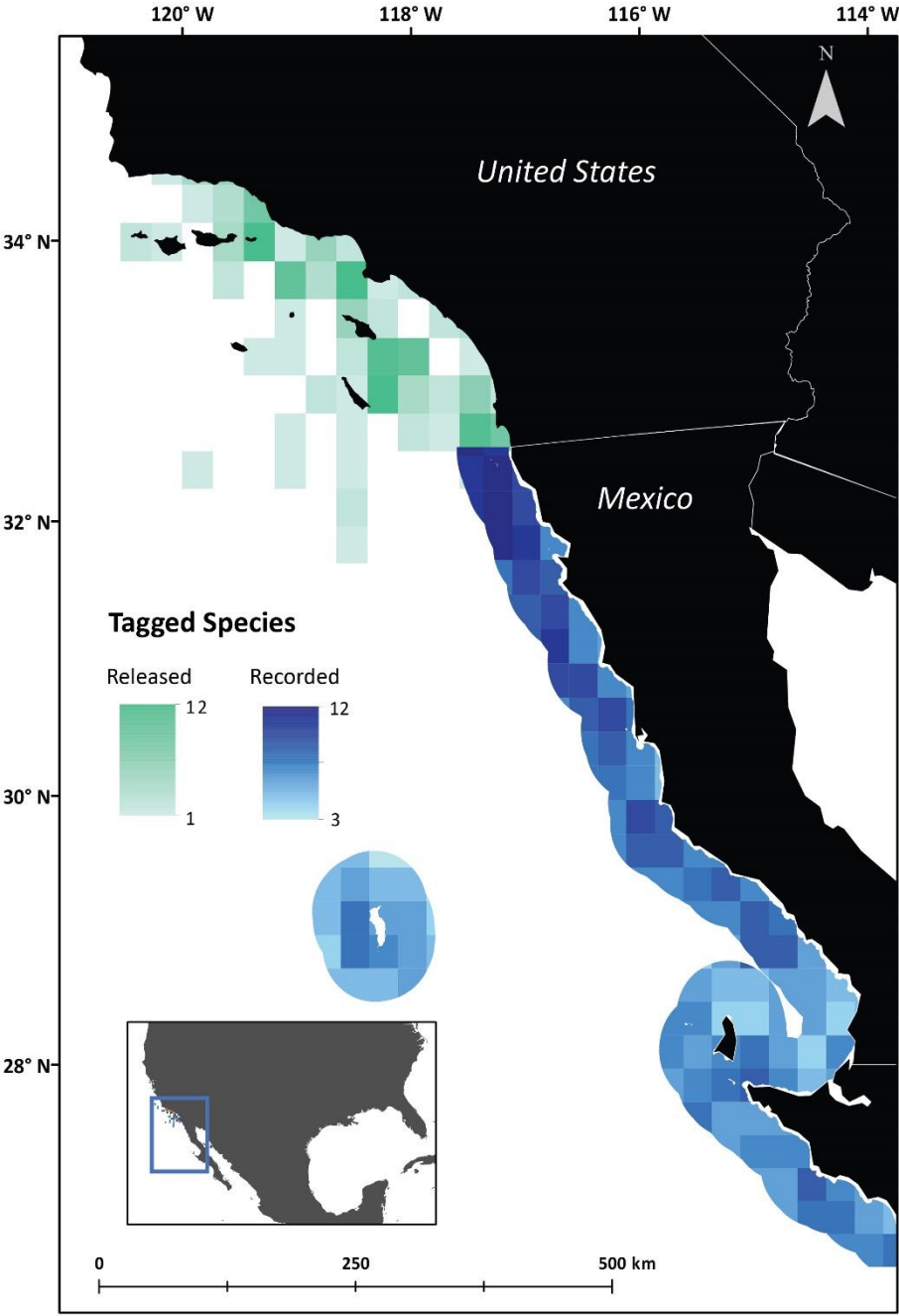
Fig 5. Transboundary connectivity of species moving from California to the Peninsula of Baja California. Green colors represent the number of studies that released species in southern California, and blue colors the number of studies that record species in Baja California. We consider blue quadrants with higher number of studies as quadrants with higher transboundary connectivity.
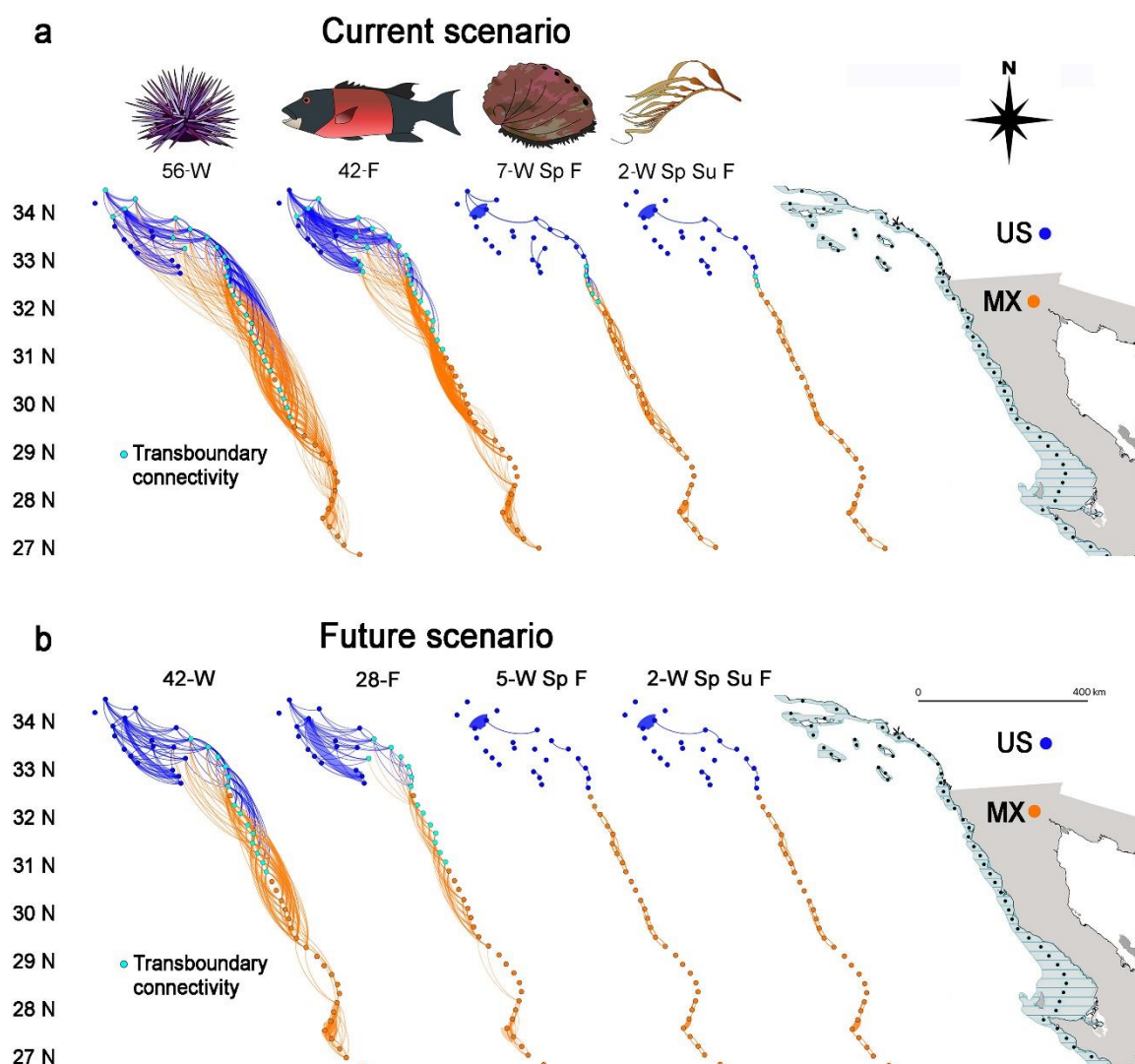
Fig 6. Networks of larval connectivity in the California Bight. Spatial networks of modelled larval dispersal for focal species (from left to right, sea urchin, California Sheephead, abalone, and giant kelp) between nodes delimited by the 200-m isobath. Connectivity polygons are shown on the far right. Line width represents the probability of larval dispersal (thicker lines have higher probability) and line colour the country of origin. Blue-coloured nodes and lines represent the USA and orange Mexico as larval origins, respectively. Sites involved in transboundary connectivity are highlighted in light blue color. For each focal species, we indicate the planktonic larval duration (PLD, in days), followed by a letter representing the spawning season (Spring = Sp, Summer = Su, Fall = F, Winter = W, See Supplementary Table 4). Images credit: Katherine E. Dale. **a** Current scenario, considering the PLD reported in the literature and the total area with giant kelp found within each polygon. **b** Future scenario, accounting for reduction of PLD and giant kelp habitat due to climate change. Sites involved in transboundary connectivity are highlighted in light blue color.
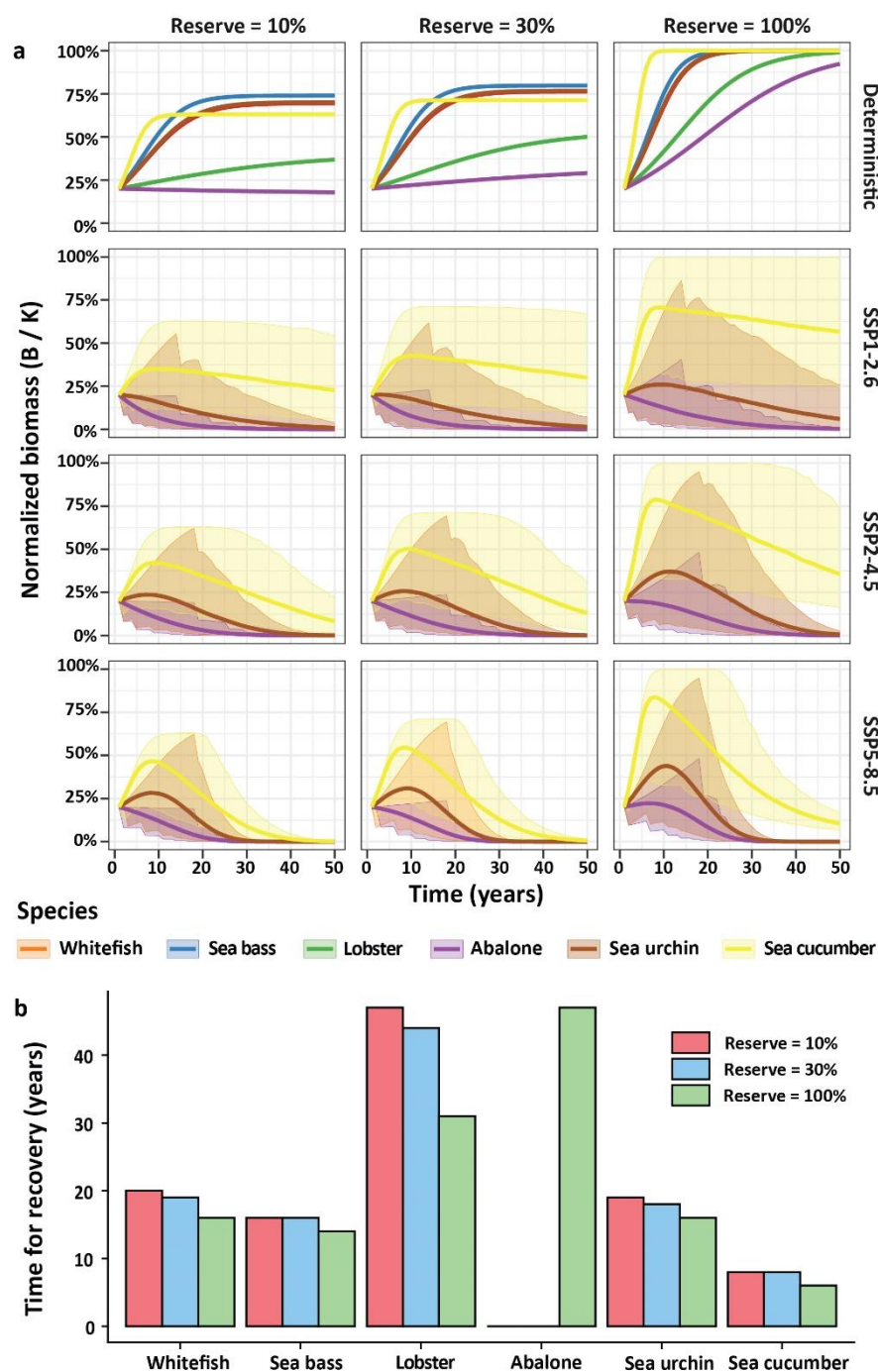
Fig 7. Simulated time to recovery for focal species under three protection scenarios in the California Bight. Recovery pathway of six species (mean ± standard deviation), **a** for scenarios of protection (10, 30, or 100%) and models. The first row of panel shows the deterministic model for all six species. Rows 2-4 show results from the stochastic models for vulnerable species (abalone, sea urchin, sea cucumber) to marine heatwaves under three climate scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5). **b** Time to reach 90% of equilibrium biomass for each of the seven species across three protection scenarios. Missing bars indicate no recovery within the simulated 50 years.
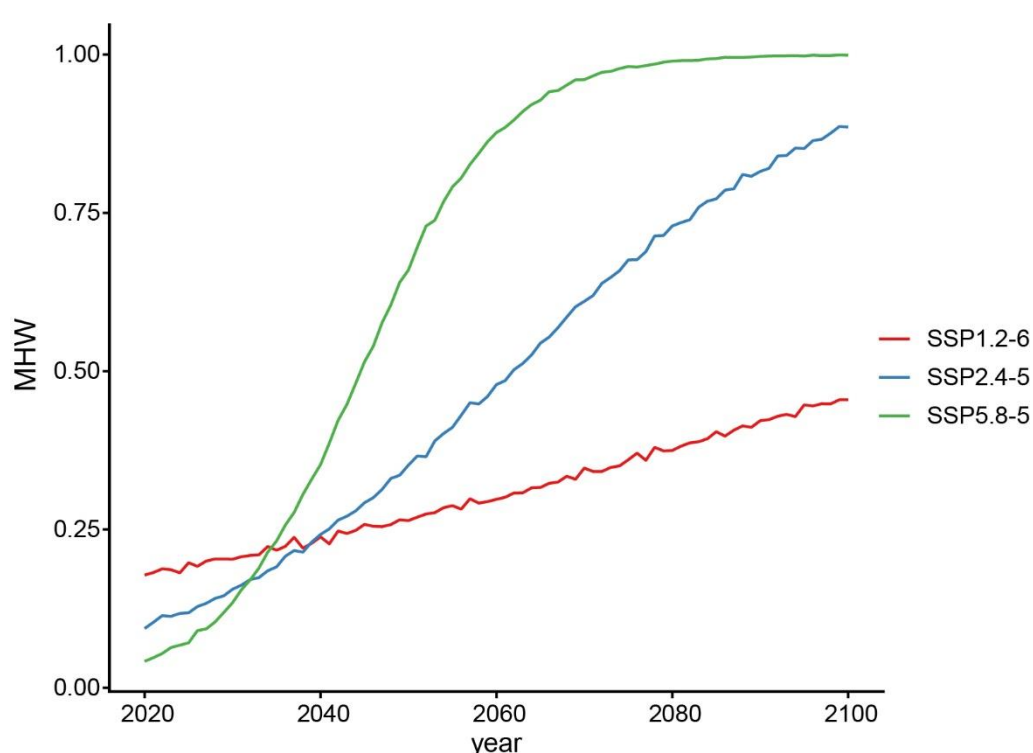
Fig. 8.- Probability of projected marine heatwaves for 2020-2100. Marine heatwaves under climate scenarios SSP1-2.6, 2-4.5, and 5-8.5 that match or exceed the cumulative intensities registered in 2014-2015 in the California Bight.
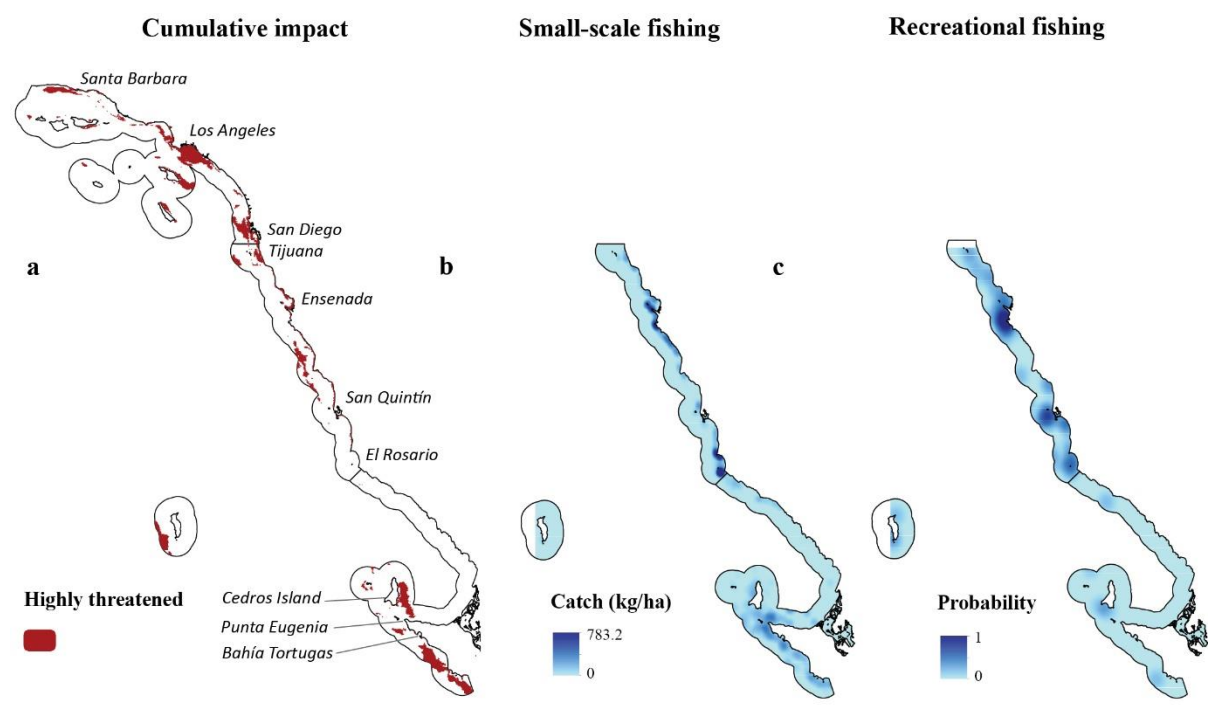
Fig. 9.- Distribution of threats and fishing in the California Bight. Maps of **a** highly threatened areas (top 10% of cumulative impacts of 13 threats), **b** cumulative catch for six small-scale fisheries and **c** probability of recreational fishing in a 100-m grid square in the three regions of Baja California.

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