Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity

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Classic marine ecological paradigms view kelp forests as inherently temperate-boreal phenomena replaced by coral reefs in tropical waters. These paradigms hinge on the notion that tropical surface waters are too warm and nutrient-depleted to support kelp productivity and survival. We present a synthetic oceanographic and ecophysiological model that accurately identifies all known kelp populations and, by using the same criteria, predicts the existence of >23,500 km² unexplored submerged (30- to 200-m depth) tropical kelp habitats. Predicted tropical kelp habitats were most probable in regions where bathymetry and upwelling resulted in mixed-layer shoaling above the depth of minimum annual irradiance dose for kelp survival. Using model predictions, we discovered extensive new deep-water *Eisenia galapagensis* populations in the Galápagos that increased in abundance with increasing depth to >60 m, complete with cold-water flora and fauna of temperate affinities. The predictability of deep-water kelp habitat and the discovery of expansive deep-water Galápagos kelp forests validate the extent of deep-water tropical kelp refugia, with potential implications for regional productivity and biodiversity, tropical food web ecology, and understanding of the resilience of tropical marine systems to climate change.

climate | oceanography | evolution | biogeography

Coral reefs are tropical hotspots of biodiversity and productivity, and their vulnerability to environmental change has prompted an acceleration of global conservation and management activities (1–3). The ecology and conservation of tropical kelp forests, however, have been largely ignored because of the rarity of tropical kelp collections and the restriction of the few described taxa to deep water. Deep-water tropical kelp forests have been viewed as rare relicts of expansive shallow-water distributions that existed during cooler oceanographic climates (4) and, thus, may be vulnerable to further sea-surface warming (5). Kelp forests represent some of the world's most productive and dynamic ecosystems (6), facilitating regional diversity through a variety of trophic and habitat associations (7). At a global scale, variability in kelp distribution patterns can drive subsequent variability in coastal ecology and human economies. Yet despite their worldwide importance, kelp-based ecosystems are considered shallow-water temperate-boreal phenomena (4, 8) because of their physiological requirements for high-nutrient concentrations and low temperatures in the narrow euphotic zones of temperate-boreal regions. Surface irradiances in the tropics typically exceed levels of saturation for kelp photosynthesis, but nutrient and temperature conditions within the shallow mixed layer are inadequate for kelp survival (4). Consequently, surface-dwelling kelp forests have never been described for tropical waters.

We coupled ecophysiological data on kelp with a global surface-to-seafloor geospatial analysis of oceanographic data to test the alternative hypothesis that tropical kelp habitats are abundant and occupy expansive deep-water refugia at the base of the euphotic zone, where enough light and nutrients are available at the sea floor to sustain kelp growth and survival. The distribution of extratropical kelp populations can be described as the intersection of a set of ecophysiological constraints with physical and chemical properties of the surface and shallow sublittoral ocean (4). This same set of environmental conditions suitable for high-latitude, surface-dwelling kelp subsistence may be encountered at greater depths in the tropics, where a deeper euphotic zone exists (9) in a manner analogous to equatorward trends in high-altitude treelines (10) and isothermal submergence of sessile marine invertebrates (11, 12). Therefore, refugia refer to habitable areas below uninhabitable surface waters. The existence and distribution of these deep refugia for temperate kelp species has not been tested with oceanographic data or field exploration.

The primary ecological and physiological requirements of kelp populations include available substrate, high nutrients (correlated with cool-water temperatures), and a minimum annual irradiance dose of >50 E·m^{-2} (13). At mid- to high latitudes, benthic irradiance is the primary limiting factor because high-nutrient concentrations fuel coastal productivity, which increases light extinction coefficients, effectively restricting kelp to littoral and sublittoral depths of <45 m (4, 14). At low latitudes, however, oligotrophic surface waters allow for high water clarity, often resulting in a euphotic zone that exceeds the depth of the mixed layer (9). The depth of the mixed layer (and associated nutricline) (see *Materials and Methods*) above the illuminated substrate may, therefore, be the best predictor of regions that could support tropical kelp populations, facilitating a deep-water kelp refuge below more conventional shallow-water tropical marine habitats (e.g., coral reefs). In the absence of this deep-water refuge hypothesis, the few existing specimens of deep tropical kelp taxa [*Eisenia galapagensis* (15), *Laminaria brasiliensis* (16), and *L. abyssalis* (16)] have been considered rare, anomalous relicts of shallow-water populations that existed during glacial periods of cooler oceanographic climate (4).

The recent development of global remote-sensing platforms and oceanographic data repositories permits rigorous testing of our tropical deep-water kelp refuge hypothesis through the use of global analysis of high-resolution 3D oceanographic data sets. We combined satellite-derived estimates of global sea-surface photosynthetically active radiation (PAR), optical depth, and bathymetry with estimates of climatological mixed-layer depth to predict the location of illuminated substrate beneath the mixed layer between the tropics of Cancer (23.5°N) and Capricorn (23.5°S) (see *Materials and Methods*). Our model predicted extensive potential deep-water kelp habitats throughout the
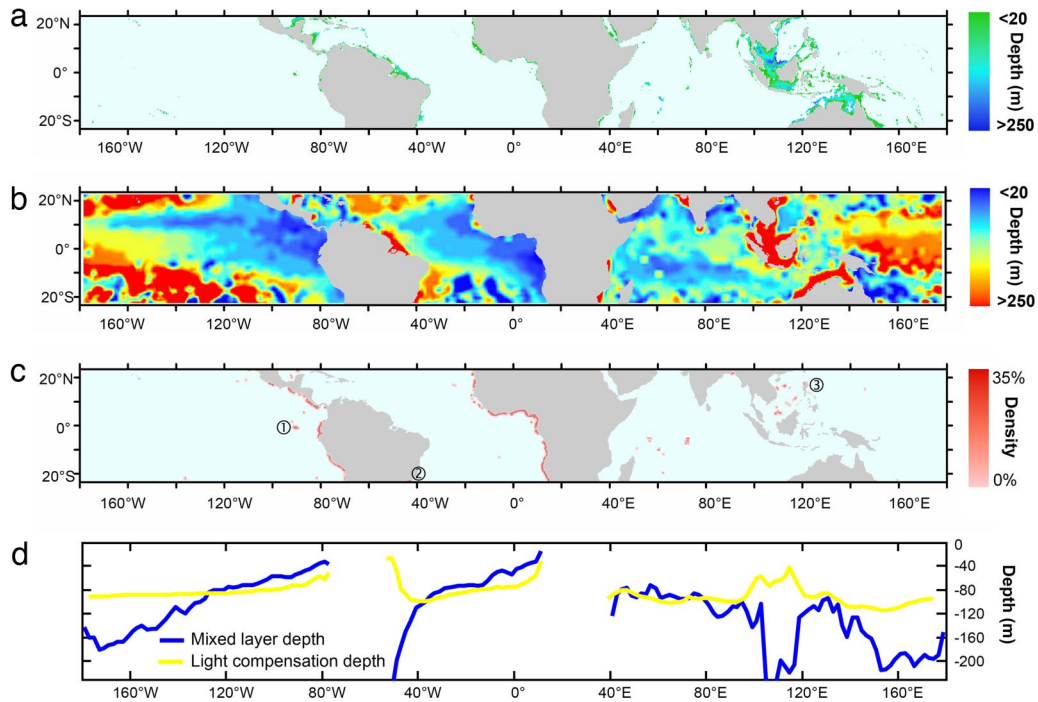
Fig. 1. Components of deep-water kelp refuge model for tropical regions worldwide. (*a*) Distribution of illuminated benthos receiving irradiance above kelp photosynthetic compensation point. (*b*) Mixed-layer depth. (*c*) Predicted location of deep-water tropical kelp populations (shading indicates frequency of predicted kelp habitats within 50-km radius). Numbers are locations of known deep-water tropical kelp taxa: 1, *E. galapgensis*; 2, *L. brasiliensis* and *L. abyssalis*; and 3, *L. philippinensis*. (*d*) Equatorial cross-section (averaged between 5°N and 5°S latitudes) showing the mixed-layer depth relative to the kelp photosynthetic compensation point.

tropics, including >23,500 km^2 of unexplored deep-water tropical kelp habitats at minimum depths of 25 to 107 m and maximum depths of 100 to 236 m depending on the ocean basin (Fig. 1 *a–c* and Table 1). The largest and shallowest predicted areas occurred in the eastern regions of the Pacific and Atlantic Oceans. Here the eastward shoaling of the mixed layer (thermocline) to 20–90 m at the equator (Fig. 1*d*) intersected the steep bathymetries of volcanic islands and the active margins of Central and South America and Central Africa. The model also predicted more limited tropical kelp habitats in the western regions of the Pacific, Atlantic, and Indian Oceans. Here the extremely deep kelp light-compensation depth surpassed the relatively deepened mixed layer (90–150 m) (Fig. 1*d*), predicting deep tropical kelp habitats in areas of both high- and low-bathymetric relief. The eastern aspect of the model captured the known distribution of *E. galapagensis* in the Galápagos Archipelago (15), whereas the western aspect encompassed collection locations of other known tropical kelp specimens (*L. brasiliensis* and *L. abyssalis* off Cabo Frio in Brazil) (16). Upon completing our analysis, we discovered a little-known reference to another

deep-water kelp species, *L. philippinensis* (17). The few *L. philippinensis* specimens known to science were collected from precisely where our model predicted deep-water kelp should occur in the Philippine Sea (Fig. 1*c*). These general east–west patterns were driven largely by the negative effects of equatorial upwelling on the depth of the mixed layer and water clarity (Fig. 1*d*), suggesting a tight linkage between deep tropical kelp distributions and global oceanographic climate.

We empirically tested the deep kelp model predictions on a research cruise to the Galápagos Archipelago in January 2007. This location was chosen because of the large area of predicted kelp distribution (427 km^2) and the broad and relatively shallow depth range of the predicted deep kelp refuge (40–80 m). Limited observations of *E. galapagensis* have occurred since its original description in 1945 (15), with observations of some specimens at only a single location after the 1982–1983 ENSO event (G. J. Edgar, K. A. Miller, and L.E.G., unpublished data). Our model, however, predicted extensive deep kelp populations at various locations in the archipelago (Fig. 2*a*). The largest predicted deep-water refuge occurred along the west coast of Isla

Table 1. Sizes and depth statistics of predicted deep-water tropical kelp habitats

Basin	Area, km^2	Mean depth, m	Min depth, m	Max depth, m
Eastern Atlantic	13,889	56.0	31	111
Western Atlantic	2,791	51.5	30	100
Eastern Pacific	5,008	51.7	25	100
Western Pacific	93	141.1	107	174
Indo-Pacific	895	93.1	76	104
Indian	828	116.9	74	236
Total (mean)	23,504	85.1	57.2	137.5

Equatorward extensions of shallow-water temperate kelp populations into the tropics have been excluded from tabulation of deep-water statistics, but are represented in Fig. 1.
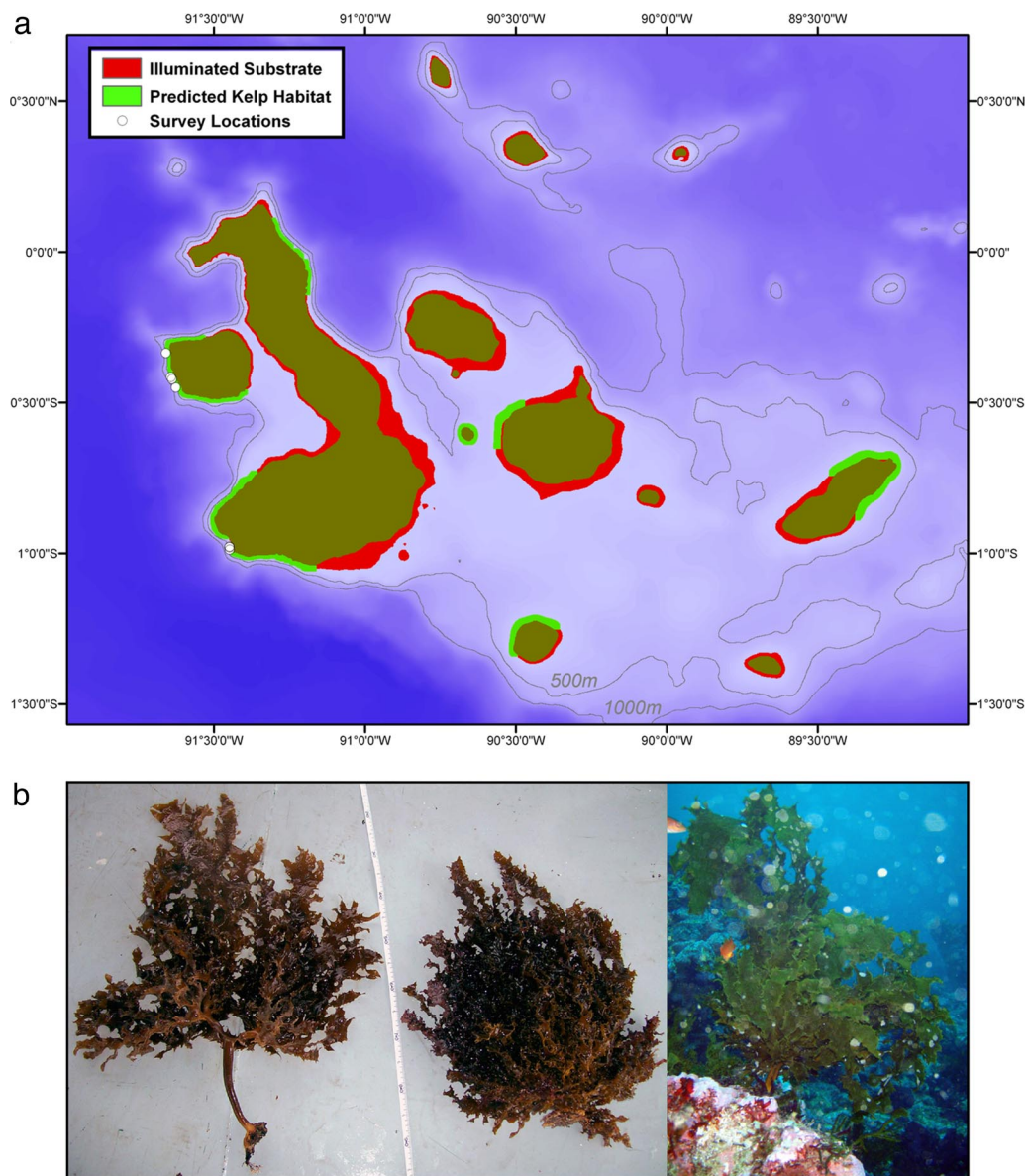
Fig. 2. Empirical support of deep-water kelp refugia model in Galápagos Archipelago. (*a*) Map of illuminated substrate (red) and predicted deep-water kelp distribution (green) with locations of newly discovered (open circles) *E. galapagensis* populations. (*b*) Deep-water (60 m) (*Left*), shallow-water (10 m) (*Center*), and underwater (*Right*) *E. galapagensis* thalli. Note the lengthened stipe in the deep-water thallus that was characteristic of sporophytes found >20 m depth. [Photograph in *b Right* is reproduced with permission from S. Connell (University of Adelaide, Adelaide, Australia) (Copyright 2007).]

Fernandina and the southwest coast of Isla Isabela, where the Equatorial Undercurrent reaches its shallowest depth and impinges directly on the steep Galápagos shoreline. Using SCUBA, we observed abundant *E. galapagensis* recruits, juveniles, and adults at all eight sampled locations (Fig. 2) (see *Materials and Methods*), with densities of ≤12 m^{-2} (comparable to temperate *E. arborea* densities in California) (18). Scattered individuals of *E. galapagensis* were observed as shallow as 10–20 m, and this shallow limit varied according to the mixed-layer depth determined by *in situ* conductivity–temperature–depth sampling. The deep limit of *E. galapagensis* could not be ascertained, but individuals increased in frequency up to our 60-m SCUBA detection limits at all sampled locations. It is unknown how far below 60 m the *E. galapagensis* populations extended at these sites. Nevertheless, individuals at 50- to 60-m depths were denser, larger, and healthier than shallower individuals observed at each sample location (Fig. 2*b*), validating the hypothesis of a

deep-water kelp refuge. Additionally, within this refuge, we observed a high abundance of a temperate macroalgal species previously unknown for the Galápagos, *Desmarestia ligulata*, suggesting that our predictive model may be applicable to cold-water macroalgae other than kelp.

The existence of a deep-water refuge for tropical kelp has profound biogeographical and evolutionary consequences. First, deep-water kelp refugia help reconcile unknown origins in the present-day distribution of surface-dwelling kelp (4). Specifically, the distribution of the kelp genera *Eisenia*, *Laminaria*, *Lessonia*, and *Ecklonia* in the southern hemisphere cannot be explained by the surface-drifting hypothesis previously developed for the giant kelp *Macrocystis* (11, 19, 20) because only *Ecklonia maxima* (endemic to South Africa) has floating thalli. However, permanent deep-water populations of *Eisenia*, *Laminaria*, and *Ecklonia*, which span the tropics, may connect northern and southern hemisphere populations along both the eastern

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and western boundaries of the Pacific and Atlantic Oceans, potentially explaining the origin of endemic kelp systems in Chile, South Africa, Australia, and New Zealand (4). Second, east–west differences in deep-water tropical kelp genera are conspicuous. The eastern tropical Pacific contains *Eisenia* only, one of the most derived genera in the kelp order Laminariales (21). The western tropical Pacific and Atlantic Oceans harbor three species of deep-water *Laminaria*, all of which have primitive traits for the Laminariales (16, 17), suggesting an ancient origin (>30 Mya) (22) and relative permanence of deep-water kelp refugia.

The identification of deep-water kelp refugia in the tropics also has significant ecological consequences, with conservation and management implications for these regions. The localized upwelling that appears to regulate shoaling of the mixed layer in the Galápagos, and thus provides for the existence of *Eisenia* forests, also may create vertical advective flows that supply kelp-derived particulate organic carbon to shallower filter-feeding invertebrate assemblages. In other kelp systems, such spatial trophic subsidies have profound impacts on trophodynamics and food web structure (23). These deep kelp assemblages also may serve as vital habitats for local fisheries species (e.g., *Semicossyphus darwini* and *Paralabrax albomaculatus*) that were observed during our SCUBA surveys in Galápagos *Eisenia* forests. Both of these genera are conspicuous predators in California kelp systems (7). Indeed, during our brief studies at Galápagos, we observed trophic and habitat associations with *E. galapagensis* individuals at both low and high *E. galapagensis* densities, including grazing by fish (*Nicholosina denticulata*), sea hares (*Aplysia* sp.), and decorator crabs typical of temperate kelp systems (7). Therefore, the global significance of these systems likely extends beyond simple ecological curiosity, with broader impacts to tropical sublittoral systems worldwide.

The relatively deep location of the tropical kelp refuge also may buffer these kelp systems from more shallow water regional ocean climate phenomena (e.g., El Niño-Southern Oscillation (ENSO)). Although tropical coral reef systems are vulnerable to ENSO (24), especially in eastern tropical regions (25), typical mixed-layer depressions of ≈20 m during ENSO events (26) are too shallow to eliminate deep kelp refugia. Furthermore, climatic processes that enhance sea-surface warming and deepen the mixed layer may impact the shallow limit of tropical deep kelp forests, whereas correlated decreases in surface productivity may increase optical clarity and simultaneously extend the depth of the euphotic zone and the deep limit of the forests. Therefore, deep kelp refugia may be old and resilient features of the tropics, supported by the fact that the deep-water tropical kelp, *L. philippinensis*, is the most morphologically and ultrastructurally primitive extant kelp taxon (17). The potentially ancient origin of kelp (22) and the resistance of deep-water kelp refugia to surface climate change may allow tropical kelp forests to develop unique communities relative to other tropical systems.

Materials and Methods

The predictive model of tropical deep kelp habitats consisted of two broad components: a set of physiological constraints on kelp distribution derived from the literature (ecophysiological model) and a geospatial analysis of light, temperature, and nutrient climatologies from the surface to the depth of the seafloor (oceanographic model). Detailed methods for processing of oceanographic data are discussed later. Chosen values of relevant physiological thresholds are listed, with appropriate citations to comprehensive reviews of laboratory and field studies on these parameters (4, 12).

We integrated monthly global climatologies of SeaWiFS-derived incident sea-surface PAR and optical depth (K_d) parameters to predict the depth of the minimal annual irradiance dose for kelp survival (50 E·m^{-2}·year^{-1}) (i.e., the kelp photo-

synthetic compensation depth) (12). The global distribution of sufficiently illuminated substrate was then predicted by the intersection of kelp compensation depth with global bathymetry from the ETOPO2 satellite altimetry-derived database (Fig. 1*a*). Because kelp is more vulnerable to nutrient limitation than temperature stress (27, 28), we used the depth of the seasonal thermocline to estimate the vertical extent of the mixed layer, and thus the zone within which deep-water nutrient replenishment occurs (Fig. 1*b*) (29). Vertical temperature profiles from the World Ocean Database (WOD2001) (30) were optimally interpolated onto a 0.5° geographic grid at standard depth levels (30) and used to estimate the monthly climatological mixed-layer depth, defined as the shallowest local maximum of second derivative of the temperature-depth function (i.e., the shallowest maximum that was at least 80% of the global maximum gradient). Calculations were restricted to the upper 550 m of water column to avoid confounding with the deeper, less biologically relevant permanent thermocline. Methods of calculating mixed-layer depth vary widely in the oceanographic literature. We chose our definition to correspond most closely with relevant properties for kelp, specifically depths that receive adequate nutrients for kelp growth (31). Detailed discussion of the correlation among nutricline, thermocline, and mixed-layer depths can be found elsewhere (29, 31). We validated our mixed-layer depths by comparison to nitrate concentration measurements from WOD2001 when available and found that they conservatively predicted NO$_3$ concentrations >2 μM, indicating suitable conditions for kelp growth (4). Thus, the mixed-layer depth was used to constrain the distribution of illuminated substrate, yielding the predicted location of illuminated substrate beneath the mixed layer (Fig. 1*c*). Because of the relative continuity of the climatological oceanographic data fields, the final resolution of the deep tropical kelp model was determined by the 2-arcminute (≈3.7-km) spatial resolution of the ETOPO bathymetric grid, allowing us to detect potential tropical kelp habitats of ≈14 km^2.

The final predictive model can be represented as the subset of bathymetric grid locations $\langle x, y \rangle$ for which the following conditions hold ($\langle x, y \rangle$ subscripts on all variables are omitted for clarity):

Coordinates of predicted kelp habitat

$$\in \{\langle x, y \rangle \mid (Z_{\text{seafloor}} \geq Z_{\text{mixed layer}}) \cap$$

$$(Z_{\text{seafloor}} \leq Z_{\text{minimum light}}) \cap (T_{\text{max, seafloor}} \leq 23°C)\}$$

$$Z_{\text{mixed layer}} = \text{mean}(Z(m)_{\text{mixed layer}})$$

$$Z(m)_{\text{mixed layer}} = \min\{z \mid \mathrm{d}^2T(m, z)/\mathrm{d}z^2$$

$$\geq 0.8 \cdot \max(\mathrm{d}^2T(m, z)/\mathrm{d}z^2)\} + 5 \text{ meters}$$

$$Z_{\text{minimum light}}$$

$$= \max\{z \mid \Sigma[\text{PAR}(m)\exp(-K_d(m)\cdot z)] \geq 50 \text{ E·m}^{-2}\cdot\text{yr}^{-1}\}$$

$$T_{\text{max, seafloor}} = \max\{T(m, Z_{\text{seafloor}})\},$$

where *m* denotes the number of the month; $m \in \{1, 2, \ldots, 12\}$; *z* denotes the depth in meters; $z \in \{1, 2, \ldots, 550\}$; and T, PAR, K_d, and Z_{seafloor} are temperature, light, and bathymetry inputs from the WOD2001, SeaWiFS, and ETOPO2 databases, respectively. A 23°C maximum monthly climatological temperature constraint and a +5-m buffer on the mixed-layer depth were applied to generate a conservative set of predictions; depending on local physiological adaptation to light and nutrient fluxes, the extent of potential deep kelp habitats may be greater.

Using model predictions, eight locations were chosen for SCUBA surveys of deep kelp habitat. Divers were positioned on

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the sea floor at 10-m depth and initiated vertical transects along the bottom to depths of 60 m. The depth of the first *E. galapagensis* sporophyte along the transect was recorded, and 10–20 sporophytes were collected during each dive for morphometric analysis (sporophyte length, stipe length and diameter, fertility), genetic analysis, and preparation of herbarium voucher specimens. The deep limit of *E. galapagensis* was never observed in SCUBA surveys because of divers' depth safety limitations (i.e., no dives were >60 m). Duplicate specimens were deposited in the herbarium at the Charles Darwin Research Station and the Marine Biological Collection/Global Kelp Archive at the Moss Landing Marine Laboratories. Horizontal transects also were sampled at 20-m depth at each study location. Densities of *E. galapagensis* sporophytes and mobile invertebrates were estimated in 1-m^2 quadrats, percent cover of benthic algae was estimated by using random point contacts, and fish species lists were created by using visual surveys.

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