Spatial and temporal variability of invasive macroalga, *Sargassum horneri*, in beach-cast wrack on San Nicolas Island, California

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**Abstract**

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**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, such as extinction, invasion, and alternative stable states in donor system can cause persistent effects from resource subsidies (Yang et al. 2008). Furthermore, anthropogenic perturbations like nutrient depositions, overharvesting, shifts in predator guilds, and climate change are increasingly modifying natural ecosystems (Falkowski et al. 2000, Worm et al. 2006, Greig et al. 2012). Consequently, the quality and quantity of subsidies will likely change as humans alter ecosystems through species introductions and range shifts associated with climate change (Gorman et al. 2009). However, our understanding of how biological invasions in donor communities influence the supply and timing of subsidies to recipient habitats remains limited. Thus, it is important to assess how invasive species affect subsidy exports to fully comprehend the impact of biological invasions.

Differing life history and reproductive strategy between introduced species and native counterparts may result in complementary timing of biomass contributions to a system. Invasive species can drastically reshape ecosystems through various mechanisms such as increasing competition with, and predation of native species, reducing biodiversity, hybridizing with native species, and introducing pathogens (Vitousek et al. 1996, Ruiz et al. 1997, Mack et al. 2000, Crooks 2002, Bruno et al. 2003, Rodriguez 2006). However, 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).

Marine phytodetritus, dislodged seagrasses, and seaweeds washed ashore (collectively termed “wrack”) are a crucial food source and have significant ecological consequences to shore and nearshore habitats (Duggins et al. 1989, Bustamante et al. 1995, Orr et al. 2005). Thus, invasions in subtidal kelp forests may impact the timing and magnitude of wrack subsidies from these donor systems to recipient coastal communities. For example, the recent growing invasion of *Sargassum horneri* in kelp forests in the California Bight (Marks et al. 2015) has the ability to reduce kelp abundance (Caselle et al. 2018, Sullaway and Edwards 2020), thus, changing wrack composition on kelp-subsidized coasts. *Sargassum horneri* embodies the traits commonly associated with successful biological invaders: rapid growth, local dispersal, high densities, and prolific reproduction(Marks et al. 2018). Moreover, *S. horneri* is an annual species whose biomass peaks in the winter and spring (Marks et al. 2018) while most dominant native macroalgae in the region, including Giant kelp, *Macrocystis pyrifera,* are perennials whose biomass peak during summer and falls (Reed et al. 2009, Harrer et al. 2013, Marks 2018). Consequently, the contribution of *S. horneri* to wrack may be complementary to that of native seaweeds.

Here, we surveyed wrack at seven sites on San Nicolas Island (SNI) to quantify the contribution of *S. horneri* to wrack over the course of one year. 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 exhaustive timed searches for *S. horneri* at each site. To detect a temporal pattern of *S. horneri* wrack, we conducted these surveys in March, May, September, and December 2022. To understand spatial patterns, 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). Due to nesting birds, we were unable to sample Cosign in March and May.

**Methods**

We assessed the spatial and temporal deposits on seven sites that often receive wrack deposits on San Nicolas Island, California (Fig. 1). To determine the relative contribution of *S. horneri* to wrack, we surveyed large (>1m) wrack piles deposited on beaches and rocky shorelines and measured the proportion of the pile surface area *S. horneri* represented. This qualitative metric of *S. horneri* prevalence allowed us to quickly and instructively sample wrack piles at various sites along the coast. We measured all wrack piles we encountered along a haphazardly placed 50 m transect, identified the dominant seaweed species, and calculated the 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*).

Because beached seaweeds are often dislodged by physical forces that fracture stipes and seaweeds further break down on the shore, we also quantified the presence of *M. pyrifera* and *S. horneri* fragments on sites that included sandy beaches (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. We used a measuring wheel starting from three randomly selected points on the transect, counted and measured every fragment of seaweed that intercepted the wheel from the transect to the waterline.

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 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. We repeated these statistical analyses between sites at each time point. Because *S. horneri* was low in abundance on wrack piles, we did not conduct a formal statistical analysis and present the proportion of wrack pile surface area represented by *S. horneri*.

We used the same series of analyses as above to test for differences in seaweed total seaweed fragments per length of beach 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.

**Results**

Wrack piles on all sites primarily consisted of *M. pyrifera* throughout the year (Fig. 2). Total wrack area differed over time (Kruskal-Wallis: *X* 2 =38.336, df = 3, p <0.001) with most wrack occurring in May and September. Although total wrack area did not differ between May and September (p=0.08), we only found wrack piles larger than 1m at three out of the seven sites in May (Fig. 2C, E, F). During March, wrack area was significantly higher at Bachelor, Red Eye, and Tender and there was no statistical difference between them (p>0.05). In May, wrack area was significantly higher in Tender than both Cissy and Red Eye (p<0.005). In September, there was no difference between wrack area at the sites except Tranquility had less wrack than Bachelor (p=0.01) and Cosign (p<0.001). In December, there was no difference between wrack area with the exception of Tender which had more wrack cover than Artist (p=0.03) and Cosign (p<0.001). It should be noted that at this time point, wrack piles at Artist were dominated by *Stephanocystis spp*. *Sargassum horneri* presence was sporadic on pile surfaces, quantified only at Cissy and Red Eye in March (combined 2.5 ± 1.7 %) and Cissy and Tender in May (combined 0.3 ± 0.2 %).

Overall, the number of seaweed fragments (*M. pyrifera* and *S. horneri*) per length of beach differed between sites (Kruskal-Wallis: *X* 2 =16.283, df = 4, p =0.002) but not over time (p= 0.09; Fig. 3). The number of seaweed fragments per meter of beach was higher at Tender than all sites (p<0.05) except Red Eye (p=0.19). Cissy was left out of this and the next analysis due to vastly different sample sizes because the site was not accessible during March and May. *Sargassum* *horneri* was present at Cissy during March and May, Artist, Red Eye, and Tender in September but was low in abundance and not adequate for formal statistics (number of *Sargassum* fragments found at Cissy: 1 in March and 1 in May; Artist: 1 in September, Red Eye: 6 in September, Tender: 25 in September).

Lengths of seaweed fragments differed between sites (Kruskal-Wallis: *X* 2 =16.374, df = 4, p =0.003) but not over time (p=0.51, Fig. 4). Seaweed fragments were longer at Tender than every other site (p<0.05) except Red Eye (p>0.05). Lengths at Tender and Red Eye did not differ over time (p>0.05). The length of *S. horneri* did not vary over time (p=0.60) or by site (p=0.25).

We found *S. horneri* through exhaustive searches in March, May, and December but none in September (Table 1). All *S. horneri* individuals found 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, two of the sites that are near the Nav Fac 100 kelp forest monitoring site (Kenner and Tomoleni 2021), were dominated by *Stephanocystis* spp. wrack piles in March, a dominant fucoid in the Kenner and Tomoleni (2021) monitoring site. 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, 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 on 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 their potential impacts to native habitats both in the wrack and attached to substrage.

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.

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**Figure and table captions**

Figure 1

Map of San Nicolas Island field sites

Figure 2

Total surface area of 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 species that dominated wrack piles. \* Denotes sites we were unable to access.

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 and bars represent mean ± standard error. \* 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 and bars represent mean ± standard error. \* 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

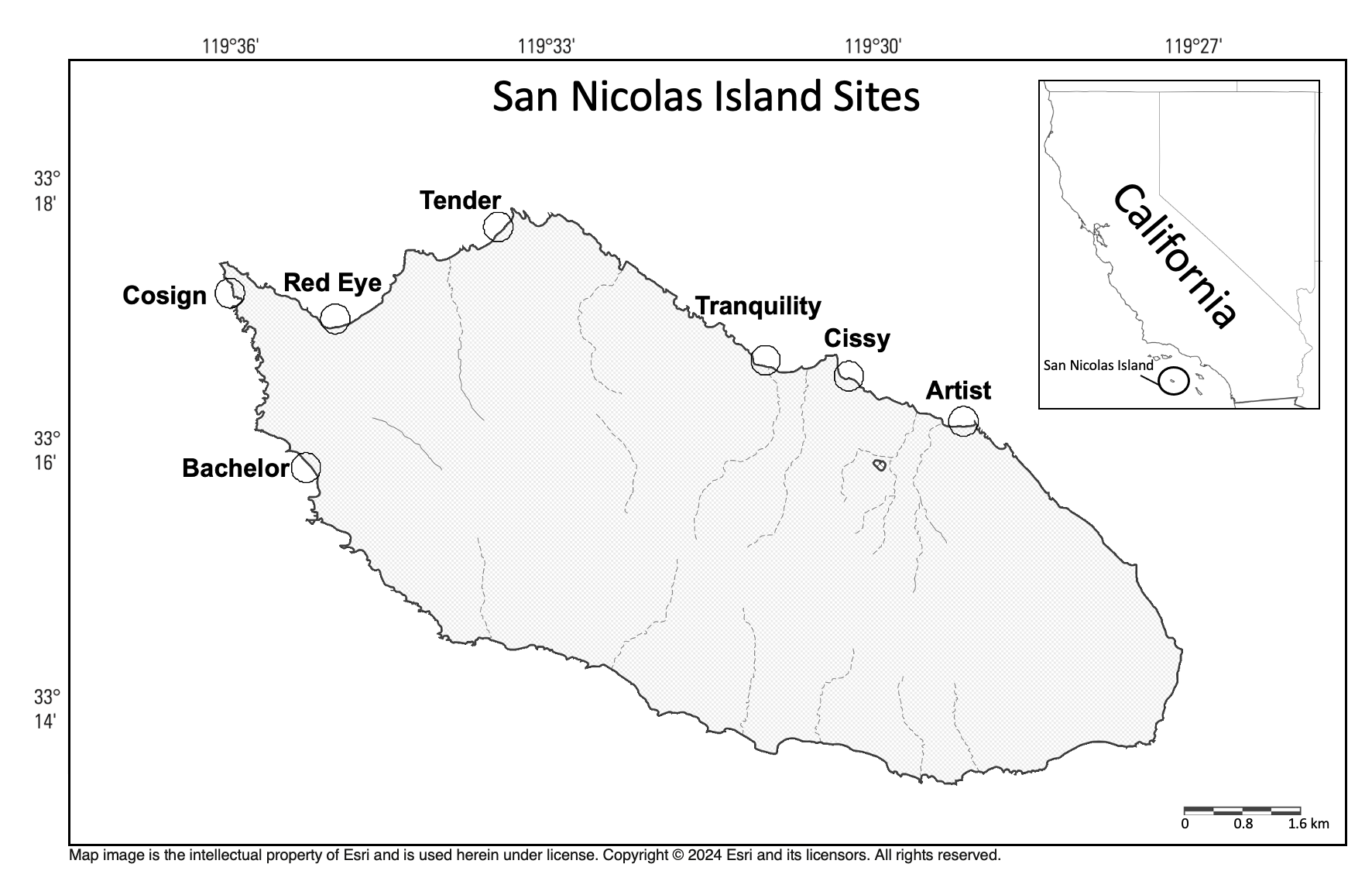


Figure 2

**A chart with text and green squares

Description automatically generated with medium confidence**

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)** | **SE** |
| March 2022 | Artist | 2 | 0.83 | 0.01 |
| March 2022 | Bachelor | 3 | 0.74 | 0.18 |
| March 2022 | Cissy | 8 | 0.72 | 0.14 |
| March 2022 | Red Eye | 5 | 0.48 | 0.10 |
| March 2022 | Tender | 2 | 0.75 | 0.13 |
| May 2022 | Cissy | 3 | 0.38 | 0.18 |
| May 2022 | Red Eye | 2 | 0.36 | 0.07 |
| May 2022 | Tender | 2 | 0.08 | 0.01 |
| December 2022 | Bachelor | 1 | 0.52 | 0 |
| December 2022 | Tender | 3 | 0.37 | 0.63 |