Title

Spatiotemporal patterns of invasive Devilweed *Sargassum horneri* in beach-cast seaweed wrack on San Nicolas Island, California

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Abstract

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). The quality and quantity of subsidies will likely change as humans alter ecosystems through species introductions and range shifts associated with climate change. For example, lowered palatability of subsidies from replacement by less desirable invaders may 1) reduce the use of such subsidy by consumers, 2) shift consumption pressure onto native species, or 3) disproportionately impact some consumers of such subsidies. However, life histories, reproductive strategy, and resistance to physical perturbations by introduced species may result in differing and sometimes complementary timing compared to native counterparts. Thus, understanding the seasonality and composition of resource pulses is needed to better understand if invasive species either reduce the quality and quantity of subsidies or serve as an additional subsidy.

The flow of subsidies between ecosystems is often in the form of seasonal inputs from a donor to recipient ecosystems, however, physical perturbations from climatic events (e.g., storms, El Niño / La Niña) may change the timing and magnitude of some subsidies. These events may be brief and rare but account for a substantial proportion of all available resources in a system and can have important, sometimes persistent, effects on a wide range of communities (Ostfeld and Keesing 2000, Yang et al. 2008). Moreover, anthropogenic perturbations such as nutrient depositions, overharvesting, altered predator guilds, and climate change are altering natural ecosystems [(Falkowski et al., 2000, Greig et al., 2012, Worm et al., 2006)](https://www.zotero.org/google-docs/?WGalYb), thus, altering the quality and quantity of subsidies. However, we lack an understanding of how biological invasions in donor communities can change the supply and timing of organisms and materials to recipient habitats. Thus, monitoring of resource pulses in subsidized ecosystems may help us understand if invaders overlap or complement native resources.

Many beaches and rocky intertidal shores worldwide receive large inputs of wrack from offshore donor systems. It is well established that marine phytodetritus, dislodged seagrasses, and seaweeds washed ashore (collectively termed “wrack”) have significant ecological consequences to nearshore and shore habitats [(Bustamante et al., 1995, Duggins et al., 1989, Orr et al., 2005)](https://www.zotero.org/google-docs/?25X4OH). Moreover, climate change is expected to increase the ranges of some species, and human activities increasingly move non-indigenous species beyond their natural ranges [(Rilov and Crooks, 2009, Ruiz et al., 1997)](https://www.zotero.org/google-docs/?ygqfQW). For example, the recent growing invasion of Devilweed (*Sargassum horneri*) in kelp forests of southern California and Channel Islands [(Marks et al., 2015)](https://www.zotero.org/google-docs/?0ijcyF) may impact wrack-associated communities, including protected Black abalone (*Haliotis cracherodii*) and their habitats.

Devilweed exhibits the characteristics that make biological invaders successful; Devilweed is fast-growing, disperses locally, occurs in high densities, and invests in copious reproduction (Marks et al. 2018). Moreover, life history components such as early, late, or extended flowering periods can enhance reproductive fitness of invaders in novel environments and promote invasion success (Pyšek and Richardson 2007, Marks et al. 2018). Although, most dominant native macroalgae in the region are perennial (Reed et al. 2009; Harrer et al. 2013; Marks 2018) their biomass peaks seasonally during summer and fall, Devilweed is an annual whose biomass peaks in the winter and spring (Marks et al. 2018). Thus, Devilweed is co-occurs with native macroalgae but this differing seasonality will likely result in variable contributions to wrack. Here, we sampled wrack on seven sites on San Nicolas Island to quantify Devilweed’s wrack contribution on wrack the surface of wrack piles, as fragments on beaches, and through exhaustive timed searches.

**Methods**

We assessed the presence of Devilweed in the wrack on seven sites on San Nicolas Island, California (Fig. 1). To determine the relative contribution of Devilweed to wrack, we surveyed large (>1m) wrack piles deposited on beaches and rocky shorelines and measured the proportion of the pile surface area Devilweed represented. This qualitative metric of Devilweed 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 measured the surface area. We calculated 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 Devilweed 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 Devilweed individuals and divided it by the surface area of the pile to estimate the proportion of wrack that consisted of Devilweed. Using this method, the relative contribution of Devilweed to wrack for a large pile could be estimated in minutes as opposed to hours (DeSantiago et al. *in prep*).

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 Kelp and Devilweed 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 Devilweed 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 Devilweed stipes and fragments were measured and recorded.

**Data Analysis**

**Results**

Wrack on all sites was dominated by giant kelp throughout the year (Fig. 2). Devilweed was only found on the surface of wrack piles in March (2.5 ± 1.7 m2) and May (0.3 ± 0.2 m2). Total wrack area differed over time (Kruskal-Wallis: *X* 2 =38.336, df = 3, p <0.001) with the highest wrack area in May and September. Although 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 and most of the wrack area was found at the Tender site. Wrack area did not differ between March and December (p=0.09) and was lower than that of May and September (p<0.01).

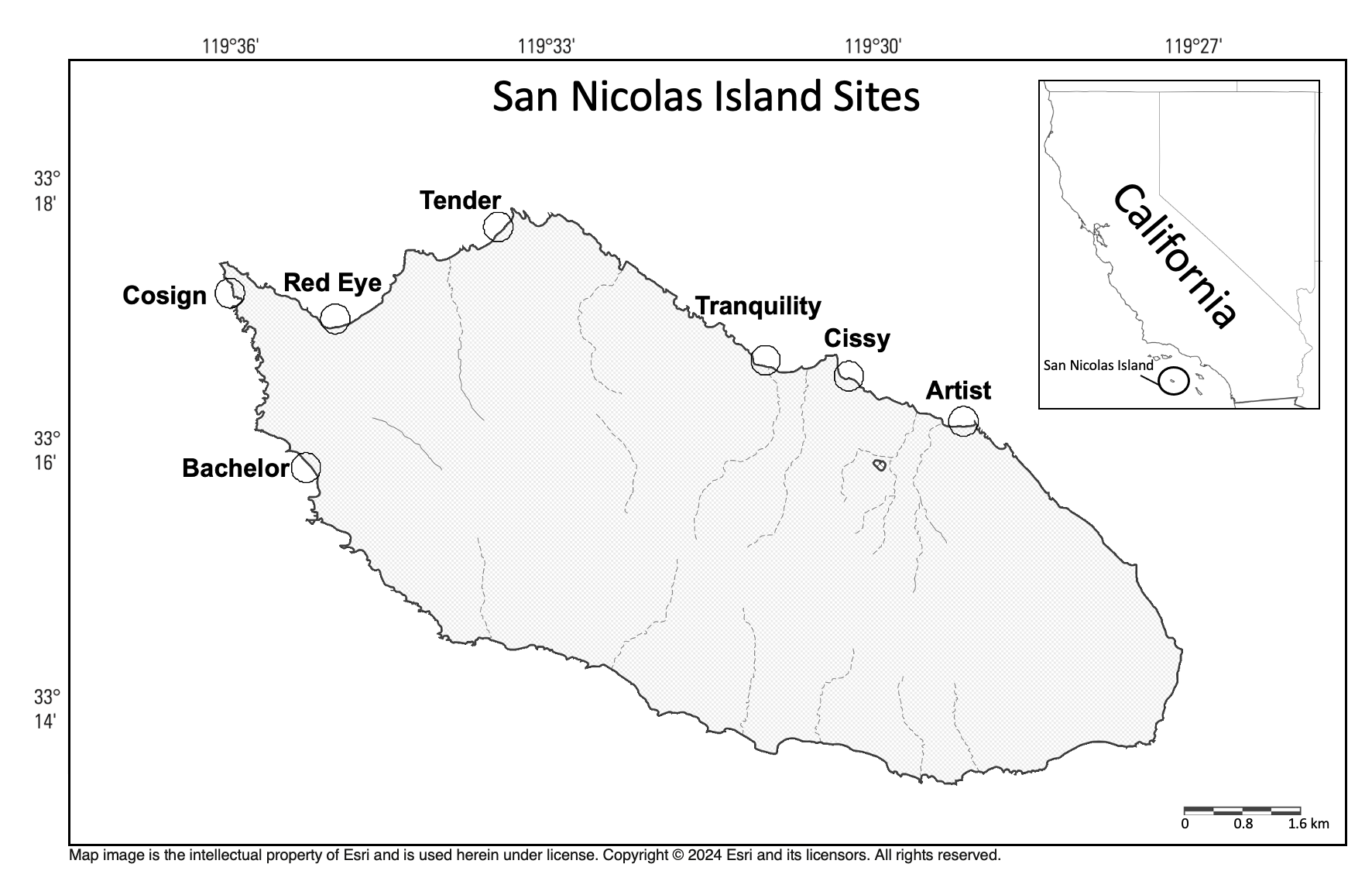
The number of seaweed fragments per meter of beach did not differ over time (p= 0.65) or between sites (p=0.67; Fig. 3). Devilweed fragments per meter of beach were marginally higher September than other trips (ANOVA: F3,53 =2.84, p =0.04), but were overall fewer than kelp fragments (two-sample t test: t57.44 = 8.06, p <0.001). Seaweed fragment length differed between sites (2-Way ANOVA: F4,96 =2.96, p =0.02) but not over time (p=0.95) and the two factors did not interact (p=0.59; Fig. 4). Seaweed fragments were longest at Tender and Red Eye and did not differ beteen each other (Tukeys HSD: p=0.98).

Inconsistent with the previous surveys, we found Devilweed through exhaustive searches during March, May, and December but none in September (Table). All Devilweed individuals found in exhaustive searches were adults, and those found in May included reproductive parts.

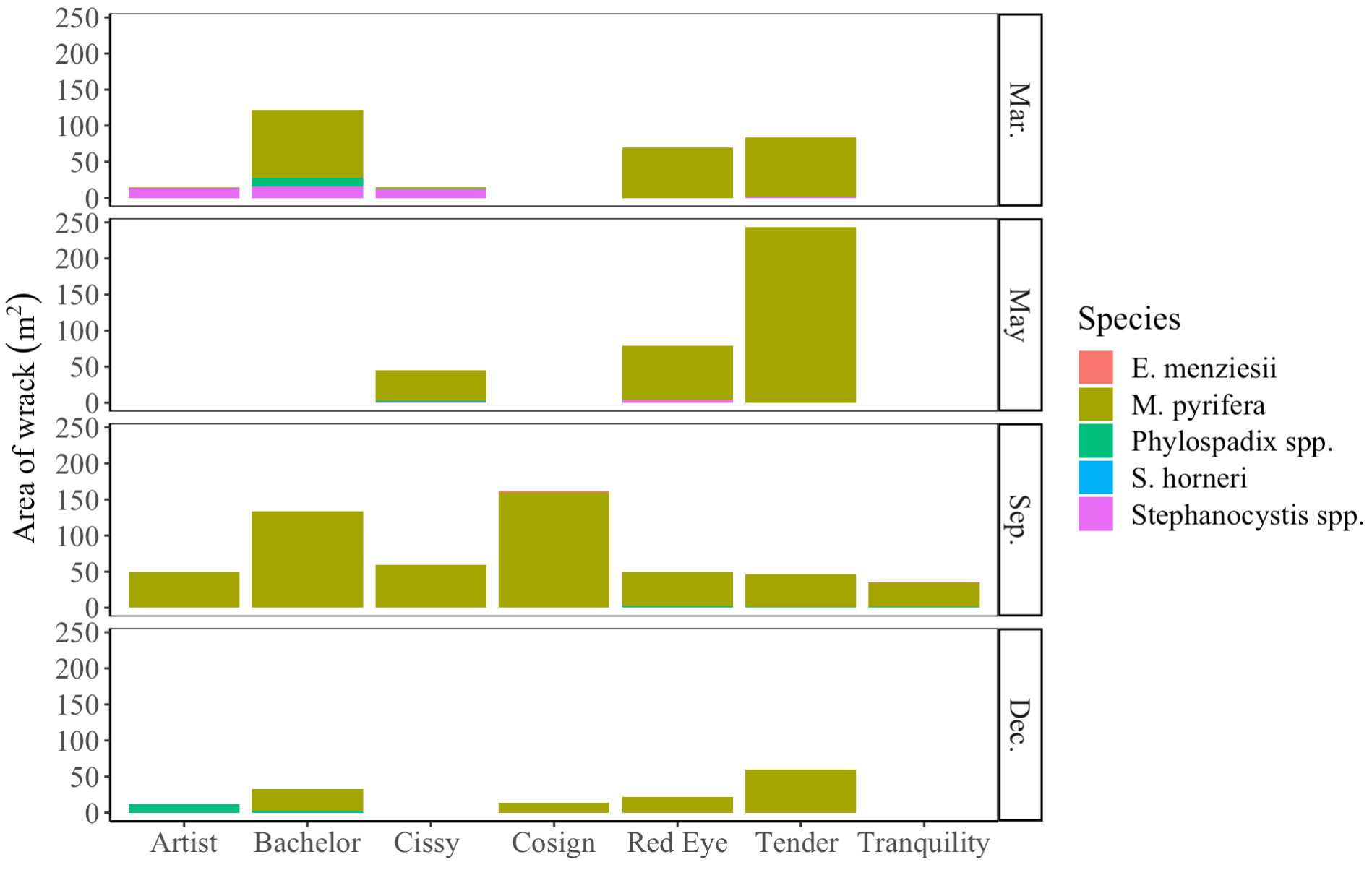
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Figures



Total surface area of wrack piles larger (> 1m) by species by site per sampling trip

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Three-dimensional surface area of wrack piles larger than 1m using the formula for half of an ellipsoid (see below). On the y axis is the area in squared meters by site, separated by month. As you can imagine, the weight of bars is primarily Macrocystis. This graph does not show S. horneri very well as it only accounts for a small portion of the wrack. When detected in piles, Sargassum horneri consisted of 2.4 +/- 1.6% of the surface area of those piles.

Total number of beached seaweed fragments found per m

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The Mean fragment size seem to be centered around 32mm – 64 mm occurrences of s. horneri only really showing up in September. More S. horneri per unit time found in March and may, some found in December but none in September.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **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 | Redeye | 5 | 0.48 | 0.10 |
| March 2022 | Tender | 2 | 0.75 | 0.13 |
| May 2022 | Cissy | 3 | 0.38 | 0.18 |
| May 2022 | Redeye | 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 |

**Discussion**