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RESEARCH ARTICLE

The ecology of giant kelp colonization and its implications for kelp forest restoration

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Abstract

The success and cost-effectiveness of kelp forest restoration hinges on understanding the colonization ecology of kelps, particularly with respect to dispersal potential, recruitment success, and subsequent establishment. To gain needed insight into these processes we examined spatial patterns and temporal trajectories of the colonization of a large artificial reef by the giant kelp *Macrocystis pyrifera*. The 151 ha artificial reef complex was constructed in three phases over 21 years, enabling dispersal, recruitment, and subsequent establishment to be examined for a wide range of environmental conditions, dispersal distances, and source population sizes. Natural colonization of all phases of the artificial reef by giant kelp was rapid (within 1 year) and extended across the entire 7-km-long reef complex. Colonization density declined with distance from the nearest source population, but only during the first phase when the distance from the nearest source population was ≤3.5 km. Despite this decline, recruitment on artificial reef modules farthest from the source population was sufficient to produce dense stands of kelp within a couple of years. Experimental outplanting of the artificial reef with laboratory-reared kelp embryos was largely successful but proved unnecessary, as the standing biomass of kelp resulting from natural recruitment exceeded that observed on nearby natural reefs within 2–3 years of artificial reef construction for all three phases. Such high potential for natural colonization following disturbance has important implications for kelp forest restoration efforts that employ costly and logistically difficult methods to mimic this process by active seeding and transplanting.

KEYWORDS
artificial reef, density dependence, dispersal, disturbance ecology, ecological restoration, kelp forest, *Macrocystis pyrifera*, recovery

INTRODUCTION

Ecological succession, stability, and species diversity are defining attributes of natural systems that are inextricably linked to disturbance (Dayton, 1971; McIntosh, 1999; van der Maarel, 1993). Not surprisingly, ecologists have long sought to understand the processes by which populations, communities, and ecosystems recover from varying forms and degrees of disturbance (reviewed in Noble & Slatyer, 1980, Sousa, 1984, Pickett & White, 1985, Platt & Connell, 2003). Most of this research has focused on plants, with considerable

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Abbreviations: ANOVA, analysis of variance; COVID-19, Corona 19 virus disease; ha, hectare; PVC, polyvinyl choloride; SCE, Southern California Edison; SE, standard error; SONGS, San Onofre Nuclear Generating Station.

interest in determining the extent to which their recovery from disturbance is limited by factors that influence seed dispersal, seedling recruitment, and the subsequent establishment of older individuals (Clark et al., 1998; Howe & Smallwood, 1982; Nathan & Muller-Landau, 2000).

The concepts underlying disturbance ecology are central to the more recently evolving discipline of restoration ecology, an applied science aimed at informing the practice of ecological restoration, which involves either actively or passively assisting the recovery of ecological systems that have been degraded, damaged, or destroyed (Halle, 2007a; Hobbs et al., 1996; Suding et al., 2015). Guiding principles of ecological restoration are rooted in ecological theory (Palmer et al., 1997) and include allowing for natural succession to occur whenever possible (Halle, 2007b) and accounting for ecological interactions such as facilitation and density- and frequency-dependence that shape it (Crandall & Knight, 2015; Scotton, 2019; Silliman et al., 2015). Ecological restoration typically incorporates socioeconomic values and interventions aimed at returning and maintaining a system in a desirable ecological state, irrespective of what caused the system to decline to a less valued state (Abelson et al., 2016; Choi, 2007; Martin, 2017). Regardless of the underlying motivation, the success of ecological restoration hinges on identifying the factors limiting the transition of a system from a less desirable to a more desirable state (Halle, 2007b; Hobbs et al., 1996).

Large brown algae in the order Laminariales (collectively known as kelps) form highly productive marine forests on shallow reefs in temperate and polar seas worldwide (Dayton, 1985; Teagle et al., 2017; Wernberg et al., 2019) and are common targets of ecological restoration (Morris et al., 2020). A variety of natural and anthropogenic disturbances associated with climate, fishing, overgrazing, and pollution cause kelp forests to fluctuate between desirable “forested” and less desirable “unforested” states. The forested state is highly valued for its goods and services, and efforts to restore unforested areas or accelerate their transition to a desirable forested state date back to the 16th century (Eger, Marzinelli, et al., 2022). More recently, heightened concerns that the unforested areas dominated by low-lying turf algae or denuded by intensive grazing are becoming more prevalent have led many stakeholders to advocate for the global protection and restoration of kelp forests aimed at maximizing their cover throughout their historically observed distribution (Eger et al., 2023). Although guidelines and methods for restoring kelp forests have been developed (Eger, Layton, et al., 2022; Schiel & Foster, 1992), considerable knowledge gaps in the colonization ecology of early life stages of kelps remain (reviewed in Edwards, 2022, Veenhof et al., 2022), which can hinder cost-effective restoration (Eger et al., 2020).

Artificial reefs are commonly used to create desirable habitats and mitigate the loss of natural habitats (Lee et al., 2018; Pickering et al., 1999). Although artificial reefs are not typically used to restore naturally occurring kelp forests, they can be used to create kelp forests in soft-bottom habitats that previously did not support kelp forests (Davis et al., 1982; Deysher et al., 2002). Such afforestation projects can provide novel insight into patterns and processes controlling kelp colonization, which is critical for guiding cost-effective restoration of degraded kelp populations on natural reefs. Unlike most natural disturbances that leave some survivors (Platt & Connell, 2003), colonization and succession on newly constructed artificial reefs occur in the absence of any prior residents. Such conditions, which are more akin to those following “catastrophic disturbances” (sensu Platt & Connell, 2003), are particularly useful for isolating the effects of variation in dispersal, recruitment, and subsequent growth and survivorship on population and community recovery.

Artificial substrates have long been used in small-scale, short-term experiments to examine factors influencing kelp recruitment (e.g., Foster, 1975; Kennelly, 1983; Layton et al., 2019). The use of larger artificial reefs for this purpose has the potential to contribute novel insight into the ecology of kelp colonization especially when they are sufficiently large to be influenced by abiotic and biotic interactions characteristic of natural reefs and when their constructions are replicated over time and space to account for environmental variation in factors that influence dispersal, recruitment, and subsequent establishment (Dayton et al., 1999). Such is the case for the Wheeler North Reef, a large (151 ha) artificial reef complex spread across 7 km^2 of sandy habitat in southern California, USA. The artificial reef was constructed in three phases over a 21-year period for the specific purpose of supporting a kelp forest dominated by the giant kelp *Macrocystis pyrifera*. Giant kelp populations in this region are regulated by density-dependent interactions that are modified by disturbance and other stochastic processes that act in a density-independent fashion (Dayton et al., 1992, 1999; Nisbet & Bence, 1989).

Here, we examined spatial patterns and temporal trajectories of dispersal, recruitment, and subsequent establishment of giant kelp for each phase of Wheeler North Reef to gain insight into the processes most likely to limit its recovery from catastrophic disturbances, which is highly relevant to kelp forest restoration. Specifically, we sought to determine: (1) how spatial patterns of giant kelp colonization varied in relation to distance from the nearest source population, (2) the extent to which density dependence during early stages of colonization influenced patterns of adult kelp abundance and biomass, and (3) the amount of time for the standing biomass of giant kelp at the artificial reef to approach levels comparable to that at nearby natural reefs. In addition, we evaluated the efficacy of outplanting laboratory-reared kelp embryos to the artificial reef as a useful and necessary tool for accelerating the establishment of giant kelp. Our results improve understanding of the ecological processes underlying kelp forest dynamics particularly with respect to recovery from disturbance, which is needed for designing cost-effective restoration programs aimed at re-establishing kelps on natural reefs where they have declined.

METHODS

Species characteristics

The giant kelp, *Macrocystis pyrifera*, is the world's largest alga and has a heteromorphic diplohaplontic life history that is characteristic of all kelps in the order Laminariales. The large diploid sporophyte produces and releases trillions of microscopic haploid female and male spores (Buschmann et al., 2006; Reed et al., 1996). Following a brief dispersal period, spores settle on the sea floor and germinate into free-living microscopic gametophytes. Female and male gametophytes engage in sexual reproduction to produce embryonic sporophytes that ultimately grow and develop into macroscopic sporophytes (hereafter referred to as "plants" sensu Bolton, 2016). Mature plants consist of a bundle of vine-like fronds anchored by a common holdfast. The buoyant fronds extend throughout the water column to produce a floating canopy at the sea surface. Plants may contain hundreds of fronds that reach up to 60 m in length and collectively weigh as much as 500 kg wet (Schiel & Foster, 2015).

Giant kelp spores need to settle at high densities ($>1\cdot \text{mm}^{-2}$) to ensure fertilization between female and male gametophytes (Reed et al., 1991). This requirement, coupled with the drastic difference in size between spores (0.01 mm) and mature plants, promotes strong negative density-dependent growth, reproduction, and survival in all phases of giant kelp's life history (Dayton et al., 1984; Dean et al., 1989; Reed, 1990; Reed et al., 2008; Reed & Foster, 1984). Such density-dependent effects can be diminished by stochastic density-independent processes to affect demographic rates and the dynamics of local kelp populations (Dayton et al., 1992, 1999; Nisbet & Bence, 1989). For example, gametophyte reproduction and the subsequent recruitment and survival of juvenile sporophytes are influenced by local environmental conditions (most notably light, temperature, and nutrients; Deysher & Dean, 1986), competition with other species (Dayton et al., 1984; Reed & Foster, 1984), and grazing (Dean et al., 1989; Henríquez et al., 2011), independent of gametophyte or juvenile sporophyte density. Similarly, periodic disturbance from large swells, marine heatwaves, and intensive grazing by sea urchins can greatly reduce or eliminate entire stands of larger giant kelp plants regardless of stand density (Dayton et al., 1992; Ebeling et al., 1985; Edwards, 2004; Tegner & Dayton, 1987). The relatively long duration of this study (1999–2023), coupled with the large size of Wheeler North Reef allowed us to investigate the extent to which density-dependent interactions shaped spatial and temporal patterns of colonization and subsequent establishment of giant kelp during a period that encompassed considerable stochastic environmental variation.

Study site description

Wheeler North Reef (hereafter "artificial reef") is a large artificial reef complex in southern California that was built to mitigate the loss of giant kelp forest habitat caused by the turbid discharge plume of the San Onofre Nuclear Generating Station (SONGS). It is located ~1 km offshore of San Clemente, California, USA (33.40210, −117.62420) at 13–16 m depth in an expansive area of sandy habitat that is near, but outside, the influence of the SONGS discharge plume. The artificial reef was designed as a low-relief (<1 m tall) boulder reef to mimic the physical structure of natural reefs in the region that supported giant kelp, including the reef located directly offshore of SONGS that was impacted by its operations (Elwany et al., 2011; Reed, Schroeter, et al., 2006).

The artificial reef was constructed in three phases over a 21-year period. Phase 1 was built in the summer of 1999 and designed as a randomized block experiment that tested two types of reef material (quarry rock boulders and concrete rubble) and three nominal bottom coverages (42% ± 2% *SE*, 63% ± 1% *SE*, and 86% ± 1% *SE*). The blocks were arranged along a distance gradient from San Mateo Reef, a 166-ha low-relief boulder reef with a large population of giant kelp that was the nearest known source of kelp spores for the artificial reef (Reed et al., 2004). The experiment consisted of 42 reef modules (40 m × 40 m) clustered in seven blocks (six modules per block) located at distances ranging from 0.6 to 3.5 km up coast of San Mateo Reef (Figure 1). Three of the six modules in each block were built from quarried rock boulders, and the other three were built from concrete rubble. The two reef materials differed in their size and shape, which caused the modules to differ slightly with respect to small-scale topography (Elwany et al., 2011; Reed et al., 2004).

Concerns were raised during the environmental review of Phase 1 that giant kelp would not colonize along the entire length of the artificial reef due to limitations in spore dispersal and subsequent sporophyte recruitment. To address this concern, the design of the Phase 1 reef was modified to include outplanting

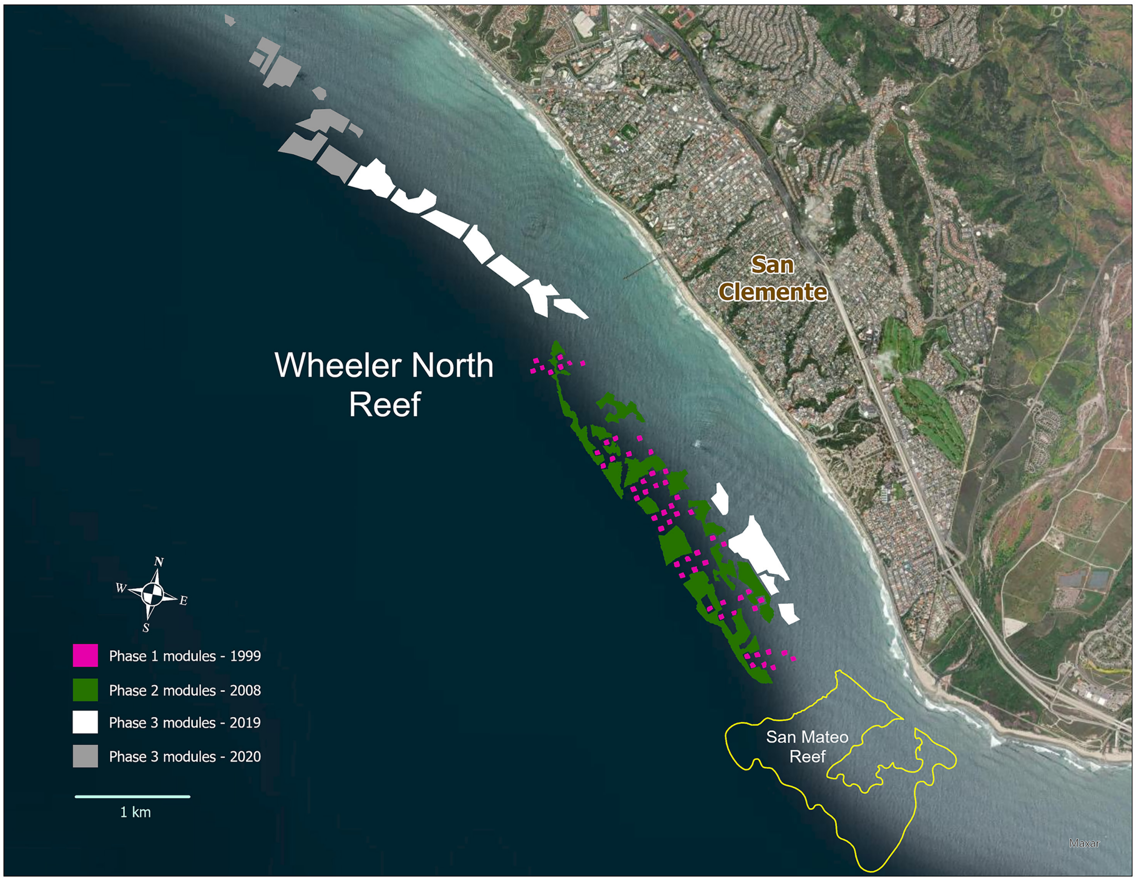


FIGURE 1 Map of the study area showing the configuration, locations, and construction dates of the different phases of Wheeler North Reef. [Color figure can be viewed at wileyonlinelibrary.com]

laboratory-reared giant kelp to 14 additional modules (one rock and one concrete module with medium bottom coverage in each of the seven blocks) to assess the feasibility of this method for augmenting giant kelp abundance in the event that its colonization on the artificial reef was limited by spore dispersal. Collectively, the 56 Phase 1 modules (42 + 14) extended along 3.5 km of shoreline and covered about 10 ha of the sea floor in an area encompassing approximately 144 ha (Figure 1).

Phase 2 of the artificial reef was built in the summer of 2008 and consisted of 18 irregularly shaped modules of varying size (0.6–16 ha) that were interspersed among the Phase 1 modules (Figure 1). The design of the Phase 2 reef was informed by results from the Phase 1 experiment showing that bottom coverage of reef material, but not the type of reef material, significantly affected the abundance and diversity of species on the artificial reef (Reed, Schroeter, et al., 2006; Schroeter et al., 2015). Consequently, the Phase 2 modules were constructed entirely of quarried rock boulders placed in a single layer covering an average of 45% of the bottom and extending <1 m above the sea floor (Elwany et al., 2011).

Results from monitoring the Phase 1 and Phase 2 reefs from 2009 to 2015 showed that their collective area was not large enough to consistently meet all of the artificial reef's objectives (Schroeter et al., 2018). Therefore, a third phase of the artificial reef was constructed in the summers of 2019 and 2020 (referred to hereafter as Phases 3a and 3b, respectively) to ensure full compensation for losses of kelp forest habitat caused by the operations of SONGS. Phases 3a and 3b were designed similarly to Phase 2 and collectively added 80 ha of low-relief quarried rock boulders in 20 irregularly shaped modules (0.6–12 ha in area) that covered an average of 45% of the sea floor. Nineteen of the 80 ha were in four modules located immediately inshore of the southern portion of Phases 1 and 2 with the remaining 61 ha of Phase 3 extending 0.5–3.5 km up coast of the northernmost portion of the Phase 2 reef (Figure 1). Collectively, the three phases of the artificial reef combined for a total reef area of 151 ha that extended along 7 km of coast.

Data collection

Data from annual diver surveys in summer (June through mid-September) were used to determine the effects of distance from the nearest source population of reproductive giant kelp on its initial colonization and subsequent establishment on the different phases of the artificial reef. For all phases, we used plants <1 m tall to characterize the initial colonization of the artificial reef by small kelp recruits and plants ≥1 m tall to characterize the establishment of larger individuals that have a much higher probability of survival (Dayton et al., 1984). Forests, whether terrestrial or marine, are often characterized by the density of their standing biomass (i.e., mass per unit area), which determines a wide array of ecological patterns and processes (Barnes et al., 1997; Pan et al., 2013). Such is the case for giant kelp for which biomass density has been shown to be inextricably linked to net primary production (Rassweiler et al., 2018; Reed et al., 2008); population fecundity (Castorani et al., 2017); and the structure, diversity, and stability of the kelp forest community (Castorani et al., 2018; Lamy et al., 2020; Miller et al., 2018). Although obtaining direct estimates of the standing biomass of giant kelp is logistically challenging, it can be predicted from non-destructive measurements of the density of fronds, which are readily obtained by diver surveys (Rassweiler et al., 2018; Reed et al., 2009). Hence, we used the density of fronds ≥1 m tall as a proxy for standing biomass density.

Sampling of the 42 Phase 1 modules not outplanted with kelp began in summer 2000 approximately 9 months following the completion of reef construction (data available in Reed et al., 2024a, 2024b, 2024c). Divers recorded the number and individual size (estimated as the number of fronds) of plants ≥1 m tall in a 2-m wide band centered along a 40-m long permanent transect. Two parallel transects separated by 20 m were sampled on each module.

Data collection at Phase 2 began in the summer of 2009 (approximately 9 months following the completion of reef construction) at 40 locations distributed uniformly across the 18 Phase 2 modules in proportion to their area (data available in Reed et al., 2023a, 2023b, 2023c). Each sampling location consisted of two 50-m long parallel transects separated by 25 m that were defined by permanent geographical coordinates at 0 m and a fixed magnetic heading. At each location, divers recorded the number of fronds >1 m tall for each giant kelp individual occurring within five uniformly spaced 10 m × 2 m quadrats oriented perpendicular to the transect line. Plants <1 m tall were counted in 1 m^2 quadrats placed adjacent to the transect line within the larger 10 m × 2 m quadrats ($\pi=$five 1-m^2 quadrats per transect). The same sampling design was used to record the abundance and size of giant kelp along a single 50-m transect at 59 locations distributed among the 20 Phase 3 modules beginning in the summer of 2020. The one exception was that restrictions on research caused by the COVID-19 pandemic shortened our sampling season and prevented us from collecting densities of small plants in 1 m^2 quadrats on the Phase 3 modules in the summer of 2020.

For comparison, we used the same methods as described above for the different phases of the artificial reef to concurrently survey giant kelp at two nearby natural reefs (San Mateo and Barn) located 0.5 and 10 km down the coast of the southern edge of the artificial reef.

Outplanting laboratory-reared kelp

As noted above, the design of the Phase 1 reef was expanded to assess the feasibility of manually planting giant kelp in the event that it failed to colonize naturally. For this purpose, giant kelp was reared in the laboratory by seeding a 7 mm diameter braided nylon line with spores obtained from adult kelp in the study region. Seeded lines were cut into 8-cm long segments and placed in laboratory culture conditions optimal for sporophyte production (Deysher & Dean, 1984) until embryonic sporophytes were visible with the unaided eye (~1 mm). During June and July 2000 segments of braided line containing kelp embryos were outplanted to 14 of the Phase 1 modules by fastening them with nylon ties to a 10 cm × 30 cm polyvinyl chloride (PVC) plate secured to the reef with a stainless steel bolt. An average of 28 (range 23–30) outplant units (PVC plates with a seeded line containing kelp embryos) were installed in a uniform array approximately 2 m from each of the two transect lines of the 14 transplant modules ($n=778$ total outplant units deployed). We sampled each outplant unit in September and October 2000 (~3 months after installation) and May and June 2001 (~11 months after installation) for the presence/absence of the PVC plate, the presence/absence of giant kelp on the seeded line of the PVC plate, and the size of outplanted kelp (data available in Reed et al., 2024d). Measurements of size were categorical and included individuals <1 m tall, ≥1 m tall with <8 fronds, and ≥1 m tall with 8 or more fronds. For comparison, the density and size of naturally recruited giant kelp on the 14 outplant modules were sampled concurrently within a 2-m wide swath centered on each transect line.

Data analysis

The influence of proximity to the nearest source population on the recruitment and subsequent development of giant kelp was evaluated annually for each phase of the artificial reef using linear regression. Three different dependent variables were evaluated in these analyses: (1) density of plants <1 m tall, (2) density of plants ≥1 m tall, and (3) density of fronds ≥1 m tall. Plants <1 m tall represent newly recruited individuals, and the extent to which their densities varied with distance from the nearest source population of giant kelp was used to evaluate dispersal potential. Documenting temporal changes in the relationships between the densities of plants and fronds ≥1 m tall and source proximity allowed assessment of the time course over which spatial variation in dispersal and recruitment influenced subsequent patterns of adult kelp abundance and standing biomass. Because kelp only colonized the portion of the sea floor covered by hard substrate (i.e., rock or concrete) and the percent cover of the sea floor covered by hard substrate varied among sampling locations, the densities of plants and fronds at a given sampling location were standardized to the percent cover of hard substrate of that sampling location. Unlike the cover of hard substrate, the densities of plants and fronds were largely unaffected by the type of hard substrate (Appendix S1 in the Supporting Information: Figure S1). Consequently, analyses for Phase 1 did not discriminate between modules of the two substrate types.

The independent variable (i.e., distance from the nearest source population) in the regression analyses varied for the different phases of the artificial reef. Source proximity of the Phase 1 modules was measured as the distance from the centroid of a block of six modules to the upcoast edge of San Mateo Reef. Because prior phases of the artificial reef had the potential to serve as source populations of kelp for later phases of the artificial reef, we used two measures of source proximity as the independent variables in analyses of the Phase 2 and Phase 3 reefs: (1) distance from San Mateo Reef, and (2) distance from previously constructed phases of the artificial reef. For Phase 2, proximity to previously constructed portions of the artificial reef was measured as the distance between a Phase 2 sampling location ($n = 40$) and the nearest Phase 1 module. Similarly, proximity to the previously constructed artificial reef for Phase 3 was measured as the distance between a Phase 3 sampling location ($n = 37$ for Phase 3a and $n = 20$ for Phase 3b) and the nearest Phase 2 sampling location. The dependent variables examined were mean densities of plants <1 m tall, plants ≥1 m tall, and fronds ≥1 m tall, standardized to the cover of the hard substrate at that sampling location. Separate analyses were done for each combination of independent and dependent variables and year for each phase of the artificial reef.

The survivorship of the outplant units bolted to the 14 Phase 1 modules and the proportion of outplant units with outplanted kelp (as indicated by kelp attached to the seeded line rather than the PVC plate) were evaluated at 3 and 11 months after installation. Differences between outplanted and naturally recruited giant kelp in the mean proportion of individuals in each of the three size classes 11 months after outplanting were evaluated with separate one-way ANOVAs.

RESULTS

Spatial and temporal patterns of giant kelp colonization

Phase 1: 2000–2003

Giant kelp colonized the Phase 1 reef within the first year after its construction (Figure 2a). Recruitment varied widely among the 42 reef modules ranging from near 0 to 14 plants · m^{-2}. Average plant densities on the modules generally decreased with increasing distance from the putative spore source at San Mateo Reef indicating diminishing dispersal with distance. Nonetheless, recruitment at the most distant block of modules from San Mateo averaged as much as 1.5 plants · m^{-2}, demonstrating substantial dispersal over distances of at least 3.5 km.

High densities of small plants in Year 1 led to a dramatic increase in the density of larger plants in Year 2, which also generally declined with distance from San Mateo (Figure 2b). Modules with relatively high densities of plants ≥1 m tall (i.e., >1 plant · m^{-2}) declined over time. This decline was due to the density-dependent thinning of smaller plants by larger individuals as evidenced by an increase in average plant size with time after reef construction that accompanied the decline in the density of plants ≥1 m (Appendix S1: Figure S2) coupled with much lower recruitment of new plants <1 m tall in subsequent years (Figure 2a). Plant thinning on modules with the highest densities caused the pattern of declining plant density with distance from San Mateo to disappear by Year 3 (Figure 2b). This thinning resulted in a relatively uniform density of plants ≥1 m tall across the 42 modules in Year 4, which averaged ~0.5 plants · m^{-2}.

The standing biomass of giant kelp (as estimated by the density of fronds ≥1 m tall) was very low in Year 1 when it consisted almost entirely of small plants (Figure 2c). Frond density increased sharply beginning in Year 2 creating a dense surface canopy on all 42 modules by Year 3 (Appendix S1: Figure S3a). Spatial patterns in biomass generally matched those of plants ≥1 m tall as frond densities in Years 1–3 declined with increasing distance from San Mateo out to 3.5 km (Figure 2c). This spatial pattern disappeared in Year 4; however, this was not due to density-dependent thinning as was the case with plant density. Instead, the disappearance of declining frond density with distance from San Mateo was caused by an increase in the standing biomass of modules farthest from San Mateo rather than a decrease in the standing biomass of modules closest to San Mateo.

Phase 2: 2009–2012

Similar to Phase 1, giant kelp rapidly colonized the Phase 2 reef in the first year after it was built, with little to no new recruitment in the subsequent 3 years (Figure 3a). Although spatial variability in the density of plants <1 m tall in Year 1 was substantial (range 0.5–46.5 plants · m^{-2}), it did not appear to be influenced by proximity to nearby sources of spores, as it was unrelated to distance from the kelp forest at San Mateo (Figure 3a) or distance from the nearest Phase 1 module (Appendix S1: Figure S4a). Given these results, it was not surprising that we observed little correlation between the densities of plants and fronds

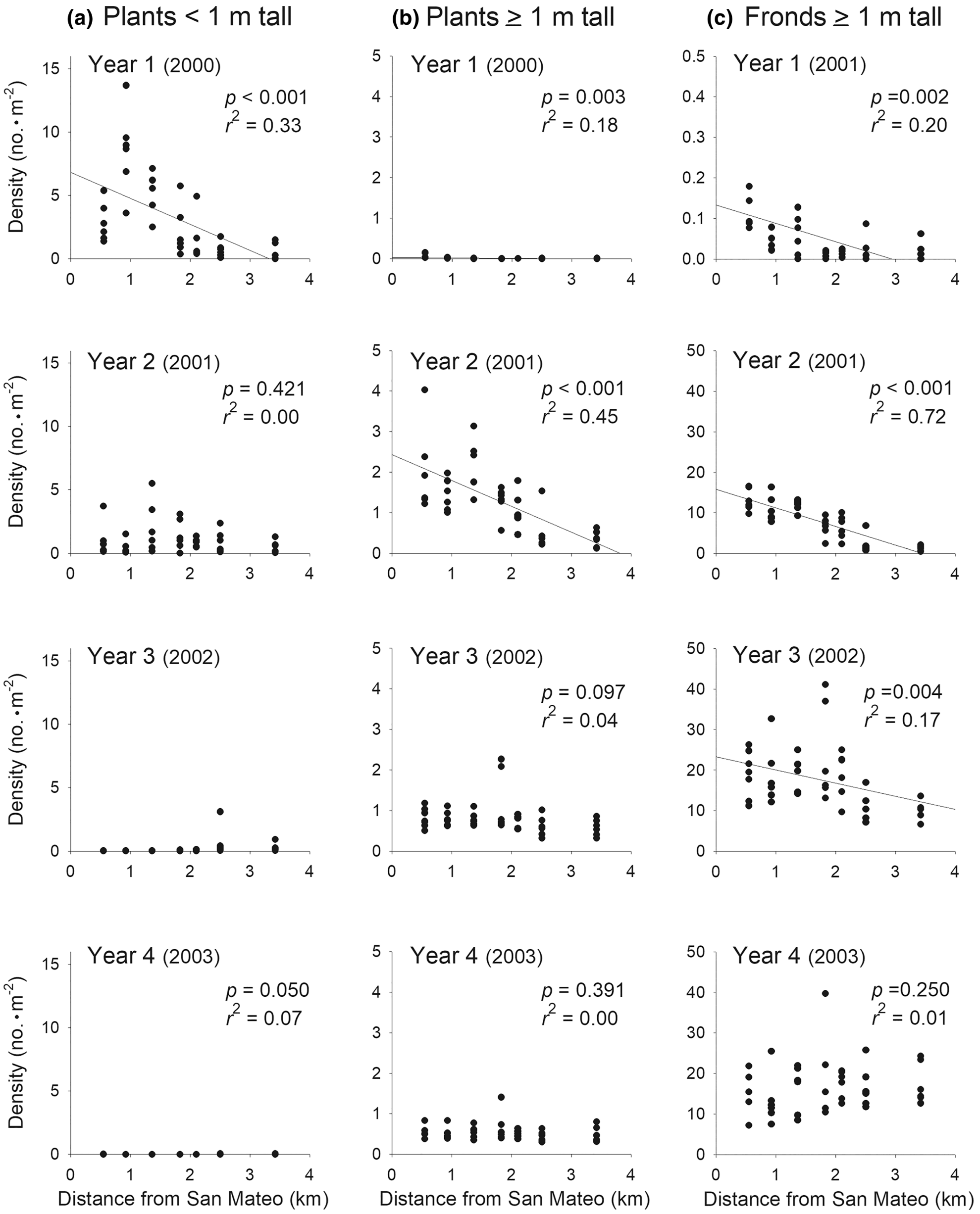


FIGURE 2 The relationship between the density of (a) plants <1 m tall, (b) plants ≥1 m tall, and (c) fronds ≥1 m tall on the Phase 1 modules and their distance from San Mateo, the nearest natural population of giant kelp to serve as a spore source. Data are shown for the first 4 years following the construction of the Phase 1 reef. Values represent the mean densities of 42 modules for each year. Regression lines are included where $p < 0.05$.

≥1 m tall on the Phase 2 reef and the distance from San Mateo (Figure 3b,c) or the distance from the nearest Phase 1 module (Appendix S1: Figure S4b,c). The only exceptions were slightly positive relationships between distance from San Mateo and the density of plants ≥1 m tall in Year 2 (Figure 3b) and the density of fronds ≥1 m tall in Year 1 (Figure 3c). Much like Phase 1, spatial variation in the density and biomass of giant kelp declined over time and a dense surface canopy formed over all the Phase 2 modules within 2 years after construction (Appendix S1: Figure S3b). By Year 4 the mean (± *SE*) densities of plants and fronds ≥1 m tall on the Phase 2 modules ($0.7 \cdot \text{m}^{-2} \pm 0.04$ and $13.8 \cdot \text{m}^{-2} \pm 0.9$, respectively) were similar to those observed on the Phase 1 modules ($0.5 \cdot \text{m}^{-2} \pm 0.03$ and $16.5 \cdot \text{m}^{-2} \pm 0.9$, respectively) 4 years after the Phase 1 modules were built (Figures 2b,c vs. 3b,c), despite the density of newly recruited plants <1 m tall on Phase 2 averaging more than three times that of Phase 1 ($11.3 \cdot \text{m}^{-2} \pm 1.5$ vs. $3.1 \cdot \text{m}^{2} \pm 05$; Figures 2a vs. 3a).

Phase 3: 2020–2023

Unlike the Phase 1 and Phase 2 reefs, the colonization of the Phase 3 reef was not characterized by an

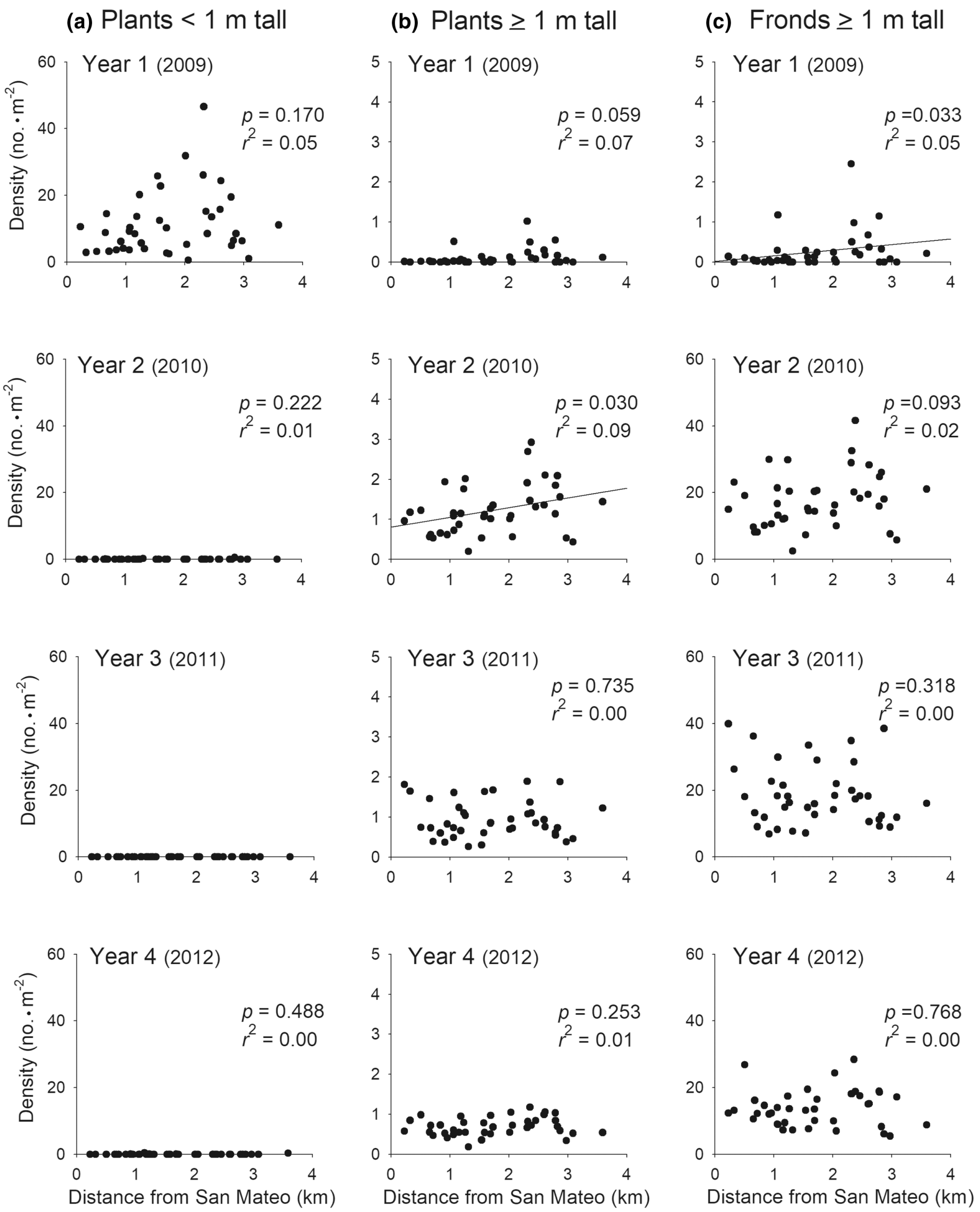


FIGURE 3 The relationship between the density of (a) plants <1 m tall, (b) plants ≥1 m tall, and (c) fronds ≥1 m tall on the Phase 2 modules and their distance from San Mateo, the nearest natural population of giant kelp. Data are shown for the first 4 years following the construction of the Phase 2 reef. Values represent the mean densities of 40 sites for each year. Regression lines are included where $p < 0.05$. No statistics are reported for plants <1 m tall in Year 3 because none were observed at any of the sites.

initial large pulse of recruits. Instead, similar densities of newly recruited plants <1 m tall were observed in successive years on Phase 3a and 3b modules (Figures 4a and 5a), albeit at densities considerably lower than those observed during the initial colonization of Phases 1 and 2 (Figures 2a and 3a). The density of larger plants and fronds on the Phase 3 modules increased in subsequent years, but because of their relatively low recruitment they did not reach the high levels observed on the Phase 1 and 2 modules (Figures 4 and 5 vs. 2 and 3). The one exception was a single site at Phase 3b where the density of plants ≥1 m tall exceeded 8 · m^{-2} in the first year after construction (Figure 5b), which was the highest recorded on any phase of the artificial reef at any time during the study. Notably, we did not see a significant declining trend in the density of small plants or larger plants and fronds at Phase 3 with distance from San Mateo (Figures 4 and 5), or from the nearest artificial reef module (Appendix S1: Figures S5, S6) except in one instance (frond density in Year 2 of Phase 3b; Appendix S1: Figure S6b). In fact, we observed just the opposite in Years 3 and 4 for Phase 3a when the density of plants and fronds increased significantly with proximity from San Mateo (a distance of 0.6–5.6 km; Figure 4) and in Year 3 for Phase 3b when

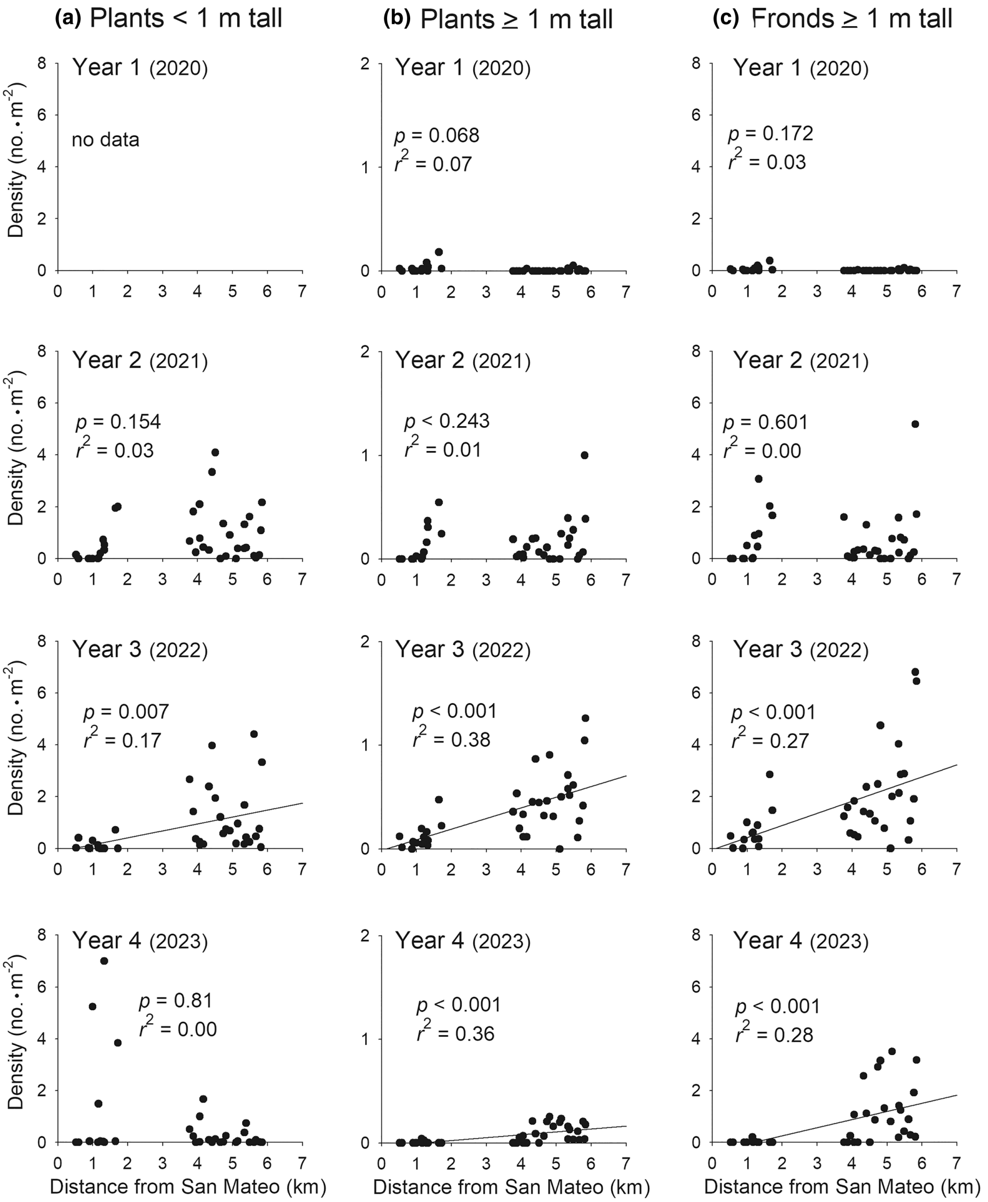


FIGURE 4 The relationship between the density of (a) plants <1 m tall, (b) plants ≥1 m tall, and (c) fronds ≥1 m tall on the Phase 3a modules and their distance from San Mateo, the nearest natural population of giant kelp. Data are shown for the first 4 years following the construction of the Phase 3a reef. Values represent the mean densities of 37 sites for each year. Regression lines are included where $p < 0.05$. Data for plants <1 m tall were not collected in 2020 due to restrictions on research caused by the COVID-19 pandemic.

the density of fronds increased significantly from San Mateo and the nearest Phase 2 module (Figure 5, Appendix S1: Figure S6).

Comparisons between the artificial reef and nearby natural reefs

Temporal variation in the density of kelp initially colonizing the artificial reef caused the standing biomass of giant kelp of the different phases of the artificial reef to differ by as much as an order of magnitude for the same number of years after reef construction (Figure 6). As noted above, kelp biomass on the Phase 3a and 3b modules was substantially lower than that on the Phase 1 and 2 modules. The biomass of giant kelp at nearby natural reefs (San Mateo and Barn) showed similar levels of temporal variability over the course of the 20-year study. Despite this variation, the rate of kelp biomass increase on the newly constructed artificial reef was relatively rapid and the average biomass of giant kelp for all phases of the artificial reef exceeded that at San Mateo and Barn within 2 or 3 years after reef construction. The low biomass of giant kelp at San Mateo from 2021 to 2023 is particularly noteworthy since the size of a spore source is directly related to the standing biomass of giant kelp (Castorani et al., 2017). The smaller source population at San Mateo during this period may

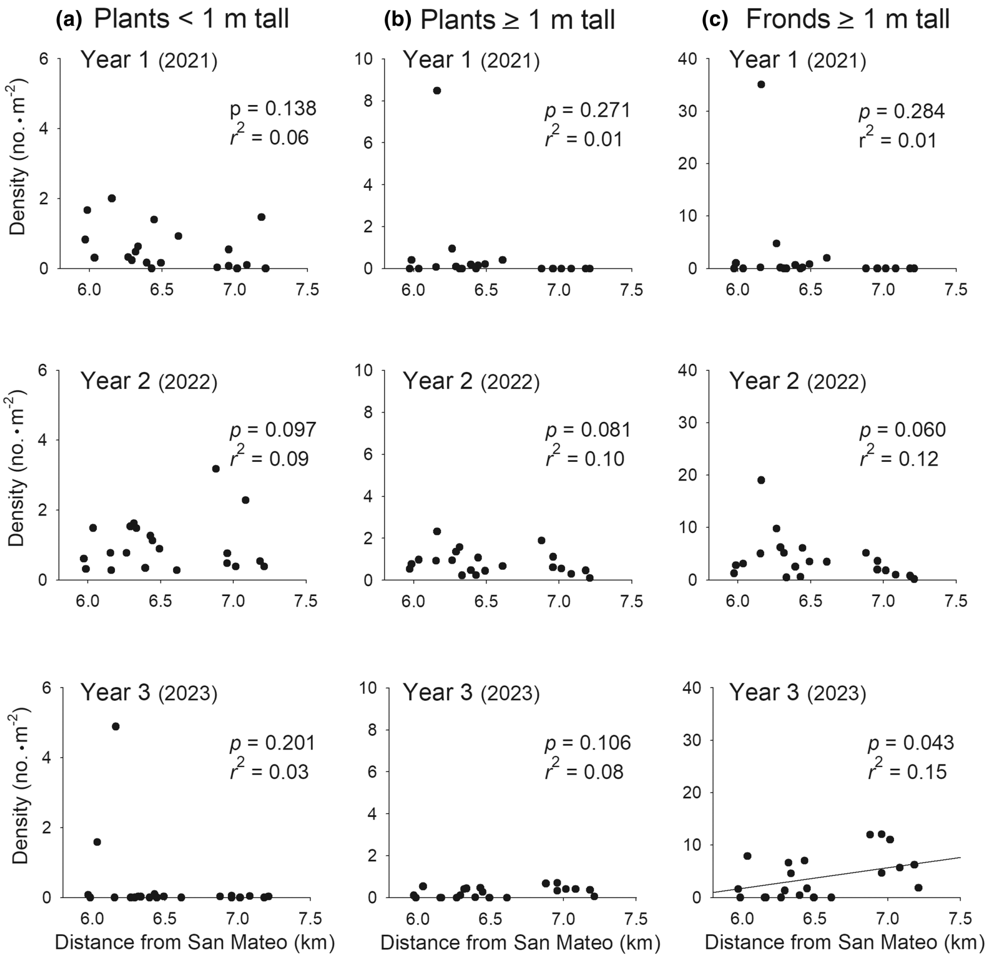


FIGURE 5 The relationship between the density of (a) plants <1 m tall, (b) plants >1 m tall, and (c) fronds >1 m tall at Phase 3b of the artificial reef and distance from San Mateo, the nearest natural population of giant kelp. Data are shown for the first 3 years following the construction of the Phase 3b reef. Values represent the mean densities of 20 sites for each year.

have contributed to the lower recruitment observed on the Phase 3 modules compared to that observed following the construction of Phases 1 (Figure 3a) and 2 (Figure 4a) when the standing biomass of giant kelp at San Mateo was much larger (Figure 6).

Survivorship and growth of outplanted kelp

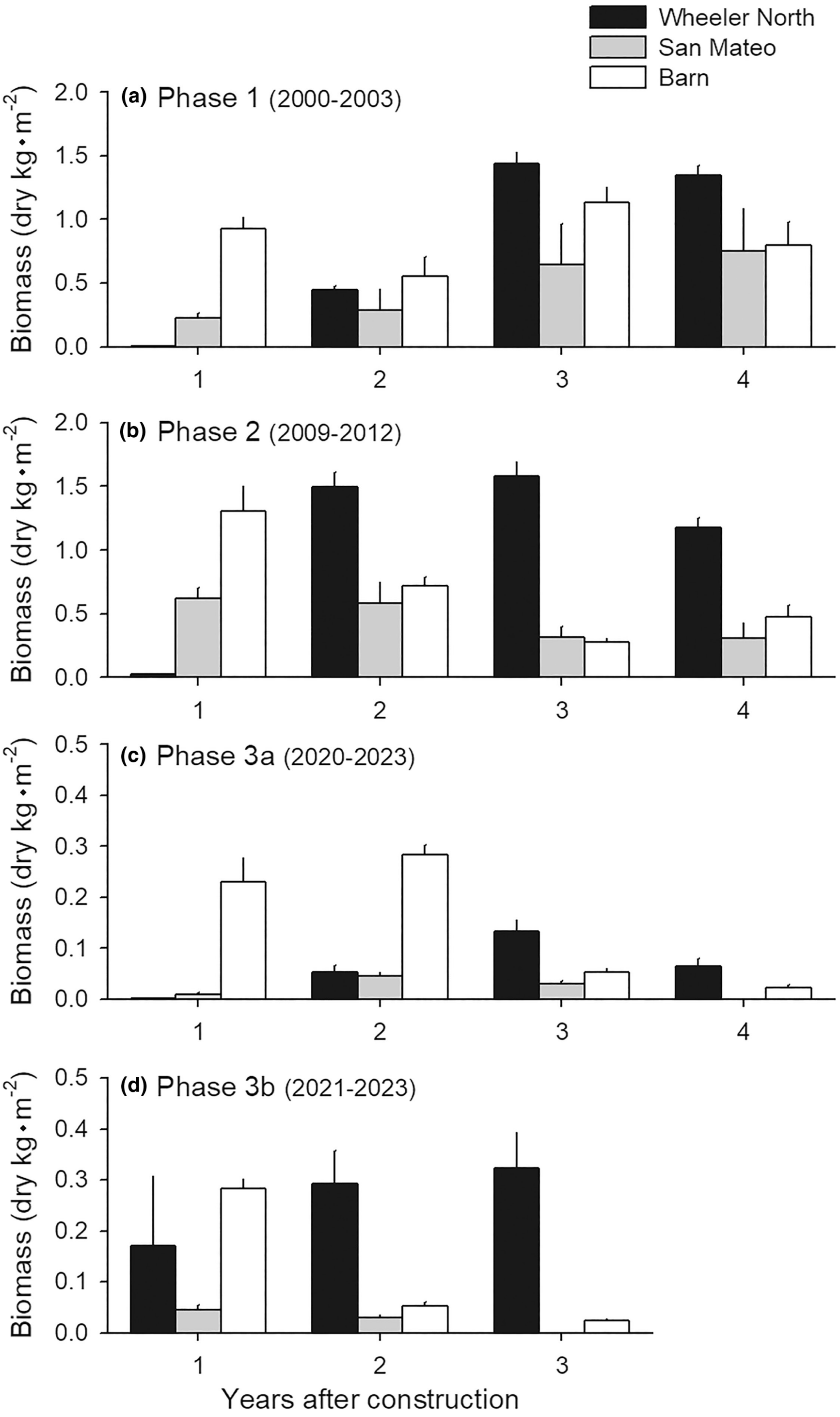
Approximately 90% of the PVC outplant units remained in place 3 months after they were installed (Figure 7a). More than 90% of these (or 81% of those initially installed) were still anchored to the artificial reef after 11 months. Outplanted giant kelp was observed on 91% of the seeded lines that remained in place 3 months after outplanting and on 75% of the lines 11 months after outplanting (Figure 7b). In total, 515 of the 778 outplant units installed (66%) supported giant kelp 11 months after outplanting. Outplanted kelp was generally smaller than naturally recruited kelp 11 months after outplanting as evidenced by a significantly higher proportion of outplanted individuals in the small size class and a significantly lower proportion in the medium size class compared to naturally recruited individuals (Figure 7c; ANOVA $F_{1,26} > 7.5$, $p = 0.01$ for both small and medium size classes).

Density-dependent competition with natural recruits on the modules may have influenced the survival and growth of outplanted kelp on the seeded lines. Evidence for this was the observation that the proportion of seeded lines with outplanted kelp after 11 months was inversely correlated to the initial colonization density of naturally recruited kelp (Figure 8a), while the proportion of outplanted kelp in the smallest size category (i.e., <1 m tall) 11 months after outplanting was positively related to the initial colonization density of naturally recruited kelp (Figure 8b).

DISCUSSION

Giant kelp forests are primarily restricted to shallow coastal reefs that are inherently patchy. Local

FIGURE 6 The mean biomass of giant kelp at the artificial reef (Wheeler North) and two nearby natural reefs (San Mateo and Barn) vs. the number of years after construction for (a) Phase 1, (b) Phase 2, (c) Phase 3a and (d) Phase 3b of the artificial reef. Error bars are 1 *SE*.



populations fluctuate greatly in response to a suite of both predictable and unpredictable factors (Graham et al., 2007; Schiel & Foster, 2015), and discrete giant kelp patches commonly go extinct and reappear at irregular intervals (Cavanaugh et al., 2011; Edwards, 2004; Tegner & Dayton, 1987). Such spatial characteristics and temporal dynamics are best explained by giant kelp functioning as a metapopulation in which extant patches serve as donor populations that rescue extinct patches (Castorani et al., 2015; Reed, Kinlan, et al., 2006). The colonization of Wheeler North Reef by giant kelp is consistent with this concept, as the newly constructed reef modules, which were akin to severely disturbed reefs with no survivors, were rapidly colonized by spores dispersed from donor populations that were at least several kilometers away.

Like most plants, dispersal in giant kelp declines exponentially with distance from the source population (Anderson & North, 1966; Gaylord et al., 2002, 2006). Nonetheless, simulations of modeled and

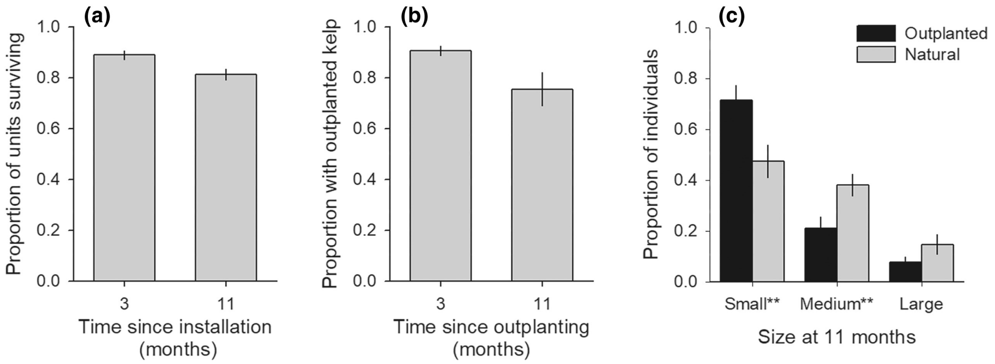


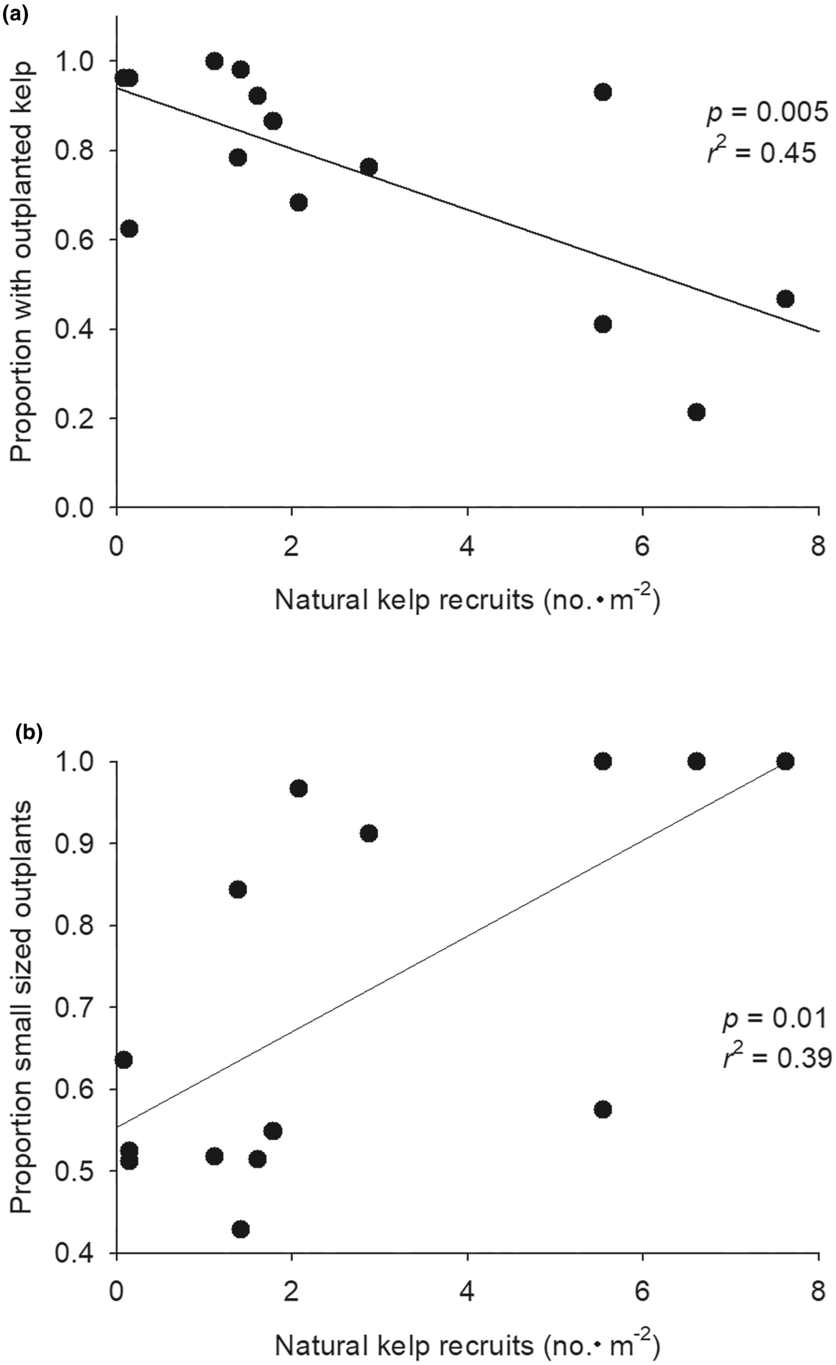
FIGURE 7 Results of outplanting giant kelp on modules of the Phase 1 reef with respect to (a) the proportion of outplant units (PVC plates containing a nylon line with laboratory-reared kelp embryos) that survived for 3 and 11 months after installation, (b) the proportion of outplant units with outplanted kelp 3 and 11 months after outplanting, and (c) the proportion of outplanted and naturally recruited kelp in the small (<1 m tall), medium (≥1 m tall, <8 fronds), and large (>1 m tall, ≥8 fronds) size class 11 months after outplanting. Values are means (± *SE*), $n = 14$ modules. ** in (c) indicates the mean proportion of plants in small and medium size classes differed significantly between outplanted and naturally recruited kelp ($p = 0.01$).

empirical estimates of kelp spore dispersal show that most kelp beds in southern California are connected via spore dispersal to several neighboring kelp beds for a wide range of oceanographic conditions (Reed, Kinlan, et al., 2006). This level of connectivity, even among nearby patches, appears to result from a relatively small fraction of dispersing spores traveling far beyond the average dispersal distance. Importantly, a small fraction of dispersing spores can result in dense colonization when the size and per capita fecundity of the source population are large. This pattern occurs because fluctuations in source population fecundity, rather than oceanographic processes affecting dispersal distance, have been shown to account for most of the observed variation in patch connectivity and metapopulation dynamics in southern California (Castorani et al., 2017). This phenomenon likely contributed to giant kelp's ability to rapidly colonize the most isolated portions of Wheeler North Reef that were relatively far from the closest source populations.

Recolonization of locally extinct kelp patches isolated from nearby sources of spores has often been explained by local dispersal from floating plants or plant fragments that drift through the area (see reviews by Dayton, 1985, Graham et al., 2007, Edwards, 2022). Although this mode of dispersal may be important for range extensions and genetic connectivity (Batista et al., 2018; Macaya & Zuccarello, 2010), it is unlikely to account for rapid and widespread recruitment commonly observed during kelp colonization events following local patch extinctions (Reed, Kinlan, et al., 2006). A more parsimonious explanation for these events is distant spore dispersal that depends on the tails of the dispersal curve, which may be the norm rather than the exception (Reed et al., 2004). Observations of widespread dispersal and rapid recolonization by non-floating kelp species support this hypothesis (Christie et al., 2019; Ebeling et al., 1985; Johnson & Mann, 1988; Norderhaug & Christie, 2009) and the notion that spore dispersal is unlikely to be the bottleneck preventing the recolonization of Laminarian kelps following local extinction (Andersen, 2013; Castorani et al., 2017).

One of the more striking observations of our study was the high spatial variability in the initial colonization of Wheeler North Reef, as the density of kelp recruits on the modules differed by as much as 100-fold for a given phase of the artificial reef. The extent to which this high variability resulted from variation in source population fecundity, oceanographic transport affecting dispersal, or unknown stochastic processes affecting gametophyte reproduction and sporophyte recruitment is uncertain. However, filling this knowledge gap is not critical for determining the main processes affecting kelp establishment in this instance. The high spatial variation in kelp abundance initially observed on the artificial reef modules declined substantially over time due to strong density-dependent survival and growth, which caused the densities of larger plants and fronds to become more evenly distributed. Thus, even when colonization declined significantly with distance from the source population (as was the case for Phase 1), recruitment was still sufficient at the most distant modules to result in high-standing biomass that produced a surface canopy within a couple of years of reef construction. The exception was the Phase 3 modules, which supported much lower densities of plants and fronds than Phases 1 and 2 did. The lower densities of giant kelp observed for Phase 3 may have been due to smaller source populations leading to lower spore settlement and/or unfavorable conditions for kelp recruitment and growth, which were characteristic of the region (as indicated by the low-standing biomass of kelp at nearby natural reefs during this time). That the biomass of giant kelp on all phases of the artificial reef quickly attained levels similar to or greater than that of nearby natural reefs highlights the rapid regenerative capacity of many giant kelp populations in North America commonly observed following catastrophic disturbances that cause

FIGURE 8 (a) Survival (as indicated by the proportion of outplant units with outplanted kelp) and (b) growth as indicated by the proportion of outplanted kelp in the small size class (<1 m tall) as functions of the density of naturally recruited giant kelp. $n = 14$ modules.



local extinctions (Castorani et al., 2015; Cavanaugh et al., 2019; Edwards, 2004; Tegner & Dayton, 1987).

A variety of methods of kelp "seeding" (i.e., dispersing spores and planting small juvenile life stages) have been tried in order to restore diminished kelp forests to a more densely forested state (Eger, Marzinelli, et al., 2022; North, 1976). The method used for outplanting embryonic giant kelp to the artificial reef in this study was relatively successful in that kelp survived for at least 11 months on 66% of the outplant units installed. Despite this level of success, outplanting proved unnecessary due to the widespread natural colonization by giant kelp the first year after the artificial reef was constructed. This finding is important from a restoration context because the effort and expense involved in culturing kelp in the laboratory and in fabricating and installing the outplant units in the field were substantial. That this effort involved only 14 of 56 modules covering ~20% of 10 ha of the Phase 1 reef and produced an average plant density ($0.02 \cdot m^{-2}$) that was ~75 times lower than the average density of natural recruits <1 m tall on the modules farthest from the nearest spore source ($1.5 \cdot m^{-2}$), highlights the enormous effort that would be needed to mimic natural recolonization on deforested reefs via outplanting.

Broadcasting laboratory-reared kelp embryos attached to small substrates has been promoted as a potentially more cost-effective means of seeding kelp for restoration (Eger, Marzinelli, et al., 2022; Fredriksen et al., 2020; North, 1976). We are not aware of any quantitative studies documenting the effectiveness of this method in restoring kelp populations on deforested reefs. North (1976) estimated that only one in 100,000 embryos will reattach successfully to the sea floor and develop into a juvenile plant using this technique. Based on this estimate, 150,000 seeded substrates per m^2 of ocean bottom would have been needed to match the density of recruits observed at the most distant modules of the Phase 1 reef having the lowest recruit densities. Broadcasting such an extraordinarily large number of substrates as a means of restoring kelp on even small reefs only a few hectares in the area would require a massive effort.

Seeding degraded kelp forests with mesh bags filled with sporogenous kelp tissue has been used as a means of providing local sources of spores when recovery is assumed to be limited by spore dispersal (Eger, Layton, et al., 2022; Westermeier et al., 2014). That this method has had limited success in restoring diminished kelp populations (Eger, Marzinelli, et al., 2022) is not surprising given the importance of the size and fecundity of the spore source in promoting colonization (Anderson & North, 1966; Castorani et al., 2017). The number of spores released from a single mesh bag is comparable to that released from a single plant over a few days. Therefore, a relatively high density of bags spread across a large area and replenished with reproductive tissue on a frequent basis would be needed to mimic the spores produced and released by even a small kelp forest. For context, the size of the spore source at San Mateo Reef in the spring of 2000 when the Phase 1 reef was first colonized averaged 0.1 plants $\cdot$ m^{-2} over 166 ha of reef, totaling an estimated 48,000 m^2 of fertile sorus tissue (Reed et al., 2004). A spore source even a small fraction of this size would be extremely difficult to replicate with bags filled with reproductive tissue.

Identifying the cause(s) of kelp decline and the reasons preventing its reestablishment is fundamental to developing a cost-effective plan for restoring diminished populations to a desirable level (Morris et al., 2020). Knowledge of the ecology of kelp colonization is critically important for informing this process. Our results and those of others (Christie et al., 2019; Dayton et al., 1992; Ebeling et al., 1985; Edwards, 2004; Norderhaug & Christie, 2009) documenting the rapid widespread colonization of kelps on deforested reefs, highlight the high potential for degraded kelp forests to recover quickly without human intervention provided the stressors causing degradation (e.g., eutrophication, sedimentation, overgrazing) have been ameliorated (Foster & Schiel, 2010; Scheibling, 1986). Indeed, even the loss of 90% of bull kelp (*Nereocystis luetkeana*) along >350 km of coast in northern California during a severe marine heatwave in 2014–2015 has shown potential for rapid recovery, as the canopy area abruptly increased in 2021 to levels commonly observed during the 30 years preceding the massive decline (Cavanaugh et al., 2023). Such potential for dispersal and widespread colonization, coupled with the enormous effort, high cost, and large uncertainty involved in attempting to mimic these processes by seeding and transplanting provides much incentive for kelp restoration practitioners to follow the guiding principles of ecological restoration, which rely extensively on knowledge gained from research of how communities develop over time (Palmer et al., 1997) and allow for natural colonization and succession to occur whenever possible (Halle, 2007b).

AUTHOR CONTRIBUTIONS

Daniel C. Reed: Conceptualization (lead); formal analysis (lead); funding acquisition (equal); methodology (equal); project administration (equal); writing – original draft (lead); writing – review and editing (equal). **Stephen C. Schroeter:** Conceptualization (supporting); funding acquisition (equal); methodology (equal); project administration (equal); writing – review and editing (equal). **David Huang:** Data curation (lead); formal analysis (supporting); methodology (equal); writing – review and editing (equal). **Denise Weisman:** Data curation (supporting); formal analysis (supporting); writing – review and editing (equal). **Kathryn M. Beheshti:** Conceptualization (supporting); funding acquisition (supporting); project administration (supporting); writing – review and editing (equal). **Rachel S. Smith:** Conceptualization (supporting); funding acquisition (supporting); project administration (supporting); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

All data are housed in the data repository of the Environmental Data Initiative funded by the U.S. National Science Foundation at the locations listed as: Phase 1 giant kelp plant density <1 m: https://doi.org/10.6073/pasta/4e3e5630b861e1584d8302857e3e4565. Phase 1 giant kelp plant and frond density >1 m: https://doi.org/10.6073/pasta/a71750d9c19fc7b36d5f69a68abb7138. Phase 1 rock percent cover: https://doi.org/10.6073/pasta/43a916ccdb946586418ebe870699650b. Phase 1 Survivorship and size of outplanted giant kelp: https://doi.org/10.6073/pasta/16ee5acb21d744f777da223276fff121. Phases 2 and 3 giant kelp plant density <1 m: https://doi.org/10.6073/pasta/3fac38f0633532d33b963c67f80d01f2. Phases 2 and 3 giant kelp plant and frond density >1 m: https://doi.org/10.6073/pasta/075e353f81754b2b5d7ee45638cf30a6. Phases 2 and 3 rock percent cover: https://doi.org/10.6073/pasta/87de677073e08534b30a6fcc5696388.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. The ecology of giant kelp colonization and its implications for kelp forest restoration.

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Supplemental Material

The ecology of giant kelp colonization and its implications for kelp forest restoration

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Figure S1. The colonization of giant kelp on rock and concrete modules of the Phase 1 artificial reef for the first five years following construction. Shown are the means (± *SE*) for: (a) the densities of small plants < 1 m tall, (b) the densities of larger plants ≥ 1 m tall, and (c) the densities of fronds ≥ 1 m tall. n = 21 modules for each reef type. Results of two-way ANOVAs in which reef type (rock vs. concrete) and year after construction were considered fixed factors, showed that the densities of plants (small and large) and fronds on rock and concrete modules were similar in every year ($F_{4,60} < 0.24$, $p > 0.64$ for the effects of reef type and reef type*year interaction in all cases).

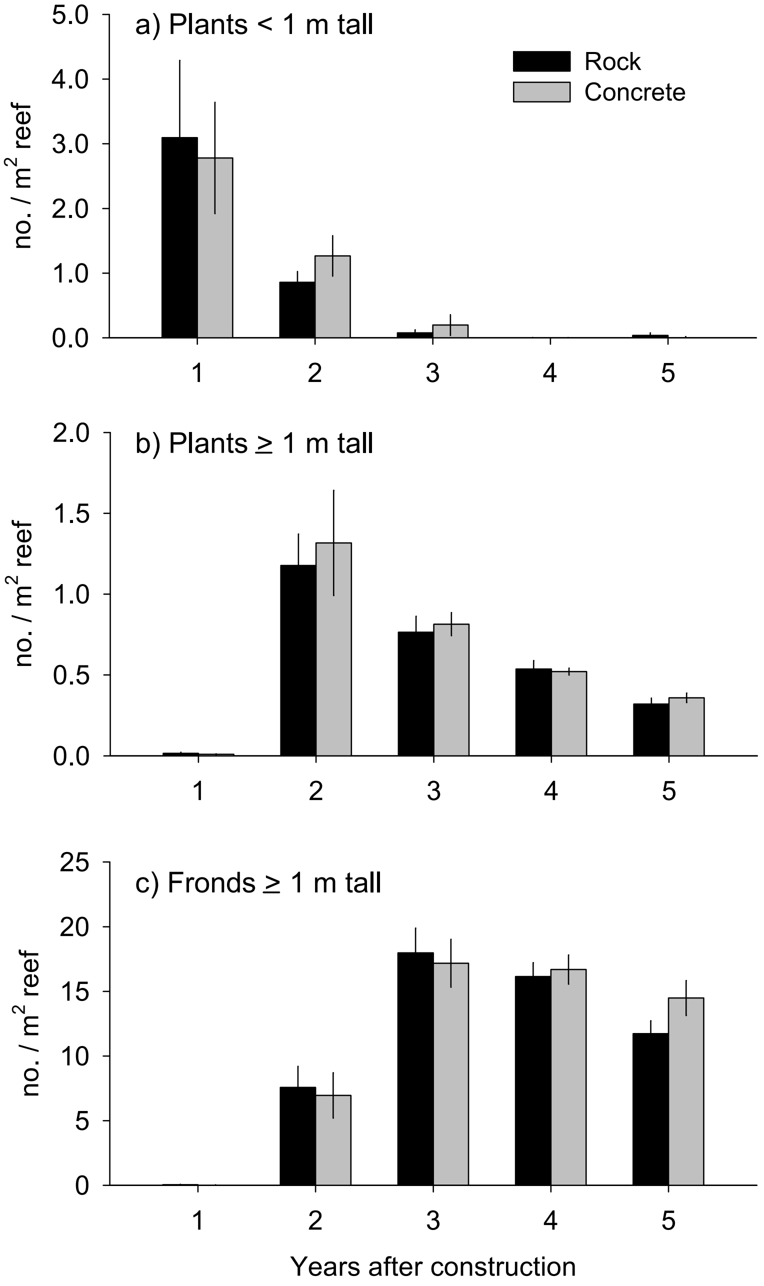

Figure S2. Temporal patterns of giant kelp abundance and size on the Phase 1 modules of Wheeler North Reef during the first 5 years following their construction. Values are means (± *SE*) averaged over 42 modules for: (a) plant size as estimated by the number of fronds ≥ 1 m tall per plant, and (b) plant density.

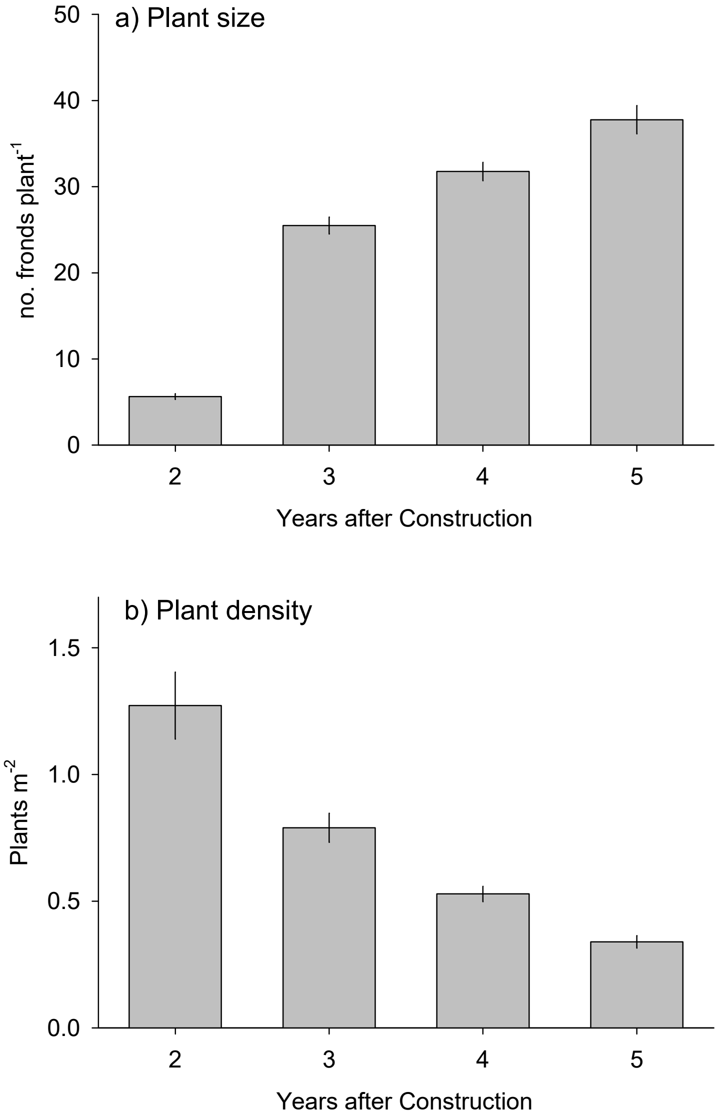

Figure S3. (a) Schematic drawing of phases 1 and 2 of Wheeler North Reef and San Mateo Reef. (b) infrared Google Earth image in 2002, three years after the construction of Phase 1, and (c) color enhanced infrared Landsat image in 2010 two years after the construction of Phase 2. The distribution of surface canopy of giant kelp shown in red in (b) and (c) closely matches the distribution of the artificial reef modules shown in (a).

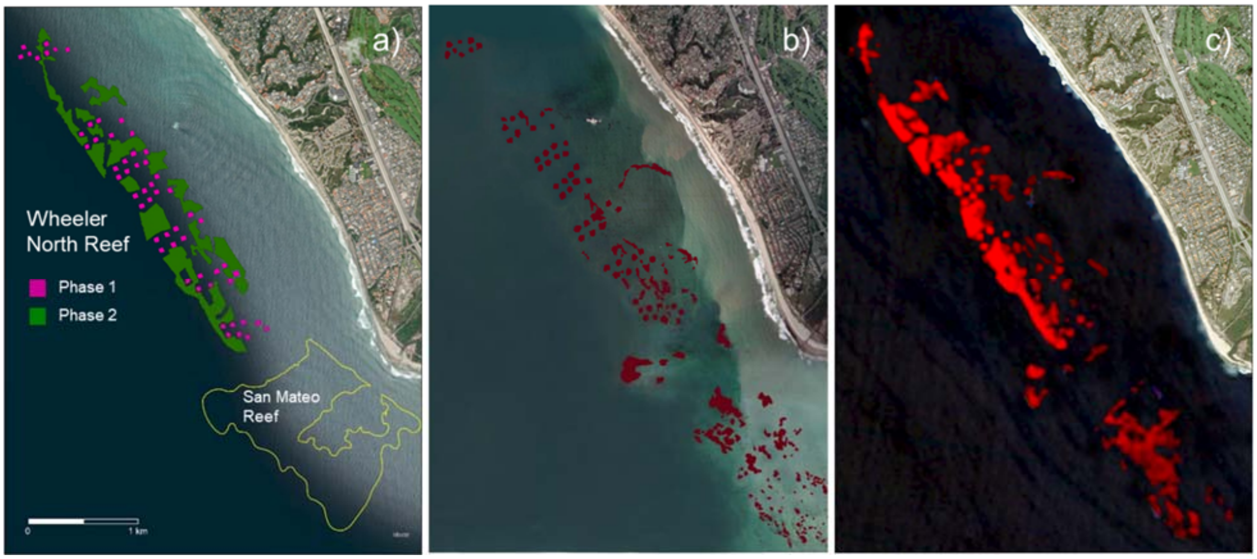

Figure S4. The relationship between the density of: (a) plants < 1 m tall, (b) plants ≥ 1 m tall, and (c) fronds ≥ 1 m tall on the Phase 2 modules and their distance from the nearest Phase 1 module for the first four years following artificial reef construction. Values represent mean densities recorded at 40 sites for each year. No statistics are reported for plants < 1 m tall in year 3 because none were observed at any of the sites.

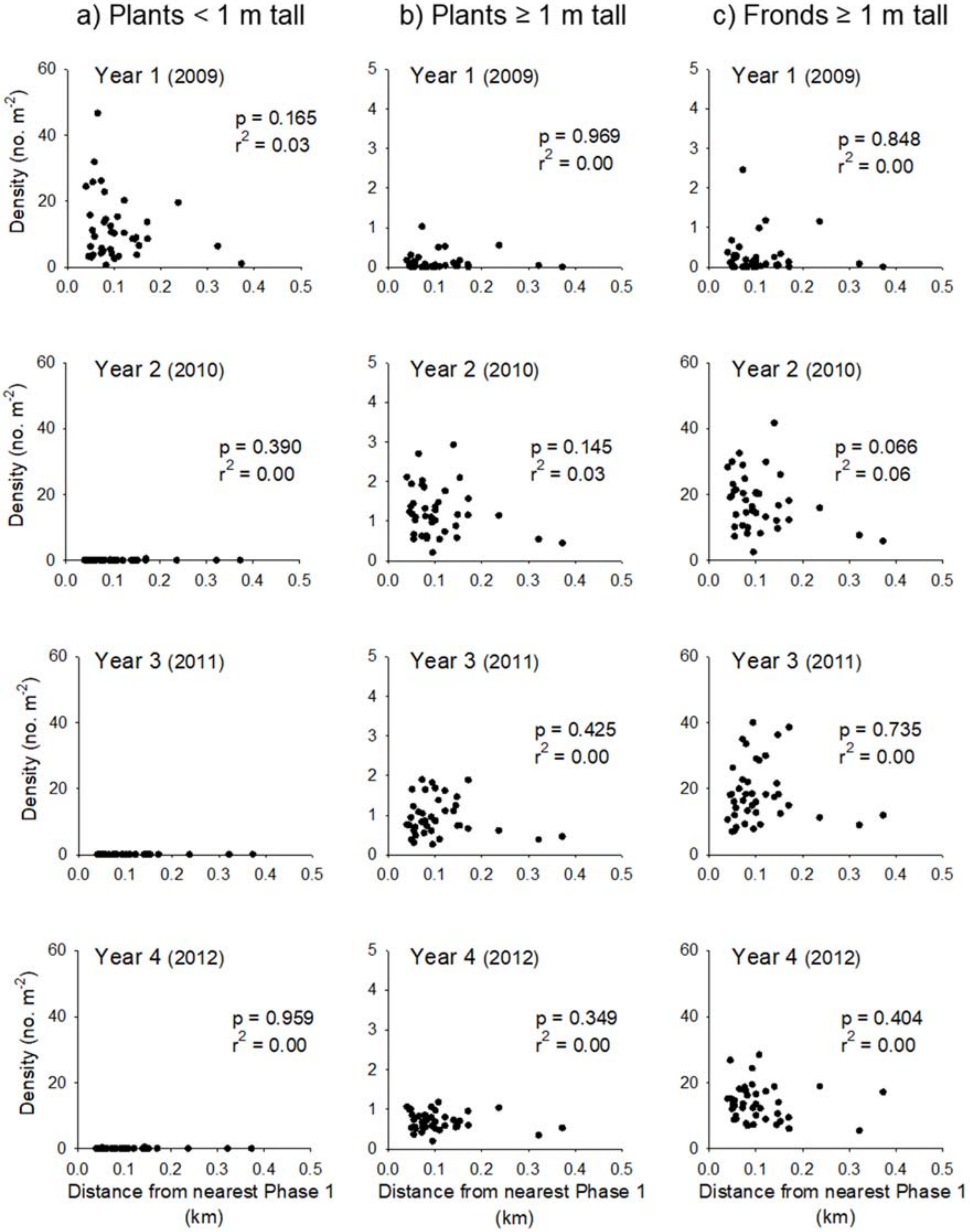

Figure S5. The relationship between the density of: (a) plants < 1 m tall, (b) plants > 1 m tall, and (c) fronds > 1 m tall at Phase 3a of the artificial reef and distance from the nearest kelp population on a previously construction portion of the artificial reef. Data are shown for the first 4 years following the construction of Phase 3a. Values represent mean densities of 37 sites for each year. Regression lines are included when $p < 0.05$. Data for plants < 1 m tall were not collected in 2020 due to restrictions on research caused by the COVID-19 pandemic.

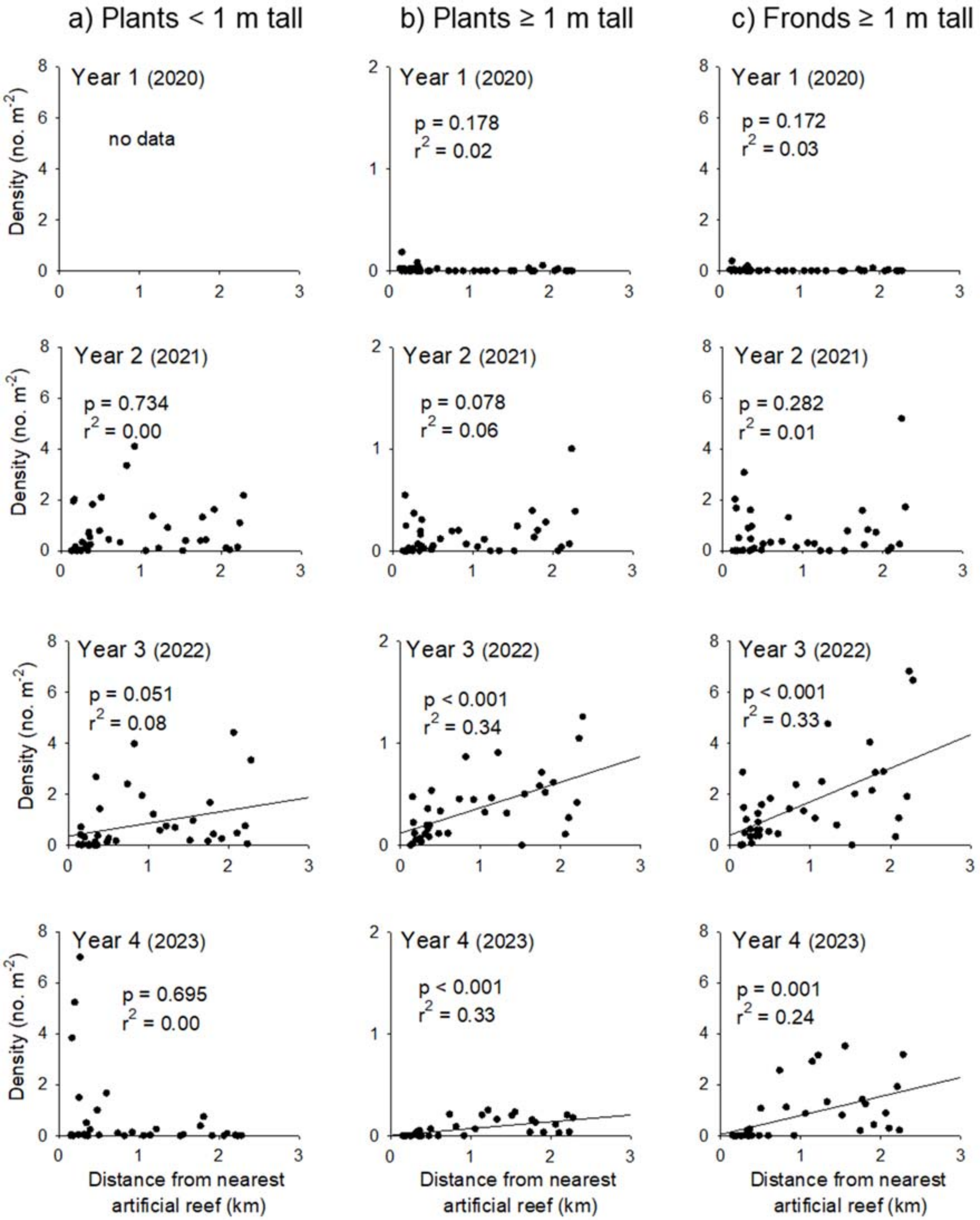

Figure S6. The relationship between the density of: (a) plants < 1 m tall, (b) plants > 1 m tall, and (c) fronds > 1 m tall at Phase 3b of the artificial reef and distance from the nearest kelp population on a previously construction portion of the artificial reef. Data are shown for the first 3 years following the construction of Phase 3b. Values represent mean densities of 20 sites for each year. Regression lines are included when *p* < 0.05.