Spatial and temporal variability of beach-cast wrack and the contribution of an invasive macroalga, *Sargassum horneri*

Ric DeSantiago1,2,3and Jeremy D. Long1,2

1 Department of Biology, San Diego State University, San Diego, CA 98182 USA

2 Coastal and Marine Institute, San Diego State University, San Diego, CA 92106 USA

3 Department of Environmental Science and Policy, University of California, Davis, CA 95616 USA

**Abstract**

Habitat subsidies can strongly shape the structure and function of recipient ecosystems. Human-mediated changes to donor ecosystems via species invasions and climate change could influence the impact of these subsidies. However, the spatiotemporal variation in native and invasive wrack deposition is largely unknown. With respect to spatial variation, the distribution of native and invasive species in donor systems may differ. With respect to temporal variation, native and invasive species may subsidize adjacent systems at different times of the year. Such variation could essentially extend the season during which subsidies influence recipient systems. We surveyed seaweed wrack on beaches that receive large inputs from adjacent kelp forests but that have recently been invaded by the seaweed *Sargassum horneri*. We conducted surveys at seven sites on one of the California Channel Islands at four time points across 2022. We observed spatiotemporal variation in native and invasive wrack inputs to beaches. Kelp dominated wrack inputs throughout the year and *S. horneri* was relatively rare (never exceeding 3% of all wrack found). Kelp was most abundant on west-northwest facing shores, but *S. horneri* was even more rarely found on west-facing shores. The peak period of deposition for these two species also differed, with kelp deposition peaking in September and *S. horneri* deposition peaking in March. These findings highlight the complex spatiotemporal variation in native and invasive wrack inputs, highlighting the complex interplay between these species and their potential to shape recipient communities.

**Introduction**

Habitat subsidies can strongly shape the structure and function of recipient ecosystems (Polis and Hurd 1996, Menge et al. 1997, 2003, Nakano et al. 1999, Jefferies 2000, Palumbi 2003, Spiller et al. 2010). Changes in community structure in donor systems mediated by species invasions and climate change can influence recipient systems (Yang et al. 2008). However, our understanding of how biological invasions in donor communities influence the supply and timing of subsidies to recipient habitats remains limited. Given the strong influence of subsidies on recipient systems, it is important to assess how invasive species affect subsidy exports to fully comprehend the impact of biological invasions.

Marine phytodetritus, dislodged seagrasses, and seaweeds washed ashore (collectively termed “wrack”) critically shape coastal ecosystems (Duggins et al. 1989, Bustamante et al. 1995, Orr et al. 2005). Thus, invasions in subtidal communities may impact the timing and magnitude of wrack subsidies from these donor systems to recipient coastal communities. However, the impact of invasive macroalgae on detrital subsidies to shorelines remains difficult to predict. On the one hand, invasive species can present a lower quality resource for detritivores in recipient systems. On the other hand, non-native primary producers can also diversify detrital food webs by providing an additional food resource to detritivores and decomposers (Rodriguez 2006). For example, a non-native red macroalga *Agarophyton vermiculophyllum*, provides a complementary source of labile organic matter relative to native *Spartina alterniflora* in intertidal salt marshes and mudflats of the southeastern USA (Haram et al. 2020). Similarly, beach-cast tissues of the invasive subtidal macroalga, *Undaria pinnatifida,* provide an alternative food source to native kelps consumed by talitrid amphipods on beaches in southern New Zealand (Suárez-Jiménez et al. 2017).

An example of an invasive seaweed whose impacts on wrack and recipient communities are difficult to predict is *Sargassum horneri*. Because this seaweed can reduce kelp abundance in the California Bight (Marks et al. 2015, Caselle et al. 2018, Sullaway and Edwards 2020) and *S. horneri* is a lower preference food to gastropod detritivores, this invasion may reduce the quantity and quality of wrack (DeSantiago et al., in review). However, the different phenology between *S. horneri* and native seaweeds suggest that this invasion could positively impact recipient habitats. *S. horneri* is most abundant in the subtidal in the winter and spring (Marks et al. 2018) while most dominant native macroalgae in the region, including Giant kelp, *Macrocystis pyrifera,* is most abundant in the summer and fall (Reed et al. 2009, Harrer et al. 2013, Marks 2018). Consequently, although *S. horneri* may be a lower quality food than kelp to some consumers, it may extend the amount of time that wrack is available to intertidal detritivores.

Here, we surveyed wrack at seven sites on one of the California Channel Islands (San Nicolas Island, hereafter SNI) at four time points across one year (March, May, September, and December 2022). At each survey, we measured the proportion of *S. horneri* on the surface of large wrack piles, quantified *S. horneri* and *M. pyrifera* fragments on sandy beaches, and conducted timed searches for *S. horneri* at each survey. Because subtidal kelp and *S. horneri* abundance is non-randomly distributed around the island, we selected four sites on the windward side of SNI (Bachelor, Cosign, Red Eye, and Tender) and three sites on the leeward side (Tranquility, Cissy, Artist).

**Methods**

We surveyed wrack on seven sites on San Nicolas Island, California (Fig. 1). To determine the relative contribution of *S. horneri* to wrack, we measured the proportion of the surface area of large kelp wrack piles (length > 1m) represented by *S. horneri*. This qualitative metric of *S. horneri* prevalence allowed us to quickly and non-destructively sample wrack piles at various sites along the coast. Along a 50 m transect, we measured all large wrack piles, identified the dominant seaweed species, and calculated the pile and *S. horneri* surface area. We estimated the three-dimensional surface area of wrack piles using the formula for a hemi ellipsoid A ≈ 2π \* ( ((a\*b)1.6+(a\*c)1.6+(b\*c)1.6)/3 )1/1.6 + π \* b \* c, where “a” is the depth, “b” and “c” are the semi major axis lengths of the pile. For each *S. horneri* individual encountered on the surface of the pile, we measured its longest length and width to calculate the area using the equation for an ellipse (A=πab), where “a” and “b” are the semi major axis lengths. For a single pile, we calculated the sum area of all *S. horneri* individuals and divided it by the surface area of the pile to estimate the proportion of wrack that consisted of *S. horneri*. Using this method, the relative contribution of *S. horneri* to wrack for a large pile could be estimated in minutes as opposed to hours (DeSantiago et al. *in review*).

To survey wrack not associated with large piles, we also quantified the presence of *M. pyrifera* and *S. horneri* fragments at five of our sites (Artist, Cissy, Red Eye, Tender, Tranquility). To do this, we haphazardly placed a 50m transect parallel with the water on the highest end of each beach, adjacent to the transects in the survey described above. From this transect, we used a measuring wheel starting from three randomly selected points on the transect and moved towards the waterline. Along this “vertical” transect, we counted and measured every fragment of seaweed that was touched by the wheel.

To quantify any *S. horneri* that was not captured by the foregoing methods, we exhaustively searched for *S. horneri* at all sites for 30 minutes by one person or 15 minutes with two people. We conducted these surveys in areas adjacent to the surveys described above to avoid overlap. The length of all *S. horneri* stipes and fragments were measured and recorded.

**Data Analysis**

To compare the total surface area of wrack piles over time, we used a Kruskal-Wallis non-parametric test due to the non-normal distribution of data. We conducted a Dunn’s post-hoc pairwise comparisons test with a Bonferroni adjustment to further investigate the contributions of sites to the variability of wrack area over time. Because *S. horneri* was low in abundance on wrack piles, we did not conduct a formal statistical analysis.

We used the same series of analyses as above to test for differences in seaweed fragments and fragment length per length of beach over time and between sites and conducted Dunn’s post-hoc pairwise tests where appropriate. Since sitewide *S. horneri* occurrence surveys resulted in very few *S. horneri* individual counts, no formal statistics were conducted. All statistical analyses and visualizations were conducted using the R Programming Language (R Core Team, 2023) and ArcGIS® software by Esri.

**Results**

Total wrack abundance displayed spatial variation between sites on San Nicolas Island, with more wrack generally being deposited along sites facing the west to northwest (Bachelor Beach, Cosign, Red Eye, Tender) than sites facing the north to northeast (Tranquility, Cissy, Artist; Fig. 2-4). Three observations about the area of large wrack piles supported this pattern (Fig. 2). First, in March, wrack area was higher at Bachelor, Red Eye, and Tender (p>0.05). Second, in May, wrack area was higher in Tender than Cissy (p<0.005). In September, Bachelor and Cosign had more wrack area than Tranquility (p=0.01 and p<0.001, respectively). Large wrack piles were always dominated by *M. pyrifera*.

Our fragment density surveys revealed a similar spatial pattern whether we considered number of fragments or length of fragments per unit length (Fig. 3, Kruskal-Wallis: *X* 2 =16.283, df = 4, p =0.002 and Fig. 4, Kruskal-Wallis: *X* 2 =16.374, df = 4, p =0.003) but not over time (p= 0.09; Fig. 3). The density of seaweed fragments was higher at Tender (a northwest facing beach) than all sites (p<0.05) except Red Eye (also a northwest facing beach, p=0.19). Tranquility was excluded from this analysis because the site was not accessible during March and May. In these fragment density surveys, *Sargassum* *horneri* was found rarely and only at the northwest/north facing shorelines [one fragment at Cissy (March and May) and Artist (September), 6 fragments at Red Eye, and 25 fragments at Tender (September)]. Similarly, when fragment length was considered, *S. horneri* was most prevalent at Red Eye and Tender (Fig. 4).

Total wrack abundance of large piles (as determined by calculating the sum of the large pile surface area) displayed temporal variation (Kruskal-Wallis: *X* 2 =38.336, df = 3, p <0.001) (Fig. 2-4). These large wrack piles were dominated by *M. pyrifera* throughout the year (Fig. 2). For any given site, *M. pyrifera* was most abundant in May or September. Although total area of large wrack piles did not differ between May and September (p=0.08), large piles were only found them at three out of the seven sites in May suggesting September was the peak period (Fig. 2C, E, F). *Sargassum horneri* was rare on pile surfaces, and was only seen in March (2.5 ± 1.7 % of pile surface area at Cissy and Red Eye) and May (0.3 ± 0.2 % of pile surface area at Cissy and Tender).

*S. horneri* was most prevalent in our March timed searches whether we considered number of sites where it was found, number of thalli found at a site, or length of thalli found (Table 1). Unlike *M. pyrifera* which was common in September, we found no *S. horneri* in our September timed searches. All *S. horneri* individuals found in March and December were partial or complete sections of adult plants, and those found in May were complete, reproductive adults.

**Discussion**

Wrack piles on San Nicolas Island were dominated by *M. pyrifera* throughout time. However, in March, wrack piles at Artist and Cissy were dominated by *Stephanocystis* spp. and *Phylospadix* spp. dominated wrack piles at Artist in December. In a few instances, there were no piles larger than 1m to conduct this survey (Artist and Bachelor in May; Cissy and Tranquility in December). We did not have access to Tranquility and Cosign in March and May. Wrack cover by pile surface area was highest in May and September, however, most of the wrack cover in May was due to the large piles on Tender (Fig. 2F). *S. horneri* was present during March and May but only accounted for a small percent of the surface area (2.5 ± 1.7 % in March and 0.3 ± 0.2 % in May). There was no strong temporal pattern of seaweed fragment frequency per length of beach but there were more fragments at Tender and Red Eye. Similarly, fragments were generally longer at Tender and Red Eye. *Sargassum horneri* fragments were rare but identified in March, May, and September. Surprisingly, exhaustive searches did not reveal any *S. horneri* in September but were found at every other sampling period (March, May, and December).

While there were no strong temporal patterns, wrack subsidies may reflect the *S. horneri* invasion of nearby kelp forests. For example, kelp forests around SNI are dominated by canopy-forming Giant kelp *M. pyrifera*, which in turn dominated the wrack. Moreover, wrack piles at Artist and Cissy were dominated by *Stephanocystis* in March, a dominant fucoid in a nearby kelp forest monitoring site (Nav Fac 100; Kenner and Tomoleni 2021). Furthermore, Nav Fac 100 has been invaded by *S. horneri* since it was first observed in 2015 and has occurred on every subsequent monitoring trip (Kenner and Tomoleni 2021). Although sources of macrophyte drift on coasts is dependent on currents, wind, wave action, morphological features and exposure of recipient habitats, it is likely that this invaded kelp forest exported *S. horneri* to nearby sites.

The pattern of the *S. horneri* invasion on San Nicolas Island kelp forests remains unclear. For example, *S. horneri* densities at Nav Fac 100 are low during the spring and increase several-fold in the fall (Kenner and Tomoleni 2021), in concurrence with its reproductive lifecycle. However, *S. horneri* densities have decreased every spring since it was initially recorded. While our year-long monitoring effort allowed us to see differences in seasonal and spatial variability of *S. horneri*, a longer monitoring effort may better estimate the impact of this kelp forest invasion. Furthermore, *S. horneri* has not been recorded at any other kelp forest monitoring site, yet our study found that *S. horneri* was also in the wrack at Bachelor (SNI west end, windward side), Red Eye and Tender (SNI northwest, windward side), Artist and Cissy (SNI north, leeward side), in at least one of three surveys. It should be noted that although we were unable to access Cosign (September and December), *S. horneri* has previously been quantified in the wrack on this site (DeSantiago et al. *in review*). Moreover *S. horneri* has been observed attached intertidally at Cosign (S. Graham, unpublished data, 2020, cited within Kenner and Tomelini 2021; DeSantiago pers. ob. 2020).

The distribution of *S. horneri* on SNI suggests that the invasion has spread beyond kelp monitoring sites. It is unlikely that local hydrology facilitated the movement of *S. horneri* from the known invaded site (Nav Fac 100) to the west-facing windward coast. Moreover, our exhaustive surveys found that *S. horneri* plants found in March were reproductive adults at all sites, suggesting that although densities may be low in Nav Fac 100, reproductive *S. horneri* may be propagating on other sites at SNI. Despite *S. horneri’*s local recruitment, its ability to self-fertilize, and pneumatocysts that allow it to float, make it a highly successful gamete propagator (Marks et al. 2015). Additionally, *M. pyrifera* detached by wave action could also detach *S. horneri*, evidenced by our wrack pile surveys that reveal *S. horneri* intertangled with *M. pyrifera*.

Our results suggest that *S. horneri* can be found in the wrack throughout the year. This was surprising due to *S. horneri*’s known reproductive cycle in which biomass is low during winter when *S. horneri* are small tufts of seaweed, yet we found mature adults in the wrack in December. While it is known that *S. horneri* has the features to be a highly successful invader, it is unknown to us if the genotype of this species found on SNI and other Channel Islands has adapted to a differing reproductive cycle to that of its native range. For example, *S. horneri* adults have been established in at least two intertidal sites on San Clemente Island throughout the year (Pollard et al., *unpublished data;* DeSantiago *pers. ob.* 2021). Our study suggests there is a complexity to *S. horneri* that is not easily captured by a single survey type. We highlight the importance of using various methods when monitoring invasive species to properly assess spatial and temporal distribution.

Although we did not find strong evidence to support complementary timing of *S. horneri* compared to native wrack species, *S. horneri* may provide an additional food source for some species while reducing fitness of others. For example, sandy beaches and the macrofauna that inhabit them are almost entirely supported by allochthonous subsidies (Dugan et al. 2003). Recent studies revealed that native amphipods, *Megalorchestia* *benedicti*, exhibited lower preference for *S. horneri* and lower performance on diets of *S. horneri* compared to *M. pyrifera* in the lab, and smaller *M. benedicti* were associated with *S. horneri* in the field. Moreover, abalone fed *S. horneri* and a mixed diet that included *S. horneri*, grew less than those fed *M. pyrifera* alone (DeSantiago et al. *in review*). In a separate study, abalone who were fed *S. horneri* diets displayed lower performance and higher mortality than those fed *M. pyrifera* and an invasive alga, *Undaria pinnatifida* (Bauer et al. 2023). Conversely, although black turban snails, *Tegula funebralis*, did not show a preference for *S. horneri,* they grew more on diets that included it (DeSantiago et al. *in review*). Understanding the distribution of invasive *S. horneri* in the wrack is critical in assessing its potential impacts on subsidy-dependent communities in both rocky and sandy beaches, as it has the potential to impact detritivores and consumers at both.

**Acknowledgements**

We thank the Navy Marine Ecology Consortium for facilitating access to San Nicolas Island Field sites. This work could not have been completed without the support of students and technicians who assisted in the field: Jessica Patzlaff, Halina Perez, Lauren Strope, and Anthony Truong. We would also like to thank William F. Hoyer III for his guidance and vast knowledge of the natural history of San Nicolas Island and the sites within and Jennifer Dugan for assistance in method development and her inspirational work. This project was funded by the U.S. Navy (Cooperative agreement N62473-20-2-0007) . R. Desantiago was supported by the University Graduate Fellowship at San Diego State University.

**Literature cited**

Bauer, J., R. Beas-Luna, M. Emeterio-Cerecero, J. Vaca-Rodríguez, G. Montaño-Moctezuma, and J. Lorda. 2023. Growth and survival of juvenile red abalone ( *Haliotis rufescens* ) fed invasive macroalgae. New Zealand Journal of Marine and Freshwater Research:1–13.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18:119–125.

Bustamante, R. H., G. M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Schleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd, and C. McQuaid. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102:189–201.

Caselle, J. E., K. Davis, and L. M. Marks. 2018. Marine management affects the invasion success of a non‐native species in a temperate reef system in California, USA. Ecology Letters 21:43–53.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166.

DeSantiago, R., W.K. White, J.R. Hyde, K.M. Swiney, and J.D. Long. In review. Consumer- and seaweed-specific impacts of invasion-mediated changes to detrital subsidies on rocky shores. Ecology.

Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science 58:25–40.

Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173.

Falkowski, P., R. J. Scholes, E. Boyle, J. Canadell, D. Canﬁeld, J. Elser, N. Gruber, and K. Hibbard. 2000. The global carbon cycle: a aest of our knowledge of earth as a system. Science 290:7.

Gorman, D., B. D. Russell, and S. D. Connell. 2009. Land-to-sea connectivity: linking human-derived terrestrial subsidies to subtidal habitat change on open rocky coasts. Ecological Applications 19:1114–1126.

Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. Global Change Biology 18:504–514.

Haram, L., E. Sotka, and J. Byers. 2020. Effects of novel, non-native detritus on decomposition and invertebrate community assemblage. Marine Ecology Progress Series 643:49–61.

Harrer S.L., D.C. Reed, S.J. Holbrook, R.J. Miller. 2013. Patterns and controls of the dynamics of net primary production by understory macroalgal assemblages in giant kelp forests. Journal of Phycology 49: 248–257.

Harrison, L.N. 2022. An invasive alga as a potential subsidy disruptor in beach wrack-associated assemblages. Thesis. San Diego State University, San Diego, California, USA.

Jefferies, R. L. 2000. Allochthonous inputs: integrating population changes and food-web dynamics. Trends in Ecology & Evolution 15:19–24.

Kenner, M. C., and J. A. Tomoleni. 2021. Kelp forest monitoring at Naval Base Ventura County, San Nicolas Island, California: Fall 2019, sixth annual report. U.S. Geological Survey Open-File Report 2021-1081.

Mack, R. N., D. Simberloff, W. Mark Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequence, and control. Ecological Applications 10:689–710.

Marks, L., D. Reed, and S. Holbrook. 2018. Life history traits of the invasive seaweed *Sargassum horneri* at Santa Catalina Island, California. Aquatic Invasions 13:339–350.

Marks, L., P. Salinas-Ruiz, D. Reed, S. Holbrook, C. Culver, J. Engle, D. Kushner, J. Caselle, J. Freiwald, J. Williams, J. Smith, L. Aguilar-Rosas, and N. Kaplanis. 2015. Range expansion of a non-native, invasive macroalga *Sargassum horneri* (Turner) C. Agardh, 1820 in the eastern Pacific. BioInvasions Records 4:243–248.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proceedings of the National Academy of Science 94:14530-14535.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences 100:12229–12234.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

Orr, M., M. Zimmer, D. E. Jelinski, and M. Mews. 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86:1496–1507.

Palumbi, S. R. 2003. Ecological subsidies alter the structure of marine communities. Proceedings of the National Academy of Sciences 100:11927–11928.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. The American Naturalist 147:396–423.

Reed, D., A. Rassweiler, K. Arkema. 2009. Density derived estimates of standing crop and net primary production in the giant kelp *Macrocystis pyrifera*. Marine Biology 156: 2077-2083.

Rodriguez, L. F. 2006. Can invasive species facilitate native species? evidence of how, when, and why these impacts occur. Biological Invasions 8:927–939.

Ruiz, G. M., J. T. Carlton, E. D. Grosholz, and A. H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. American Zoologist 37:621–632.

Spiller, D. A., J. Piovia-Scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, and T. Iwata. 2010. Marine subsidies have multiple effects on coastal food webs. Ecology 91:1424–1434.

Suárez-Jiménez, R., C. D. Hepburn, G. A. Hyndes, R. J. McLeod, R. B. Taylor, and C. L. Hurd. 2017. Importance of the invasive macroalga *Undaria pinnatifida* as trophic subsidy for a beach consumer. Marine Biology 164:113.

Sullaway, G., and M. Edwards. 2020. Impacts of the non-native alga *Sargassum horneri* on benthic community production in a California kelp forest. Marine Ecology Progress Series 637:45–57.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

**Figure and table captions**

Figure 1

Map of San Nicolas Island field sites.

Figure 2

Total surface area of large wrack piles (m2) over sampling period (March, May, September, December) by site Artist (A), Bachelor (B), Cissy (C), Cosign (D), Red Eye (E), Tender (F), Tranquility (G). Colors represent dominant wrack species. \* Denotes sites we were unable to access, and zeroes (0) denote there was no wrack piles found on that site.

Figure 3

Mean seaweed fragment frequency per meter of sandy beach by site in March (A), May (B), September (C) and December (D). Colors represent seaweed species. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier ranges.\* Denotes sites we were unable to access.

Figure 4

Mean seaweed fragment length per meter of sandy beach by site in March (A), May (B), September (C) and December (D). Colors represent seaweed species. Lines inside boxes are median values, box limits are Q1 and Q3, and whiskers represent non-outlier ranges.\* Denotes sites we were unable to access.

Table 1

Results of total *Sargassum horneri* thalli found in exhaustive timed searches by sampling period and site. Mean length of total *S. horneri* found on each site during that sampling period and standard error are reported in each column.

**Figures and tables**

Figure 1

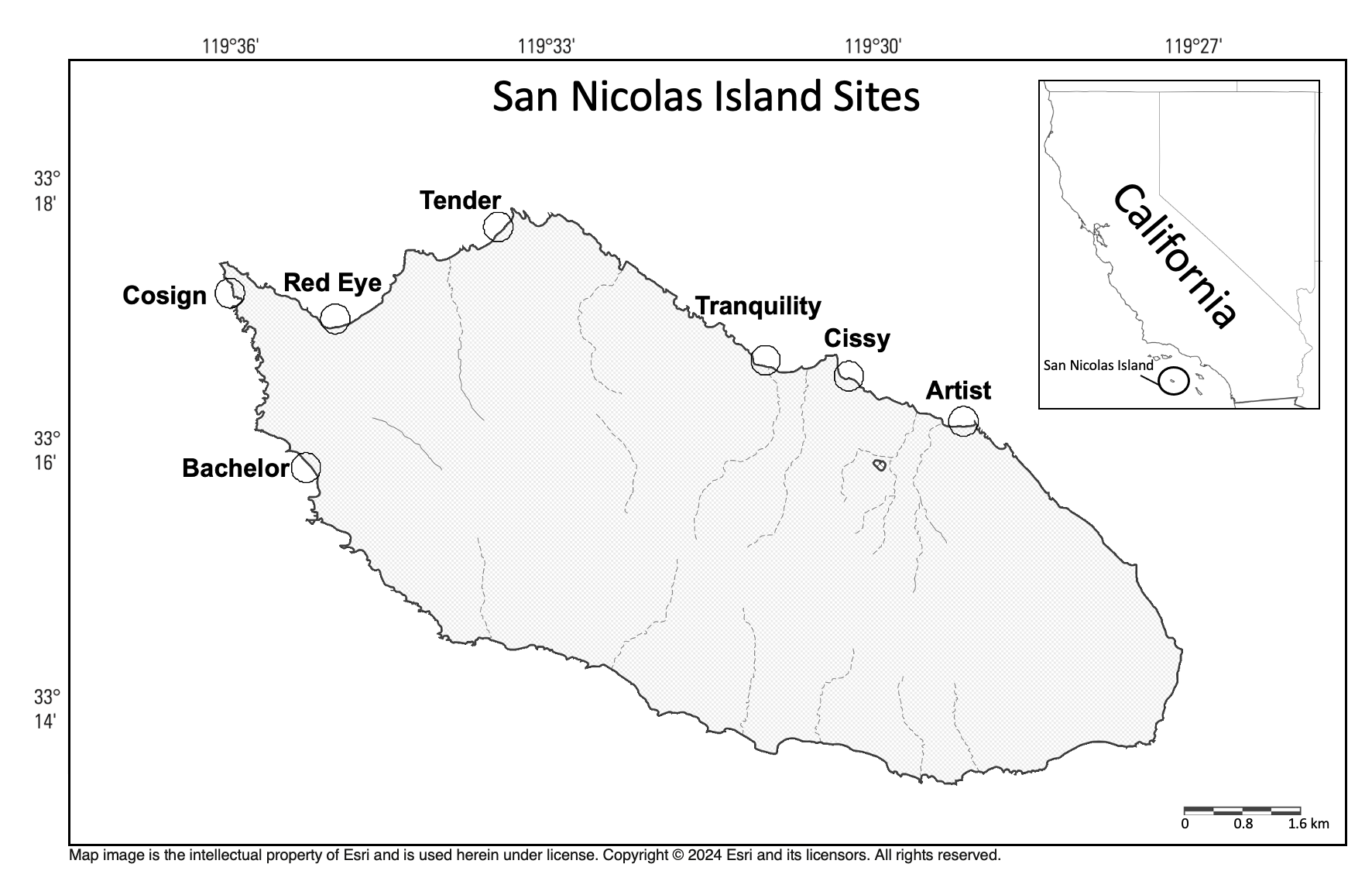


Figure 2 **A chart with different colored squares

Description automatically generated**

Figure 3

**A chart of different types of seaweed

Description automatically generated**

Figure 4

**A chart of different types of seaweed

Description automatically generated**

Table 1

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Trip | Site | # of thali | Mean length (m) | Length SE |
| March | Bachelor | 3 | 0.74 | 0.18 |
| Cosign | NA | NA | NA |
| Red Eye | 5 | 0.48 | 0.10 |
| Tender | 2 | 0.75 | 0.13 |
| Tranquility | NA | NA | NA |
| Cissy | 8 | 0.72 | 0.14 |
| Artist | 2 | 0.83 | 0.01 |
| May | Bachelor | NA | NA | NA |
| Cosign | NA | NA | NA |
| Red Eye | 2 | 0.36 | 0.07 |
| Tender | 2 | 0.08 | 0.01 |
| Tranquility | NA | NA | NA |
| Cissy | 3 | 0.38 | 0.18 |
| Artist | NA | NA | NA |
| September | Bachelor | NA | NA | NA |
| Cosign | NA | NA | NA |
| Red Eye | NA | NA | NA |
| Tender | NA | NA | NA |
| Tranquility | NA | NA | NA |
| Cissy | NA | NA | NA |
| Artist | NA | NA | NA |
| December | Bachelor | NA | NA | NA |
| Cosign | NA | NA | NA |
| Red Eye | NA | NA | NA |
| Tender | 3 | 0.37 | 0.63 |
| Tranquility | NA | NA | NA |
| Cissy | NA | NA | NA |
| Artist | 1 | 0.52 | 0 |