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Deposition, Persistence, and Utilization of Kelp Wrack Along the Central California Coast

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DEPOSITION, PERSISTENCE, AND UTILIZATION OF KELP WRACK ALONG THE CENTRAL CALIFORNIA COAST

A Thesis
Presented to the
Faculty of the
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In Partial Fulfillment
of the Requirements for the Degree
Master of Science

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by
Jarred A. Klosinski
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CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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DEPOSITION, PERSISTENCE, AND UTILIZATION OF KELP WRACK ALONG THE CENTRAL CALIFORNIA COAST

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ABSTRACT

Deposition, Persistence, and Utilization of Kelp Wrack
Along the Central California Coast
by
Jarred A. Klosinski
Master of Science in Marine Science
California State University Monterey Bay, 2015

Kelp wrack occurs year round along temperate coastlines providing food to a low productivity environment; few efforts however, have been made to quantify wrack's variability in deposition, persistence, and utilization along beaches and the rocky intertidal. Knowing the biomass deposited, persistence (amount of time a piece of wrack is found in an area), and how primary and secondary consumers respond to wrack allows for a better understanding of how these three variables work together to promote a food web and the ecological implications of the presence/absence of wrack within an area. My work focused on spatiotemporal variation in wrack deposition, persistence, and utilization by kelp flies and bacteria in central California from April 2013 to August 2014. Changes in wrack biomass density, persistence on the shore, phlorotannin concentration, bacterial density, and kelp fly density were measured along with a suite of other factors including species composition, condition (individual or fragmented), and burial. Over the study period, a significant difference in biomass density was found between substrates with higher amounts of wrack on the rocky intertidal. In addition, persistence maps indicating hotspots of prolonged wrack accumulation showed a significant increase in kelp wrack at greater distances from the shoreline, such as the berm on beaches and the high intertidal in the rocky intertidal, although no difference between substrate was observed. In terms of utilization, phlorotannin concentration did not appear to affect bacterial abundance or fly density, which suggested that the levels present in kelp wrack were not a strong deterrent for bacteria and flies. A two-week experiment was also conducted, which manipulated the weight of the giant kelp *Macrocystis pyrifera* to determine its effect on the above-mentioned factors. The rate of water loss and persistence was measured daily, while utilization changes occurred on a slower scale and were measured weekly. During this time, kelp fly density changed significantly between substrate, while phlorotannins decreased significantly over time. Again, there was no relationship between phlorotannin concentration, bacterial abundance, or fly density, although bacterial abundance and fly density increased when wrack was rehydrated by high tides after initial desiccation. Quantifying deposition, persistence, and utilization of kelp wrack is important to establish baselines, make comparisons, and understand the interactions taking place that can affect wrack's ecological role as a subsidy.

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INTRODUCTION

Highly productive systems serve an invaluable ecological role as energy sources for marine systems (Mann 1972, Duggins 1980, Fasham 1984, Simenstad and Wissmar 1985, Carpenter 1986, Duggins et al. 1989). Ecosystems with high primary productivity can directly sustain higher trophic levels, whereas areas of low productivity often rely on subsidies as their energy source (Vetter 1994, Polis and Hurd 1996, Orr et al. 2014). Subsidies are defined as “a donor controlled resource (prey, detritus, nutrient) from one habitat to a recipient (plant or consumer) from a second habitat, which increases population productivity of the recipient, potentially altering consumer resource dynamics in the recipient system” (Polis et al. 1997). The flow of energy outside of these highly productive environments can support secondary production, which supplies food and nutrients to surrounding low productivity environments.

Terrestrial organisms in low productivity marine systems (such as beaches and the rocky intertidal) utilize subsidies of organic material for energy like beach wrack (detached macroalgae and sea grass) and carrion (animal carcasses) (Polis and Hurd 1996, Ince et al. 2007). The removal of seaweeds from a kelp forest is one of the main sources of marine subsidies to the shore (Zobell 1971, Dugan et al. 2003). The addition of kelp wrack to beaches and the rocky intertidal has been shown to increase the species abundance and diversity of consumers (Dugan et al. 2003, Ince et al. 2007, Mellbrand et al. 2011), increase dune vegetation on beaches (Dugan and Hubbard 2010), and increase the abundance of primary and secondary consumers in terrestrial food webs (Duggins et al. 1989, Bustamante and Branch 1996, Mellbrand et al. 2011). The presence of kelp subsidies along temperate coasts allows for wrack-associated communities to flourish.

Kelp detritus is critical to secondary production on the coast and its presence or absence drives the abundance of populations of consumers (Duggins et al. 1989, Bustamante et al. 1995, Bustamante and Branch 1996, Dugan et al. 2011). Therefore, beach-cast kelp can be instrumental in supporting diversity in low productivity areas.

The production of kelp detritus is regulated primarily by oceanographic conditions. Waves from winter storms frequently remove kelp from the substrate and set them adrift (Zobell 1971, Dayton et al. 1984, Ebeling et al. 1985, Witman 1987, Seymour et al. 1989, Dayton et al. 1992, Graham et al. 1997). Seasonal cycles of high wrack abundance in winter and low wrack abundance in summer relates to the timing of these storms (Zobell 1971, Koop and Field 1980). However, kelp loss does not occur only in the winter, as frond erosion occurs all year long (Gerard 1976, Mazure and Field 1980, Jarman and Carter 1981, Newell et al. 1982, Griffiths et al. 1983, Soares et al. 1997). The balance between uprush and backwash varies; backwash is higher on reflective beaches than on dissipative beaches, and wave uprush is stronger than backwash (Masselink and Hughes 2003) leading to a net deposition of wrack on beaches and the rocky intertidal. Once kelp thalli are removed from the substrate, some float to the surface as rafts. Drifting kelp can act as a mechanism for kelp dispersal where the fronds, which are still alive, can release spores and travel up to 7 km/day (Hernandez et al. 2006). In the Southern California Bight, there is approximately 14,000 to 376,000 tons of drifting kelp annually (Hobday 2000). Similarly, it is estimated that 130,000 tons of *M. pyrifera* are exported from Monterey Bay kelp forests (Harrold and Lisin 1989) and can be deposited on the shore after 5-7 days at sea (Harrold and Lisin 1989). Currents are responsible for the transport of the rafts; however, drift kelp from Monterey Bay generally stays near Monterey Bay

(Harrold and Lisin 1989). In addition, currents are important in allowing drift seaweed to accumulate within bays (Bustamante et al. 1995), indicating that coastal morphology can magnify the amount of wrack deposited. In general, the storms that are responsible for removing the kelp do not transport it far from the kelp forest (Zobell 1971).

The residence time of wrack on the beach varies spatially and temporally (Zobell 1971). It is not uncommon for detritus deposition to be uneven across the beach since wrack is strongly influenced by abiotic factors such as exposure, slope, and buoyancy (Orr et al. 2005, McLachlan and Brown 2006, Duong and Fairweather 2011). Nearshore water movement determines where kelp wrack will be deposited (Zobell 1971), but the distribution of wrack along a beach is controlled primarily by tides, with wrack deposited during incoming tides and removed during outgoing tides (Zobell 1971, Orr et al. 2005). Wrack that is higher on the beach will be less likely to be removed (Rodil et al. 2008). Mixed semi-diurnal tides can reach different levels of the shore creating a constant addition and removal of wrack over time. Factors including slope, beach area, grain size, and wave exposure can be important in determining the amount of wrack that stays on the beach (Zobell 1971, Orr et al. 2005, Barreiro et al. 2011). For instance, wrack deposited during higher tides remains on the beach longer (Rodil et al. 2008) and is typically found along the high tide mark of the beach (McLachlan and McGwynne 1986). Depending on tides and waves, detritus can be retained for more than a week (Zobell 1971, McLachlan and McGwynne 1986).

The majority of the California coastline is composed of beaches, with only 28% being rocky shoreline (Storlazzi and Field 2000). Along the coastline, wrack is added daily (Bustamante et al. 1995, Orr et al. 2005). Since wrack input is known to be spatially variable (Zobell 1971, Orr et al. 2005) and oceanographic conditions differ between beaches and the rocky intertidal (Zobell 1971, Barreiro et al. 2011, Orr et al. 2005), wrack deposition and persistence should also differ between beaches and the rocky intertidal leading to differences in utilization within the food web.

Wrack deposition can vary based on the type of substrate, as seen on the 2005 study by Orr et al. in British Columbia, which found significant differences between the amounts of detritus that accumulated on beaches of different grain sizes from cobble to sand. The Monterey Bay coast can consist of a range of sediment sizes, for example, beach sediments can be comprised of sand or gravel derived from the watershed and the continental shelf sources (Bird 2000, Sallenger et al. 2002, Smith et al. 2005), although rivers are the main source (Patsch and Griggs 2006). In central California, the origin of the beach sand includes the Salinas, Pajaro, and San Lorenzo Rivers, erosion from coastal cliffs, dunes, and offshore sands (Dingler and Reiss 2002). For sand to accumulate on beaches, sediment transport occurs through littoral cells, which move sediment from sources (i.e. rivers) to sinks (i.e. submarine canyons) by alongshore currents (Storlazzi and Field 2000, Frihy and Dewinder 2003, Patsch and Griggs 2006). In Monterey Bay, at least two littoral cells exist, one in northern Monterey Bay where transport is to the south and flows in a clockwise motion, and one in southern Monterey Bay, which is less defined (Thornton et al. 2006). It is possible that substrate types as well as the different water movement patterns found throughout the region are responsible for the different amounts of wrack deposited on the coast.

Marine algae allocate resources for chemical defense (Geiselman and McConnell 1981, Steinberg 1984, Steinberg 1985, Tugwell and Branch 1989, Steinberg and van

Altena 1992, Duggins and Eckman 1997, Hammerstrom et al. 1998, Levinton et al. 2002). Members of the brown algae (class Phaeophyceae) produce phlorotannins that may deter bacteria and herbivory (Geiselman and McConnell 1981, Harrison 1982, Levinton et al. 2002, Nagayama et al. 2002). The concentration of phlorotannins varies among kelp species (order Laminariales), which in general have low levels compared to species of the order Fucales (Van Alstyne et al. 1999a, Van Alstyne et al. 1999b). No longer photosynthetically active, detritus ceases production of phlorotannins, and phlorotannin concentration decreases during the decay process (Duggins and Eckman 1997, Levinton et al. 2002) making detrital kelp more available for consumption. Therefore, drift kelp deposited at the high tide line should have lower phlorotannin concentrations than kelp at low tide since it has been on the shore longer.

The most abundant and important organisms in the wrack are bacteria, which are responsible for remineralizing the detritus back into nutrients (Koop et al. 1982, Mann 1988, McGwynne et al. 1988, Inglis 1989). As a primary consumer of kelp wrack, bacterial growth is affected by the presence of phlorotannins (Duggins and Eckman 1997, Nagayama et al. 2002) and the abundance of bacteria on detritus is based on the age of wrack (Duggins and Eckman 1997). Bacteria have been shown to increase with drier wrack (Imamura et al. 2011) and seasonally vary in abundance (Stenton-Dozey and Griffiths 1983, McGwynne et al. 1988). Regardless of bacterial abundance, decomposition, and the complete breakdown process can take up to a year (Valiela et al. 1985). Once the nutrients are released, flushing of the shore by tides and waves can return the nutrients to the sea, which in turn can support primary production in the ocean (Koop et al. 1982, Newell et al. 1982). The long decomposition process allows phlorotannins to decay making organic matter available for remineralization (Duggins and Eckman 1997).

The presence of kelp flies on wrack serves as an indication of wrack's nutritional quality. Kelp flies are members of the order Diptera, which solely inhabit kelp wrack and are early colonizers of wrack appearing within four days of being deposited onto the shore (Lavoie 1985, Mellbrand et al. 2011). The utilization of kelp wrack by kelp flies varies depending on where it is deposited in relation to the water line and the length of time on the shore. Adult flies consume the mucilage excreted by the kelps as well as bacteria on the surface of the algae (Bender 1975, Griffiths and Stenton-Dozey 1981, Cullen et al. 1986), whereas their larvae consume the alga when bacterial decomposition begins (Kompfner 1974). Therefore, flies may be indirectly affected by phlorotannins since they consume the bacteria that are present based on phlorotannin concentration. Overall, flies can be both primary and secondary consumers of wrack, whose variability in deposition and retention determines the species that uses it as a subsidy.

To understand the processes responsible for the deposition and persistence of wrack, as well as determining how usage of wrack by bacteria and kelp flies is affected by phlorotannins, field surveys, experiments, and laboratory work were completed. Surveys and experiments were designed to address the following hypotheses:

1) Kelp wrack biomass varies spatially and temporally between beaches and the rocky intertidal.
2) Kelp wrack persistence varies spatially and temporally between beaches and the rocky intertidal.

3) Phlorotannin concentrations in *M. pyrifera* affects the presence of bacteria and kelp flies on the surface of the wrack.

METHODS

Study sites and sampling design

Research was conducted at six sites alternating between rocky coastline and beaches in central California, spanning from Davenport to Carmel, to capture variability around Monterey Bay and also to distinguish sites as independent replicates of beaches and rocky intertidal. Beach sites included Salinas River State Beach (SRSB), Monterey State Beach (MSB), and Carmel River State Beach (CRSB); and rocky shore sites included Davenport Landing Beach (DLB), Stillwater Cove (SWC), and Soberanes Point (SP) (Figure 1). The sites were chosen due to limited human disturbance and the sites were variable distances from kelp forests. Data collected within each site were averaged to obtain one value for each type of substrate and hereafter, sites will be referred to as *beaches* or the *rocky intertidal*. Approximately two 50 m x 50 m quadrats from the water line at MLLW to the beginning of the sand dune or sea cliff were randomly sampled from April 2013 to June 2014. One quadrat was used to collect persistence data and the other quadrat was used to collect deposition and utilization data. The MLLW line was determined using NOAA's vector shoreline ESRI shapefile, which includes data from a 20 year average along the California coast. Sampling for deposition and utilization occurred monthly over a two-week period and persistence was estimated weekly. Beaches were classified as intermediate in morphology due to their high temporal variability, sand storage at the beach and surf zone, and bars and troughs in the surf zone

(McLachlan and Brown 2006). Rocky intertidal sites ranged from exposed, high wave energy headlands to protected low wave energy bays (Easterbrook 1999).

Kelp wrack density

To test the hypothesis that kelp wrack density (kg/m^2) was higher at the rocky intertidal than beaches, and varied seasonally, the density of kelp detritus within each site quadrat was measured once a month at low tide for a total of 2,938 samples. Wrack was separated by species, consisting of the most common phaeophytes on central California beaches, which were members of the orders Laminariales, Fucales, and Desmarestiales. All parts of the kelp were included in the biomass density except for unattached pneumatocysts. Wrack was categorized as either an individual (entire wrack is intact with holdfast and frond(s)) or a fragment (holdfast, stipe, or frond). Wet weight wrack biomass was quantified per quadrat using a SK-20KD A&D scale to 0.01 kg.

Deposition of kelp wrack was compared to significant wave height (H_s), since storms are one of the main contributors to kelp removal (Zobell 1971, Ebeling et al.1985, Seymour et al. 1988). H_s data were collected from the National Buoy Data Center Station 46042 and one average for all sites was used for a Julian week, since sampling at all six sites did not occur on the same day.

Kelp wrack persistence

To test the hypothesis that persistence of kelp wrack was longer on beaches than in the rocky intertidal, the persistence quadrat at each of the six sites was visited at low tide approximately once a week during the study period. On average, beach sites were visited

48 times, while rocky sites were visited 38 times; rocky sites were visited less due to weather conditions and the low frequency of tides low enough to collect data. A total of 14,720 data points were collected. The quadrat was cleared once of all algal detritus one day prior to the first sampling. During each sampling event thereafter, species of phaeophyte detritus from the orders Laminariales, Fucales, and Desmarestiales within the quadrat were identified to species and the location of wrack was recorded using a Garmin eTrex® GPS (latitude and longitude) with an accuracy of 1-5 m, but independently confirmed at 1.8 m. Percent burial of wrack on beaches was also recorded and estimated on a sliding scale, where 0% = 0-10% sand, 25% = 11-40% sand, 50% = 41-60% sand, and 75% = 61-99% sand. Samples that were more than 99% buried would not have been visible and therefore were not recorded.

GPS data from each sampling period were mapped using ArcGIS to determine the persistence of detritus mounds at the sites. Persistence was determined based on how often a wrack pile was found in an area of the quadrat. Persistence was measured by importing latitude and longitude coordinates onto an ArcGIS world map, overlaying a fishnet, a grid made of 2 m x 2 m cells, and using the spatial join feature, that counted the number of times a wrack coordinate was within one of the 2 m x 2 m cells. Grid dimensions were chosen based on of the error on the GPS.

To test the hypothesis that persistence changed with beach morphology, seasonal monitoring occurred during winter and summer for beach slope and sand grain size. Triplicate beach slope measurements were taken 1 m above the ground and were measured across 50 m from the base of the berm to the swash zone at low tide in February 2014 and June 2014 at the three beaches. Measurements from a Brunton Pocket

Transit inclinometer were averaged and slope was recorded to the nearest 0.5°. Additionally, one sample of approximately 100 g of sediment was collected by hand from all beaches at the swash zone, beach face, and base of the berm in February 2014 and June 2014 for a total of 18 samples (1 sample x 3 zones per beach x 3 beaches x 2 seasons). Sediments were dried at 60°C for two days and sieved to remove sediments and debris larger than 2 mm. Sediments were analyzed for mean grain size using arithmetic statistics to determine the change in sand grain size across zones as well as beaches between winter and summer using a Beckman Coulter LS Particle Size Analyzer (Beckman Coulter Inc. 2011).

Utilization of Macrocystis pyrifera detritus

To test the hypothesis that phlorotannin concentrations in *Macrocystis pyrifera* negatively affected the presence of organisms utilizing kelp wrack, and that phlorotannins, bacteria, and flies varied spatially and temporally, approximately three samples of kelp from each zone on the beach (swash zone, beach face, and berm) and rocky intertidal (low, mid, and high) were collected from random *M. pyrifera* detritus within the deposition quadrat. For beaches, I defined the zones with their approximate ranges from the shoreline as: swash zone- turbulent area of run-up and backwash of water (0-15 m), beach face- sloping section below the berm (16-30 m) and berm- highest point reached by normal swash to the base of the dunes where vegetation began (31-50 m). The beach face was less apparent in fall and winter due to erosion from waves and was pushed closer to the berm. For the rocky intertidal, Low intertidal- lowest low tide to the upper limit of kelps (0-20 m), mid intertidal- upper limit of kelps to upper limit of barnacles (21-40 m), and high intertidal- lower limit of barnacles to sea cliff (41-50 m) (Nybakken and Bertness 2005). The same wrack piles were used to measure biomass density, phlorotannin concentration (% dry mass), bacterial density and (cells/g), and kelp fly density (flies/cm^2/hour). Samples were gathered from *M. pyrifera*, which was the most common species of detritus at all sites and the preferred habitat and food for kelp flies (Kompfner 1974). Phlorotannin concentration and fly density samples were collected monthly over a two week period in the middle of the month, while bacterial density (colony forming units/μL) was collected seasonally (July and October 2013, and January and April 2014) and bacterial density (cells/g) was counted for July 2013 and January 2014 samples only.

Utilization of Macrocystis pyrifera detritus: Phlorotannin concentration

Multiple blades were collected from the randomly chosen *Macrocystis pyrifera* wrack piles throughout the quadrat and brought to the lab where they were weighed to the nearest 1 g wet weight. A separate 1 g sample of the blade was oven-dried at 60°C for 48 hours. A total of 311 samples were collected. The blade has a high surface area on *M. pyrifera* and was connected more securely to the pneumatocyst, ensuring the blade would be deposited on the shore. Also, the phlorotannin concentration within an individual kelp can vary significantly (Van Alstyne et al. 1999b). Phlorotannin levels (% dry mass, calculated using: (ppm phlorotannins/dry weight) x 100)) were measured using the Folin-Ciocalteu assay, which also quantifies non-phenolic hydroxylated aromatic compounds, however, the non-phenolic compounds comprise <5% of the total Folin-Ciocalteu reactive compounds in phaeophytes (Van Alstyne 1995). Absorbance was read at 765 nm using an OceanOptics USB 2000 spectrophotometer. Phloroglucinol dihydrate was used as a standard (Val Alstyne 1995).

Utilization of Macrocystis pyrifera detritus: Bacterial density

A 10 cm section of stipe from the randomly chosen *Macrocystis pyrifera* wrack piles throughout the quadrat was brought to the lab in a sterile plastic bag, where the stipe was wet weighed to the nearest 1 g. A total of 101 stipes were collected and used to measure bacterial density since they were sufficiently abundant at all zones along beaches and the rocky intertidal. To measure the density of bacteria on the surface of wrack, two methods were used. The first method used the number of bacterial cells that grew into colonies and the second used the total number of cells on the surface of the 1 g sample. The two methods were used due to the uncertainty of success of enumerating bacteria. Both methods began by using the same setup where stipe samples were vortexed for 5 min in 20 mL of distilled water (adapted from Epstein and Rossel 1995).

To count the maximum number of colonies, 1 µL of vortexed solution was plated on BD Difco™ R2A agar and incubated at room temperature (21°C) for two weeks. One colony of each pigment was picked per plate since each pigment was considered a different species and stained with Crystal violet Best Science Supplies to identify cell morphology (S. Rech, pers. comm.). Morphology data were collected since Koop et al. (1982) found a succession from coccus to bacillus with age of detritus. Lastly, samples were preserved using 4% formalin (Porter and Feig 1980) and stored at 4°C for up to year.

Total cell counts were conducted using the direct count method, where 1.0 mL vortexed solution was filtered through a 0.4 µm polycarbonate filter, cells were stained with DAPI at a concentration of 0.01µg/mL for 5 minutes, rinsed with 1 mL sterile seawater, and 15 fields of view were counted under an epifluorescence microscope (Porter and Feig 1980, Kemp et al. 1993, Epstein and Rossel 1995). Bacterial density was calculated using the following equation:

$$\text{cells/g} = [SC - BC) * CF * F] / V$$

SC = mean of sample counts/quadrat, BC = mean of background counts per quadrat (contamination of stain), CF = filter area, F = volume of preserved sample, and V = volume of preserved sample filtered (Kemp et al. 1993).

Bacteria have a variety of roles in the environment, especially for decomposition and remineralization of organic material. A genetically sequenced biofilm sample of freshly deposited *M. pyrifera* collected from Salinas River State Beach in April 2014 showed a diversity of bacterial families inhabiting the surface biofilm from a class project pilot study (Figure 2). The sample consisted of 3,474 sequences of 300-350 base pairs using a PowerSoil® DNA Isolation Kit Mo Bio Laboratories and an Ion Torrent™ Life Technologies. These bacteria were gram negative and responsible for sulfur and nitrogen reduction, algal decomposition, as well as a fecal indicator (Jensen and Finster 2005, Madigan and Matinko 2005, Jensen et al. 2010, Barbeyron et al. 2011).

Bacteria cultured on R2A agar grew six different species identified as distinct based on pigment, gram stain, and morphology (Table 1). Collected samples were from different stages of decomposition at both beaches and the rocky intertidal. Bacteria from surveys and experiments were later separated by pigment, which was determined to be a separate species, and their density within the petri dish was measured and later compared between substrate as well as seasonally to observe spatiotemporal changes.

Utilization of Macrocystis pyrifera detritus: Kelp fly density

Kelp fly density (flies/cm^2/hour) was determined using one roll of Victor® Fly Ribbon flypaper placed approximately 10 cm above the same wrack pile used previously for deposition and utilization data. A total of 318 flytraps were collected. In addition, triplicate flytraps were collected for background flies, which was done using flypaper that was placed more than 2 m away from the nearest wrack within the three zones of the beach and rocky intertidal. A total of 315 flytraps were collected. Fewer background flytraps were collected than expected since collection did not begin until September 2013 and not all zones had *M. pyrifera* wrack. Flypaper was wrapped in wax paper to be transported to the lab where flies were counted and identified to the order Diptera (Huckett 1971).

Deposition, persistence, and utilization of Macrocystis pyrifera experiment

Additionally, to test the hypotheses that persistence of kelp wrack was longer on beaches than the rocky intertidal, phlorotannin concentrations in *Macrocystis pyrifera* negatively affected the presence of organisms utilizing kelp wrack, and that phlorotannins, bacteria, and flies varied spatially and temporally, a short experiment was conducted in the summer of 2014. The experiment manipulating the weight of kelp wrack to determine the effects of biomass loss, persistence, and utilization lasted for 14 days, the duration of a tide cycle. Fresh *M. pyrifera* was harvested offshore of Cannery Row in

Monterey, CA, cut into three weight classes, and placed on the coast on the same day. Weight classes were based on the most common wet weights of kelp wrack that occurred along the coast: 0.5 kg, 1 kg, and 3 kg. Three replicates of each weight class were randomly placed in a 50 m x 50 m quadrat in the swash zone, beach face, and berm at low tide at Salinas River State Beach in July 2014 for a total of 27 samples. This was replicated at Soberanes Point in the low, mid, and high intertidal two weeks later in August 2014. Numbered pink plastic bands were attached to the stipe of each wrack pile for identification during each sampling. The area where the mounds were placed was cleared of wrack prior to placement so that it did not influence the amount of flies. Prior to each day's sampling, newly added wrack was removed. The same methods were used as those for determining kelp wrack density, persistence, and utilization of *M. pyrifera* detritus. Each day, mounds were wet weighed, percent burial over the course of the day was determined, GPS location was recorded for persistence, and fly density was collected. Samples for phlorotannin concentration and bacterial density through colony counts and total cell counts were collected when kelp was initially collected as well as on the 7th and 14th day.

Statistical analyses

All statistical analyses were performed using SPSS. To test the hypothesis that kelp wrack density was higher in the rocky intertidal than on beaches, and that wrack density was higher in winter than summer, a 2-way ANOVA was used with month and substrate as fixed factors. To test whether the amount of fragmented wrack was different from individual wrack, a t-test was used. H_s data were compared to individuals and fragments in addition to biomass density using a linear regression. Also, H_s data were compared amongst seasons using a 1-way ANOVA. Individuals, fragments, and wrack wet weight from experiments were dependent factors, while time and substrate were fixed factors in a 2-way ANOVA.

To test the hypothesis that kelp wrack persistence was higher on beaches than the rocky intertidal and seasonally, a 2-way ANOVA was used with month and substrate as fixed factors. The effects of burial on persistence were determined using a heterogeneity chi square for site, season, and beach zone. Persistence was compared to wrack pile's distance from the shoreline using a quantile regression to find the upper bound of the data. To test the hypothesis that persistence changed with beach morphology, 1-way ANOVAs were used with log sand grain size and slope as dependent factors and persistence and season as fixed factors. Two-way ANOVAs were used with grain size and burial as dependent factors and season, substrate, zone, and weight class as fixed factors.

To test the hypotheses that phlorotannin concentration, bacterial density, and fly density varied spatially and temporally, a 2-way ANOVA was used with month and site as fixed factors. Phlorotannin concentration as percent dry mass was calculated using:

((concentration as ppm/dry mass of the blade)*100).

To determine the effect of phlorotannin concentration on bacterial colony density, total colony density, and kelp fly density, linear regressions were performed. In addition, a regression was used to test whether bacterial colony density was similar to total bacterial density, and whether fly density was correlated to wrack biomass density. Two-way ANOVAs were used to determine the significance between bacterial colony density with season, substrate, color, and morphology as fixed factors. Fly density was standardized for surveys since a t-test showed a significant difference between kelp flies on sand or rock compared to kelp wrack (Appendix 1), but not with the fly density experiments (Appendix 2).

RESULTS

Kelp wrack deposition

During the 15-month survey period, a total of 2,938 samples of kelp wrack with a biomass of 7,435 kg were washed into the study sites from 11 different species (Table 2). Of those samples, 55% (1,603) were from beaches and 45% (1,335) were from the rocky intertidal (Table 2). Wrack species composition varied between locations, with 6 species found on beaches and 11 species found on the rocky intertidal (Table 2). The most abundant species of kelp wrack on beaches and the rocky intertidal was *M. pyrifera.* There were 75% more pieces of *M. pyrifera* than all other species combined on beaches, but was only 33% on the rocky intertidal (Table 2).

Fragments and individuals were not evenly distributed across substrates. Fragments comprised a significantly higher amount of the wrack than individuals among all species on both beaches (t-test: t_{10}=3.0; $p<0.01$) and the rocky intertidal (t-test: t_{10}=3.5; $p<0.005$). Throughout the study, the number of wrack individuals changed significantly between months and substrates (Table 4), however, this was not the case for fragments, which did not change significantly between months or substrates (Table 5). The percentage of individuals that washed ashore were not significantly different between substrates (t-test: t_{10}=1.6; $p<0.10$) and ranged from 0.5%-11.5% with an average of 5.6 (± 0.81 SE) on beaches, to 3%-53% with an average of 16.5 (± 3.17 SE) on the rocky intertidal (Figure

3). In addition, individuals that comprised the wrack were not significantly correlated to H_s on beaches (Appendix 3) (Regression: F_1=0.029; p=0.867; r^2=0.002) or on the rocky intertidal (Appendix 4) (Regression: F_1=1.775; p=0.206, r^2=0.120). Individuals within the kelp wrack were a small portion of the total amount and conditions were not appropriate for their deposition to be higher along the shore.

Wrack biomass density varied significantly between beaches and the rocky intertidal, but not monthly (Table 6; Figure 4). Biomass density on beaches was lower than on the rocky intertidal in all months except August 2013, when biomass density on beaches was 12% higher than the rocky intertidal. Beaches ranged in biomass density from 0.003 kg/m^2 to 0.03 kg/m^2 with an average of 0.01 kg/m^2 (± 0.002 SE). Likewise, biomass density on the rocky intertidal varied by an order of magnitude ranging from 0.01 kg/m^2 to 0.2 kg/m^2 with an average of 0.05 kg/m^2 (± 0.01 SE). Wrack biomass density along the shore constantly changed and higher wet weights of wrack were consistently found on the rocky intertidal.

H_s was not correlated to biomass density on beaches (Appendix 5; Regression: F_1=0.086; p=0.775; r^2=0.007) or the rocky intertidal (Appendix 6; Regression: F_1=0.067; p=0.799; r^2=0.005). In addition, H_s did not significantly differ between seasons (Table 7; Figure 4). During the study period, H_s changes were not enough to cause differences in wrack biomass density.

Kelp wrack persistence

There was no significant difference in kelp wrack persistence between seasons or across substrates (Table 8). During the 15-month period of surveys, a total of 14,720 samples of wrack from 14 different species were identified (Table 9). Species composition of wrack varied between locations with 11 species found on beaches and 14 species on the rocky intertidal (Table 9). Of those samples, 66% (9,732) were from beaches and 34% (4,988) were from the rocky intertidal. The most abundant species on beaches and the rocky intertidal was *M. pyrifera*.

Beaches generally had higher maximum persistence during all seasons compared to the rocky intertidal, although the average persistence did not change between substrates (Table 10). The average seasonal persistence ranged between 1-4 occurrences, but was typically 2 occurrences across seasons (Table 10). The lowest maximum persistence was seen in fall for both beaches and the rocky intertidal, while spring and summer generally had the highest persistence at beaches and the rocky intertidal.

Burial was thought to contribute to wrack persistence, but wrack burial was not significantly different among seasons, between beach sites, or between beach zones (Table 11; Figure 5). Only 23% of the samples were buried and the majority came from *M. pyrifera* (Table 9). Burial typically occurred from the beach face to the beginning of the berm and was caused by aeolian transport as well as suspended sediment in water that accumulated on top of wrack during high tide (personal observation).

Beach morphology characteristics such as sand grain size and slope did not significantly affect kelp wrack persistence (Tables 12a and 12b). Additionally, sand grain size on the swash zone, beach face, and berm did not differ significantly between winter 2014 and summer 2014 (Table 12c), although there was an increase in grain size from winter to summer in the swash zone and beach face, but a decrease in grain size at the berm (Figure 6). The beach slope also changed over the course of the year and increased by an average of 2° (± 1.2 SE) from winter to summer, but this was not significant (Table 13).

Persistence was found to significantly increase with distance from the shoreline on beaches and the rocky intertidal (Appendices 7-12), however the relationship was not significant during all seasons on the rocky intertidal (Tables 14 and 15; Figures 7-14; Appendices 15-20).

Kelp wrack utilization

No significant difference in phlorotannin concentration was found between beaches and the rocky intertidal, or between months (Table 16; Figure 13). Phlorotannin levels on beaches ranged from 0.01% to 0.22% dry mass with an average of 0.10% dry mass (± 0.02 SE), while levels on the rocky intertidal ranged from 0.006% to 0.34% dry mass with an average of 0.15% dry mass (± 0.03 SE) (Figure 13).

In addition, phlorotannins did not have an effect on bacterial colony density (Appendix 21; Regression: $F_{1,96}$=3.535; p=0.063; r^2=0.037), total bacterial density (Appendix 22; Regression: $F_{1,49}$=0.608; p=0.439; r^2=0.013), or kelp fly density (Appendix 23; Regression: $F_{1,301}$=1.448; p=0.232 r^2=0.018). Lastly, total bacterial density did not affect fly density (Appendix 24; Regression: $F_{1,57}$=1.441; p=0.235; r^2=0.025).

Beaches had a higher bacterial colony abundance than the rocky intertidal, although there was no significant difference between substrate or season (Table 17; Figure 14). The highest abundance for both beaches and the rocky intertidal was October 2013 with 2,040 CFU/µL and 111 CFU/µL respectively, while April 2014 was the lowest for beaches at 104 CFU/µL and January 2014 was the lowest for the rocky intertidal at 10 CFU/µL (Figure 14).

Colony pigment was used to separate the different groups cultured on a petri dish. Throughout the study, five different pigments were identified: white, gold, yellow, pink, and clear. There was a significant difference in the abundance of different colonies, but no difference between substrates (Table 18) or season (Table 19). The white colonies were the majority during all seasons as well as between beaches and the rocky intertidal at 75-98% of the cultured bacteria.

Morphology of colonies did not significantly differ between season or substrate (Tables 20 and 21). Coccus bacteria dominated (94%) colony morphology. Pennate diatoms were also observed growing within the colonies when they were removed from the surface of the stipe along with the bacteria.

Total bacterial abundance from direct cell counts was not significantly different between substrate of season (Table 22). Beach bacterial abundance increased from 7.6 x 10^6 cells/g in summer to 1.3 x 10^8 cells/g in winter, while rocky intertidal bacterial abundance decreased from 1.0 x 10^7 cells/g to 3.3 x 10^6 cells/g (Figure 15).

There was no significant difference in fly density between substrate or month (Table 23; Figure 16). A total of 44,986 flies were collected on 360 fly traps over 14 months (with an average density of 0.3 flies/cm^2/hour (± 0.13 SE) on beaches and 0.4 flies/cm^2/hour (± 0.21 SE) on the rocky intertidal.

In addition, there was a significant relationship between kelp fly density and wrack biomass density (Figure 17; Regression: $F_{1,359}$=11.413; p=0.001, r^2=0.031).

Wet weight experiment

Wet weights of samples showed an overall trend where the farther the sample was from the ocean the faster it lost water. There was a significant decrease in wet weight over time in the 0.5 kg samples (Table 24a), 1.0 kg samples (Table 24b), and 3 kg samples (Table 24c), but there was no difference between beaches and the rocky intertidal except for the 3 kg samples. Wrack on beaches was intact and not disturbed by herbivores, instead, weight decreased through water loss within the cells. Different sized pieces lost water at different rates within the zones where smaller pieces lost water faster than larger pieces and water loss was higher with increasing distance from the shoreline (Table 25). For the larger pieces (1-3 kg), within a week the outer surface was dried, while the inside remained wet. Water loss was higher in the high intertidal where samples were retained throughout the duration of the experiment (Table 26).

Throughout the experiment, samples were lost on the swash zone and beach face at Salinas River State Beach and in the low, mid, and high intertidal at Soberanes Point during high tide. In general, wet weight of wrack decreased over time more with the 3 kg samples than the other size classes. No data were available for wrack in the swash zone past the first day since it was removed by waves after two hours of being placed on the beach (Figure 18A).

Wrack on the beach face lost most of its wet weight within the first week, and afterwards weights remained fairly constant (Figure 18B). Half kg samples lost water the fastest compared to other weights, however, they were rehydrated on days 7-9 by high tides before drying again. One kg samples followed a similar trend as the 0.5 kg samples and lost most weight in less than a week before being rehydrated on days 7-9. Three kg samples were not affected by the high tide and were continued to lose water weight over the course of a week and a half before settling at a consistent weight on day 12. In addition, one of the 3 kg piles became covered in mud during the high tide on the first day causing it to weigh more than the starting weight.

Wrack on the berm lost most of its water within the first three days and showed a steeper water loss compared to the beach face (Figure 18C). Wet weight of samples did not appear to change after day 5, although foggy mornings rehydrated the 3 kg samples, indicated by the increase in wet weight on day 8.

In the rocky intertidal, low- and mid-intertidal samples remained consistent for several days in a row, while high intertidal samples changed continuously. At the low intertidal the 0.5 kg sample was washed into a tide pool where it remained until day 4 (Figure 19A). On day 4 it was noticed that wave action was causing blades to become detached resulting in a loss of weight. Herbivorous crabs and snails were also noticed near the wrack and could have been responsible for some weight loss.

Mid-intertidal samples were near tide pools and the high tide on day 1 washed most samples away and the remaining samples were moved into the tide pools where their wet did not change until after day 4. As 1 kg samples began to dry, 0.5 kg samples were rehydrated (Figure 19B). One of the 1 kg samples was washed into the high intertidal during the high tide on day 7 where it remained for the rest of the experiment.

Samples within the high-intertidal were able to dry for the first week and were rehydrated during the high tide on day 7 before drying again. Not all samples were reached by the incoming tide due to the complex topography at SP. The 0.5 kg samples did not change much in wet weight after day 7, while 3 kg samples were able to absorb water, however, none of the samples returned to their starting weight (Figure 19C). Herbivory by crabs was observed on wetted samples and those within tide pools towards the end of the experiment.

Persistence experiment

Persistence significantly differed by zones between beaches and the rocky intertidal (Table 27), but not by weight (Table 28). Wrack lasted on the shore longer, farther from the shoreline. Each day, on the beach, the high tide reached the beach face, while on the rocky intertidal, the tides reached up to the high intertidal. Despite the tides reaching the wrack, not all of the wrack piles were removed (Figure 20).

Samples in the swash zone regardless of wet weight were washed away in a matter of hours (Figure 20). These samples were not pushed farther up the beach by the incoming tide, but instead were resuspended and carried out to sea. The swash zone was an area of high turnover where new wrack was added every morning to the quadrat, but was removed before data was collected.

Water levels reached the beach face during the first day’s highest tide removing almost half of the samples (Figure 20). All waves did not reach the same extent of the beach face and some extended farther up the beach than others removing wrack piles at random. In some instances, wrack was rehydrated and even moved several meters horizontally by water movement, but remained within the beach face.

All berm samples lasted for the entirety of the experiment having the highest persistence (Figure 21). Wrack piles were undisturbed as water levels did not reach beyond the beach face (Figure 20).

Wrack in the high intertidal was either pushed back towards the sea cliff, or removed completely. Wrack was still buoyant and waves were able to move the wrack horizontally across the site before it was eventually pushed farther back, or washed back to sea.

Burial only occurred on the beach face but did not significantly change over time or by the wet weight of wrack (Table 33). Larger samples were typically 25% buried in wet sand deposited during high tide. Although sand was drier at the berm, aeolian transport did not cover wrack, in addition, wrack dried quickly, which prevented sand from being stuck to the mucus.

Wrack piles in the low intertidal regardless of size were washed away in less than a day besides one sample, which was caught in a tide pool for 4 days (Figure 22). These samples were not pushed farther up into the intertidal by the incoming tide, but instead were resuspended and washed out to sea.

Mid intertidal wrack was also influenced by water motion and samples were removed throughout the experiment. Samples were not removed evenly since water did not flow evenly along the site since the topography was uneven.

In the high intertidal, wrack remained the longest (Figure 23). Some samples were pushed farther back against the sea cliff during the high tide on day 7. By the end of the experiment wrack in the high intertidal was either in a tide pool or tangled around rocks.

Utilization experiment

Phlorotannin concentrations showed a significant decrease over time, but not between beaches and the rocky intertidal (Table 30a) or by zone (Table 30b). On the beach, the average initial concentrations varied between zone, but ranged from 0.16-1.08% dry mass

(Figure 24). Only initial concentrations existed for samples placed in the swash zone since they did not remain longer than a day. Some beach face samples were present throughout the experiment and showed a sharp drop on day 7 to 0.03% dry mass and remained at that concentration until day 14. Berm sample concentrations also showed a decrease from day 0 to day 7, and concentrations remained similar on day 14. Analyses showed that wrack lost almost all phlorotannins within the first week and did not appear to have any left during later monitoring.

Concentrations on the rocky intertidal were consistent between sample wet weights across zones. Initial concentrations ranged from 0.35% dry mass to 0.64% dry mass. Samples did not last longer than a week in the low and mid intertidal; therefore no samples were collected for day 7 or day 14 (Figures 25A and 25B). Samples in the high intertidal started at 0.39-0.64% dry mass before dropping to 0.06-0.12% dry mass on day 7 and 0.04-0.20% dry mass on day 14 (Figure 25C). Phlorotannin levels showed a large decrease within a week and remained low after two weeks.

There was no significant difference between bacterial colony density over time, or between beaches and the rocky intertidal (Table 31). Initial counts of bacterial abundance were highly variable between samples of different wet weights on beaches. Initial counts ranged from 7-60 CFU/µL in the swash zone, but samples were not found in the swash zone past day 0 (Figure 26A).

On the beach face, bacterial abundance on samples fluctuated over time and between sample wet weights and varied from 0-149 CFU/µL. The dry mass of samples was also included and was calculated by drying 1 g wet weight of the blade, which indicated that most of the water had been removed from day 0 to day 7 (Figure 26B). Bacterial abundance decreased over time for 0.5 kg and 1 kg samples, however, 3 kg samples showed an increase on day 7 before decreasing on day 14.

The berm also showed variable abundance over time and between sample wet weights. Bacterial abundance on the berm decreased over time from day 0 to day 7, but remained unchanged by day 14 for 1 kg and 3 kg samples (Figure 26C). The pattern in water loss of wrack was similar to the beach face where most water was lost by day 7, but regained some on day 14.

Bacteria samples lasted longer than a week only in the high-intertidal. Initial abundances were similar and ranged from 33-118 CFU/μL across all intertidal zones (Figure 27). Dry masses of the wrack also varied over time, as wrack did increase in dry mass throughout the experiment, instead, there were periods of drying from day 0 to day 7, followed by reabsorption of water between day 7 and 14.

Bacteria in the high intertidal showed no trend over time except for one of the 3 kg samples, which was rehydrated during the high tide on day 7 and produced 2,238 CFU/μL. Abundances on 0.5 kg samples dropped from 58 CFU/μL to 6 CFU/μL to 2 CFU/μL over two weeks and 1 kg wrack fluctuated from 118 CFU/μL to 2 CFU/μL to 318 CFU/μL.

Total bacterial cell counts showed no significant difference over time or between beach and the rocky intertidal (Table 32). Direct cells counts showed that bacterial abundance increased with time and also varied by the section of beach where samples were collected. Bacteria on the beach face were initially1.6 x 10^6 cells/g and increased to 6.2 x 10^7 cells/g, whereas on the berm, samples increased from 2.2 x 10^6 cells/g to 6.4 x 10^7 cells/g before decreasing to 1.6 x 10^7 cells/g (Figure 28). Bacterial abundance increased slowly with time within the high-intertidal, where samples remained the longest. Initial counts showed an average abundance of 3.0 x 10^5 cells/g and rose to 3.5 x 10^6 cells/g after two weeks (Figure 28).

Kelp fly density changed significantly over time, between beach and the rocky intertidal, as well as the interaction between time and substrate (Table 33). Densities changed between wet weights and between zones, but did not show a preference for water content. Kelp flies were only present on the swash zone for day 0 and densities were low and ranged from 0.006 flies/cm^2/hr to 0.03 flies/cm^2/hr on all weight samples. The significant interaction indicated kelp fly density was significantly higher on the rocky intertidal over time.

Flies were more abundant on the beach face and showed higher densities on larger wrack piles with 3 kg wrack having the most flies followed by 1 kg and 0.5 kg samples (Figure 29A). Fly density fluctuated over the study period and showed an increase on day 9 when wrack was wetted although densities remained relatively constant within a size class. Smaller wet weights of wrack showed the lowest densities, for example, 0.5 kg samples ranged from 0.007-0.09 flies/cm^2/hr, 1 kg samples ranged from 0.01-0.08 flies/cm^2/hr, and 3 kg samples ranged from 0.04-0.2 flies/cm^2/hr.

Fly density on the berm did not vary over time or by weight and were lower compared to the beach face. Densities were highest between days 3 and 12. 0.5 kg densities ranged from 0-0.02 flies/cm^2/hr, 1 kg samples ranged from 0.0008-0.01 flies/cm^2/hr, and 3 kg samples ranged from 0.004-0.02 flies/cm^2/hr (Figure 29B).

Since burial was low it did not likely affect the densities of flies since there was surface area of kelp that was still exposed.

Kelp flies were found on all samples within minutes of their placement in the rocky intertidal. Fly densities varied by zone and there were visible swarms of flies not only on wrack but on bare rocks, and rocks with living algae as well. Although flies were clearly attracted to the wrack, there was no significant trend between fly density and wrack biomass. Flies were present in all zones, but were less abundant in areas where there were fewer wrack piles such as the low intertidal (Figure 30A). Kelp flies were seen on both the surface of the water in the tide pools as well as the wrack floating in them.

Flies in the mid intertidal were more abundant on the 1 kg wrack as there were twice as many samples compared to the 0.5 kg wrack and no 3 kg samples after day 0 (Figure 30B). From day 0 to day 6 samples remained in a tide pool. Although the location of wrack did not change, the density of flies did fluctuating from 0 to 0.72 flies/m^2/hr.

Flies in the high intertidal were more abundant than other zones, especially by day 5 (Figure 30C). Flies preferred 1 kg and 3 kg samples although variability was high between day 5 and 9. Between days 10 and 14, flies were mostly found on the 3 kg wrack.

DISCUSSION

Deposition of kelp wrack

Species composition of wrack between beaches and the rocky intertidal differed with higher diversity in the rocky intertidal, although the same species were found on both substrates. Standing stock within the kelp forest (Zobell 1971), proximity of the site from the kelp forest (Zobell 1971, Dugan et al. 2003), and presence of pneumatocysts were likely the main factors contributing to there being more species found at the rocky intertidal. Rocky intertidal sites were adjacent to large standing stocks of subtidal kelps as well as a source for intertidal species that also became part of the wrack. Overall, *M. pyrifera* dominated the wrack along southern California beaches (Zobell 1971) as well at my central California study sites.

Regardless of species, the wrack was either a complete individual or a fragment. Both individuals and fragments can be dislodged by similar mechanisms including wave action (Koop and Lucas 1983) or entanglement, which was found to be an important mechanism of disturbance for kelps (Dayton et al. 1984). The abundance of individuals showed significant differences spatially and temporally with more being found on the rocky intertidal during fall. On southern California beaches, a considerable part of the *M. pyrifera* wrack after storms contained individuals (Zobell 1971). Since H_s did not change seasonally in central California, it was not believed to be the sole cause of the difference in the amount of individuals that washed ashore compared to fragments; other factors that were not accounted for may be responsible. Fragmented kelp material was the most common type of wrack, likewise, in southern California wrack was found as either single pieces or entanglements (Zobell 1971). Entanglement was not monitored specifically, but was commonly seen after storms deposited large stands of kelp in the swash zone and throughout the rocky intertidal. Although more rare, individuals contributed a larger biomass to the shore, however, fragments remained longer since they were deposited farther from the shoreline (personal observation).

Wrack biomass differed between beaches and the intertidal; however, seasonal differences were not as apparent. Along beaches in southern California, deposition also varied spatially and temporally (Zobell 1971). Regardless of location, deposition of wrack along the coast was due to a number of factors, mainly offshore standing stocks of kelp, water movement, and beach conditions including the area of the beach, topographical, or structural features (Zobell 1971). Kelp wrack abundance was higher than 0.01 kg/m^2 in the rocky intertidal year-round, while beaches did not exhibit seasonal differences and had consistent deposition throughout the year. Temporally, beaches and the rocky intertidal showed a fall-winter peak in deposition, although biomass that accumulated on the shore was not correlated to H_s. However, storm induced mortality is common in kelp forests (Zobell 1971, Dayton et al. 1984, Ebeling et al. 1985, Seymour et al. 1989, Dayton et al. 1992, Utter and Denny 1996, Graham et al. 1997, Duggins et al. 2003). Storms are a natural form of disturbance and can allow for juvenile recruitment (Ebeling et al. 1985, Graham et al. 1997) and effect the distribution of species (Duggins et al. 2003). Higher biomass on the rocky intertidal may be due to proximity to a larger standing stock of kelp (Zobell 1971, Dugan et al. 2003), as well as a higher wet weight. Kelp wrack within the rocky intertidal remained hydrated due to high tides that covered the intertidal daily, whereas kelp wrack on beaches dried more quickly since most wrack was deposited beyond the beach face where high tides only reached every two weeks.

Beaches and the rocky intertidal had a gradient of increasing water loss with distance from the shore. On beaches, the swash zone material remained wet throughout the day and turnover was high, to the berm where tides reached once every two weeks. In contrast, the rocky intertidal was submerged daily and zones wetted constantly by spray. Water loss in wrack was initially rapid, but become more gradual as the outer surface hardened (Griffiths and Stenton-Dozey 1981) and the interior of the wrack retained more moisture (Lavoie 1985).

This study found that on a typical year, the central California coast from Davenport to Carmel, a 113 km stretch of coastline can receive approximately 275,096 kg/year (2,491 kg/m/year on beaches and 3,010 kg/m/year on the rocky intertidal), encompassing the entire area of coast from mean lower low water to the high tide mark. Much of the previous work involving the sampling of biomass has occurred on beaches in southern California and South Africa. A study by Dugan et al. (2011) in southern California found more than 11,000 kg were deposited over 51 days in the summer at one beach, which was estimated to 840 kg/m/year. *M. pyrifera* was also the main species of wrack and had an estimated contribution of 548 kg/m/year. A study from South Africa showed based on estimates from offshore standing stocks of kelps that approximately 10% (1,630 kg/m/year) were brought ashore (Simons and Jarman 1981). In addition, South African beaches measured 2,179 kg/m/year (Stenton-Dozey and Griffiths 1983) and the rocky intertidal ranged from 1,200-1,800 kg/m/year (Koop and Field 1980).

The central California coast receives a larger amount of secondary production than these other highly productive areas. Differences in biomass may also be due to collecting methods using varying time scales, and number of sites and there area can make comparisons difficult. This study is more comprehensive because it compares multiple sites within a longer stretch of coast, the area being sampled spanned from low tide to high tide, where wrack can be found, and data was collected over all seasons, resulting in a better picture of kelp wrack deposition. Beaches comprise two-thirds of the world’s coastline (McLachlan and Brown 2006), therefore knowing the amounts of wrack along both types of coast can give a more complete picture of the biogeochemical cycling that kelp wrack undergoes in low productivity environments.

Persistence of kelp wrack

Persistence did not differ significantly over time or between beaches and the rocky intertidal during the surveys, but there was a significant difference between substrate and zone during the experiments. Wrack persistence followed zonation patterns where the farther the wrack was from the shoreline the longer it remained. In general, higher persistence on beaches was found between the beach face and berm, and at the rocky intertidal, the high intertidal accumulated the most wrack.

Wrack was rare and did not remain for more than a few hours in the swash zone/low intertidal where overall persistence was low. On beaches, waves reached the beach face and it was unlikely that a wrack pile stayed for longer than a day, although there was daily input of new kelp wrack. Wrack was typically washed back to sea or moved farther down the beach (Zobell 1971). The low rocky intertidal showed lower persistence than beaches and it was rare to find any wrack in the area. Wrack in the low intertidal was either entangled in the surfgrass *Phyllospadix scouleri*, or caught on a rock.

The beach face received much of the material that was deposited on beaches, which was a combination of wet and dry wrack depending on the tide height prior to sampling. Most kelp on the beach face and lower berm were replaced within two tide cycles (Zobell 1971), however not all wrack was removed. Between sampling, some wrack was removed entirely while some was pushed back towards the berm. In some instances, lateral movement along the beach face occurred before it was pushed towards the berm. On the rocky intertidal, it was more common for wrack to be removed completely, although there were occurrences where wrack was pushed back into the high intertidal.

The more frequent water movement from waves and tides cleared the area of any unattached debris.

Persistence was fairly even across the berm and was not as patchy as other zones. Wrack that was closest to the berm often lasted longer than the two-week tide cycle (Zobell 1971), sometimes months. In the high intertidal, wrack was deposited along the high tide mark. This often coincided with base of seacliffs and the wrack could go no further. The high rocky intertidal was reached daily by water resulting in high turnover of wrack. Since topography and other geographical features varied, hotspots of high persistence were found such as on top of boulders or wedged in crevices. In the rocky intertidal there were more confined spaces where wrack was caught.

Despite no significant changes in persistence seasonally, there were visible differences where persistence was both lower and more patchy at both beaches and the rocky intertidal during winter and fall compared to spring and summer. This may have been due to the changing morphology of the beach, although seasonal differences were also seen on the rocky intertidal. Beach morphology is modified through higher tides, large waves, and winds, which remove fine sediments (Zobell 1971, Bird 2000). During storms, which are more frequent during fall and winter, fine beach sediments are removed by backwash, whereas gentle wave action during spring and summer returns sediments to the beach face (Bird 2000). It is proposed that the changes in persistence can be explained by the more frequent storms during the fall and winter, which erode the beach, lowering the slope and removing the finer grained sand. The gentle slope in addition to the higher waves allows for wrack from the beach face to the berm to be reached more easily, decreasing the retention of wrack in this area (I. Aiello, pers.

comm). Once the slope increases in spring, wrack remains longer the farther it is from the shoreline. For the rocky intertidal, morphology did not change, but the stronger waves during fall and winter could likely reach farther into the high intertidal, increasing the turnover.

Burial of wrack on beaches was found to be insignificant and did not affect persistence. For wrack that was buried, those piles were found between the beach face and berm and caused by aeolian transport. In some instances, kelp wrack in the swash and lower beach face was buried by wet sand from crashing waves. Since most wrack was found near the berm, burial was most likely due to winds. Wrack under moist sand remained for 3-12 weeks during the summer (Zobell 1971). However, this was uncommon since less than one quarter of samples were buried. Burial has been found to enhance nutrients on the beach (Koop and Lucas 1983, McGwynne et al. 1988, Dugan et al. 2011) and promote production of dune plants (Dugan and Hubbard 2010).

Daily monitoring during the experiments allowed for higher resolution in the daily changes in tide height. The different scales of monitoring showed that depending on the zone, wrack can remain from hours to months. Sampling did not always show a distinct wrack line; sometimes there were multiple lines from different tide heights and other times the entire quadrat was covered. The GIS layer of wrack persistence facilitated effective visualization of recurring wrack piles throughout the study area.

Utilization of kelp wrack

Phlorotannins are a broad range of compounds also referred to as polyphloroglucinols consisting of phloroglucinol, phloroglucinol tetramer, eckol, phlorofucofureckol A, dieckol, 8,8’-bieckol and other unknown phenolic compounds (Nagayama et al. 2002, Shibata et al. 2004). The Folin-Ciocalteu assay measured total phenolics within the samples taking into account all isomers of phloroglucinol. There were no spatial or temporal differences in phlorotannin concentrations during the 15-month surveys, but when levels within an individual kelp were monitored during the 2-week long experiments, there was a decrease in levels over time. Experiments showed that *M. pyrifera* had a significant decrease in phlorotannin concentration within a week of being wrack and longer durations did not decrease the phenolic levels further. The cause of the decreasing concentration remains unknown. Phlorotannin concentrations from survey samples were generally low and represented the average concentration on the coast since samples were taken from all three zones, however most samples were from the berm/high intertidal.

The concentration of polyphenolics in brown algae range from undetectable to approximately 20% dry mass and are variable by location (Ragan and Glombitza 1986, Van Alstyne et al. 1999a). Differences in phlorotannin concentration are due to the higher intensity of predation in the tropics than temperate latitudes (Van Alstyne and Paul 1990). In California, samples of *M. pyrifera* from Pacific Grove, CA and Catalina Island, CA had concentrations of approximately 1% dry mass (Van Alstyne et al. 1999a). Phlorotannin concentrations from the experiment were inconsistent during the initial sampling. This may have been due to not all of the phlorotannins being extracted during homogenization, although all samples were treated the same and differences may be due to natural variability. Phlorotannins within an individual are not static and studies have shown that levels can vary seasonally (Ragan and Glombitza 1986), be affected by nutrient availability (Yates and Peckol 1993, Arnold et al. 1995, Peckol et al. 1996), light levels (Ragan and Jensen 1979, Pavia et al. 1997), life history stage (Denton et al. 1990), change with grazing pressure (Van Alstyne 1988, Peckol et al. 1996, Hammerstrom et al. 1998), and concentrations in blades significantly decreased over time after wounding (Hammerstrom et al. 1998). In addition, phlorotannins are known to leach out of the epidermal layer, although the rate of exudation is thought to be small (Jennings and Steinberg 1997). This may explain why samples that were wetted on the beach face, or were in a tide pool were found to have lower concentrations.

Research on phlorotannins has focused on its role of inhibiting herbivory (Geiselman and McConnell 1981, Steinberg 1985, Van Alstyne and Paul 1990, Steinberg and Van Altena 1991, Levinton et al. 2002) and suspension feeding (Duggins and Eckman 1997), but polyphenols also have physiological or ecological functions such as uptake of metal ions, inhibition of competitors or fouling organisms, or aid in recovery from wounding (Ragan and Glombitza 1986), protection from UV radiation (Pavia et al. 1997), and inhibition of bacterial, fungal, or viral growth (Sieburth and Conover 1965, Ragan and Glombitza 1986). Phlorotannins can deter feeding by herbivores at 2% dry mass and higher (Geiselman and McConnell 1981, Steinberg 1988, Winter and Estes 1992), although there is no data on herbivore's response to phlorotannins at levels less than 2% dry mass. It is possible that species, which were deterred by the low concentrations, were not found on wrack. Phlorotannins were not found to affect bacterial density or fly density in the surveys or experiments. Concentrations of phloroglucinol greater than 6.35 μmol/mL were not able to kill gram-positive and gram-negative pathogenic bacteria where as other phloroglucinol oligomers could (Nagayama et al. 2002). Lastly, a study by

Lastra et al. (2014) showed that phlorotannins played a minor role in deterring herbivores when decomposition began.

Bacterial density data were comparable between colony counts and direct cell counts. Abundances were in the same order of magnitude for most samples that were counted. Colony counts were typically higher than direct cell counts and may have been because the bacterial abundance was not even across the filter's fields of view where more bacteria were concentrated in the center. Direct counts may have been undercounted since debris buildup on the filter may have hidden bacteria, a larger volume than 1 μL was used during plating when fresh wrack samples caused the water to become a thick mucus, and it is possible that the species of bacteria on wrack preferred the low nutrient agar. Regardless, direct cell counts are the more reliable method since they count all cells within the sample compared to the selectiveness of the agar (S. Rech, pers. comm.).

Bacterial densities showed no significant change over time or between substrates. However, spatiotemporal differences were present between beaches and the rocky intertidal in summer and winter. Typically, most seasonal differences were seen between winter and summer, due to temperature changes (DeFlaun and Mayer 1983). Beaches had a higher bacterial abundance in fall and winter, while the rocky intertidal had more in summer. Larger bacterial populations in winter on beaches are possibly due to bacteria being transferred from sand and since there is more organic matter on beaches in general. When looking at all seasons, peak abundance in bacterial density occurred during fall at both beaches and the rocky intertidal.

In general, the high surface area of the sand allows for abundances between 0.60×10^9 to 51×10^9 cells/g (Yamamoto and Lopez 1985), and a separate study found densities that ranged from 25 x 10^{12}/m to 6,386 x 10^{12}/m (Stenton-Dozey and Griffiths 1983), while surface bacterial abundances on wrack ranged from 8.3x10^5 cells/mL on fresh seaweed and 4.6x10^8 cells/mL on decomposing seaweed (Cullen et al. 1986). These results were higher than this study, where over 2-weeks, densities on beaches and the rocky intertidal increased by an order of magnitude from 1.6 x 10^6 cells/g to 6.2 x 10^7 cells/g on the beach face, 2.2 x 10^6 cells/g to 1.6 x 10^7 cells/g on the berm, and 3.0 x 10^5 cells/g to 3.5 x 10^6 cells/g on the high intertidal. Between seasons, bacterial density increased from 7.6 x 10^6 cells/g in summer to 1.3 x 10^8 cells/g in winter, while the opposite effect was seen at the rocky intertidal with a decrease from 1.0 x 10^7 cells/g in summer to 3.3 x 10^6 cells/g in winter. Initial abundances on wrack were low, day 0 kelp was sparsely colonized with coccoid bacteria (Koop and Lucas 1983), and almost all visible bacteria cells were coccoid regardless of the age of wrack. It is possible that burial could increase decomposition as well as contribute to higher abundances over time through the transfer of bacteria from sediment to wrack. Also, in the dynamic environment of the rocky intertidal, water washing over the surface of wrack on a daily basis could cause bacteria to be removed, or hinder their reproduction if conditions such as temperature and salinity are changing throughout the day. The source of bacteria on wrack could be marine in origin instead of wrack being inoculated by adult flies (Cullen et al. 1986), but there is no data to suggest that flies are not transferring bacteria, regardless of the amount.

Bacteria are important to wrack not only for its decomposition (McGwynne et al. 1988), but also as a food source for kelp flies (Bender 1975, Stenton-Dozey and Griffiths 1983), and meiofauna may control bacterial densities (Jansson 1968, Giere 1975, Gerlach

1978). Experiments conducted on fly feeding preferences showed higher bacteria concentrations resulted in faster larval growth (Cullen et al. 1986), and an experimental feeding trial showed flies can be grown with bacteria as their food source (Cullen et al. 1986).

Kelp fly densities were found to significantly change over time as well as between substrate with the experiments, but not during the 14-month surveys. Fly density corresponded to seaweed deposition (Yamazaki 2012) and experiments showed an attraction to wet wrack. Kelp flies exhibited a significant preference for wrack during the surveys, but not during the experiments where densities were low and indistinguishable from the background flies. This might suggest that there are more favorable conditions of kelp wrack that kelp flies prefer; such as when wrack was dry there was no nutritional benefit.

Work by Koop and Lucas (1983) showed that kelp fly biomass was constant and flies were present from the start. Flies were present immediately on wrack as well as up to 2 weeks after deposition (Griffiths and Stenton-Dozey 1981). In general, flies could be found on wrack of varying age, although most studies have found that they feed on mucus and bacteria (Bender 1975, Lavoie 1985, Cullen et al. 1986, Inglis 1989). Mouthparts of adult Diptera are designed for suction (Meeuse 1988). Since dried wrack does not have mucus, it is possible that there are chemical signals that flies use to detect wrack. Insects have chemoreceptors on their body (Gullen and Cranston 2010) and the family Calliphoridae (order Diptera) can smell death from 16 km away (Gennard 2007). However, kelp flies are also present on intertidal algae exposed at low tide (personal observation).

Predation by larval flies did not appear to be a cause of decreasing biomass of wrack, instead, desiccation appeared to be most important since wrack was completely intact on beaches after the two week experiments, but were missing blades in wrack piles placed in the rocky intertidal. This was likely caused by waves, which pushed wrack against rocks as well as crabs and snails that were observed feeding on wrack in and around tide pools. In South Africa, studies of herbivory on wrack found contrasting results where Koop and Lucas (1983) found <9% of kelp wrack is consumed by grazers, and Griffiths and Stenton-Dozey (1981) found that scavengers consumed 60-80%.

Due to the influence of tides in controlling the food source of kelp flies, a life history model was proposed by Cullen et al. (1986), where timing of the high tide determined fly abundance. High adult abundances would be found several days after the high tide and low numbers before the upcoming high tides. Wrack that was not reached by the high tide would have lower adult abundances (Cullen et al. 1986). Wrack experiences desiccation and rehydration at different time-scales on the upper beach (Lastra et al. 2014) and drying and rewetting of wrack changes its palatability (Renaud et al. 1990). Without moisture, larvae died within a day (Kompfner 1974) and mucus was required for feeding and laying eggs (Lavoie 1985). After initial deposition and later wetting during the experiment, a transition from juvenile flies to adult was not seen. It is possible that either it takes longer to happen than the experiment's duration, or fly larvae were not visible. Other studies have found that fly eggs were laid immediately on kelp deposited on beaches (Koop and Lucas 1983), flies were most abundant during the first three days (Inglis 1989), and larvae were only observed on partially decomposed seaweed (Kompfner 1974). The time for the egg to hatch to the larval stage depends on species and environmental temperature, for the blow fly (order Diptera), this can take 8 hours at 21°C and metamorphosing from egg to adult can take six days (Gennard 2007). Since wrack can last on the shore for up to two weeks, a wrack pile could produce multiple generations of kelp flies.

The interaction that kelp flies have with wrack is unique compared to most organisms and their habitat. Kelp wrack has a positive effect on the on both kelp fly adults and larvae supplying food and habitat, as well as being chemically undefended. Fly larvae benefit at the expense of the wrack as a parasite or saprophyte (deriving nourishment from decaying organic matter); while the adult flies have a mutualistic direct effect by consuming the bacteria, which would decompose the wrack (Figure 31).

There is no ecological term that can correctly describe the relationship for a species that changes trophic levels throughout its life history, but remains on the same host, affecting it differently during each life stage. As a whole, the interaction between kelp fly larvae and wrack could be seen as a symbiotic parasitic relationship, but to be parasitic, the host has to be living (Allaby 1994). Hernandez et al. (2006) found that drift kelp are still alive and can produce viable sporophytes for up to 125 days after displacement. However, there have not been any studies that discuss if kelp wrack is considered alive.

Living algae require water, carbon dioxide, minerals, and light for photosynthesis and growth (Hurd et al. 2014). The equation for photosynthesis is:

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$

Once seaweed is removed from water, the photosynthetic rate changes, and is lower than when it was submerged because of the restricted carbon supply (Chapman 1986). However, seaweeds can tolerate moderate desiccation and the photosynthetic rate can increase since carbon dioxide from air can penetrate more quickly into the cells (Johnson et al. 1974). In addition, if humidity is high, photosynthesis can remain the same for long periods of time (Dring and Brown 1982). My experiments showed that larger wrack piles of approximately 3 kg retain water longer than smaller piles of approximately 0.5 kg to 1 kg.

Nutrients are also essential for kelp survival. Out of the water, kelp wrack will not be able to uptake nutrients, but they can rely on internal nitrogen reserves (Gerard 1982). Water and nutrients can be replenished during high tide. Replenishment is subject to the conditions that are site specific. For example, replenishment is more likely at the rocky intertidal where wrack could be in a puddle or in an area that receives spray, compared to beaches where tides typically only reach the area from the swash zone to the berm through the semidiurnal tides. Depending on the desiccation level, kelp wrack is likely alive from hours to days after deposition on the shore. Emersion is not detrimental to photosynthesis, but eventually the desiccation stress will become too much and the algae will die.

I describe the term “life history mutual parasite” as the interaction between a host and consumer species where the consumer spends its life with a host, where the host gains no fitness and acts as both a food source and a habitat. The effects of the consumer, both positive and negative, (i.e. direct predation on the host, predation of other predators on the host) have a change on the host from parasitism to mutualism as the consumer changes life stages. Another example in nature would be caterpillars, which consume a plant, but as butterflies, benefit the plant through pollination. The role of kelp flies is unique since the interaction can begin when the host is alive and continues after the host is dead. More studies would be needed to support the idea and better define this symbiotic relationship.

CONCLUSION

Combining data from deposition, persistence, and utilization showed that in fact these three seemingly unrelated aspects do in fact work together. Essentially, the kelp wrack that is deposited on the shoreline can remain there from hours to weeks. During this time wrack acts as a secondary producer where phlorotannins do not deter bacteria or kelp flies, which remain abundant.

Monitoring wrack along different the types of coast through long-term surveys and short-term experiments showed that beaches and the rocky intertidal can behave similarly or differently depending on the variable in question. For example, spatial differences existed between both types of substrate; however, there were only significant differences between beaches and the rocky intertidal for wrack biomass density and kelp fly density. Temporal differences were only significant in the decrease of phlorotannin concentrations over time and a change in fly density over time.

Deposition data showed that not only was *M. pyrifera* the dominant wrack species, but that the rocky intertidal received a larger biomass of kelp wrack year-round. This suggests that proximity to the source determines where the bulk of wrack will be deposited.

Persistence was found to significantly increase with distance from the shoreline, with most wrack being found closest to the berm or sea cliff. Persistence of wrack followed the seasonal pattern of geomorphology on beaches. Seasonal differences were seen where fall/winter storms eroded the beach, causing higher turnover where wrack was removed all the way to the berm, while calmer spring/summer weather built up sand on beaches preventing waves from reaching beyond the beach face and increasing persistence.

A simple interaction was described between kelp flies and wrack. Kelp flies have a unique relationship with kelp wrack where their trophic level changes with their life history, however, they remain on the same host and develop a different niche. This consumer resource interaction is unlike most in nature and is a combination of symbiotic relationships. Therefore, the new term “life history mutual parasite” explains how throughout the life history of a consumer, the species changes from a parasite to a mutualist, while the host transitions from living to dead.

Lastly, kelp wrack subsidies remain largely understudied where future directions of this work could more closely examine utilization of kelp wrack, specifically the role of bacteria and flies on wrack warrants further investigation. Certain areas include bacteria undergoing Next Generation Sequencing to look at species composition at different decay stages and the role of particular species in wrack breakdown. Similarly, research on flies could determine species composition as well as developing a life history model.

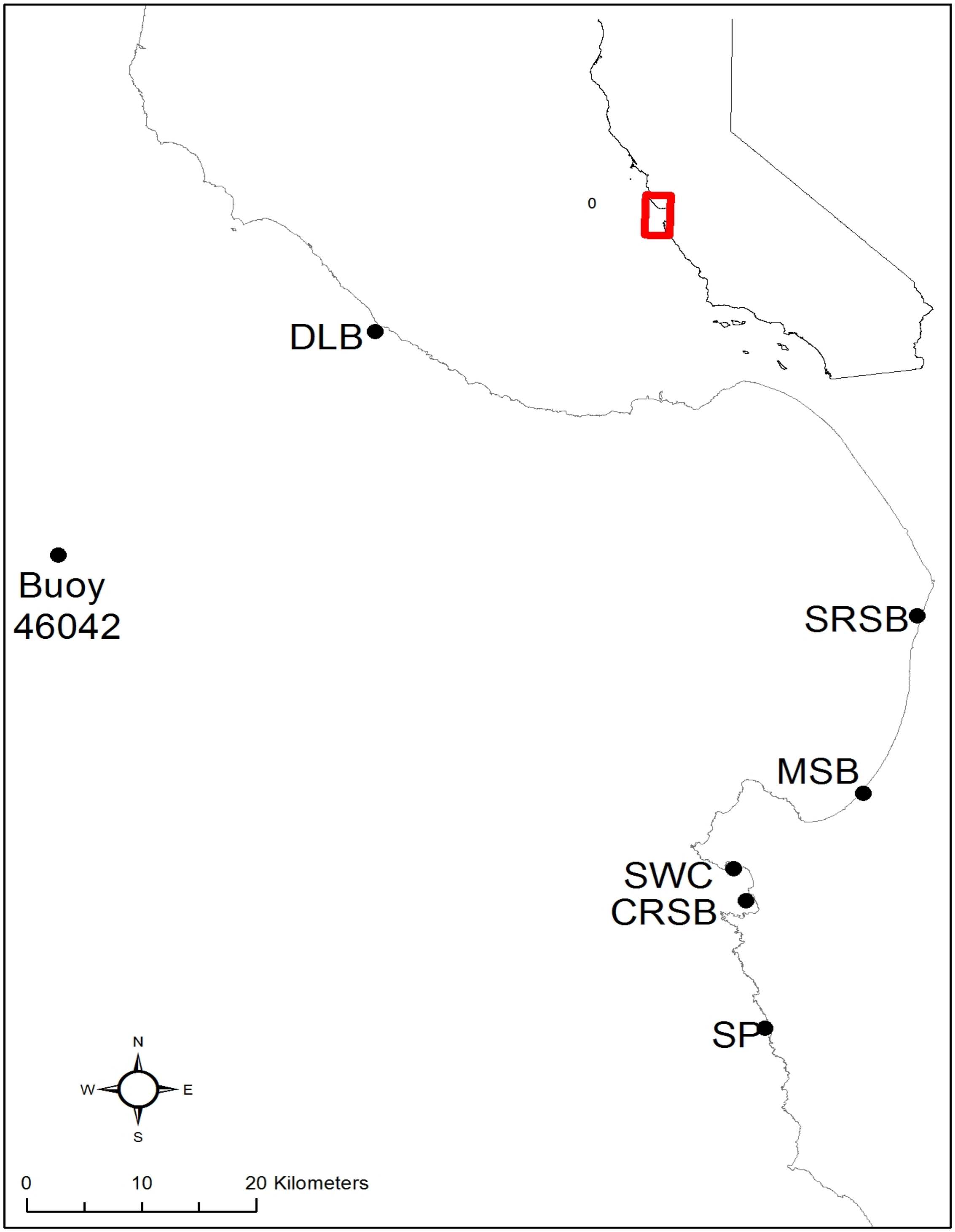


Figure 1. Location of study sites along the central California coast. Davenport Landing Beach (DLB) (rocky intertidal), Salinas River State Beach (SRSB) (beach), Monterey State Beach (MSB) (beach), Stillwater Cove (SWC) (rocky intertidal), Carmel River State Beach (CRSB) (beach), and Soberanes Point (SP) (rocky intertidal). National Data Buoy Center Station 46042 was located at 36.785 N 122.469 W.

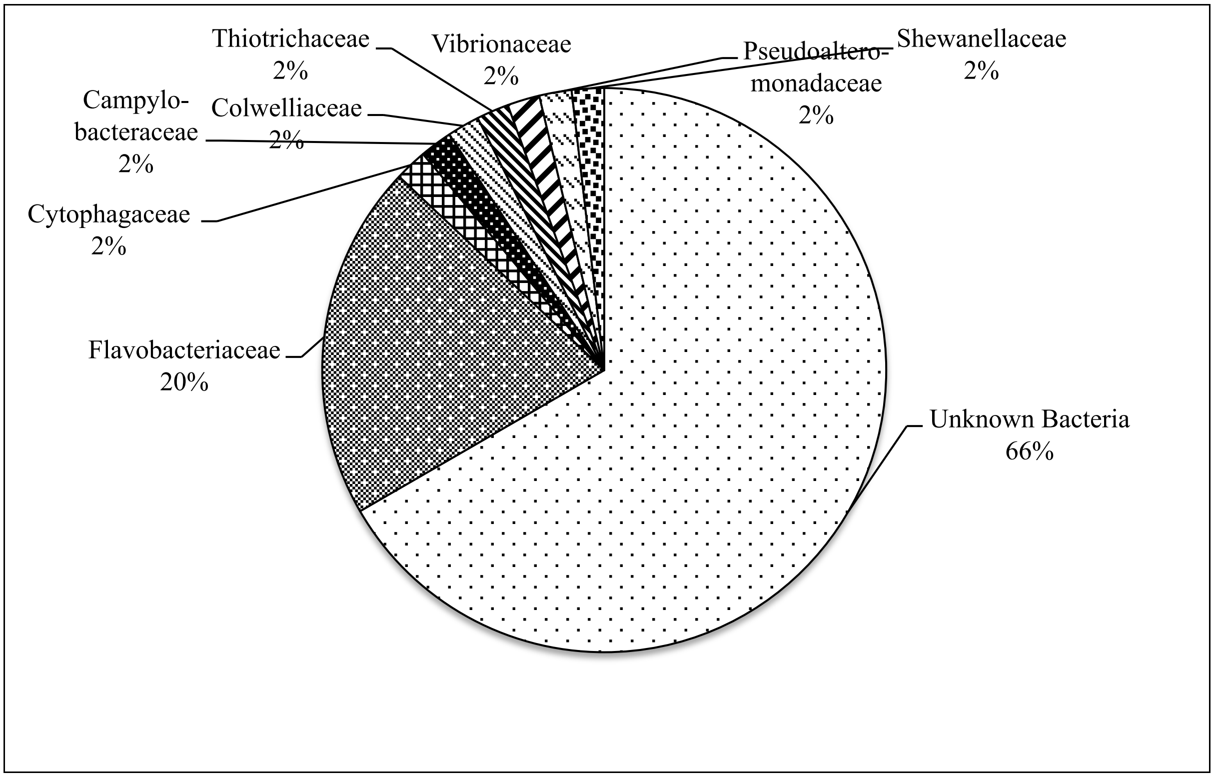


Figure 2. Taxonomic families of bacteria from a single sequenced *Macrocystis pyrifera* sample.

Table 1. Characteristics of bacterial density (colony forming units/μL) on the biofilm of *Macrocystis pyrifera* collected at beaches and rocky intertidal sites during July 2013. The pigment was the color of the colonies. Gram stain was determined using the gram stain test to identify peptidoglycan thickness in bacterial cell walls. Bacterial morphology consisted of coccus (spherical), bacillus (rod shaped), filamentous (filaments), and diploid coccus (two spheres).

Pigment	Gram Stain	Morphology
Golden-yellow	+	Coccus
Yellow	+	Coccus
Clear Mucoid	-	Bacillus
Clear	-	Coccus
White	+	Filamentous
Translucent	-	Diploid Coccus

Table 2. Species composition and their number of individuals (completely intact algae) or fragments (holdfast, stipe, or frond) at beaches and the rocky intertidal in the deposition quadrat over 15 months. The table was organized in decreasing order by the beach species abundance.

Species Composition	Beach Species Abun.	Rocky Species Abun.	Beach Ind.	Rocky Ind.	Beach Frag.	Rocky Frag.
Macrocystis pyrifera	850	547	43	65	805	482
Nereocystis luetkeana	477	219	24	34	451	185
Egregia menziesii	170	255	19	30	151	225
Stephanocystis osmundaceae	53	96	2	8	51	88
Postelsia palmaeformis	43	46	40	39	3	7
Laminaria setchellii	10	18	1	6	9	12
Pterygophora californica	0	116	0	8	0	108
Desmarestia ligulata	0	10	0	3	0	7
Fucus distichus	0	2	0	1	0	1
Dictyoneurum californicum	0	5	0	5	0	0
Alaria marginata	0	1	0	0	0	1
TOTAL	1603	1315	129	199	1470	1116

Table 3. Species composition and their percent biomass at beaches and the rocky intertidal in the deposition quadrat over 15 months. The table was organized in decreasing order by the rocky intertidal percent biomass composition of wrack.

Species Composition	Beach % Biomass Composition	Rocky % Biomass Composition
Macrocystis pyrifera	74.9	33.1
Egregia menziesii	7.6	32.7
Postelsia palmaeformis	0.7	24.7
Nereocystis luetkeana	15.3	4.2
Pterygophora californica	0	3.9
Stephanocystis osmundaceae	1.3	1.2
Desmarestia ligulata	0	0.1
Laminaria setchellii	0.2	0.04
Fucus distichus	0	0.009
Dictyoneurum californicum	0	0.004
Alaria marginata	0	0.0002
TOTAL	100	100

Table 4. ANOVA on the effects of month on substrate type (beach/rocky intertidal) individual kelp wrack.

Source	df	MS	F value	P
Month	14	35.576	3.202	0.001
Substrate	1	52.9	4.761	0.033
Month x Substrate	14	6.09	0.548	0.893
Error	60	11.111		

Table 5. ANOVA on the effects of time (month) on substrate type (beach/rocky intertidal) fragmented kelp wrack.

Source	df	MS	F value	P
Month	14	400.1	2.742	0.589
Substrate	1	1254.4	0.874	0.103
Month x Substrate	14	220.376	0.482	0.934
Error	60	457.522		

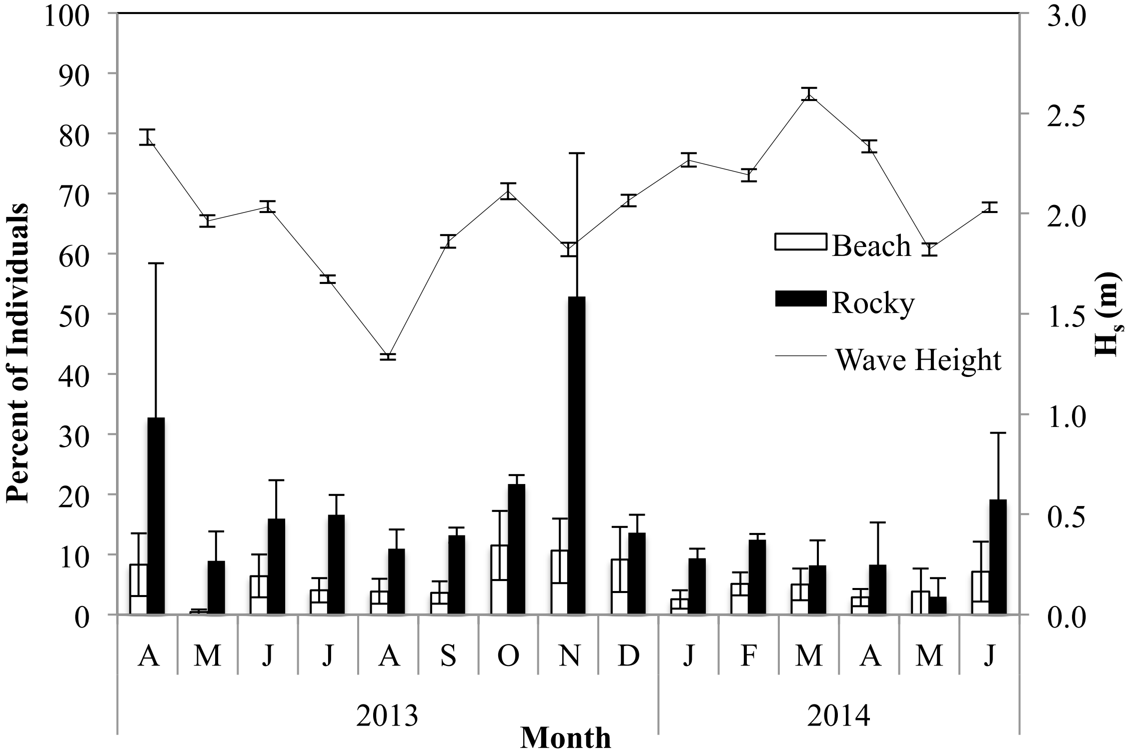


Figure 3. Temporal variability in significant wave height (H_s) and percentage of wrack that was an individual (contained holdfast and fronds) between beaches and the rocky intertidal in the deposition quadrat. Data are means ± SE, n=3.

Table 6. ANOVA on the effects of time (month) on substrate type (beach/rocky intertidal) kelp wrack biomass density (kg/m^2) of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Month	14	4.920 E-6	0.842	0.623
Substrate	1	4.055 E-5	6.937	0.011
Month x Substrate	14	4.706 E-6	0.805	0.66
Error	60	5.846 E-6		

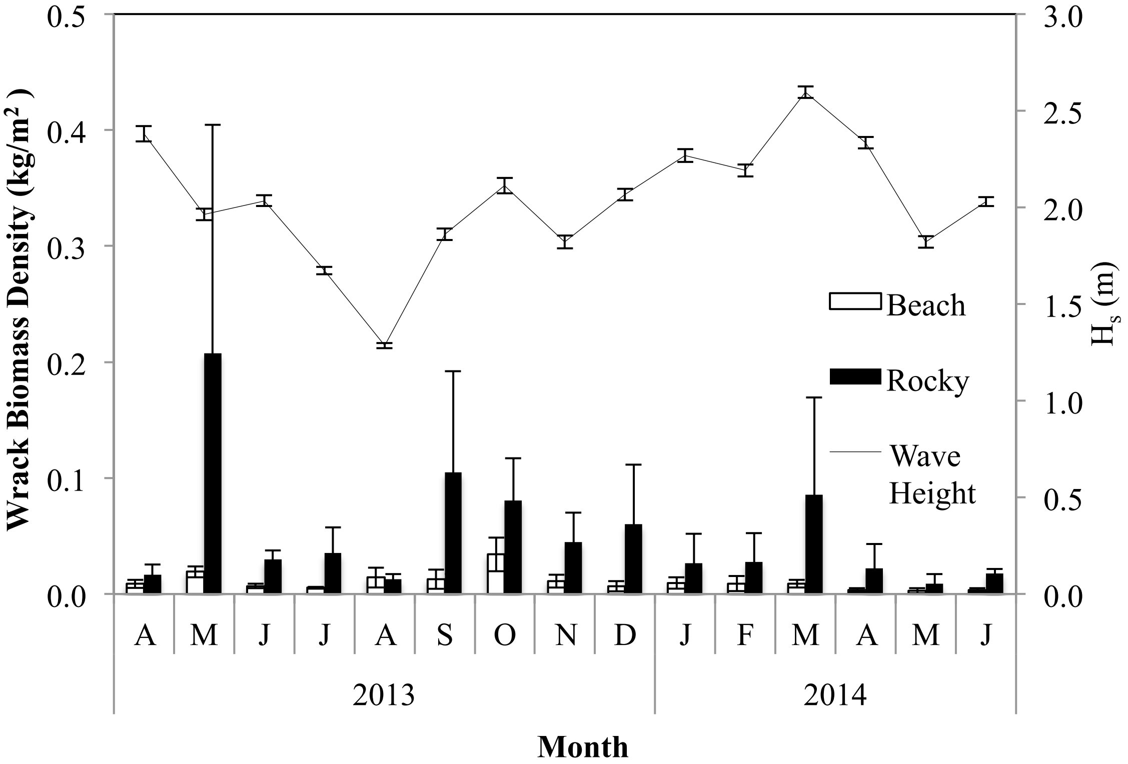


Figure 4. Temporal variability in significant wave height (H_s) and wrack biomass density (kg/m^2) between beaches and the rocky intertidal in the deposition quadrat. Data are means ± SE, n=3.

Table 7. ANOVA on the effects of season (spring/summer/fall/winter) on significant wave height (H_s) (m).

Source	**df**	**MS**	**F value**	**P**
Season	3	0.191	2.463	0.117
Error	11	0.078		

Table 8. ANOVA on the effects of substrate type (beach/rocky intertidal) on seasonal (spring/summer/fall/winter) kelp wrack persistence (# of occurrences).

Source	**df**	**MS**	**F value**	**P**
Substrate	1	0.042	0.125	0.728
Season	3	0.486	1.458	0.263
Substrate x Season	3	0.375	1.125	0.368
Error	16	0.333		

Table 9. Species composition and abundance of kelp wrack at beaches and the rocky intertidal in the persistence quadrat over 15 months. The percent of the total samples that were buried on beaches was calculated using: (number of samples buried for a species/total number of beach samples). The table was arranged in decreasing order by the beach species abundance of wrack.

Species Composition	Beach Species Abundance	Rocky Species Abundance	% Buried
Macrocystis pyrifera	5253	2152	16
Nereocystis luetkeana	2889	684	5
Egregia menziesii	704	618	2
Stephanocystis osmundaceae	589	758	0
Postelsia palmaeformis	160	214	0
Laminaria setchellii	115	43	0
Desmarestia ligulata	8	172	0
Pterygophora californica	7	327	0
Alaria marginata	3	5	0
Dictyoneurum californicum	3	8	0
Fucus distichus	1	4	0
Colpomenia sinuosa	0	1	0
Laminaria sinclairii	0	1	0
Pelvetiopsis limitata	0	1	0
TOTAL	9732	4988	23

Table 10. Temporal variability in the persistence of kelp wrack at beaches and the rocky intertidal from April 2013 to June 2014. Data were averaged ± SE, including maximum and minimum persistence during the season.

Site	Season	Average	SE	Maximum	Minimum
Salinas River State Beach	Spring	3	0.132	11	1
	Summer	2	0.122	17	1
	Fall	2	0.097	9	1
	Winter	2	0.169	14	1
Monterey State Beach	Spring	3	0.094	18	1
	Summer	2	0.082	15	1
	Fall	2	0.082	13	1
	Winter	3	0.119	21	1
Carmel River State Beach	Spring	2	0.098	10	1
	Summer	2	0.104	17	1
	Fall	2	0.095	9	1
	Winter	2	0.081	9	1
Davenport Landing Beach	Spring	2	0.092	8	1
	Summer	2	0.087	9	1
	Fall	1	0.065	4	1
	Winter	2	0.068	5	1
Stillwater Cove	Spring	2	0.07	6	1
	Summer	2	0.077	9	1
	Fall	2	0.134	10	1
	Winter	2	0.079	7	1
Soberanes Point	Spring	3	0.248	18	1
	Summer	4	0.256	23	1
	Fall	2	0.125	8	1
	Winter	2	0.133	9	1

Table 11. Heterogeneity Chi-Square values and p values of burial, beach zone (swash/beach face/berm), and interaction of burial and beach zone on kelp wrack.

			Effects		
Site	Season	X^2	Burial	Beach Zone	Burial x Beach Zone
Salinas River State Beach	Spring	29.03	<0.001	<0.001	<0.001
	Summer	54.96	<0.001	<0.001	<0.001
	Fall	0.57	<0.500	<0.001	<0.001
	Winter	10.21	<0.001	<0.001	<0.001
Monterey State Beach	Spring	88.27	<0.001	<0.001	<0.001
	Summer	4.31	<0.001	<0.001	<0.001
	Fall	68.42	<0.001	<0.001	<0.001
	Winter	55.05	<0.001	<0.001	<0.001
Carmel River State Beach	Spring	3.76	<0.025	<0.001	<0.001
	Summer	80.9	<0.001	<0.001	<0.001
	Fall	104.14	<0.001	<0.001	<0.001
	Winter	100.74	<0.001	<0.001	<0.001

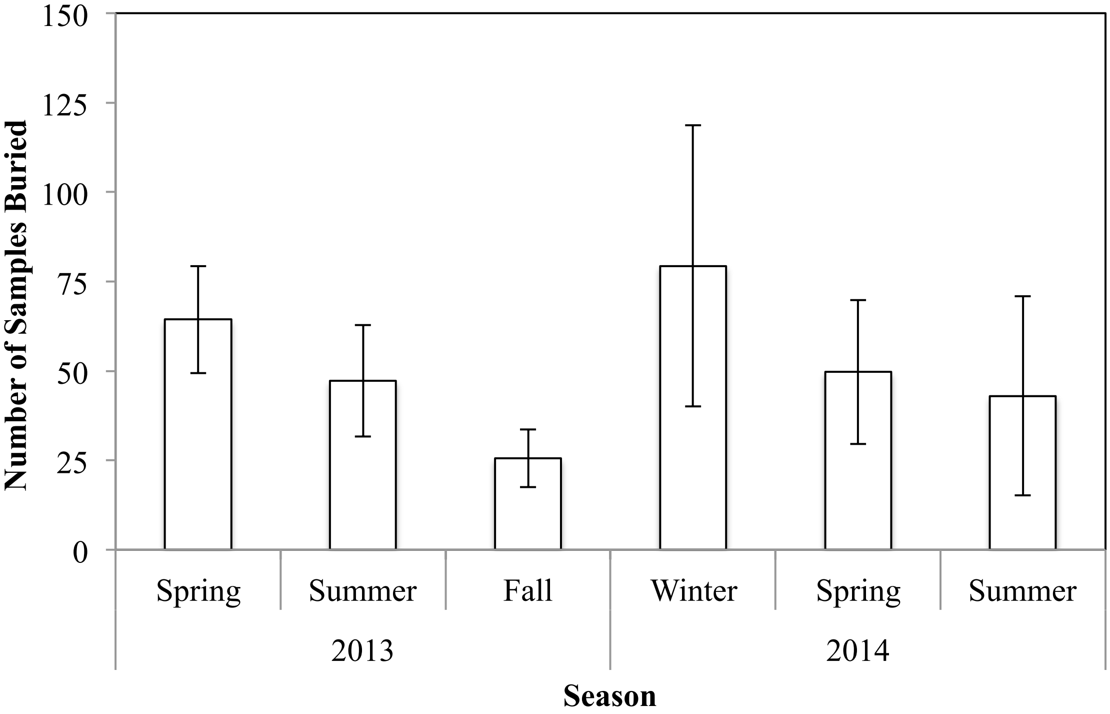


Figure 5. Temporal variability in the number of samples buried (25%, 50%, or 75%) on beaches within the persistence quadrat over 15 months. Data are means from 3 sites ± SE. Spring 2013 (April, May) n=714; Summer 2013 (June, July, August) n=2286; Fall 2013 (September, October, November) n=1,895; Winter 2014 (December, January, February) n=2,447; Spring 2014 (March, April, May) n=1,867; Summer 2014 (June) n=415.

Table 12a. ANOVA on the effects of kelp wrack persistence (# of occurrences) on sand grain size (µm).

Source	df	MS	F value	P
Grain Size	1	12925.2	2.115	0.220
Error	4	6112.57		

Table 12b. ANOVA on the effects of kelp wrack persistence (# of occurrences) on beach slope (°).

Source	df	MS	F value	P
Slope	1	5.208	0.508	0.515
Error	4	10.25		

Table 12c. ANOVA on the effects of season (winter/summer) on beach zone (swash/beach face/berm) sand grain size (µm).

Source	df	MS	F value	P
Season	1	3372.9	0.155	0.701
Zone	2	22667.3	1.042	0.383
Season x Zone	2	7981.8	0.367	0.700
Error	12	21752.4		

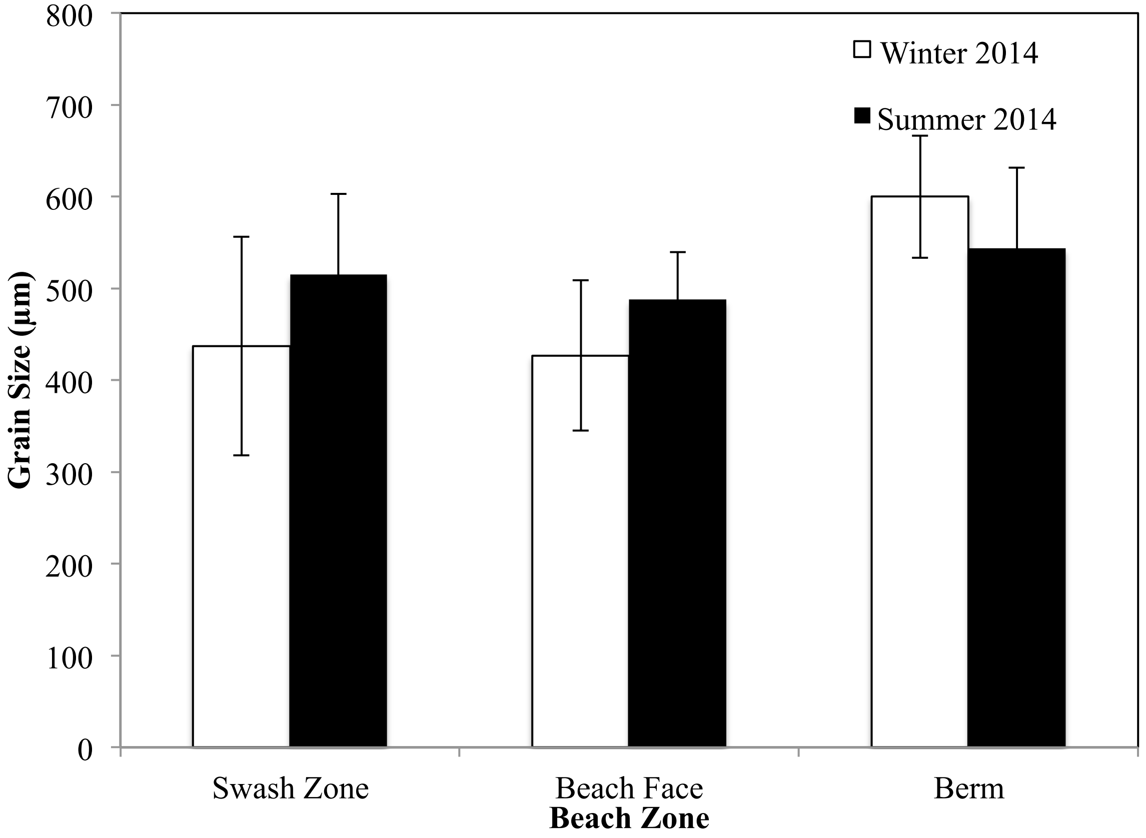


Figure 6. Temporal variability in sand grain size (µm) from winter 2014 and summer 2014. Data are means ± SE, n=3 per zone per season.

Table 13. ANOVA on the effects of season (winter/summer) on beach slope (°).

Source	df	MS	F value	P
Season	1	7.042	0.719	0.444
Error	4	9.792		

Table 14. Significance of linear regressions (distance of kelp wrack from shoreline/persistence of kelp wrack on shore) on cumulative and seasonal data for beaches and the rocky intertidal. * denotes a better fit with a quantile regression.

Site	Season	Slope	F	P	r^2
Salinas River State Beach	Cumulative *	0.2336	66.706	<0.001	0.126
	Spring *	0.0998	39.223	<0.001	0.129
	Summer *	0.0607	16.394	<0.001	0.049
	Fall *	0.0407	11.266	<0.001	0.042
	Winter *	0.0914	14.234	<0.001	0.069
Monterey State Beach	Cumulative *	0.0412	5.484	0.019	0.006
	Spring	0.02	6.286	0.012	0.011
	Summer	0.0136	3.145	0.077	0.006
	Fall *	0.0231	10.049	0.002	0.024
	Winter *	0.0245	5.88	0.016	0.011
Carmel River State Beach	Cumulative *	0.0971	75.122	<0.001	0.12
	Spring *	0.0218	9.284	0.003	0.034
	Summer *	0.0399	27.752	<0.001	0.078
	Fall *	0.0325	15.961	<0.001	0.065
	Winter *	0.0209	20.793	<0.001	0.086
Davenport Landing Beach	Cumulative *	0.0349	3.637	0.057	0.009
	Spring *	0.0377	7.653	0.006	0.04
	Summer *	0.0169	2.045	0.154	0.009
	Fall *	0.0098	1.277	0.261	0.01
	Winter *	0.0001	0	0.992	0
Stillwater Cove	Cumulative	-0.1106	102.082	<0.001	0.169
	Spring *	-0.0293	29.952	<0.001	0.107
	Summer *	-0.0277	20.067	<0.001	0.076
	Fall *	-0.073	25.579	<0.001	0.118
	Winter *	-0.0327	26.088	<0.001	0.106
Soberanes Point	Cumulative	-0.1268	4.462	0.035	0.013
	Spring *	0.0177	0.185	0.667	0.001
	Summer	-0.1023	5.35	0.022	0.024
	Fall	0.0264	1.55	0.215	0.01
	Winter	0.0185	0.881	0.349	0.005

Table 15. Significance of quantile regressions (distance of kelp wrack from shoreline/ persistence of kelp wrack) on cumulative and seasonal data for beaches and the rocky intertidal.

Site	Season	Quantile	Slope	F	P	r^2
Salinas River State Beach	Cumulative	75%	0.2336	29.822	<0.001	0.305
	Summer	50%	0.0607	12.344	0.001	0.095
	Fall	75%	0.0407	4.16	0.049	0.109
	Winter	75%	0.0914	7.849	0.01	0.246
Monterey State Beach	Cumulative	87.50%	0.0412	6.645	0.014	0.156
	Fall	50%	0.0231	11.063	0.001	0.074
	Winter	87.50%	0.0245	9.852	0.005	0.3
Carmel River State Beach	Cumulative	87.50%	0.0971	7.707	0.011	0.259
	Summer	87.50%	0.0399	5.98	0.026	0.26
	Fall	75%	0.0325	5.722	0.023	0.165
	Winter	75%	0.0209	8.338	0.007	0.223
Davenport Landing Beach	Cumulative	75%	0.0349	7.244	0.01	0.129
	Spring	50%	0.0377	6.797	0.011	0.092
	Fall	50%	0.0098	3.962	0.054	0.094
	Winter	50%	0.0001	0.964	0.33	0.014
Stillwater Cove	Spring	75%	-0.0293	14.537	<0.001	0.277
	Summer	50%	-0.0277	11.945	0.001	0.116
	Fall	75%	-0.073	5.625	0.025	0.178
	Winter	75%	-0.0327	7.244	0.012	0.218
Soberanes Point	Spring	75%	0.0177	2.256	0.151	0.117

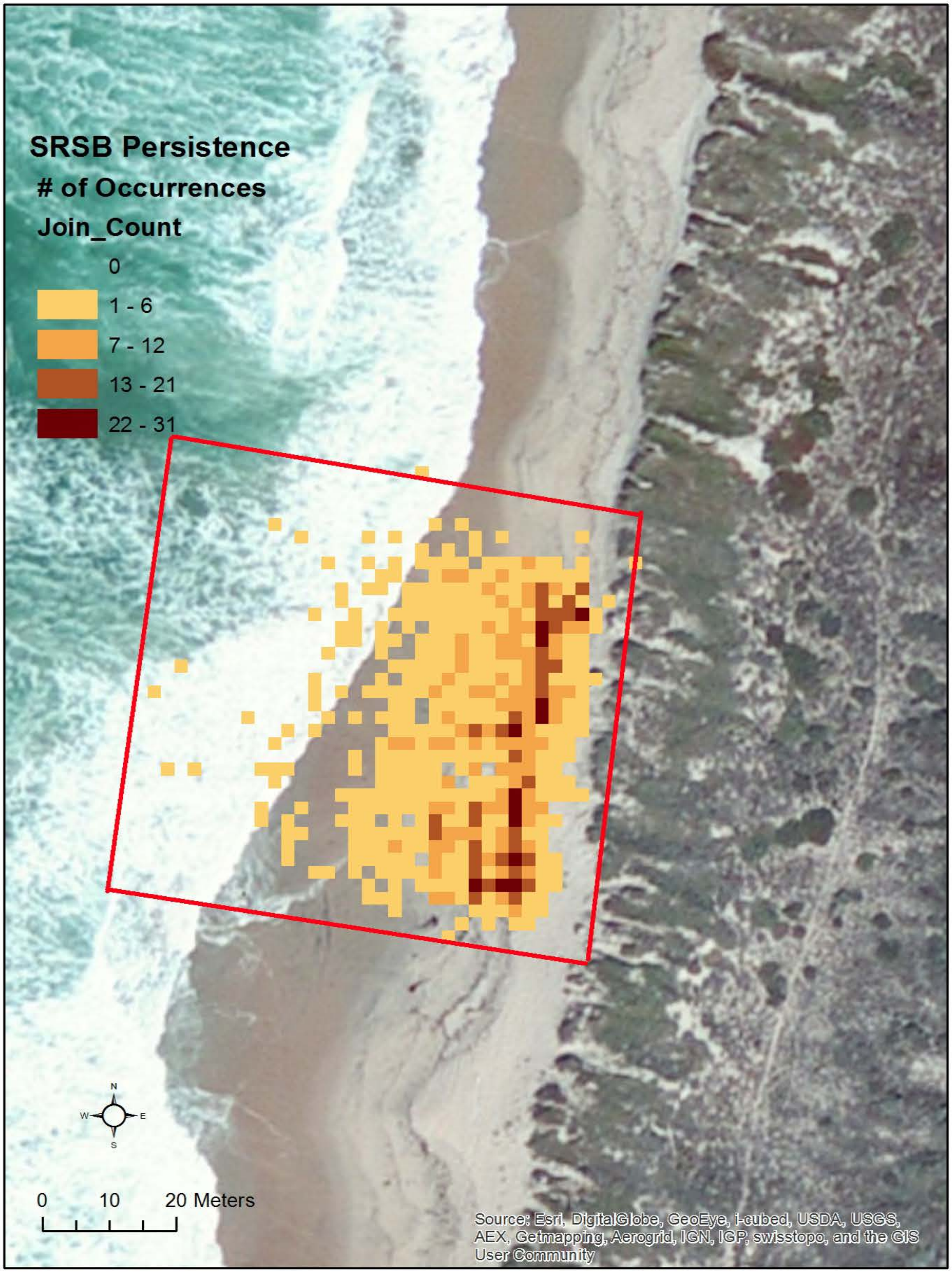


Figure 7. Total persistence of kelp wrack within the quadrat (red line) on Salinas River State Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature, n=2,568.

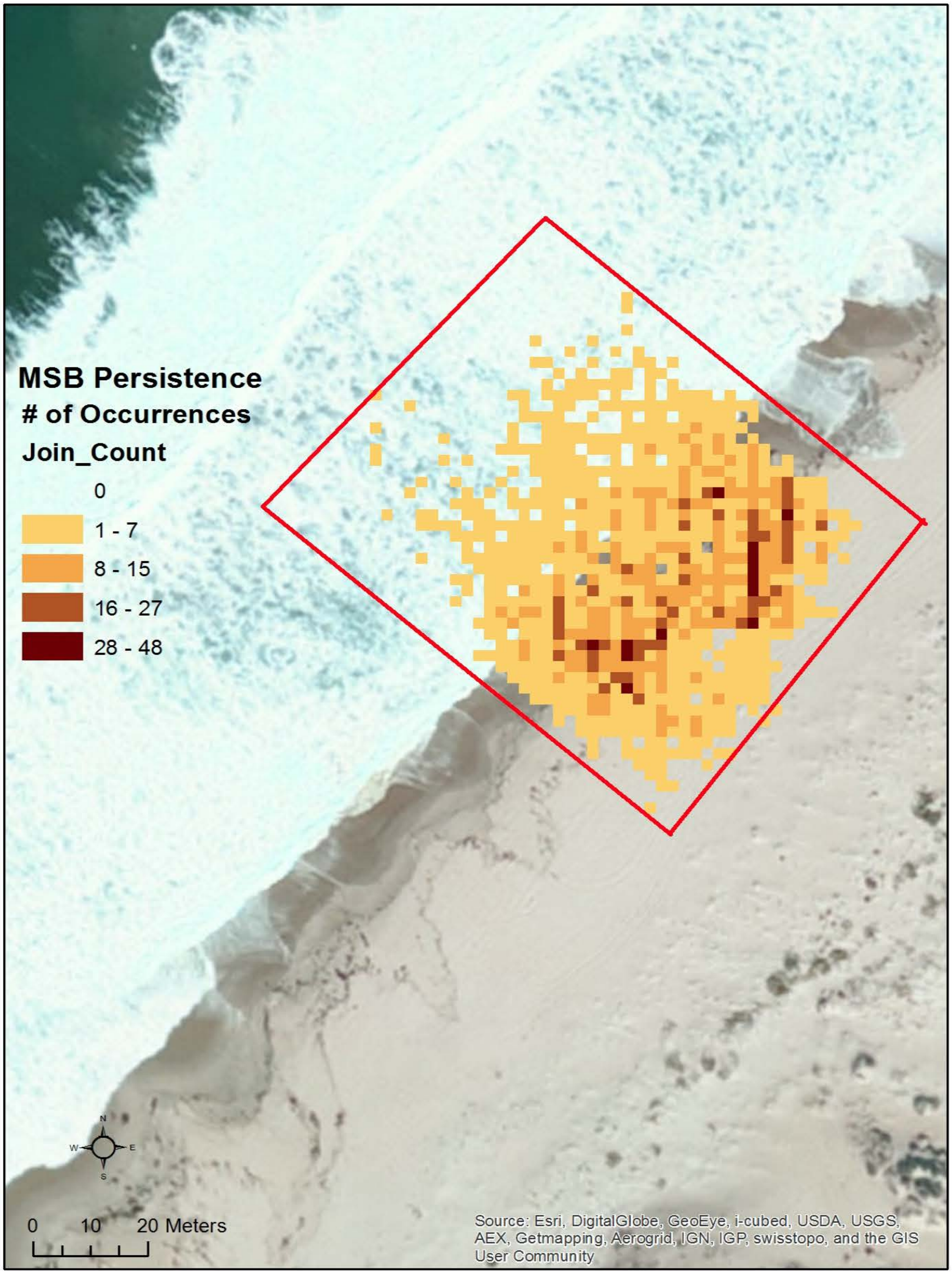
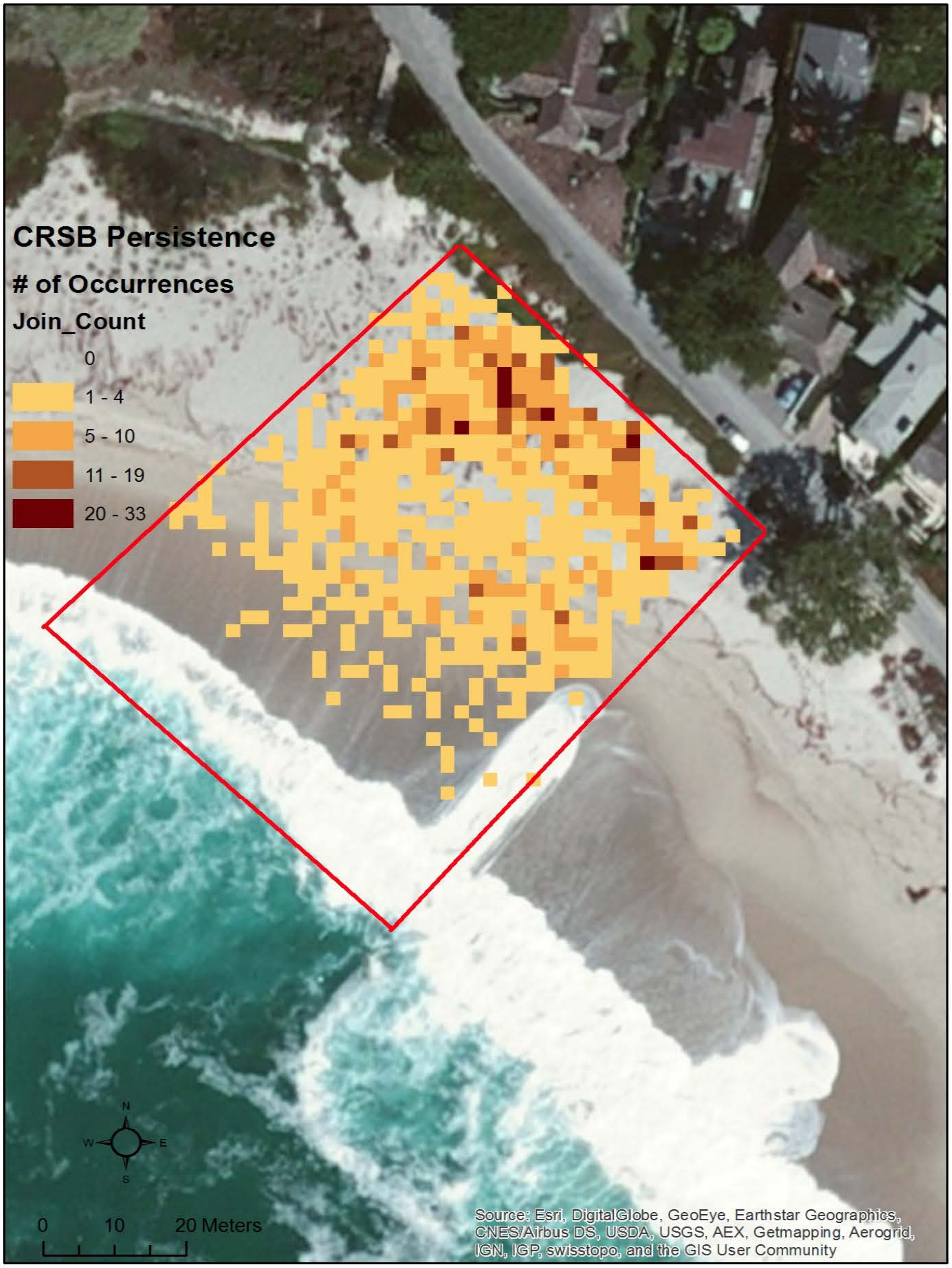


Figure 8. Total persistence of kelp wrack within the quadrat (red line) on Monterey State Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature, n=5,070.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 9. Total persistence of kelp wrack within the quadrat (red line) on Carmel River State Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature, n=2,568.

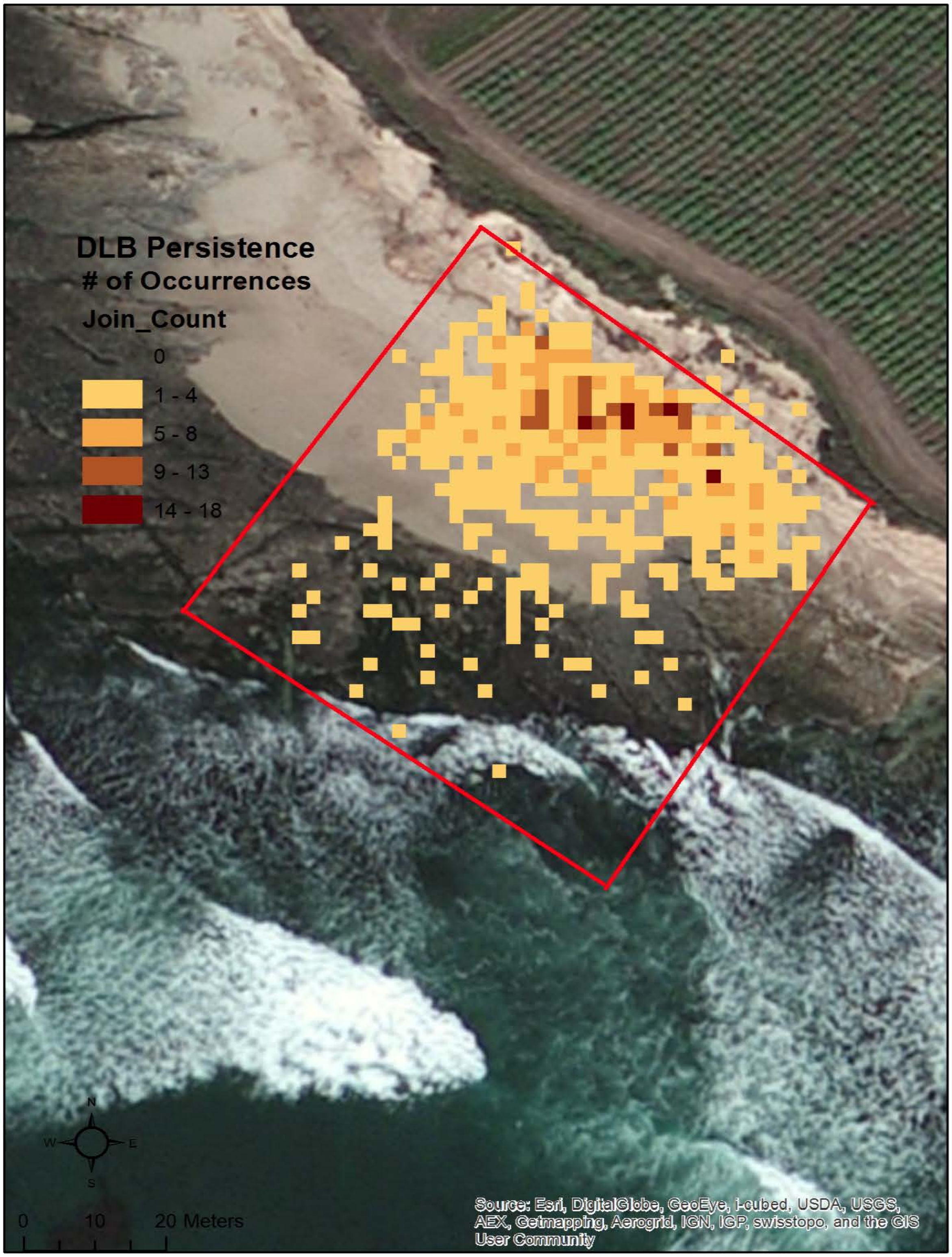


Figure 10. Total persistence of kelp wrack within the quadrat (red line) on Davenport Landing Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature, n=1,208.

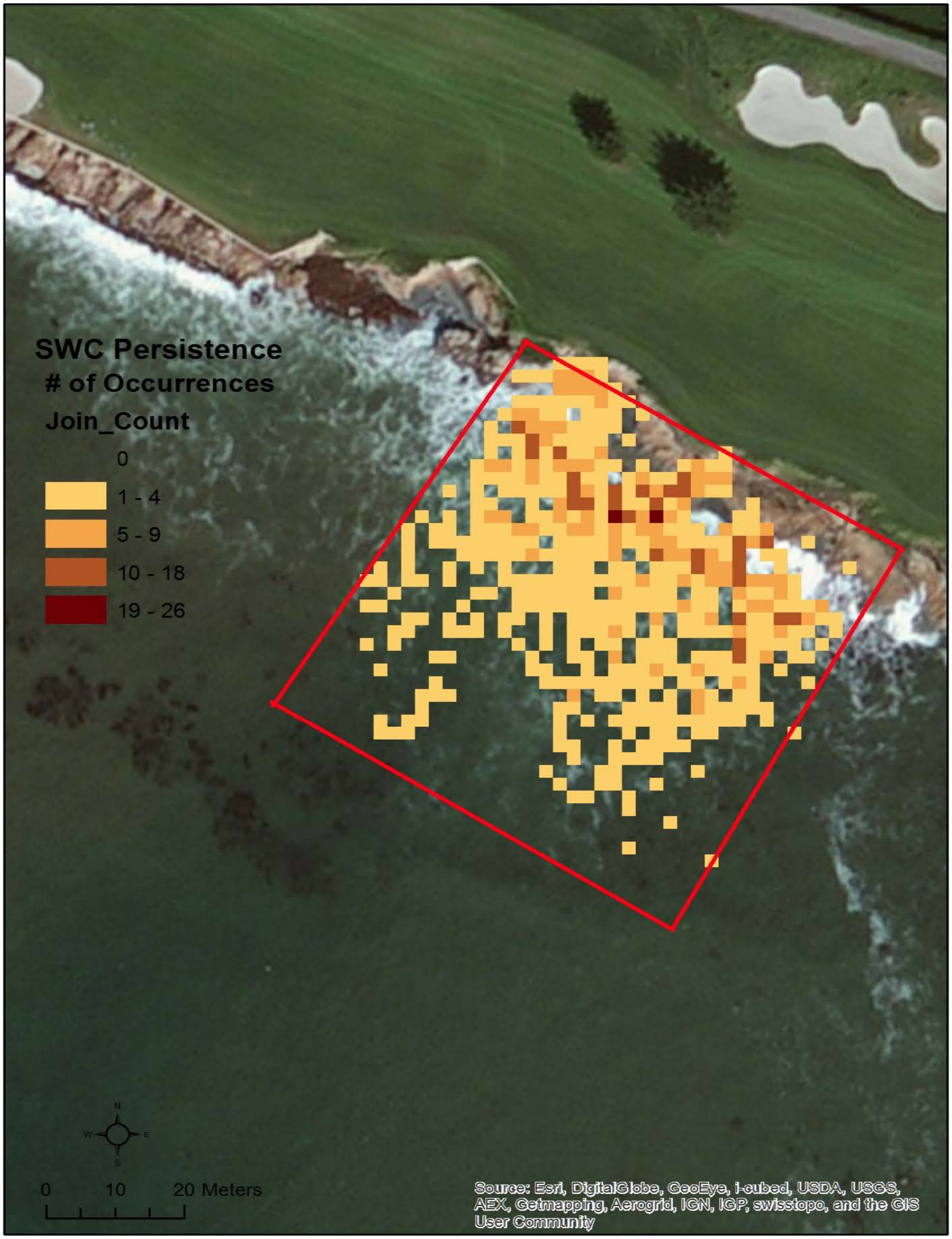
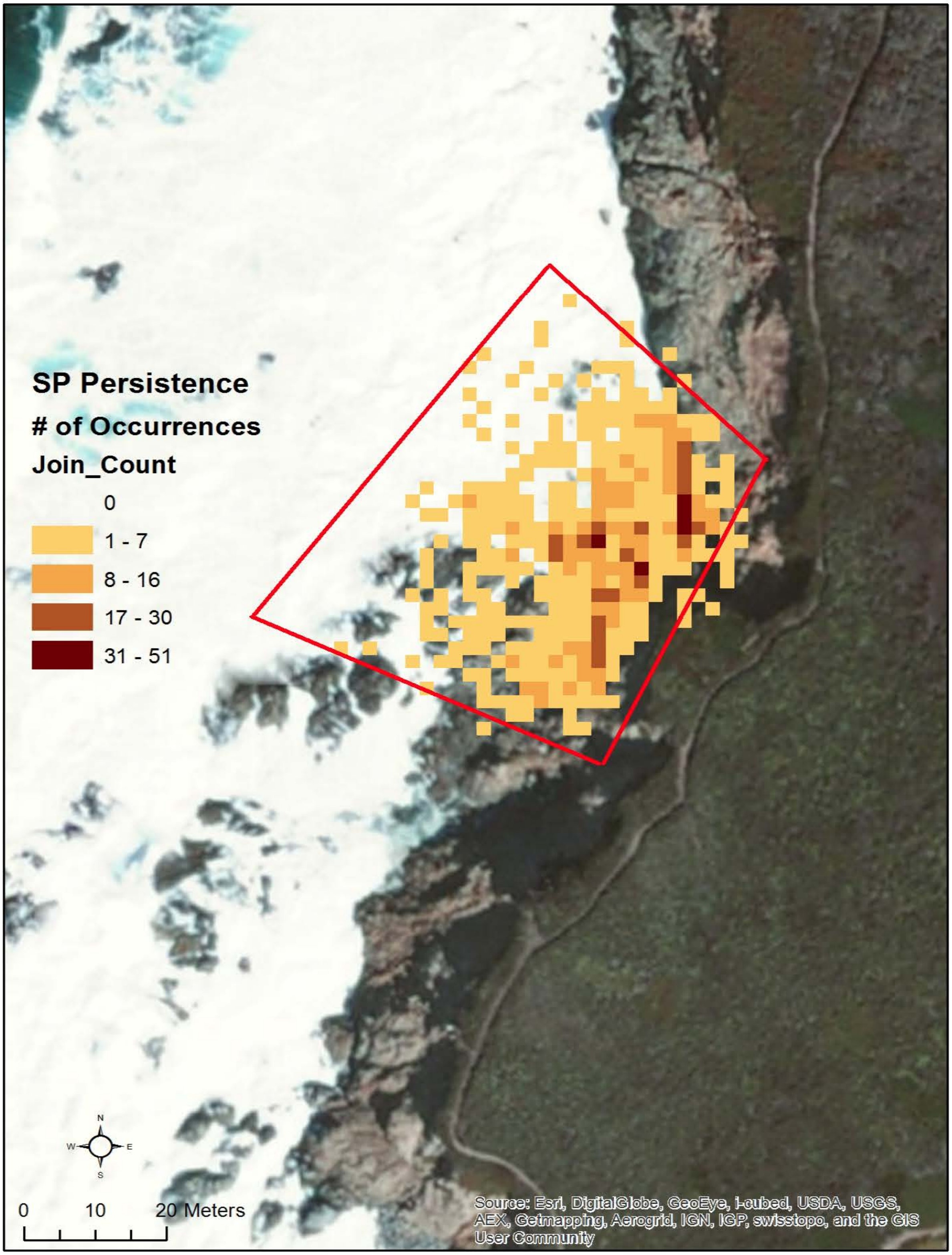


Figure 11. Total persistence of kelp wrack within the quadrat (red line) on Stillwater Cove from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the join count feature, n=1,747.



Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 12. Total persistence of kelp wrack within the quadrat (red line) on Soberanes Point from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature, n=2,073.

Table 16. ANOVA on the effects of time (month) on substrate type (beach/rocky intertidal) phlorotannin concentration (% dry mass) in *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Month	14	0.032	1.494	0.149
Substrate	1	0.043	1.967	0.167
Month x Substrate	14	0.024	1.104	0.378
Error	49	0.022		

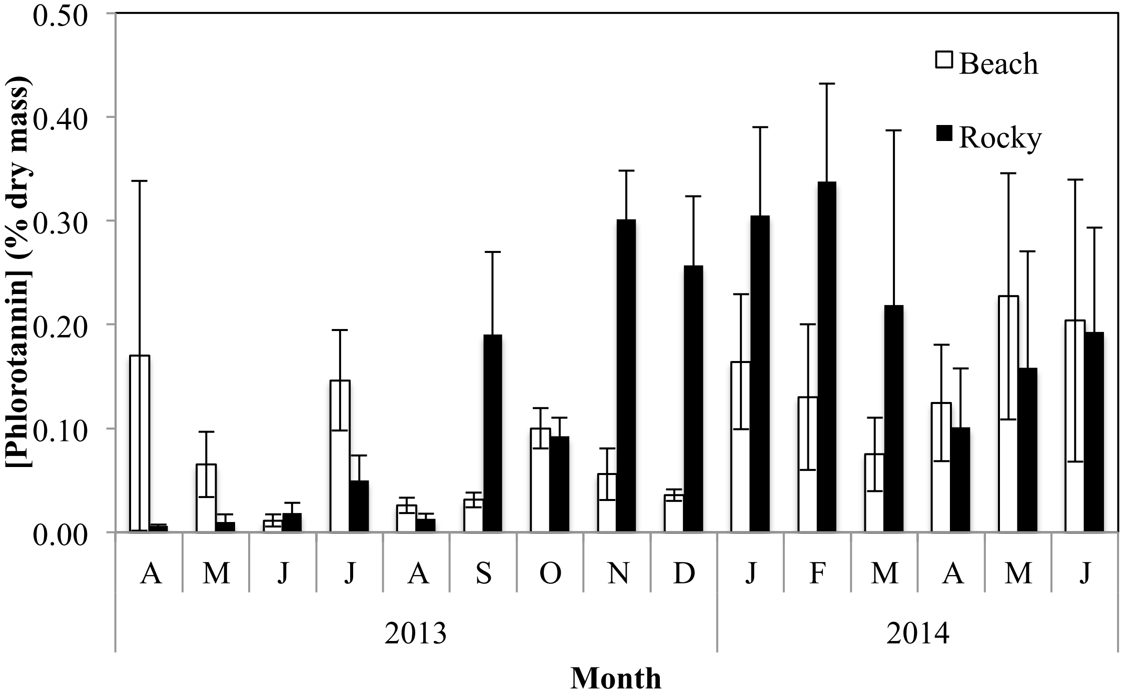


Figure 13. Temporal variability in phlorotannin concentration (% dry mass) between beaches and the rocky intertidal. Data are means ± SE, n=3.

Table 17. ANOVA on the effects of season (spring/summer/fall/winter) on substrate type (beach/rocky intertidal) bacterial colony density (colony forming units/µL) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Season	3	118236	2.372	0.109
Substrate	1	100895	2.024	0.174
Season x Substrate	3	15879.7	0.319	0.812
Error	16	49845		

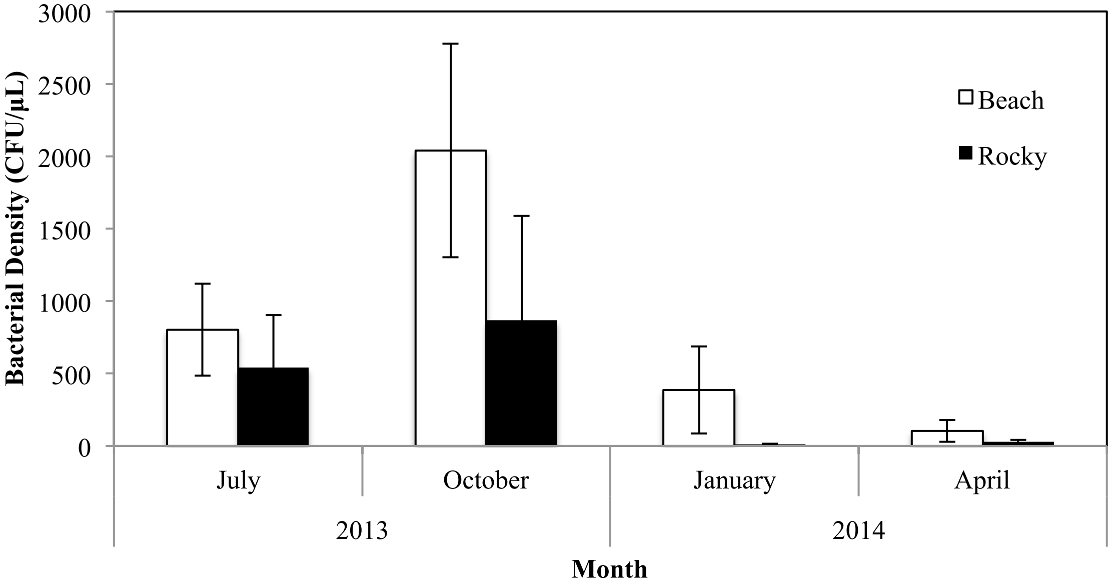


Figure 14. Temporal variability in bacterial density of colony forming units (CFU/µL) in samples collected seasonally. Data are means ± SE, n=3.

Table 18. ANOVA on the effects of substrate type (beach/rocky intertidal) on colony color (white/gold/yellow/pink/clear) bacterial colony density (colony forming units/μL) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Substrate	1	742928	1.93	0.168
Color	4	998045	2.592	0.04
Substrate x Color	4	722313	0.876	0.12
Error	110	384997		

Table 19. ANOVA on the effects of season (spring/summer/fall/winter) on colony color (white/gold/yellow/pink/clear) bacterial colony density (colony forming units/µL) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Season	3	283067	0.0683	0.565
Color	4	998045	2.407	0.054
Season x Color	12	305620	0.737	0.712
Error	100	414653		

Table 20. ANOVA on the effects of season (spring/summer/fall/winter) on colony morphology (coccus/bacillus) bacterial colony density (colony forming units/µL) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Season	3	13.521	2.29	0.093
Morphology	1	346.687	58.719	< 0.001
Season x Morphology	3	18.521	3.137	0.036
Error	40	5.904		

Table 21. ANOVA on the effects of substrate type (beach/rocky intertidal) on colony morphology (coccus/bacillus) bacterial colony density (colony forming units/µL) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Substrate	1	31.688	5.068	0.029
Morphology	1	346.688	55.543	< 0.001
Substrate x Morphology	1	25.521	4.082	0.049
Error	44	6.252		

Table 22. ANOVA on the effects of season (summer/winter) on substrate type (beach/rocky intertidal) total bacterial density (cells/g) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Season	1	4.090 E+15	1.364	0.276
Substrate	1	5.497 E+15	1.834	0.213
Season x Substrate	1	6.014 E+15	2.006	0.196
Error	8	2.998 E+15		

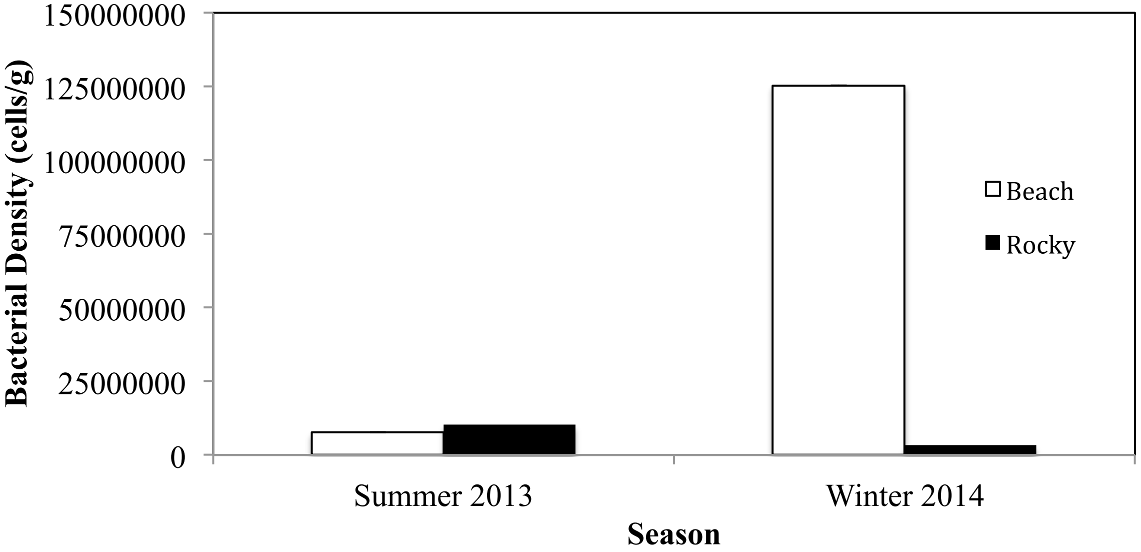


Figure 15. Temporal variability in total bacterial density using direct cell counts under an epifluorescent microscope between beaches and the rocky intertidal in July 2013 and January 2014. Data are means ± SE. Summer beach n=14, summer rocky n= 15, winter beach n=12, and winter rocky n=11.

Table 23. ANOVA on the effects of time (month) on substrate type (beach/rocky intertidal) on kelp fly density (flies/cm^2/hour) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Month	13	0.724	1.328	0.225
Substrate	1	1.041	1.909	0.173
Month x Substrate	13	0.283	0.52	0.903
Error	56	0.545		

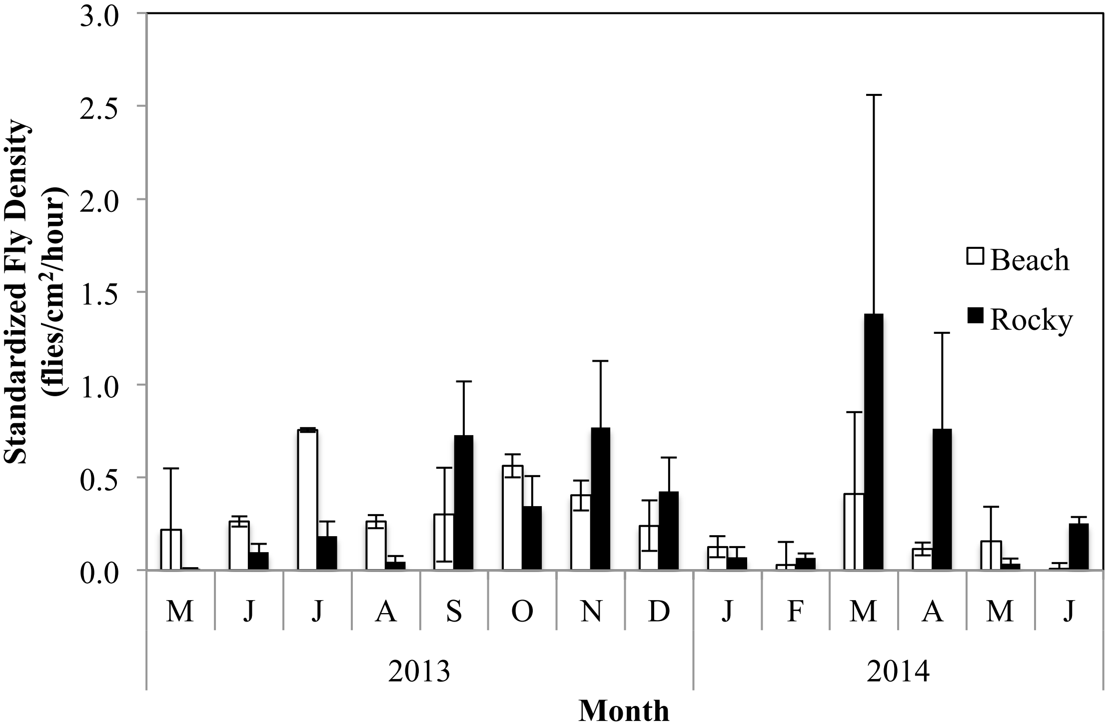


Figure 16. Temporal variability in kelp fly density (flies/cm^2/hour) between beaches and the rocky intertidal from May 2013 to June 2014. Data were standardized by subtracting flies found on sand or rock from flies found above kelp wrack. Data are means ± SE, n=3.

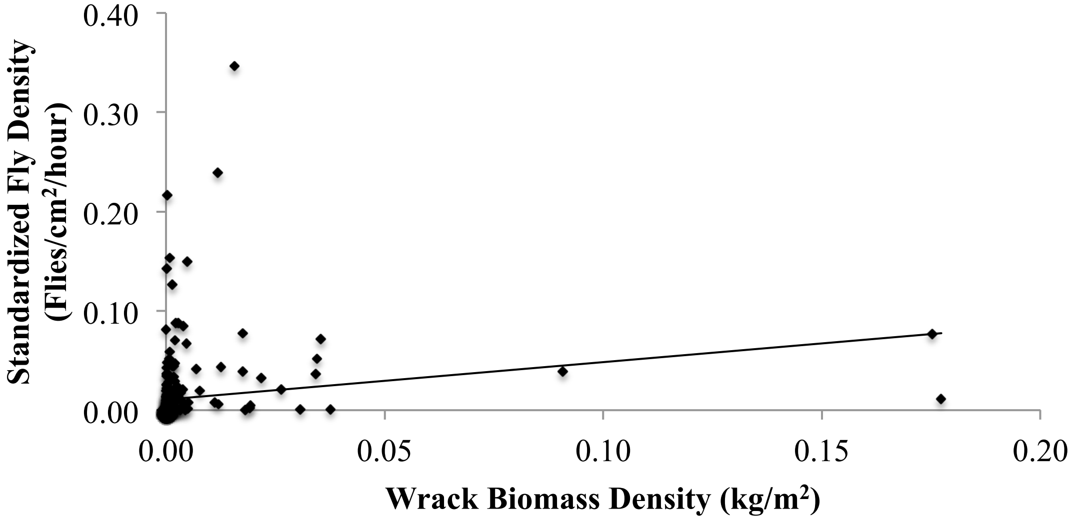


Figure 17. Relationship between kelp wrack biomass density (kg/m^2) and standardized fly density (flies/cm^2/hour) on wrack between May 2013 and June 2014 at all beaches and rocky intertidal sites. (Regression; peak fly density = 0.3768 (±0.049)* biomass density + 0.0107 (±3.123), $r^2 = 0.030$, $P = 0.001$, $F_{1,359} = 11.413$).

Table 24a. ANOVA on the effects of time (days) on substrate type (beach/rocky intertidal) on wet biomass (0.5 kg) of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	14	0.035	9.821	<0.001
Substrate	1	0.009	2.444	0.139
Time x Substrate	14	0	0.104	1
Error	15	0.004		

Table 24b. ANOVA on the effects of time (days) on substrate type (beach/rocky intertidal) wet biomass (1.0 kg) of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	14	0.137	9.395	<0.001
Substrate	1	0.027	1.883	0.19
Time x Substrate	14	0.004	0.279	0.989
Error	15	0.015		

Table 24c. ANOVA on the effects of time (days) on substrate type (beach/rocky intertidal) wet biomass (3.0 kg) of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	14	1.805	721852	<0.001
Substrate	1	5.034	2013561	<0.001
Time x Substrate	14	0.31	124090	<0.001
Error	15	2.500 E-6		

Table 25. Water loss in kelp wrack placed on beach face and berm on Salinas River State Beach in July 2014. Data are means ± SE, n=3.

	Percent Water Loss			
Weight (kg)	Beach Face	SE	Berm	SE
0.5	90	0	92	0
1	73	14	84	4.5
3	72	10.3	89	0.4

Table 26. Water loss in kelp wrack placed on low, mid, and high intertidal on Soberanes Point in August 2014. ND = No Data, data are means ± SE, n=3.

	Percent Water Loss					
Weight (kg)	Low Intertidal	SE	Mid Intertidal	SE	High Intertidal	SE
0.5	28.2	0	8.7	0	74	7.6
1	ND	ND	41	6.5	78	4
3	ND	ND	ND	ND	90	0

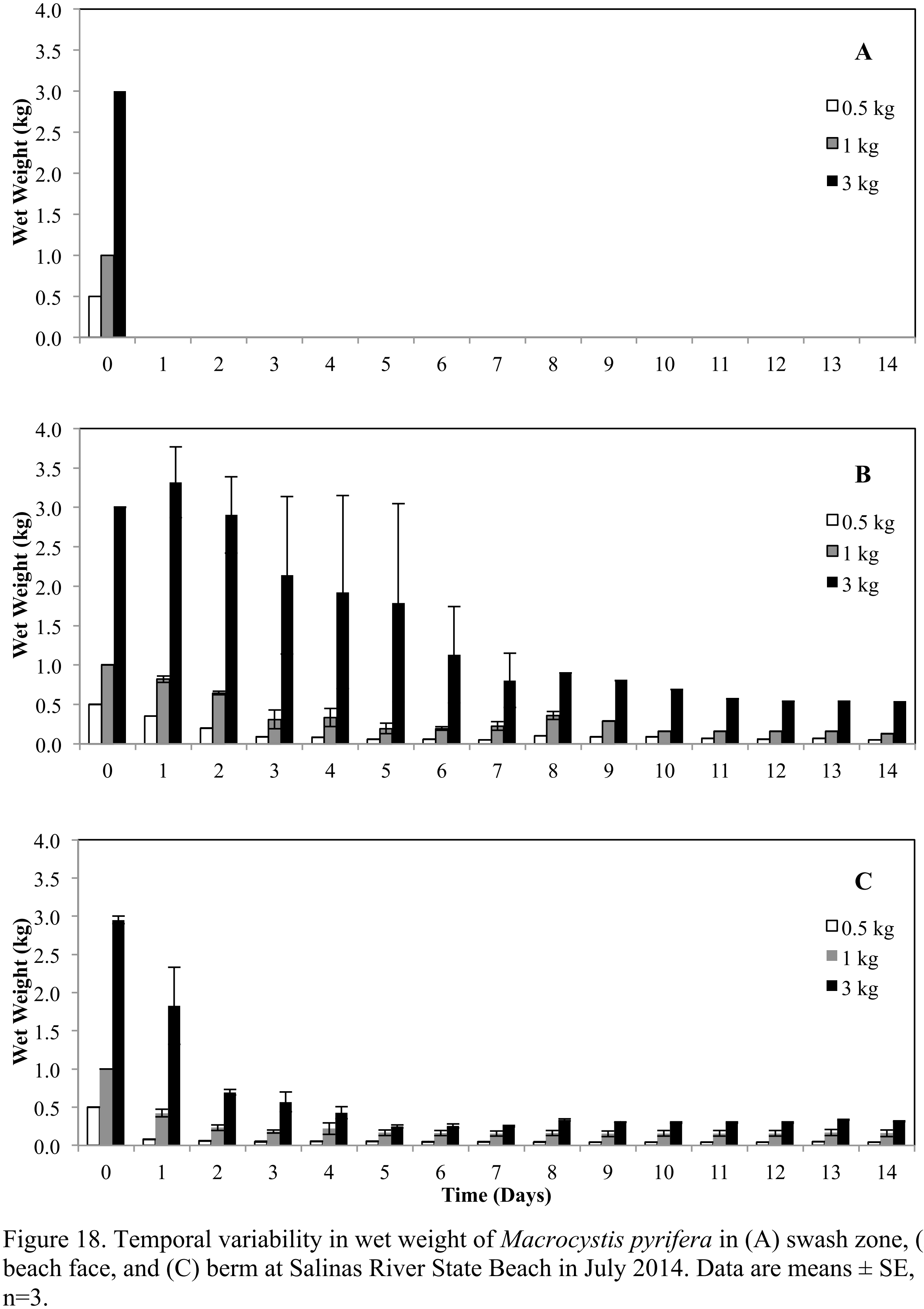


Figure 18. Temporal variability in wet weight of *Macrocystis pyrifera* in (A) swash zone, (B) beach face, and (C) berm at Salinas River State Beach in July 2014. Data are means ± SE, n=3.

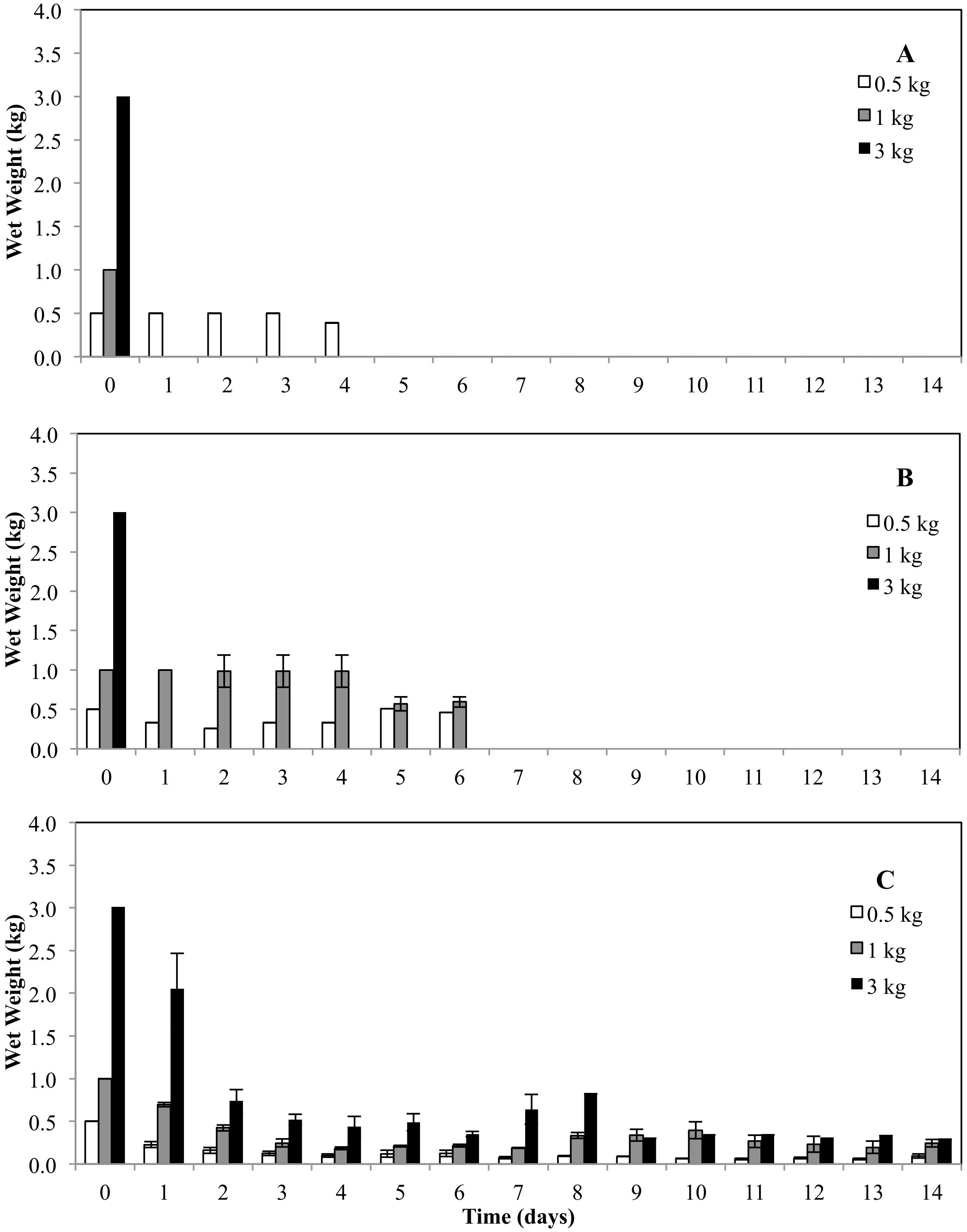


Figure 19. Temporal variability in wet weight of *Macrocystis pyrifera* in (A) low intertidal, (B) mid intertidal, and (C) high intertidal at Soberanes Point in August 2014. Data are means ± SE, n=3.

Table 27. ANOVA on the effects of substrate type (beach/rocky intertidal) on zone (swash/beach face/berm or low/mid/high) persistence of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Substrate	1	107.643	7.682	0.008
Zone	2	607.667	43.365	< 0.001
Substrate x Zone	2	36.171	2.581	0.086
Error	48	14.013		

Table 28. ANOVA on the effects of substrate type (beach/rocky intertidal) on wrack wet weight (0.5 kg/1.0 kg/3.0 kg) persistence of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Substrate	1	76.069	1.927	0.172
Weight	2	16.421	0.416	0.662
Substrate x Weight	2	6.999	0.177	0.838
Error	48	39.481		

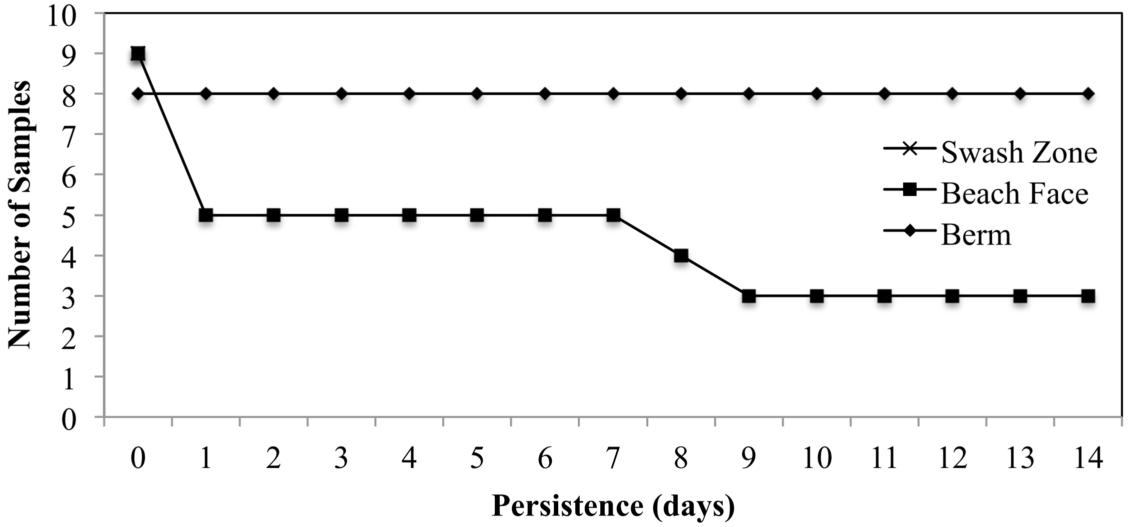


Figure 20. Temporal variability in persistence of *Macrocystis pyrifera* in the swash zone, beach face, and berm at Salinas River State Beach in July 2014. Samples were a combination of 0.5 kg, 1 kg, and 3 kg samples, n=26.

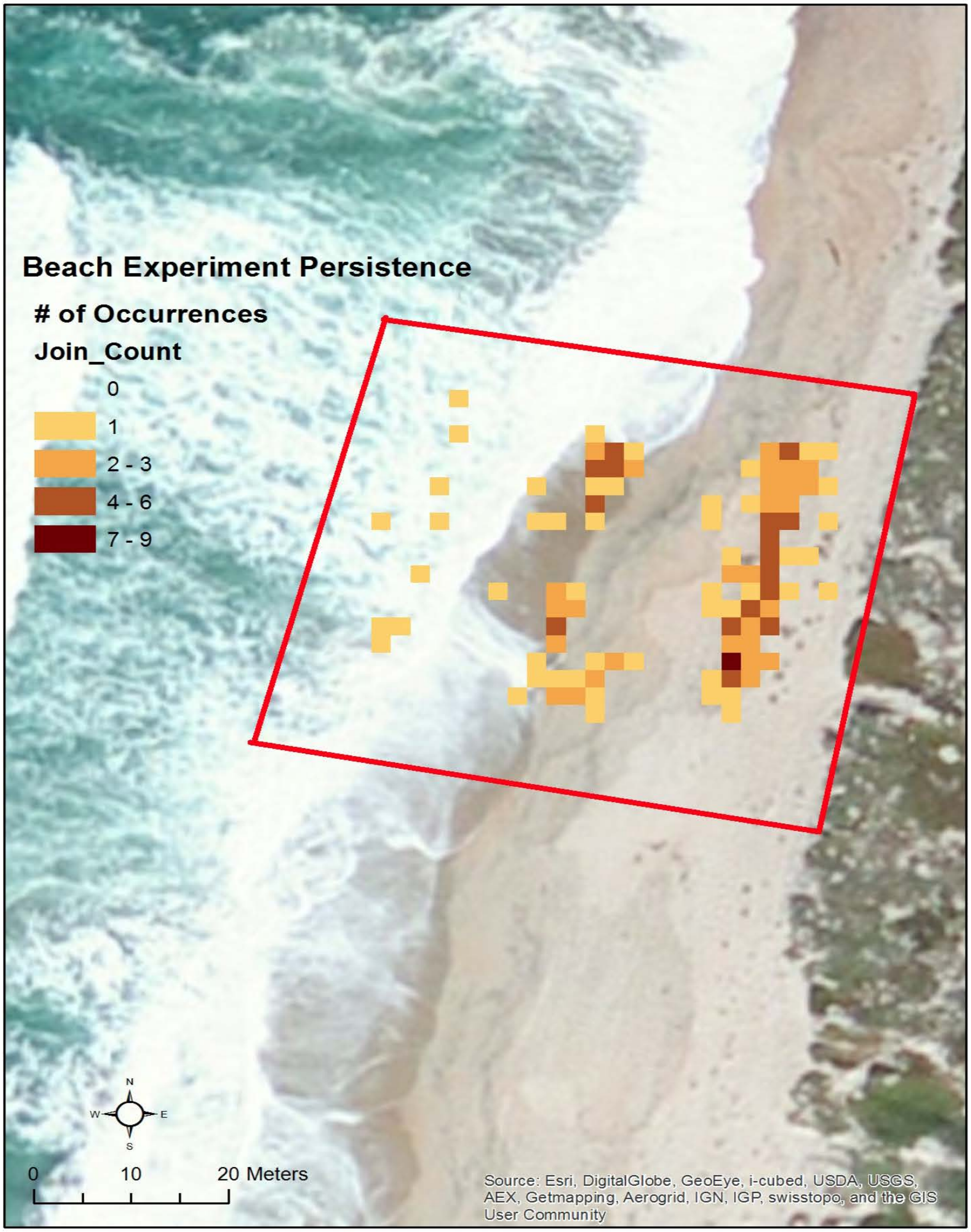


Figure 21. *Macrocystis pyrifera* persistence during the beach experiment within the quadrat (red line) at Salinas River State Beach in July 2014. Colored pixels represent the location of wrack piles and their persistence values using the Join Count feature, n=9 samples per zone, 3 zones.

Table 29. ANOVA on the effects of wrack wet weight (0.5 kg/1.0 kg/3.0 kg) on time (days) burial of *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Weight	2	0.041	0.168	0.847
Time	14	0.474	1.927	0.085
Weight x Time	28	0.111	0.451	0.975
Error	21	0.246		

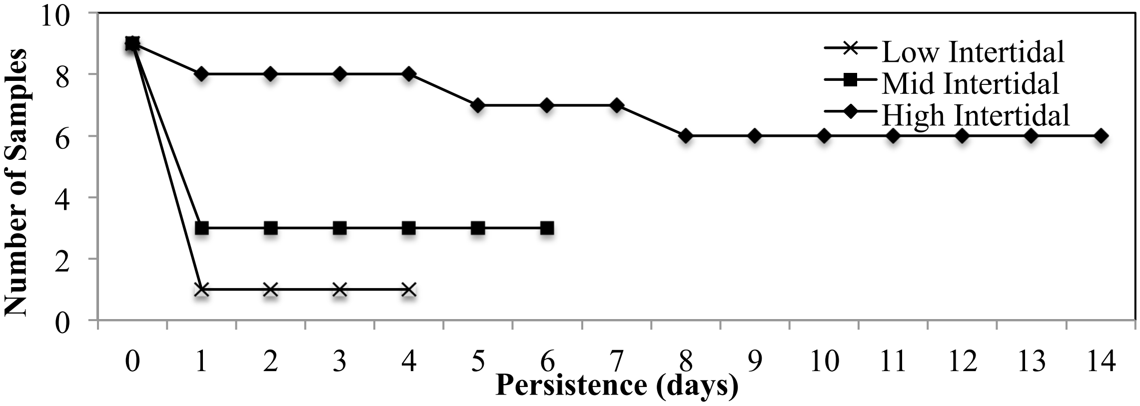
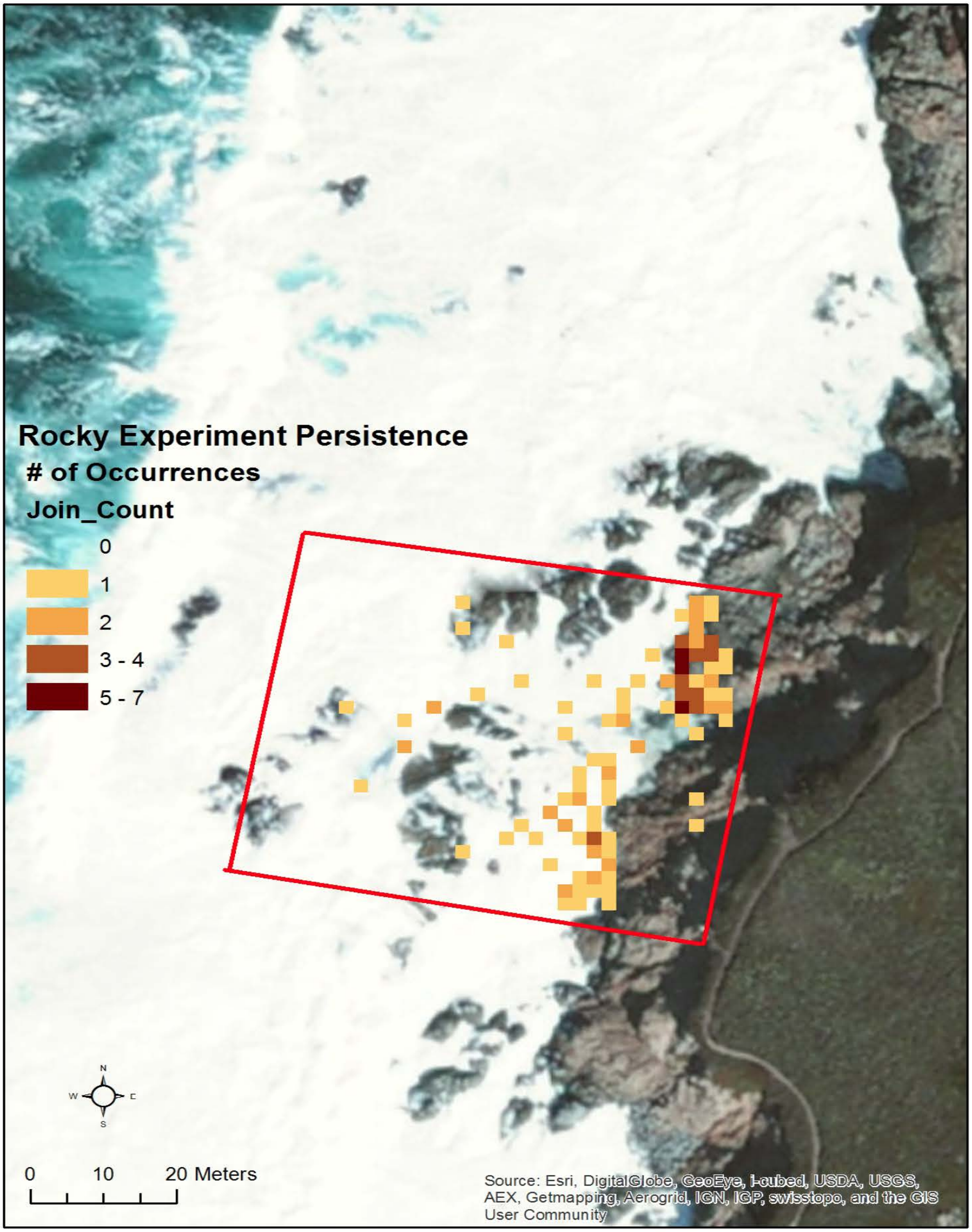


Figure 22. Temporal variability in persistence of *Macrocystis pyrifera* in the low intertidal, mid intertidal, and high intertidal at Soberanes Point in August 2014. Samples were a combination of 0.5 kg, 1 kg, and 3 kg samples, n=27.



Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 23. *Macrocystis pyrifera* persistence during the rocky intertidal experiment within the quadrat (red line) at Soberanes Point in August 2014. Colored pixels represent the location of wrack piles and their persistence values using the Join Count feature, n=9 samples per zone, 3 zones.

Table 30a. ANOVA on the effects of time (0/7/14 days) on substrate type (beach/rocky intertidal) phlorotannin concentration (% dry mass) in *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	2	0.663	20.618	<0.001
Substrate	1	0.001	0.043	0.836
Time x Substrate	2	0.01	0.306	0.738
Error	51	0.32		

Table 30b. ANOVA on the effects of time (0/7/14 days) on beach zone (beach face/berm) phlorotannin concentration (% dry mass) in *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Zone	1	0.008	0.241	0.635
Time	2	0.181	5.723	0.025
Zone x Time	2	0	0.007	0.993
Error	9	0.032		

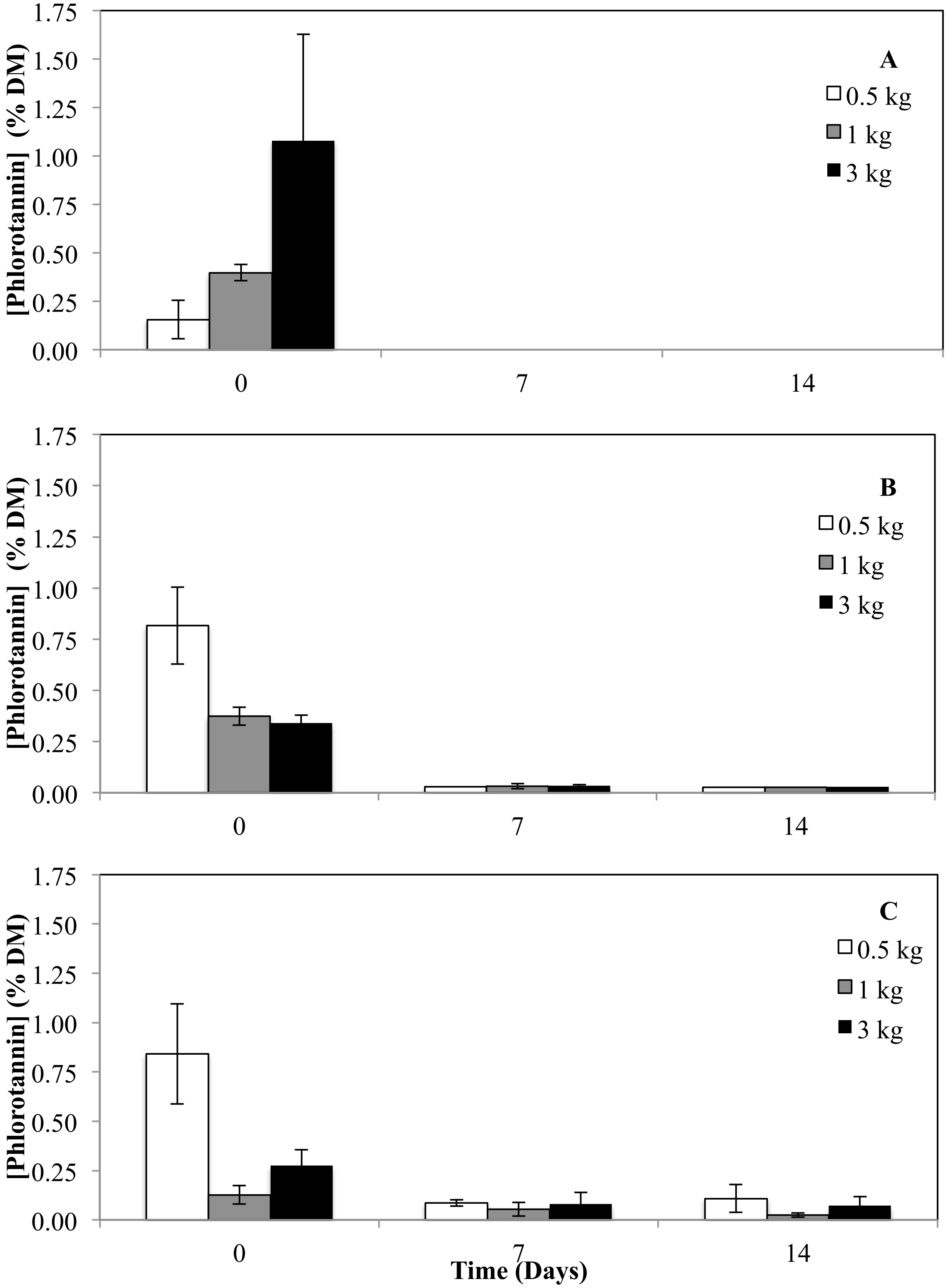


Figure 24. Temporal variability in phlorotannin concentration (% dry mass) of *Macrocystis pyrifera* on (A) swash zone, (B) beach face, and (C) berm at Salinas River State Beach in July 2014. Data are means ± SE, n=3.

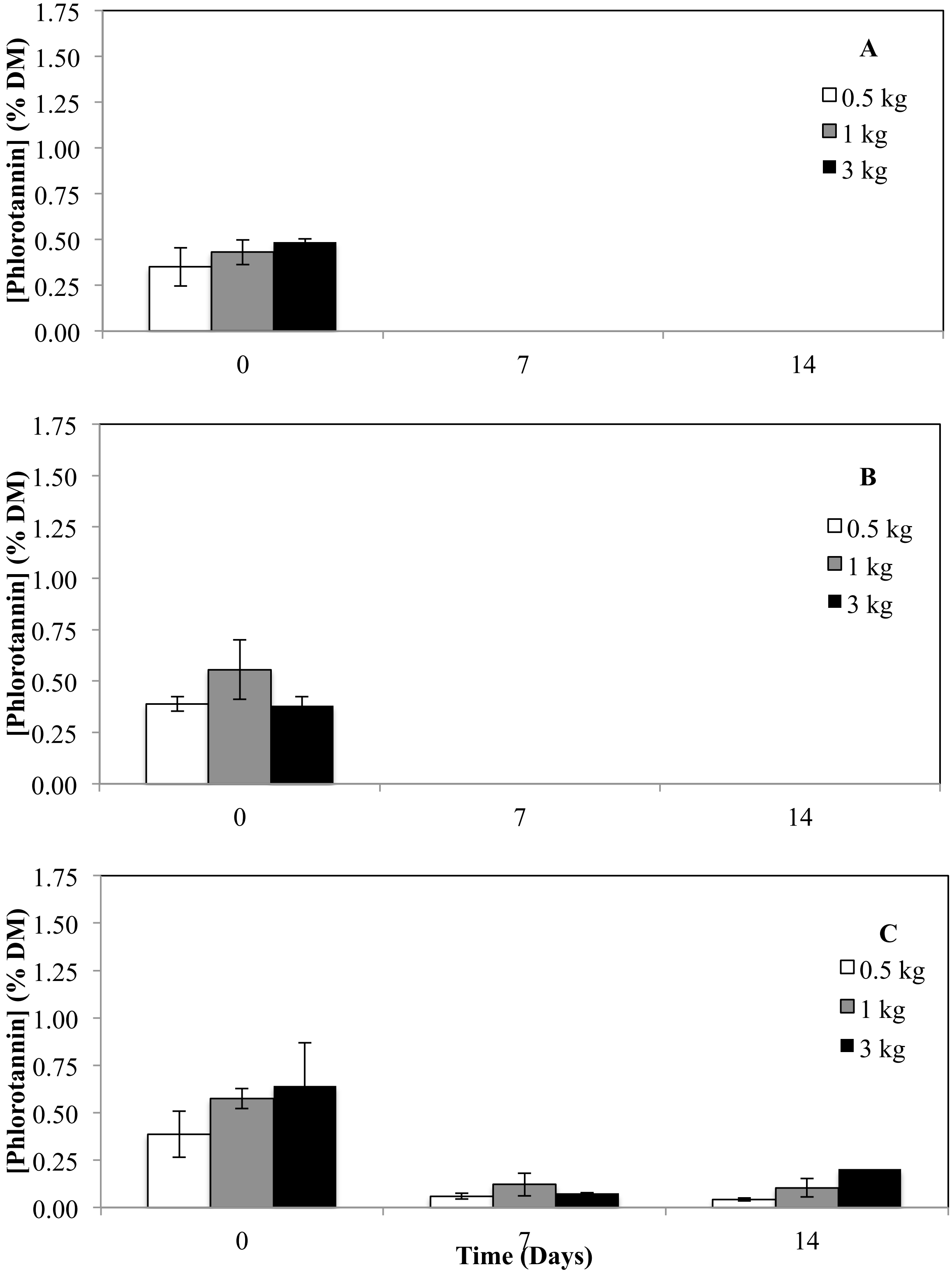


Figure 25. Temporal variation in phlorotannin concentration (% dry mass) of *Macrocystis pyrifera* on the (A) low intertidal, (B) mid intertidal, and (C) high intertidal at Soberanes Point in August 2014. Data are means ± SE, n=3.

Table 31. ANOVA on the effects of time (0/7/14 days) on substrate type (beach/rocky intertidal) bacterial colony density (colony forming units/µL) in *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	2	1357686	1.547	0.225
Substrate	1	3385821	3.858	0.056
Time x Substrate	2	1446461	1.648	0.205
Error	42	877586		

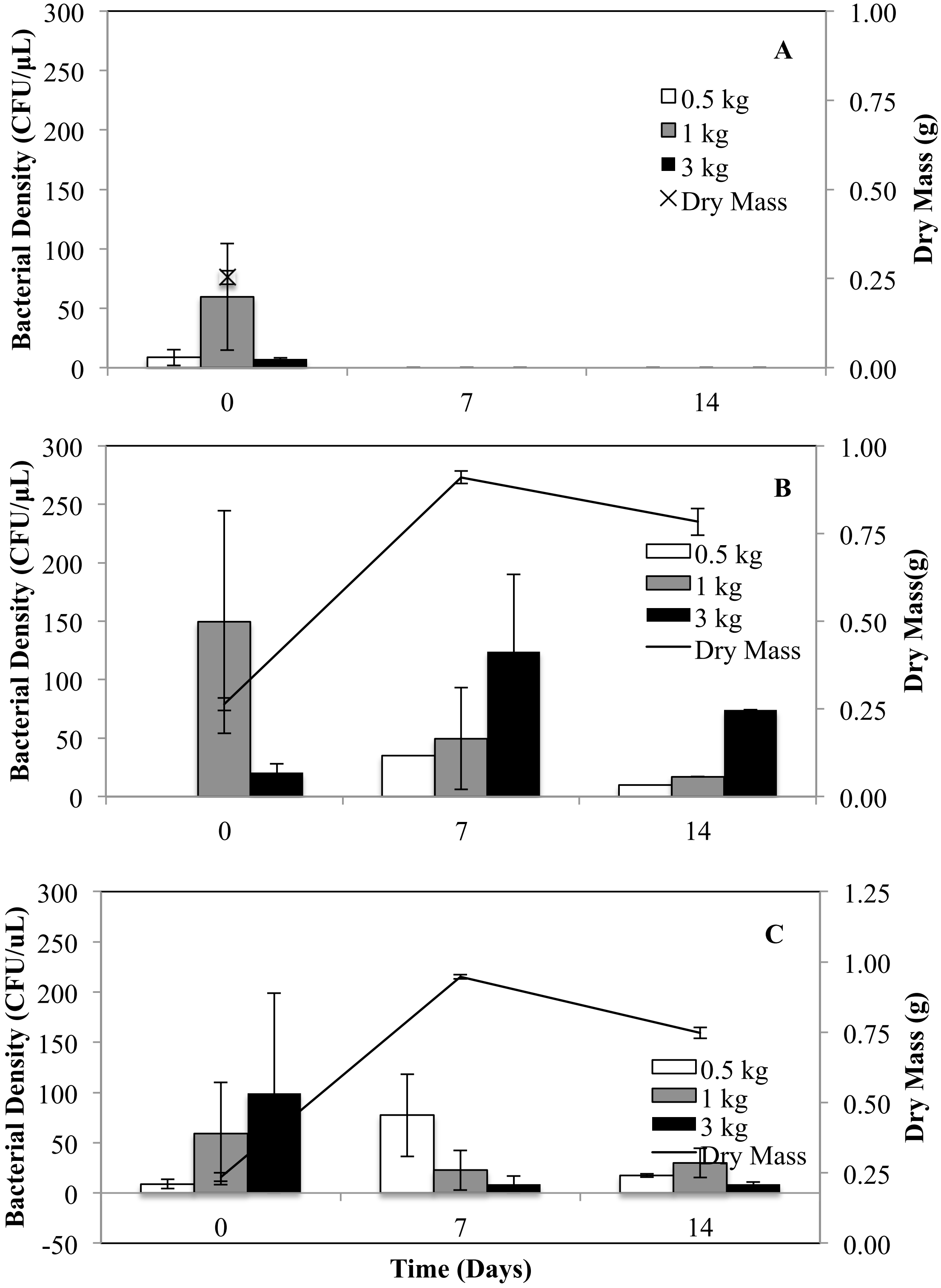


Figure 26. Temporal variability in dry mass of *Macrocystis pyrifera* and bacterial density (CFU/µL) on *Macrocystis pyrifera* in the (A) swash zone, (B) beach face, and (C) berm at Salinas River State Beach in July 2014. Data are means ± SE, n=3.

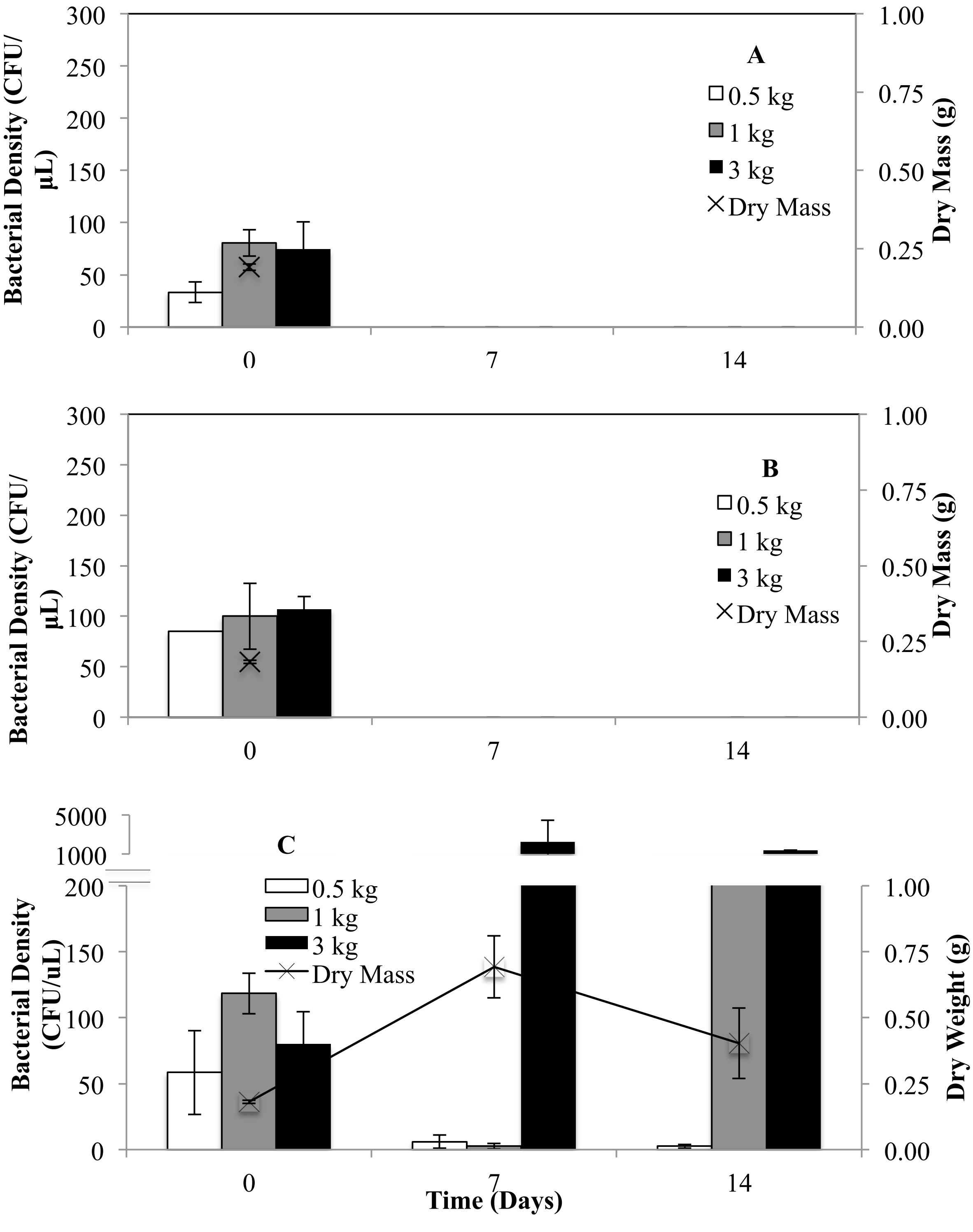


Figure 27. Temporal variability in dry mass of *Macrocystis pyrifera* and bacterial density (CFU/µL) on *Macrocystis pyrifera* in the (A) low intertidal, (B) mid intertidal, and (C) high intertidal at Soberanes Point in August 2014. The dry mass of the samples the bacteria were collected from was also included. Data are means ± SE, n=3.

Table 32. ANOVA on the effects of time (0/7/14 days) and substrate type (beach/rocky intertidal) on total bacterial density (cells/g) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	2	1.821 E+15	0.465	0.631
Substrate	1	5.950 E+15	1.521	0.225
Time x Substrate	2	1.394 E+15	0.356	0.703
Error	37	3.913 E+15		

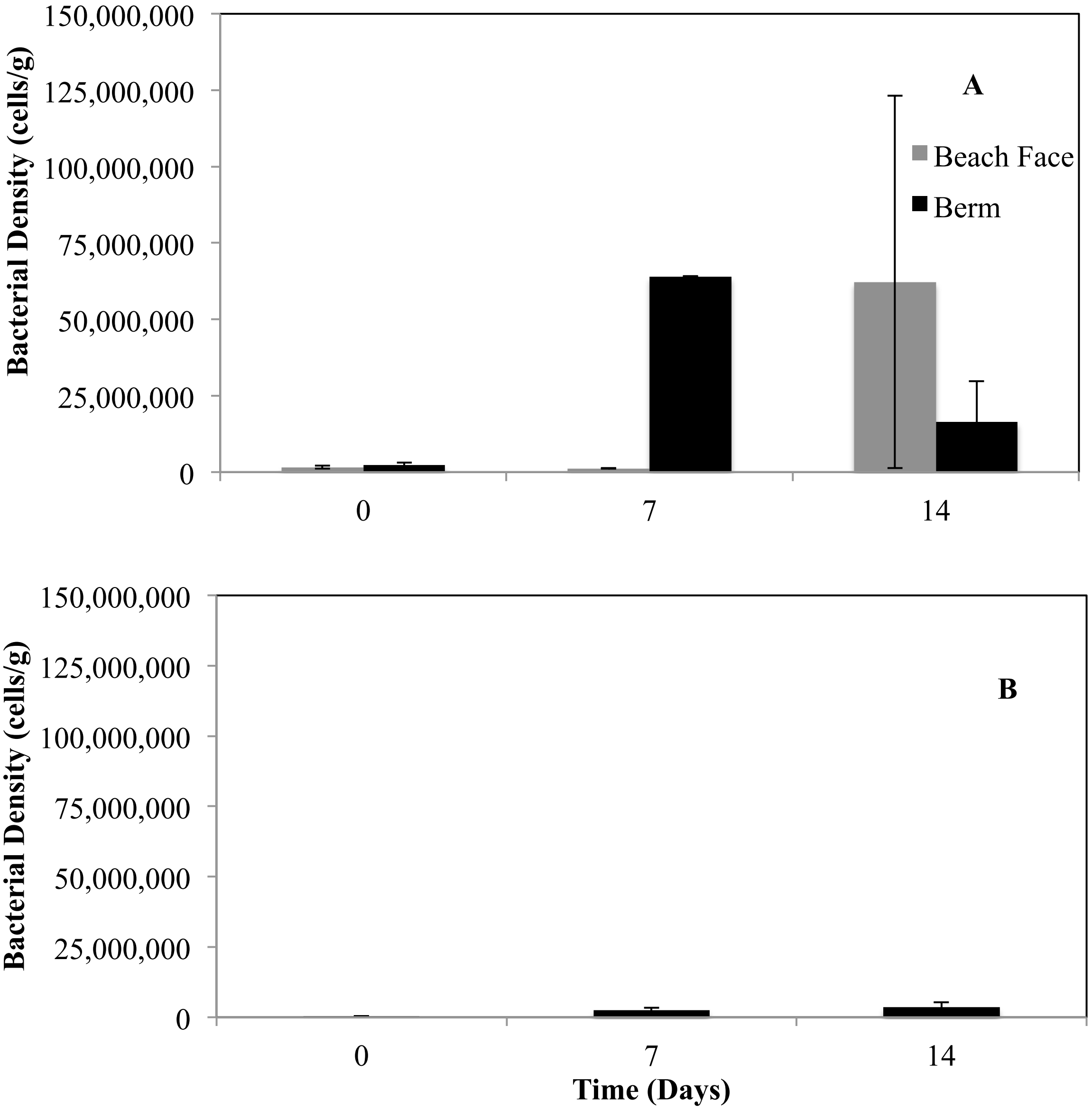


Figure 28. Temporal variability in total bacterial density (cells/g) on *Macrocystis pyrifera* using direct cell counts at Salinas River State Beach (A) in July 2014 and Soberanes Point (B) in August 2014. Salinas River State Beach data are means ± SE, n=3 and Soberanes Point data are means ± SE, n=6.

Table 33. ANOVA on the effects of time (days) and substrate type (beach/rocky intertidal) on kelp fly density (flies/cm^2/hour) on *Macrocystis pyrifera*.

Source	**df**	**MS**	**F value**	**P**
Time	14	0.063	2.584	0.003
Substrate	1	1.371	56.123	<0.001
Time x Substrate	14	0.064	2.603	0.002
Error	124	0.024		

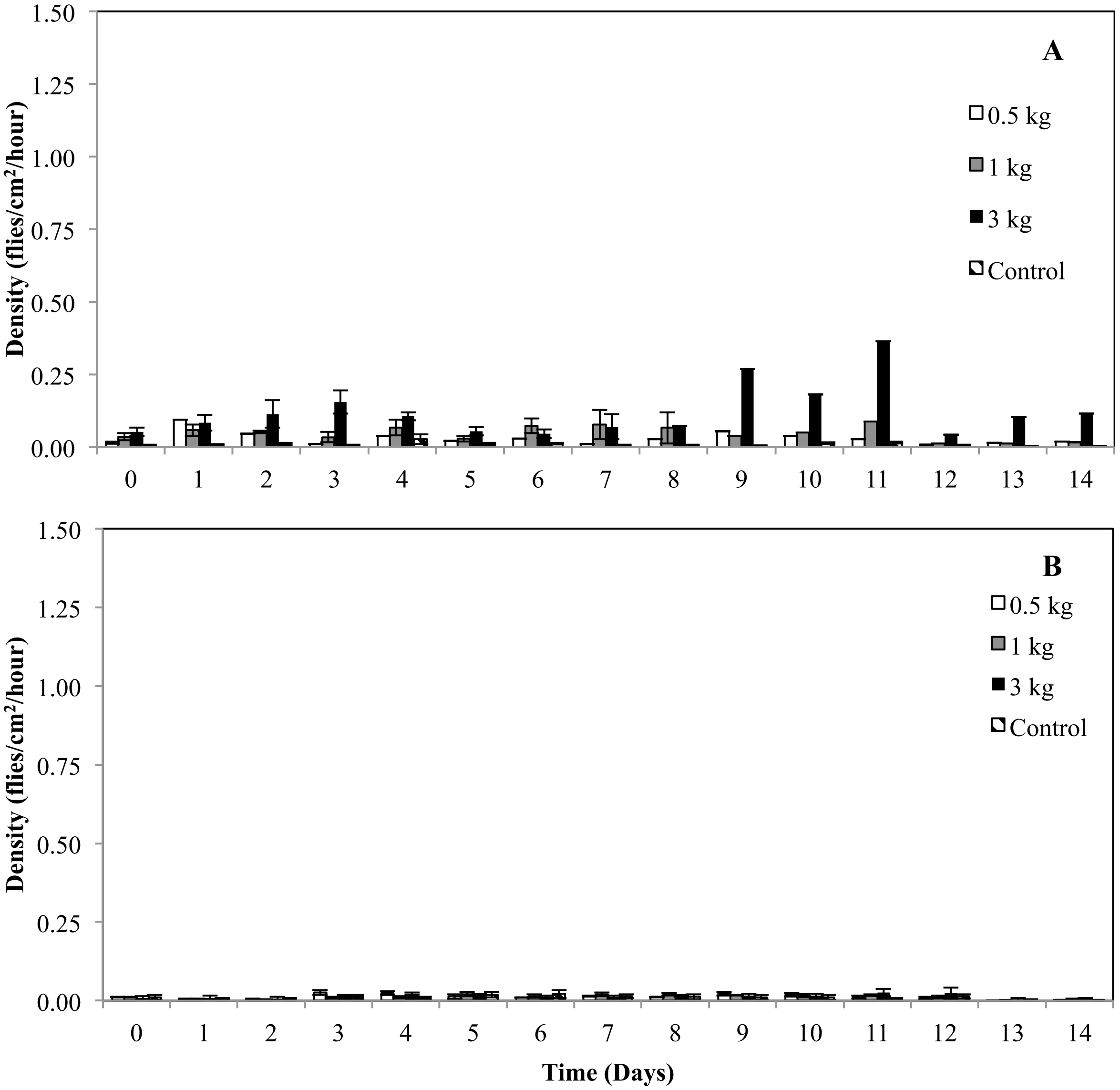


Figure 29. Temporal variability of kelp fly density (flies/cm^2/hour) on *Macrocystis pyrifera* on the (A) beach face and (B) berm at Salinas River State Beach in July 2014. Data are means ± SE, n=3.

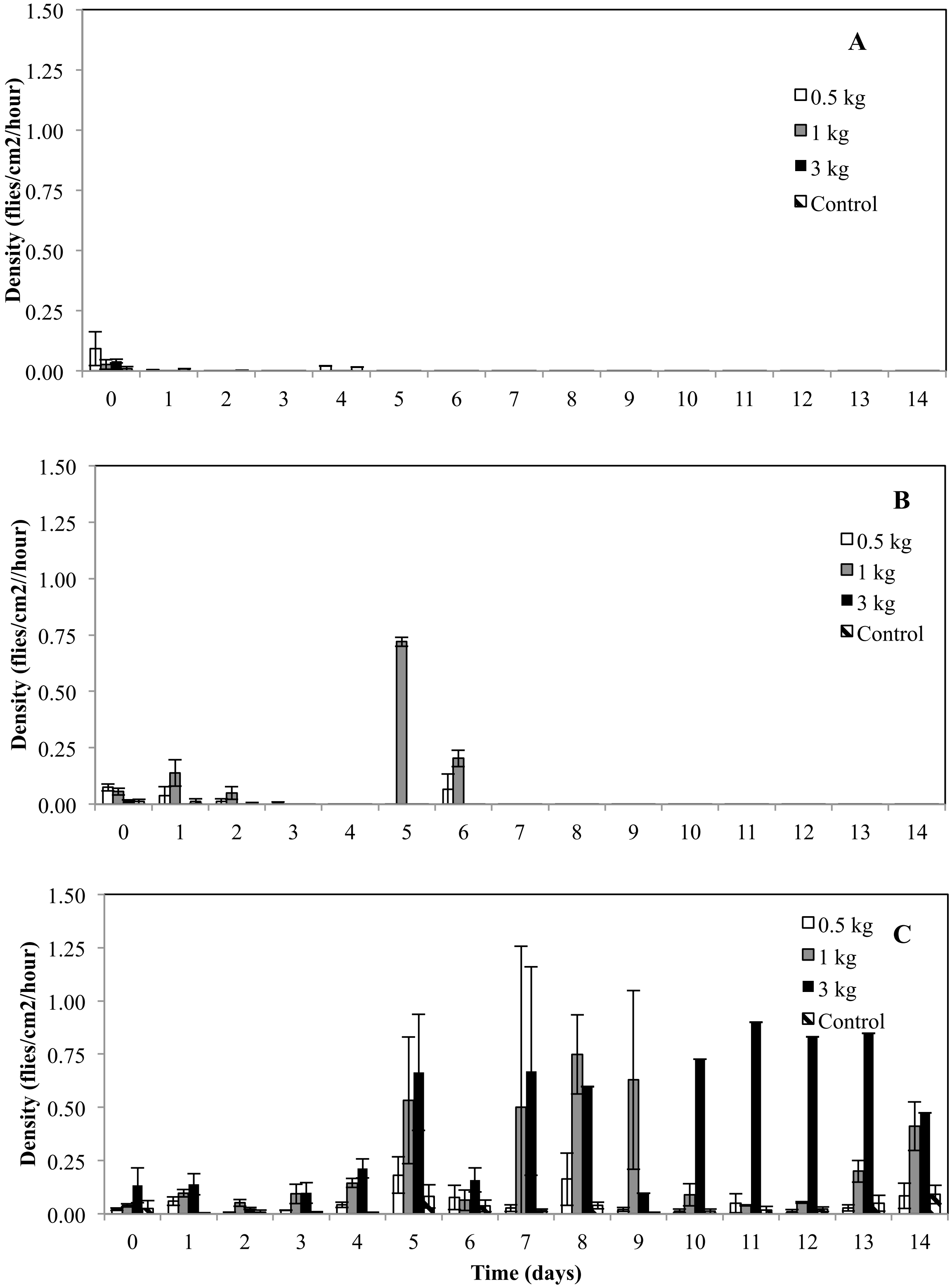


Figure 30. Temporal variability of kelp fly density on *Macrocystis pyrifera* on the (A) low intertidal, (B) mid intertidal, and (C) high intertidal at Soberanes Point in August 2014. Data are means ± SE, n=3.

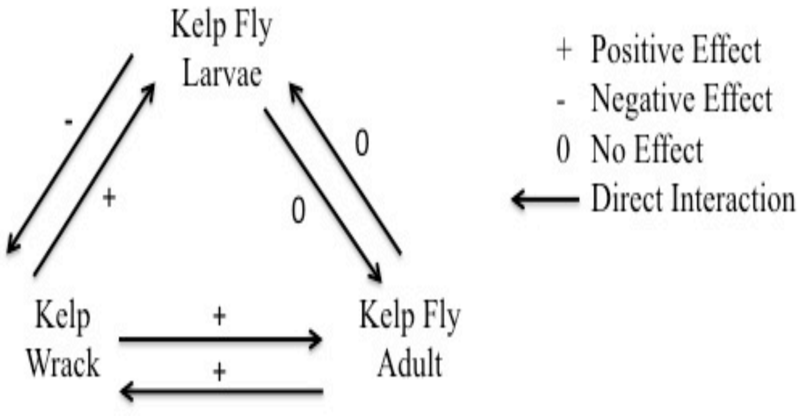


Figure 31. Kelp wrack - kelp fly interaction diagram between kelp wrack, adult kelp flies, and kelp fly larvae.

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APPENDIX A

DEPOSITION, PERSISTENCE, AND UTILIZATION FIGURES

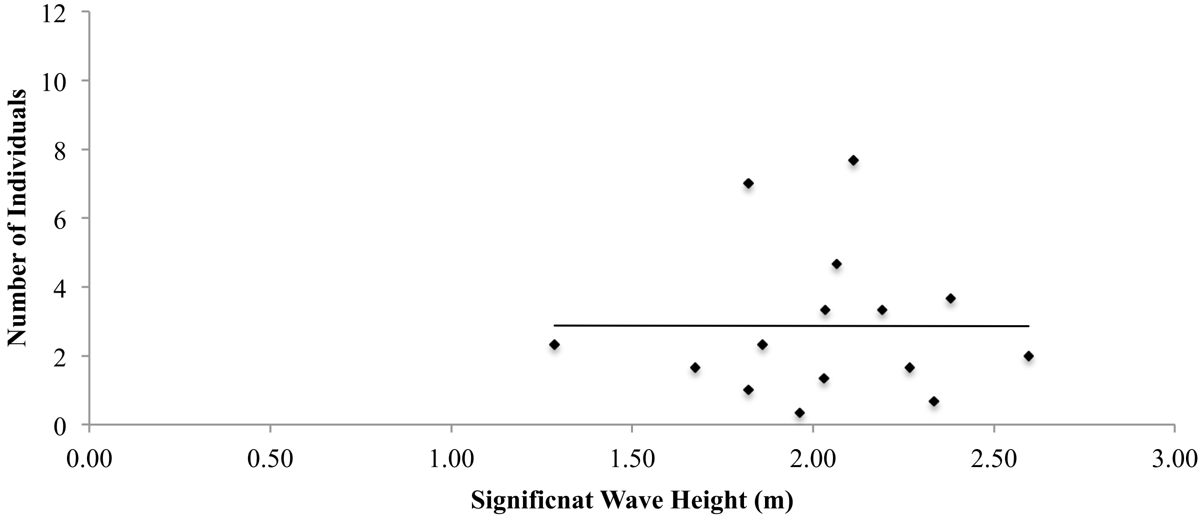
Appendix 1. t-tests on the difference between kelp fly density (flies/cm^2/hour) and control fly density (flies/cm^2/hour) on beaches and the rocky intertidal during surveys from September 2013 - June 2014 .

	t-test			
Substrate	**Month**	**T**	**df**	**P**
Beach	September	16.49	3	< 0.001
	October	3.68	6	0.001
	November	5.44	12	< 0.001
	December	5.25	10	< 0.001
	January	4.17	12	< 0.001
	February	3.52	11	< 0.005
	March	4.11	11	< 0.001
	April	4.03	9	< 0.0025
	May	4.43	6	< 0.0025
	June	3.76	6	< 0.01
Rocky Intertidal	September	4.37	7	< 0.0025
	October	3.99	12	< 0.001
	November	3.97	14	< 0.001
	December	4.25	12	< 0.001
	January	2.40	9	< 0.02
	February	4.76	12	< 0.001
	March	2.30	7	< 0 .04
	April	2.74	5	< 0.025
	May	2.31	4	< 0.05
	June	5.54	4	< 0.005

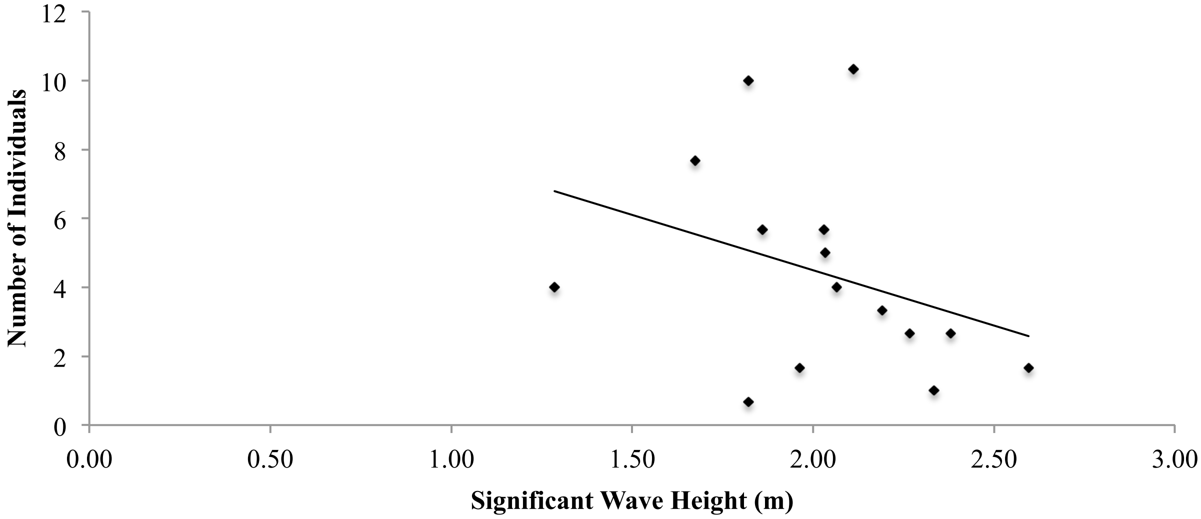
Appendix 2. t-tests on the difference between kelp fly density (flies/cm^2/hour) and control fly density (flies/cm^2/hour) on beaches and the rocky intertidal during experiments from July 2014 – August 2014.

		t-test		
Substrate	**Day**	**T**	**df**	**P**
Beach	1	2.779	3	<0.04
	2	3.661	3	<0.02
	3	2.770	3	<0.04
	4	1.710	3	<0.10
	5	2.492	3	<0.05
	6	2.702	3	<0.04
	7	2.893	3	<0.04
	8	2.484	3	<0.05
	9	3.117	3	<0.04
	10	1.936	3	<0.10
	11	2.000	3	<0.10
	12	1.757	3	<0.10
	13	6.395	3	<0.005
	14	1.702	3	<0.10
	15	1.046	3	<0.25
Rocky Intertidal	1	0.017	3	>0.40
	2	0.833	3	<0.25
	3	0.100	3	>0.40
	4	1.457	3	<0.25
	5	2.605	3	0.04
	6	0.389	3	<0.40
	7	3.609	3	<0.02
	8	0.824	3	<0.25
	9	1.474	3	<0.25
	10	3.409	3	<0.025
	11	3.632	3	<0.02
	12	3.085	3	<0.04
	13	0.188	3	>0.40
	14	2.200	3	<0.10
	15	2.500	3	<0.05

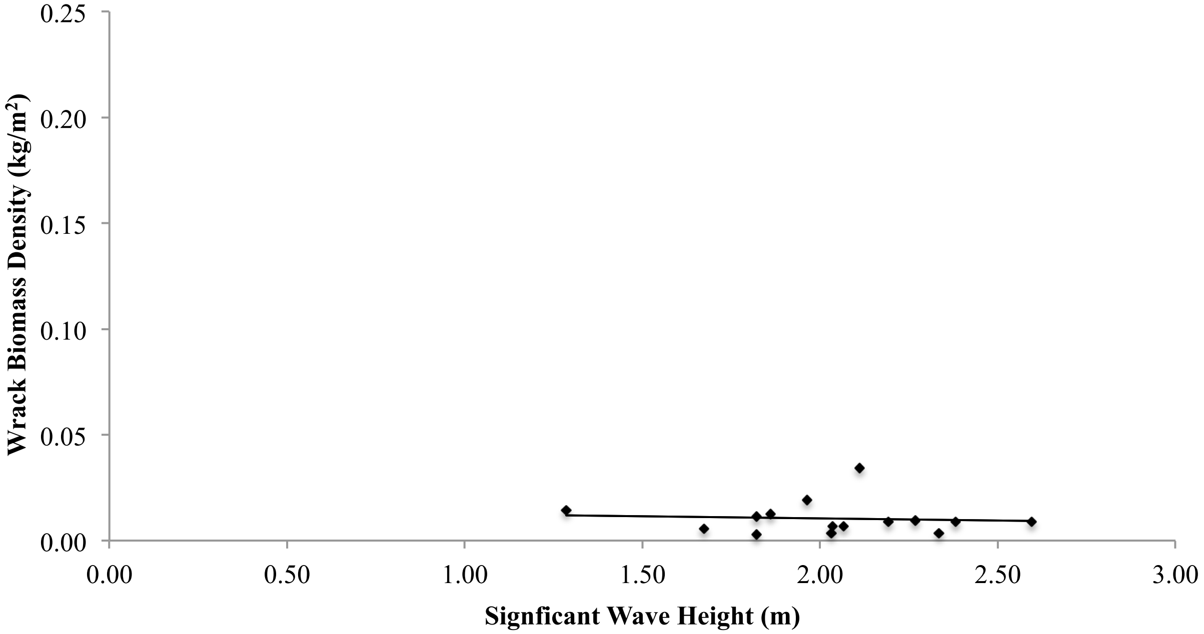
Appendix 3A. Relationship between significant wave height and the number of individual wrack pieces found on the shore at beaches. Data are monthly averages between April 2013 and June 2014. Regression: peak number of individuals = -0.0139 (±5.589)* significant wave height + 2.8948 (±2.724), $r^2 = 0.002$, $P = 0.867$, $F_{1,14} = 0.123$.



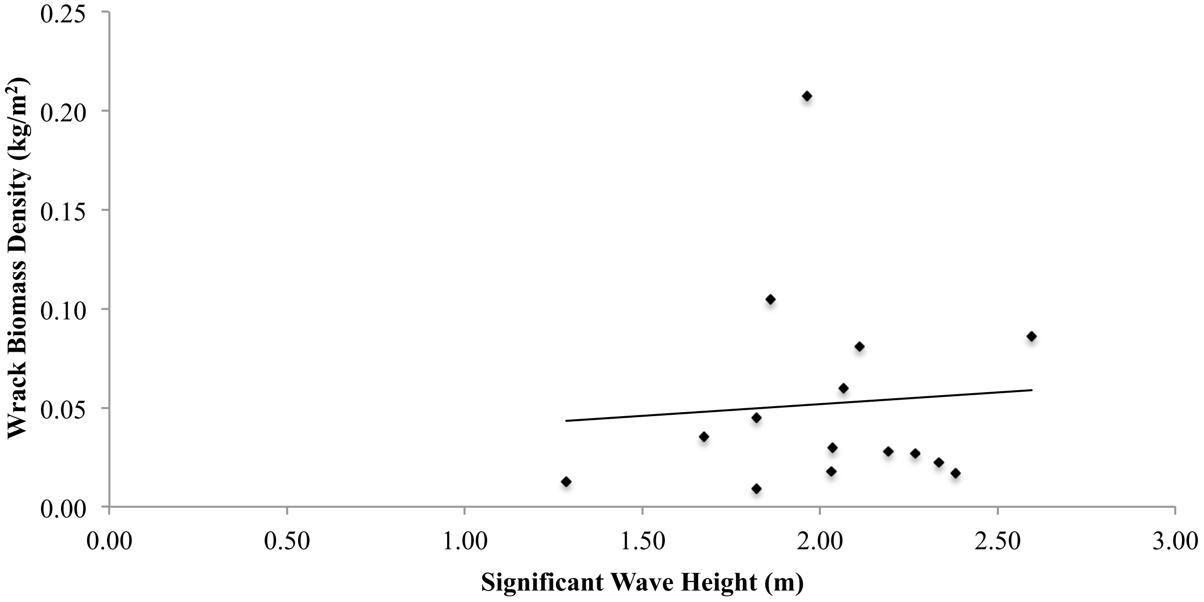
Appendix 3B. Relationship between significant wave height and the number of individual wrack pieces found on the shore at the rocky intertidal. Data are monthly averages between April 2013 and June 2014. Regression: peak number of individuals = -3.2119 (±21.113)* significant wave height + 10.918 (±10.651), $r^2 = 0.120$, $P = 0.206$, $F_{1,14} = 0.046$.



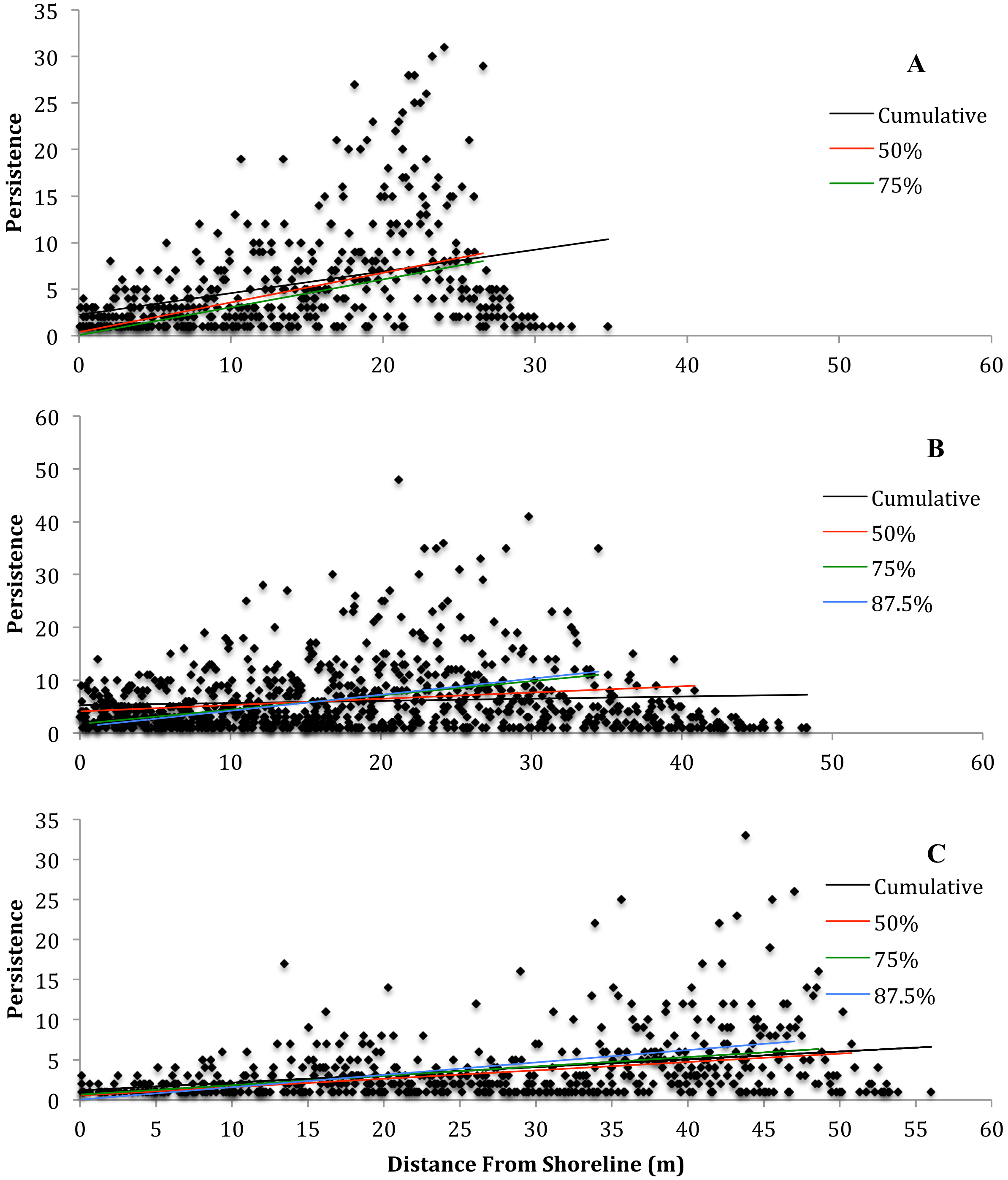
Appendix 3C. Relationship between significant wave height and wrack biomass density on beaches. Data are monthly averages between April 2013 and June 2014. Regression: peak biomass density = -0.002 (±0.144)* significant wave height + 0.0145 (±11.161), $r^2 = 0.007$, P = 0.775, $F_{1,14} = 0.086$..



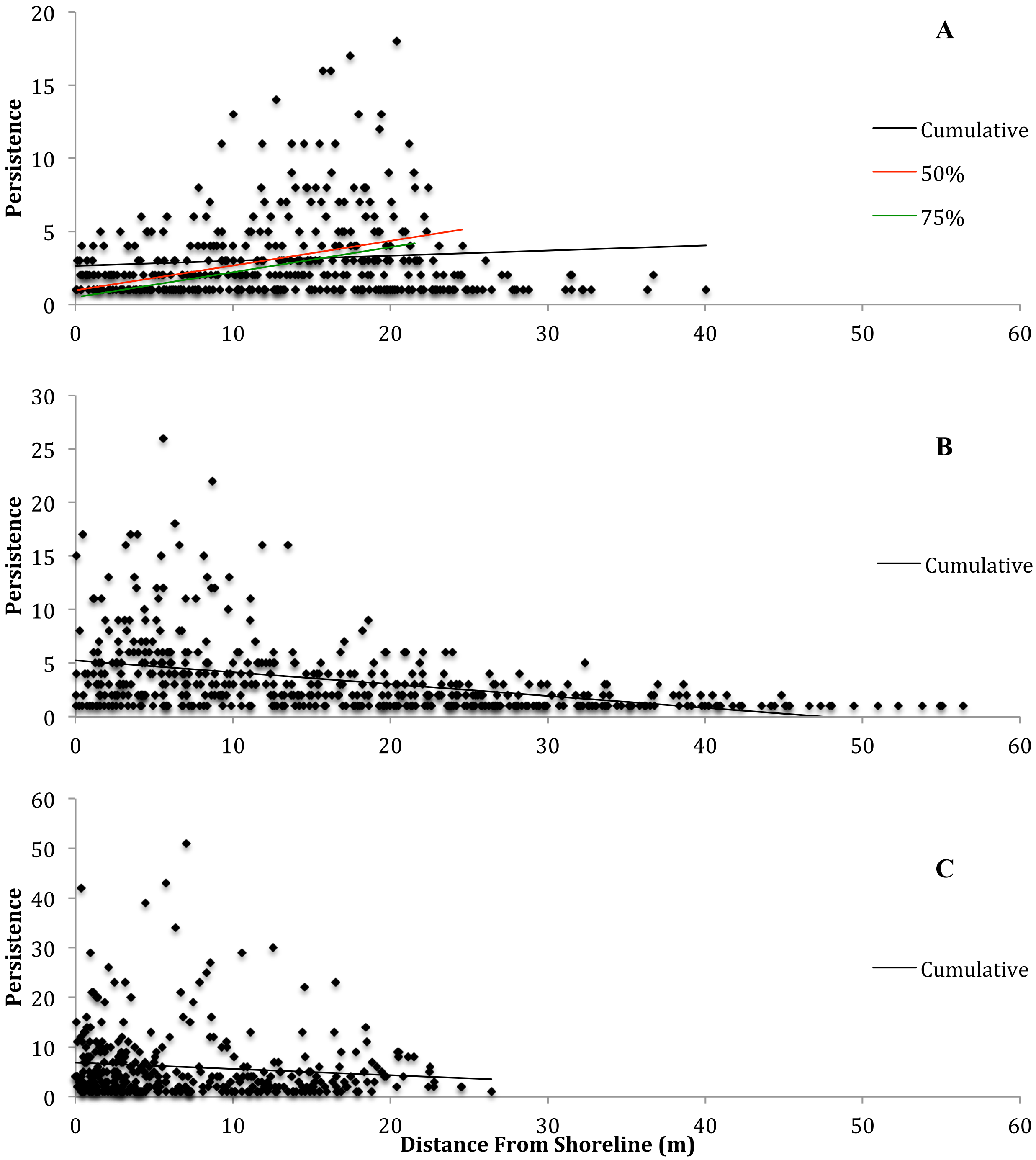
Appendix 3D. Relationship between significant wave height and wrack biomass density on the rocky intertidal. Data are monthly averages between April 2013 and June 2014. Regression; peak biomass density = 0.0118 (±0.123)* significant wave height + 0.0282 (±1.701), $r^2 = 0.005$, P = 0.799, $F_{1,14} = 0.067$.



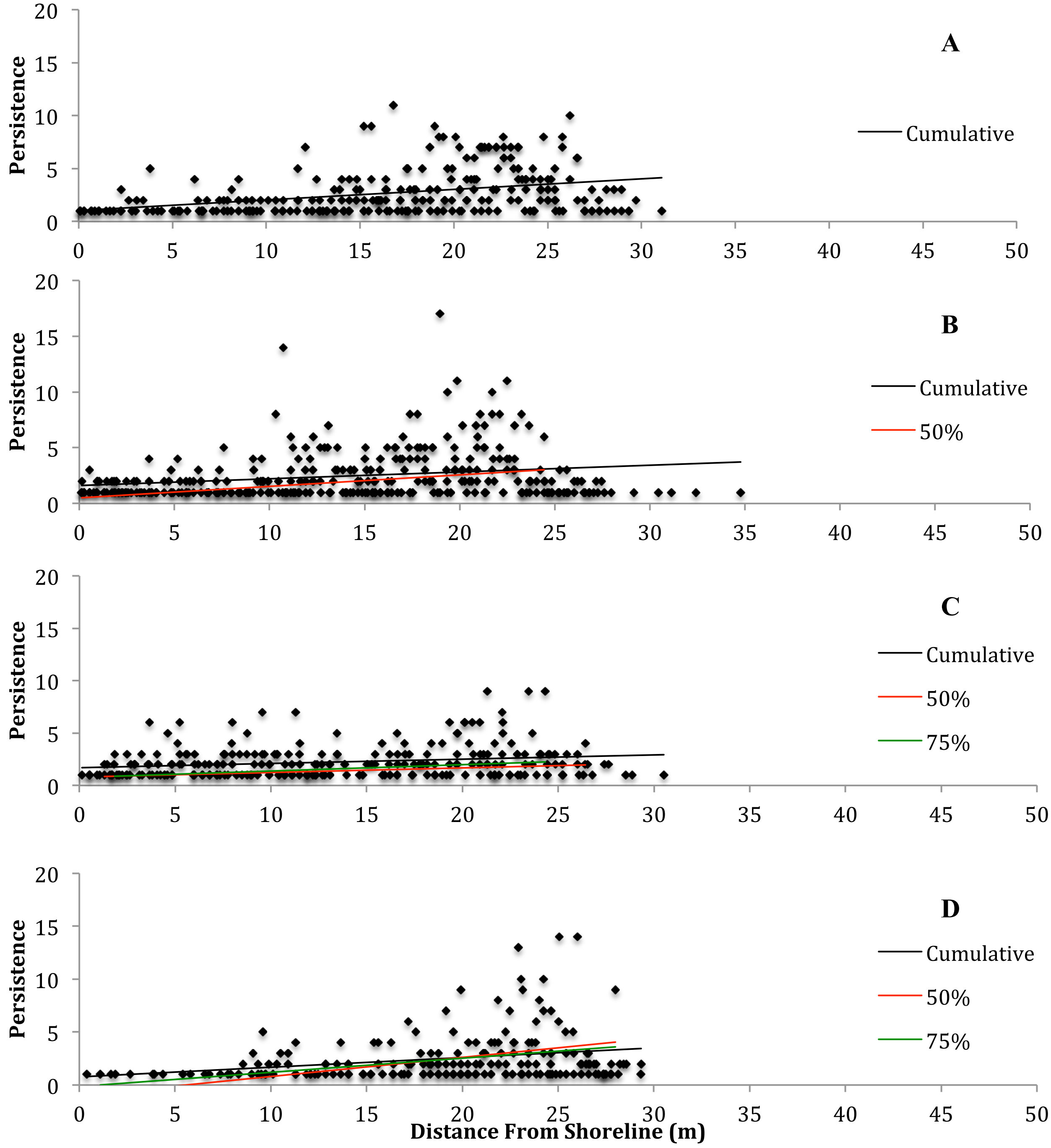
Appendix 7. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Salinas River State Beach (A) (regression: peak persistence = 0.2336 (±0.471)* distance from shoreline + 2.2301 (±0.029), $r^2 = 0.126$, $P < 0.001$, $F_{1,465} = 66.706$), Monterey State Beach (B) (regression: peak persistence = 0.0412 (±0.383)* distance from shoreline + 5.2593 (0.018), $r^2 = 0.006$, $P = 0.019$, $F_{1,845} = 5.484$), and Carmel River State Beach (C) (regression: peak persistence = 0.0971 (±0.341)* distance from shoreline + 1.1757 (±0.011), $r^2 = 0.120$, $P < 0.001$, $F_{1,554} = 75.122$).



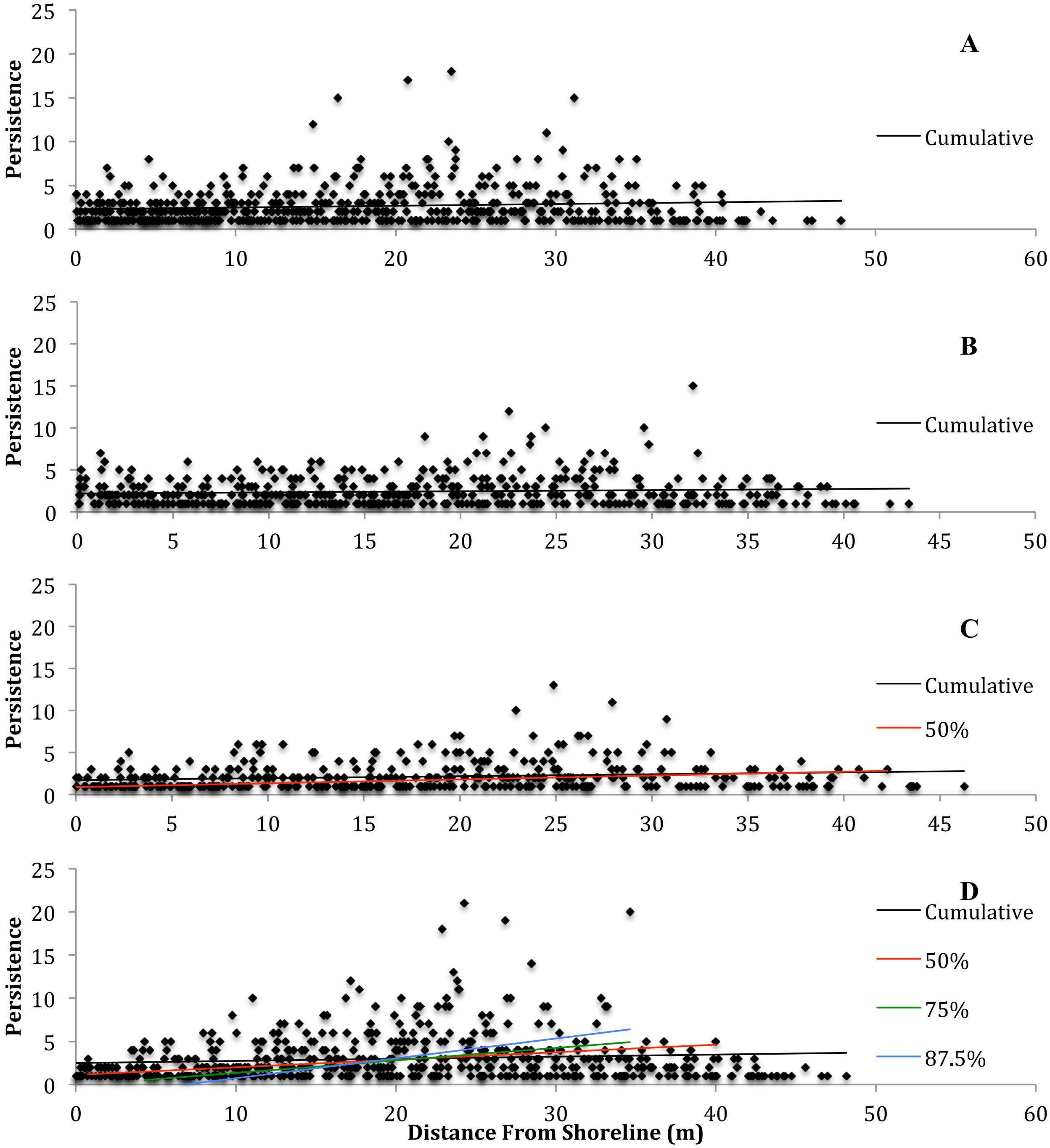
Appendix 8. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Davenport Landing Beach (A) (regression: peak persistence = 0.0349 (±0.280)* distance from shoreline + 2.6343 (±0.018), $r^2 = 0.009$, P = 0.057, $F_{1,390} = 3.637$), Stillwater Cove (B) (regression: peak persistence = -0.1106 (±0.232)* distance from shoreline + 5.2535 (±0.011), $r^2 = 0.169$, P <0.001, $F_{1,503} = 102.082$), and Soberanes Point (C) (regression: peak persistence = -0.1268 (±0.585)* distance from shoreline + 6.8569 (±0.060), $r^2 = 0.013$, P = 0.035, $F_{1,349} = 4.462$).



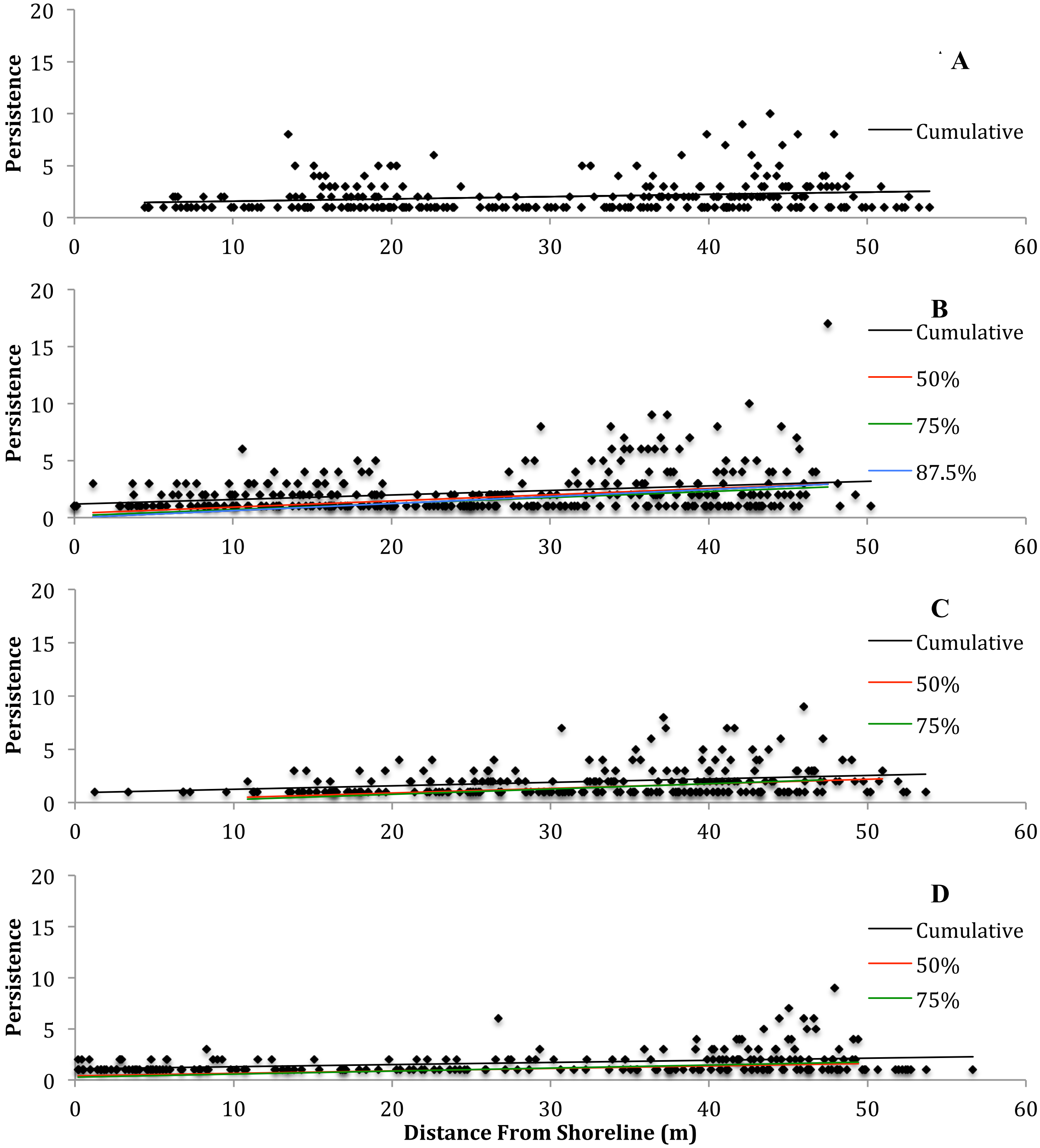
Appendix 9. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Salinas River State Beach during spring (A) (regression: peak persistence 0.0998 (±0.288)* distance from shoreline + 1.0361 (±0.016), $r^2 = 0.129$, $P < 0.001$, $F_{1,267} = 39.223$), summer (B) (regression: peak persistence 0.0607 (±0.244)* distance from shoreline +1.6103 (±0.015), $r^2 = 0.049$, P = <0.001, $F_{1,321} = 16.364$) fall (C) (regression: peak persistence 0.0407 (±0.189)* distance from shoreline + 1.6933 (±0.012), $r^2 = 0.042$, P = <0.001, $F_{1,256} = 11.266$), winter (D) (regression: peak persistence 0.0914 (±0.485)* distance from shoreline + 0.7636 (±0.024), $r^2 = 0.069$, P = <0.001, $F_{1,194} = 14.234$).



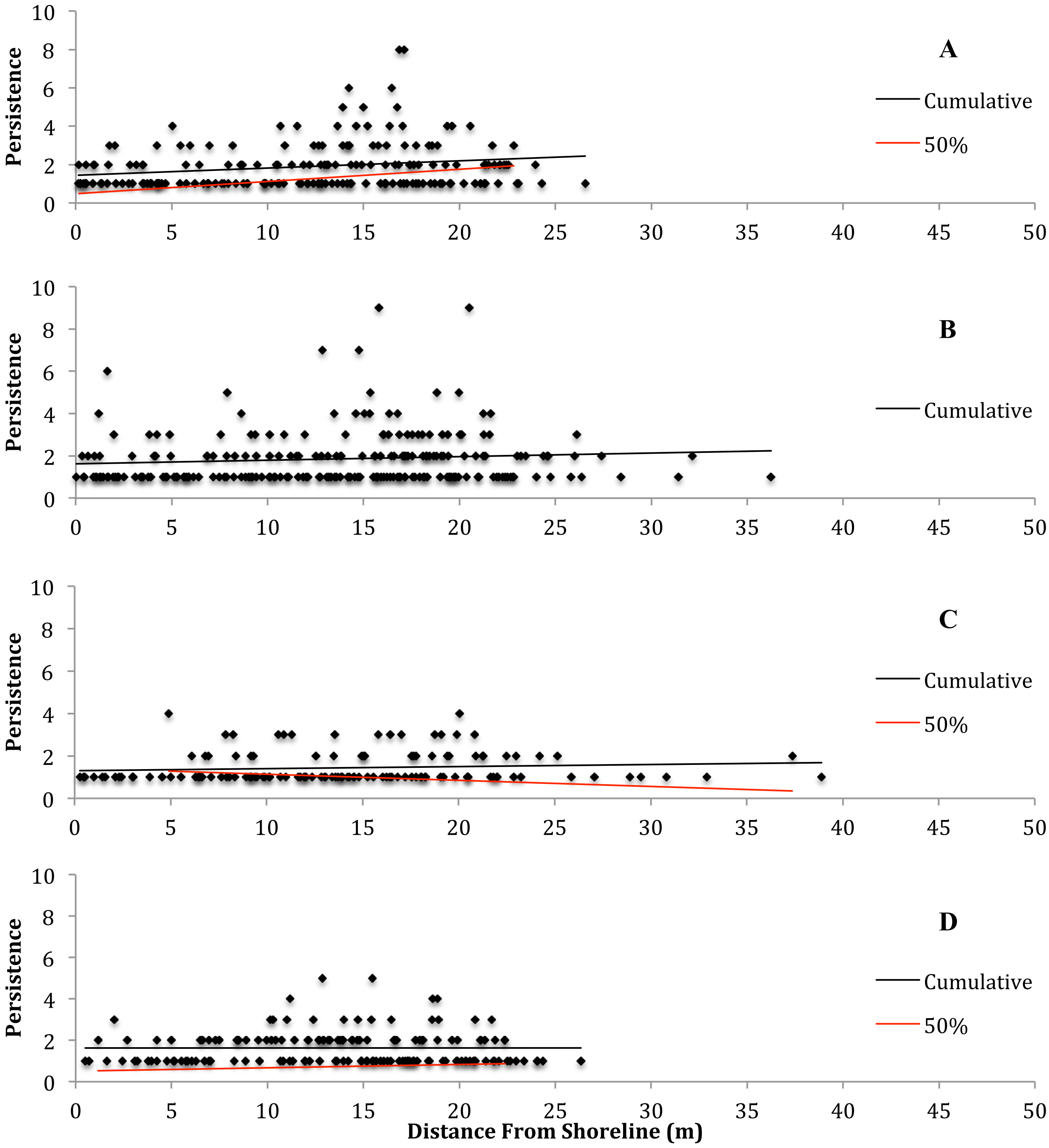
Appendix 10. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Monterey State Beach during spring (A) (regression: peak persistence 0.02 (±0.168)* distance from shoreline + 2.2775 (±0.008), $r^2 = 0.011$, $P = 0.012$, $F_{1,548} = 6.286$), summer (B) (regression: peak persistence 0.0136 (±0.155)* distance from shoreline + 2.1861 (±0.008), $r^2 = 0.006$, $P = 0.077$, $F_{1,488} = 3.145$), fall (C) (regression: peak persistence 0.0231 (±0.152)* distance from shoreline + 1.725 (±0.007), $r^2 = 0.024$, $P = 0.002$, $F_{1,408} = 10.049$), and winter (D) (regression: peak persistence 0.0245 (±0.231)* distance from shoreline +2.4895 (0.010), $r^2 = 0.011$, $P = 0.016$, $F_{1,534} = 5.880$).



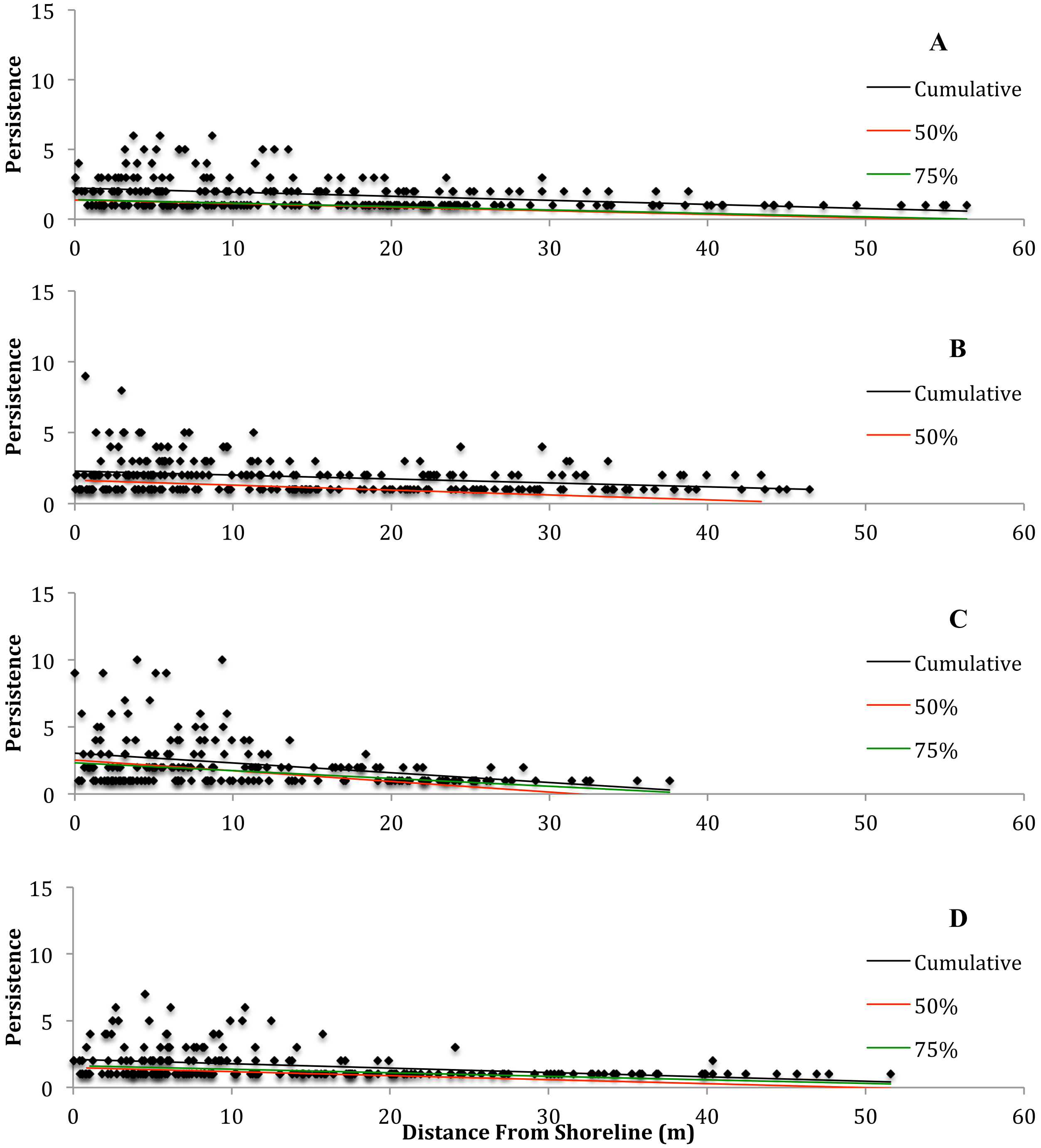
Appendix 11. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Carmel River State Beach during spring (A) (regression: peak persistence 0.0218 (±0.238)* distance from shoreline + 1.3683 (±0.022), $r^2 = 0.034$, $P = 0.003$, $F_{1,263} = 9.284$) summer (B) (regression: peak persistence 0.0399 (±0.220)* distance from shoreline + 1.1861 (±0.008), $r^2 = 0.078$, $P < 0.001$, $F_{1,327} = 27.752$), fall (C) (regression: peak persistence 0.0325 (±0.280)* distance from shoreline + 0.9175 (±0.008), $r^2 = 0.065$, $P < 0.001$, $F_{1,229} = 15.961$), and winter (D) (regression: peak persistence 0.0209 (±0.154) distance from shoreline 1.0837 (±0.005), $r^2 = 0.0086$, $P < 0.001$, $F_{1,222} = 20.793$).



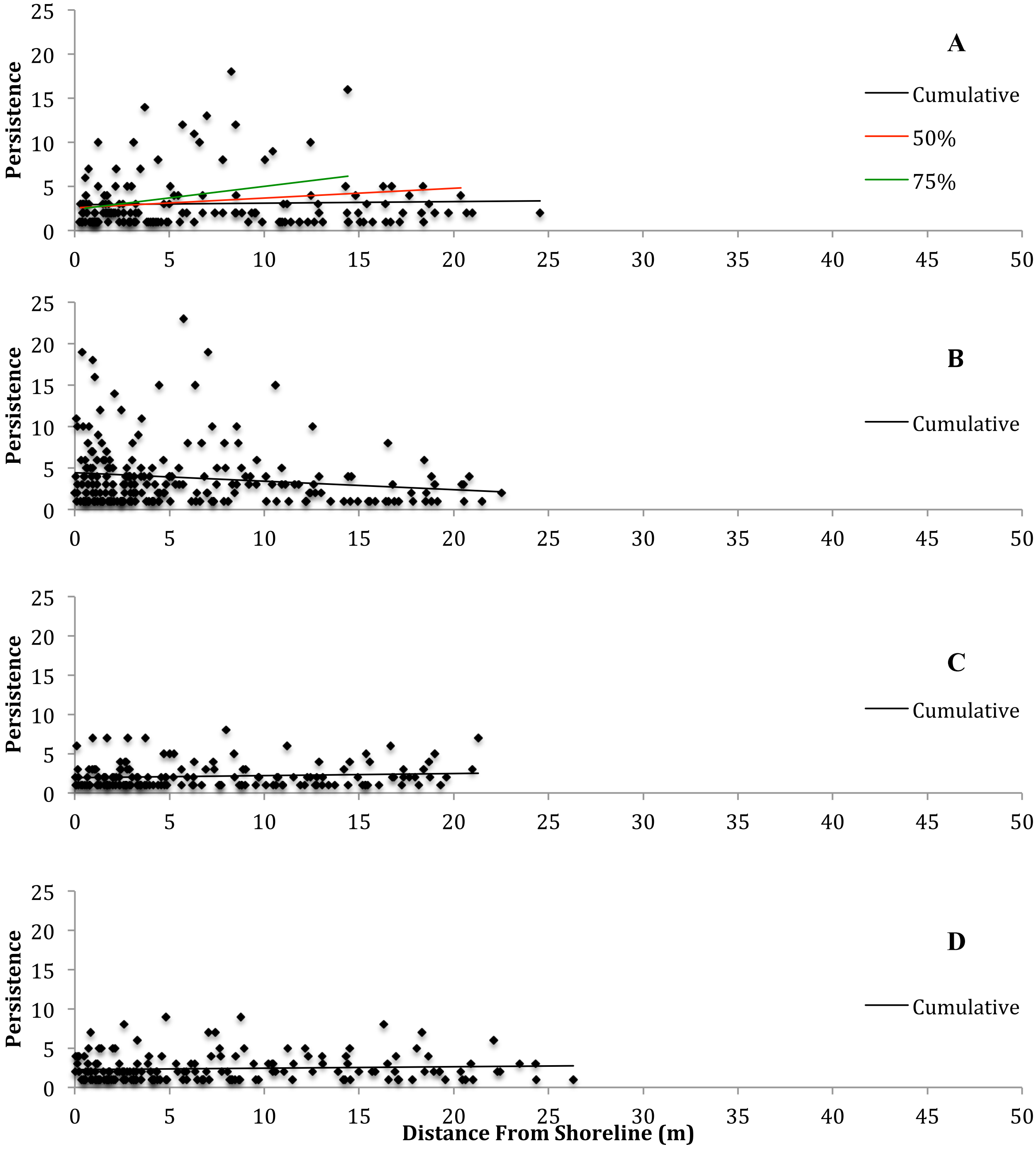
Appendix 12. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Davenport Landing Beach during spring (A) (regression: peak persistence 0.0377 (±0.189)* distance from shoreline + 1.4448 (±0.038), $r^2 = 0.040$, $P = 0.006$, $F_{1,185} = 7.653$), summer (B) (regression: peak persistence 0.0169 (±0.182)* distance from shoreline + 1.6246 (±0.012), $r^2 = 0.009$, $P = 0.154$, $F_{1,224} = 2.045$), fall (C) (regression: peak persistence 0.0098 (±0.139)* distance from shoreline + 1.3036 (0.009), $r^2 = 0.010$, $P = 0.261$, $F_{1,128} = 1.277$), and winter (D) (regression: peak persistence 0.0001 (±0.169)* distance from shoreline + 1.6276 (±0.011), $r^2 = 0.000$, $P = 0.992$, $F_{1,150} = 0.000$).



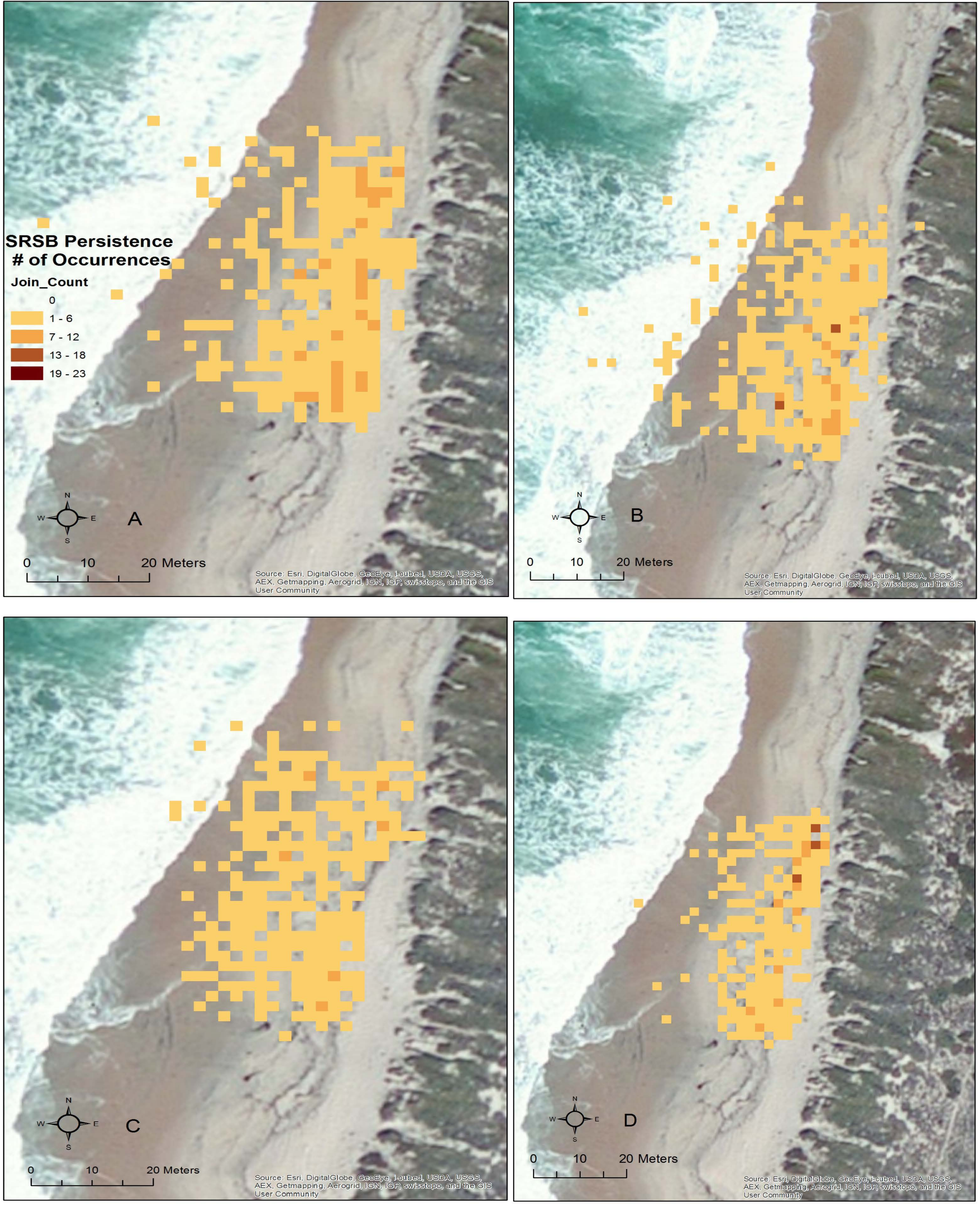
Appendix 13. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Stillwater Cove during spring (A) (regression: peak persistence -0.0293 (±0.106)* distance from shoreline + 2.2386 (±0.005), $r^2 = 0.107$, $P < 0.001$, $F_{1,250} = 29.952$), summer (B) (regression: peak persistence -0.0277 (±0.118)* distance from shoreline +2.2908 (±0.006), $r^2 = 0.076$, $P < 0.001$, $F_{1,246} = 20.067$), fall (C) (regression: peak persistence -0.073 (±0.203)* distance from shoreline 3.0454 (0.014), $r^2 = 0.118$, $P < 0.001$, $F_{1,192} = 25.579$, and winter (D) (regression: peak persistence -0.0327 (±0.118)* distance from shoreline 2.1099 (±0.006), $r^2 = 0.106$, $P < 0.001$, $F_{1,220} = 26.088$).



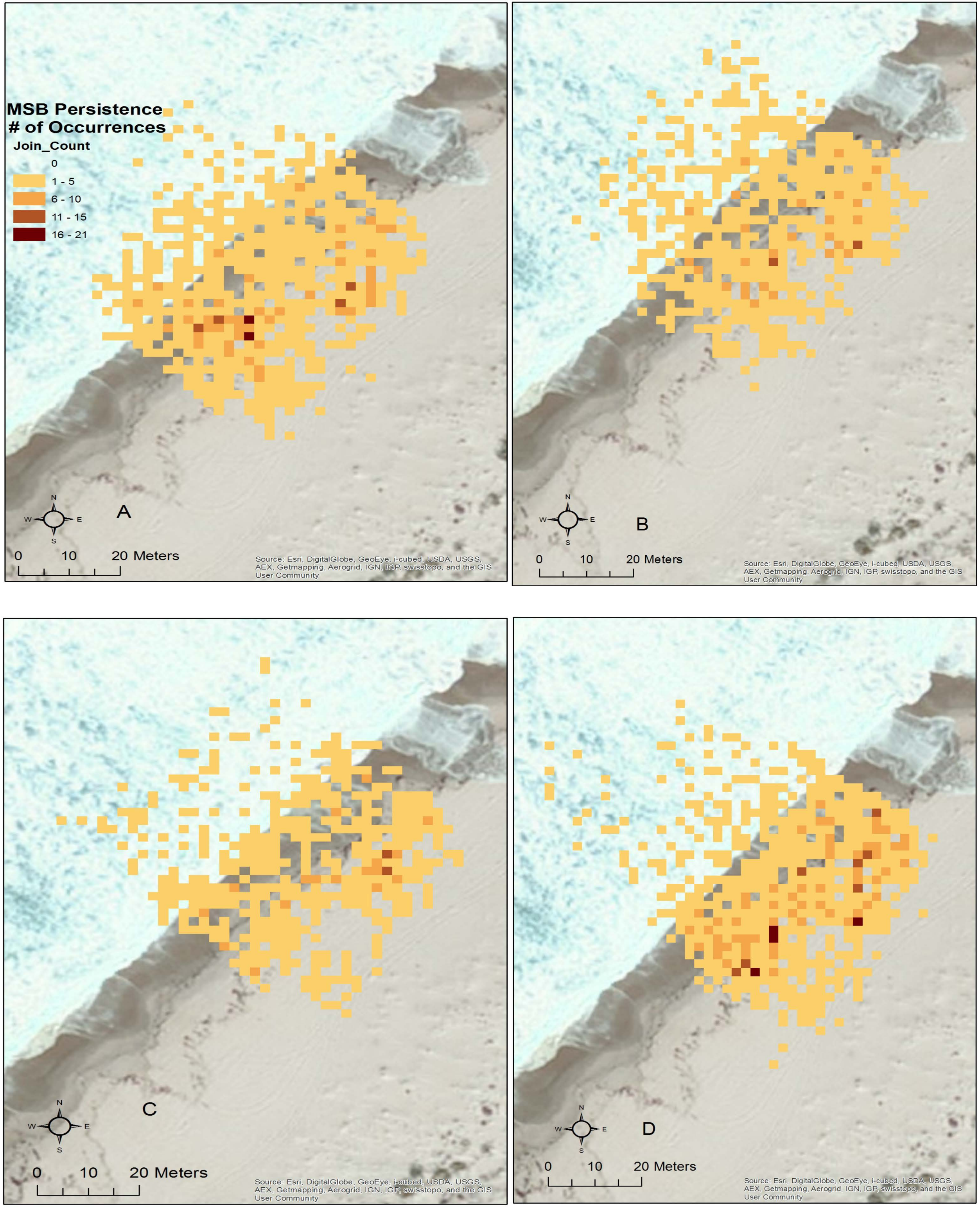
Appendix 14. Relationship between distance from the shoreline and persistence between April 2013 and June 2014 at Soberanes Point during spring (A) (regression: peak persistence 0.0177 (±0.376)* distance from shoreline + 2.9357 (±0.041), $r^2 = 0.001$, $P = 0.667$, $F_{1,157} = 0.185$), summer (B) (regression: peak persistence -0.1023 (±0.368)* distance from shoreline + 4.4462 (0.044), $r^2 = 0.024$, $P = 0.022$, $F_{1,217} = 5.350$), fall (C) (regression: peak persistence 0.0264 (±0.196)* distance from shoreline + 1.9456 (±0.021), $r^2 = 0.010$, $P = 0.215$, $F_{1,157} = 1.550$), and winter (D) (regression: peak persistence 0.0185 (±0.200)* distance from shoreline + 2.263 (±0.020), $r^2 = 0.005$, $P = 0.349$, $F_{1,170} = 0.881$).



Appendix 15. Temporal variation in kelp wrack persistence on Salinas River State Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature. Spring (A) n=714, Summer (B) n=796, Fall (C) n=573, Winter (D) n=485.



Appendix 16. Temporal variation in kelp wrack persistence at Monterey State Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature. Spring (A) n=1434, Summer (B) n=1182, Fall (C) n=869, Winter (D) n=1585.



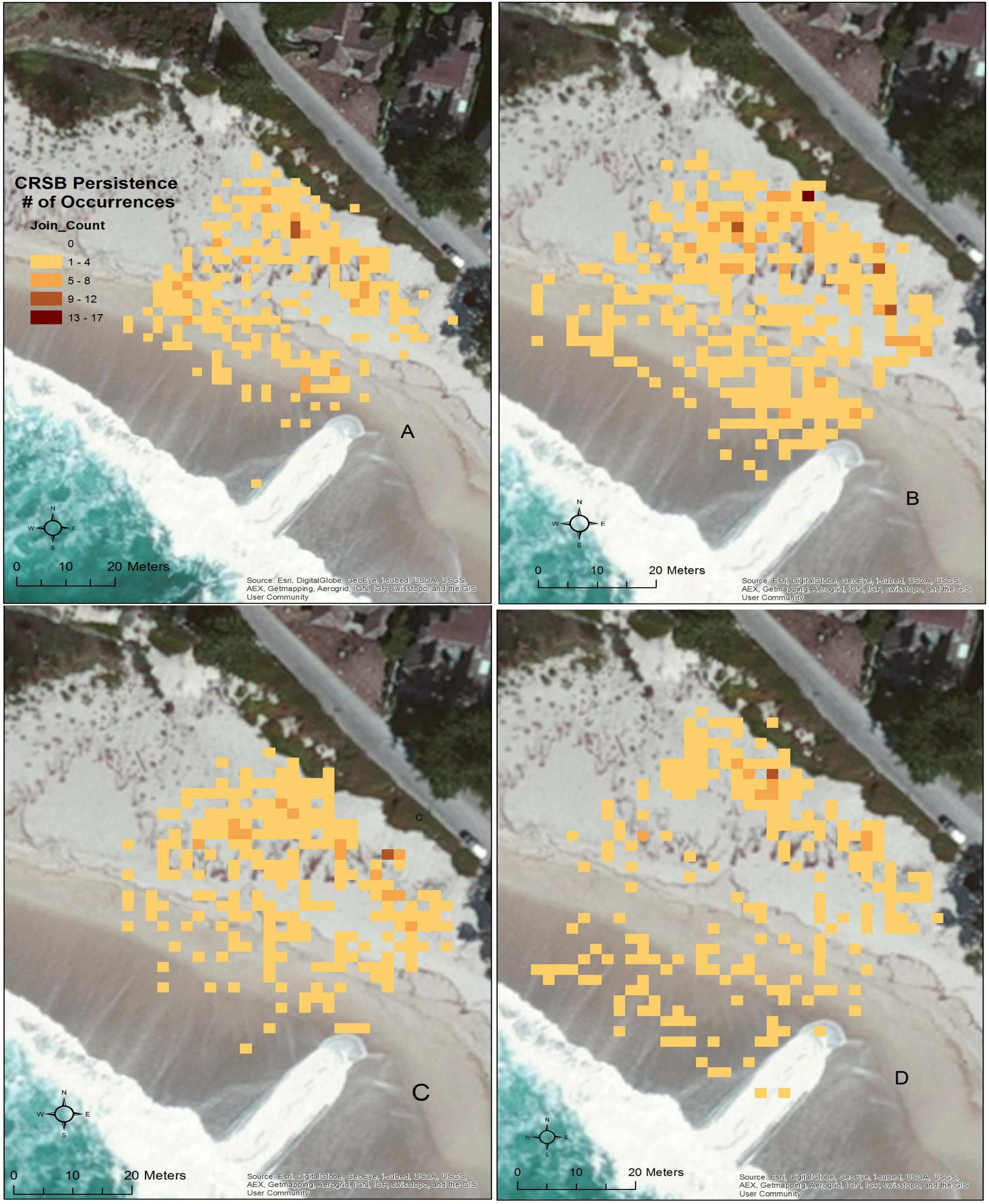
Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

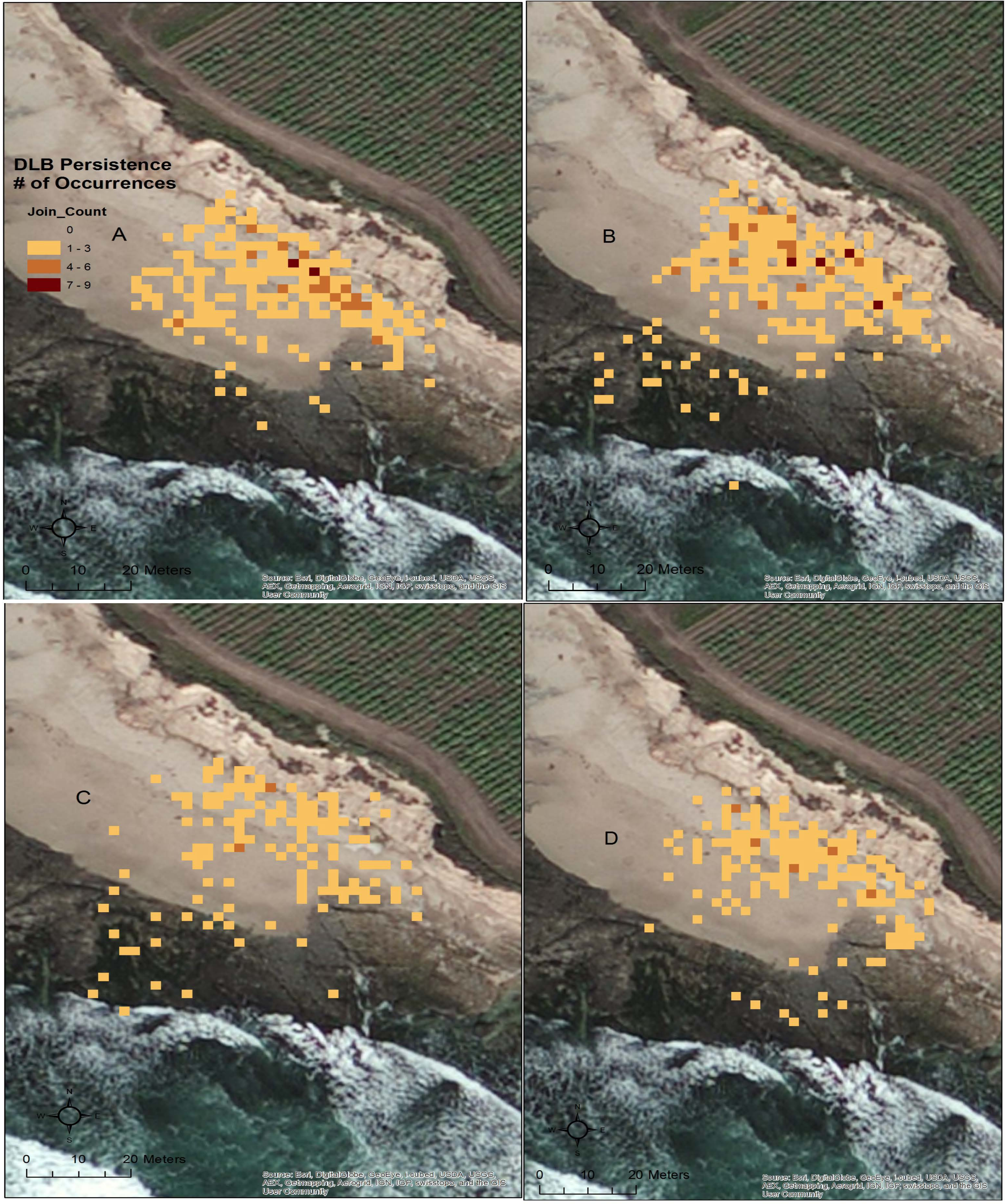
Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Appendix 17. Temporal variation in kelp wrack persistence on Carmel River State Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature. Spring (A) n=714, Summer (B) n=796, Fall (C) n=573, Winter (D) n=485.

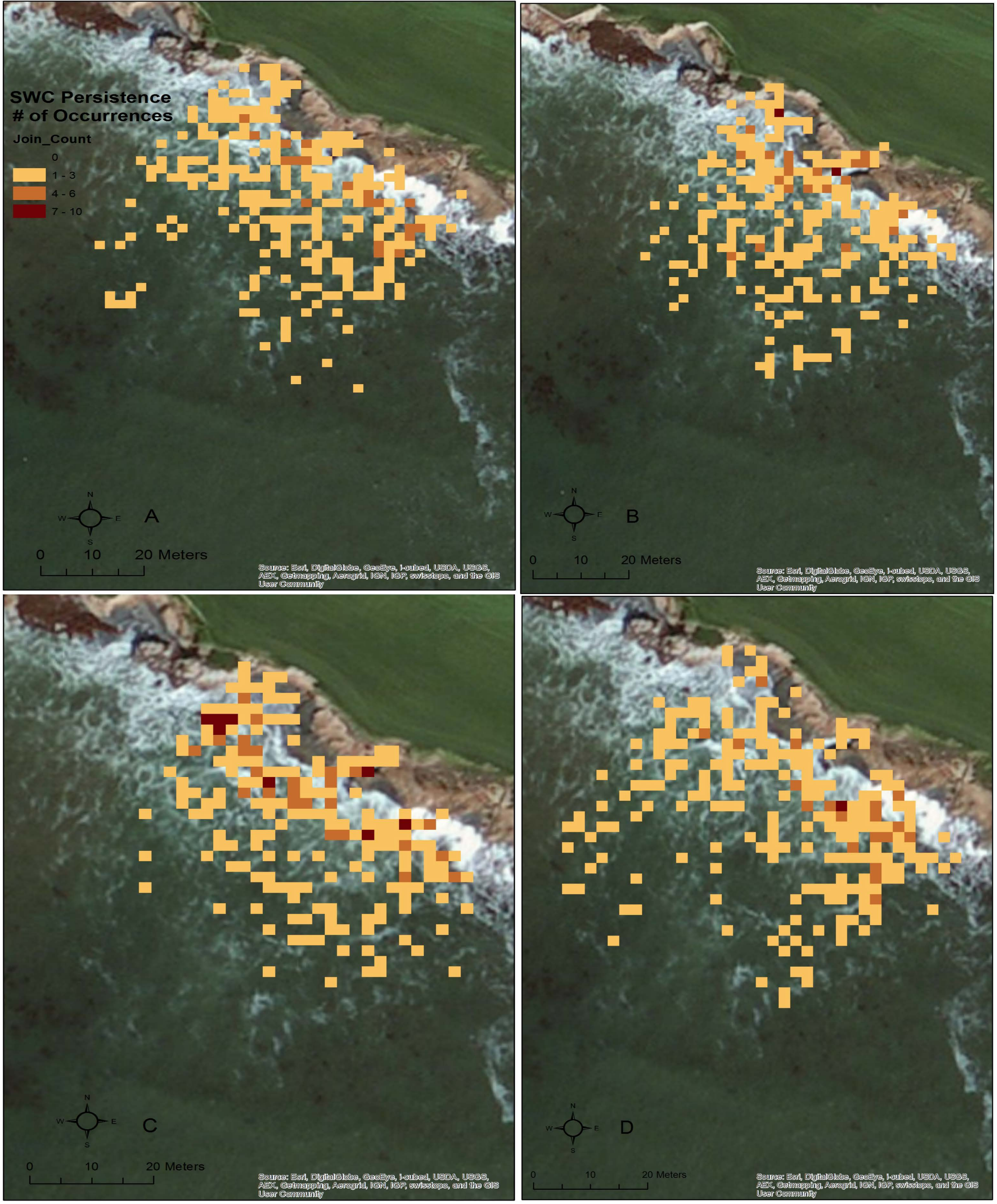


Appendix 18. Temporal variation in kelp wrack persistence on Davenport Landing Beach from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature. Spring (A) n=357, Summer (B) n=420, Fall (C) n=184, Winter (D) n=247.



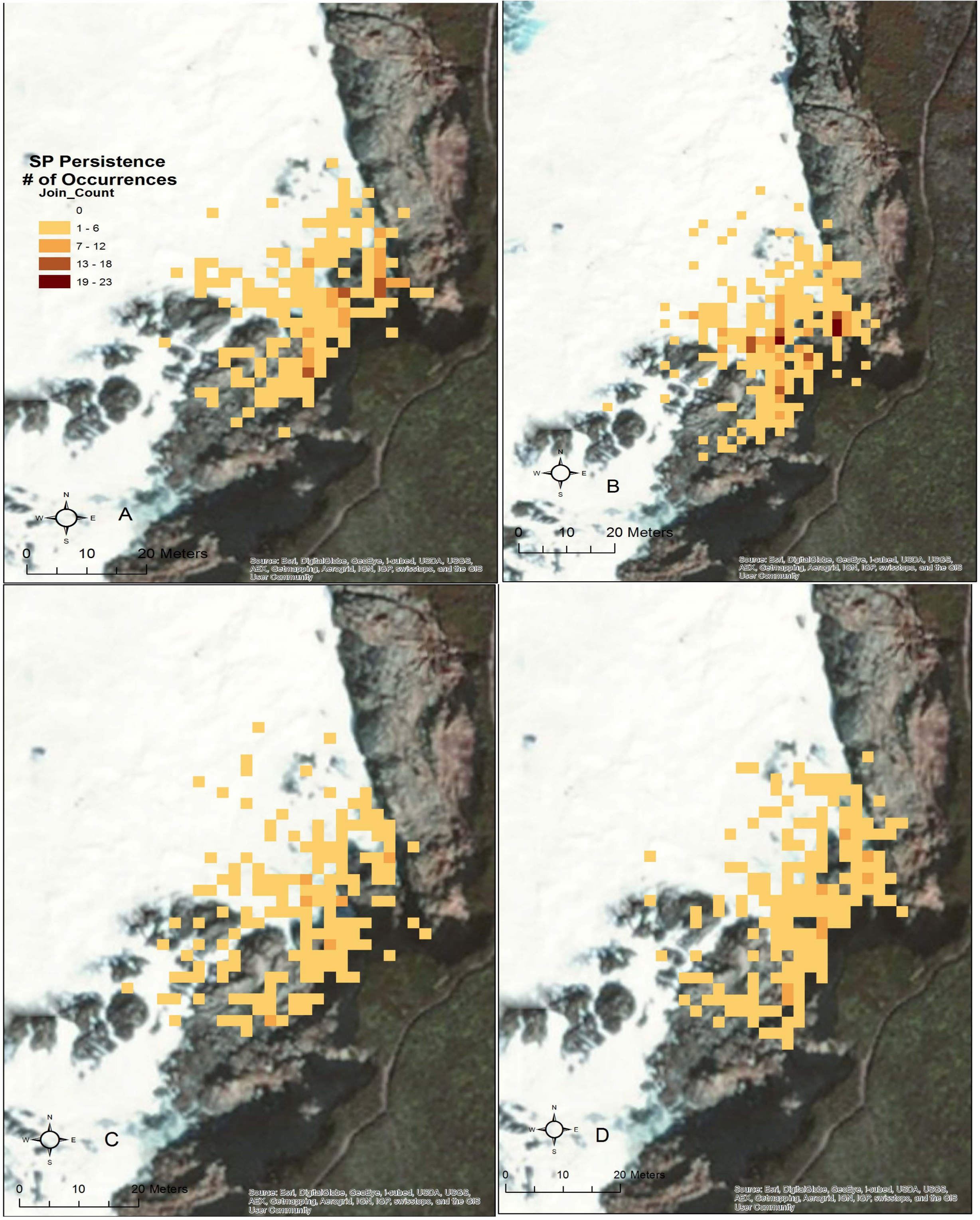
Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Appendix 19. Temporal variation in kelp wrack abundance on Stillwater Cove from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature. Spring (A) n=448, Summer (B) n=464, Fall (C) n=433, Winter (D) n=362.



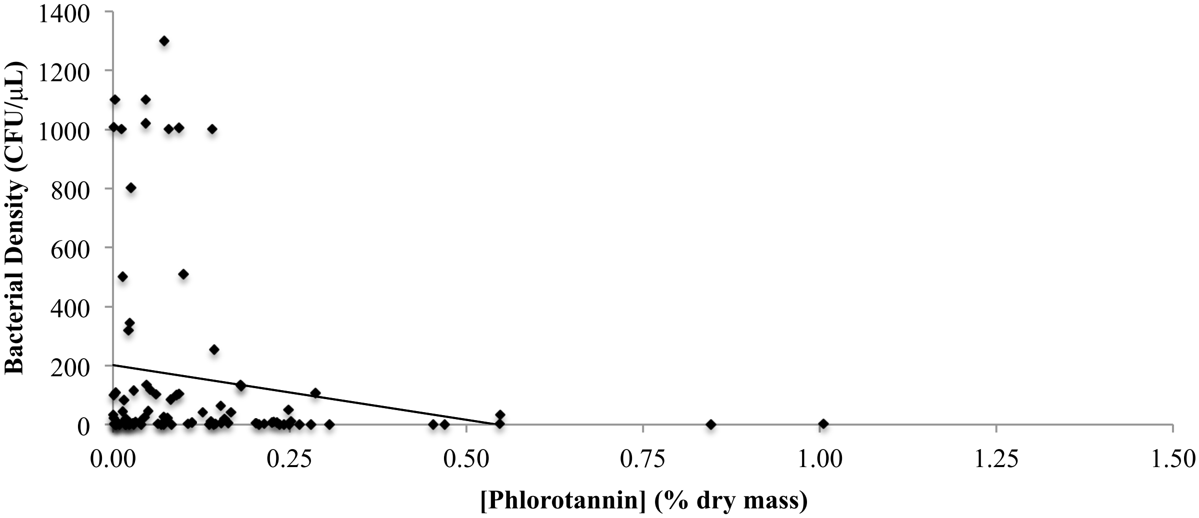
Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Appendix 20. Temporal variation in kelp wrack abundance at Soberanes Point from April 2013 to June 2014. Colored pixels represent the location of kelp wrack piles and their persistence values using the Join Count feature. Spring (A) n=483, Summer (B) n=839, Fall (C) n=337, Winter (D) n=414.

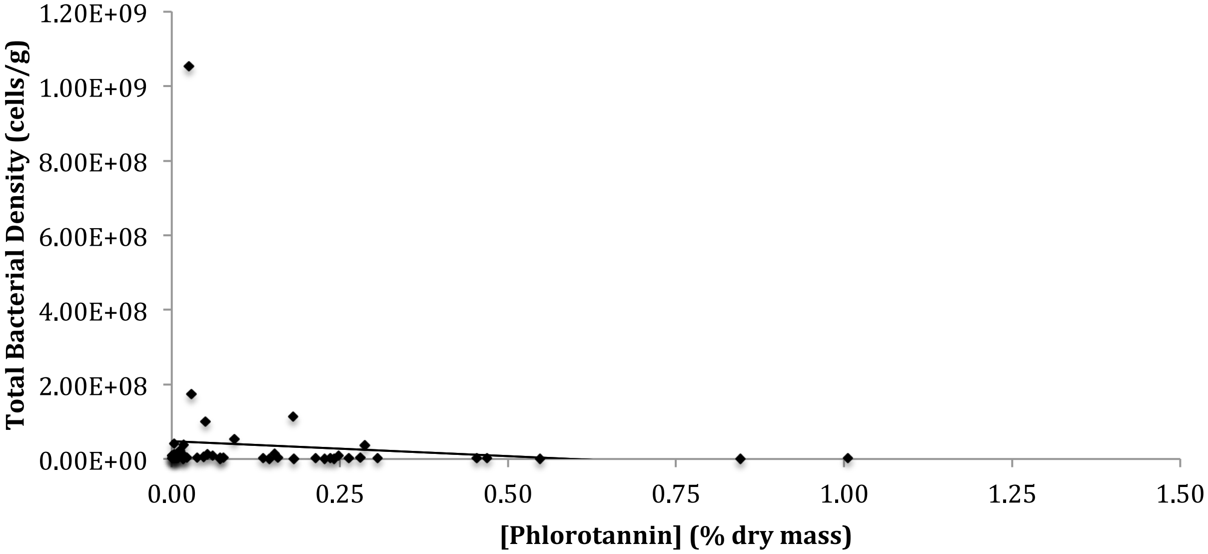


Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

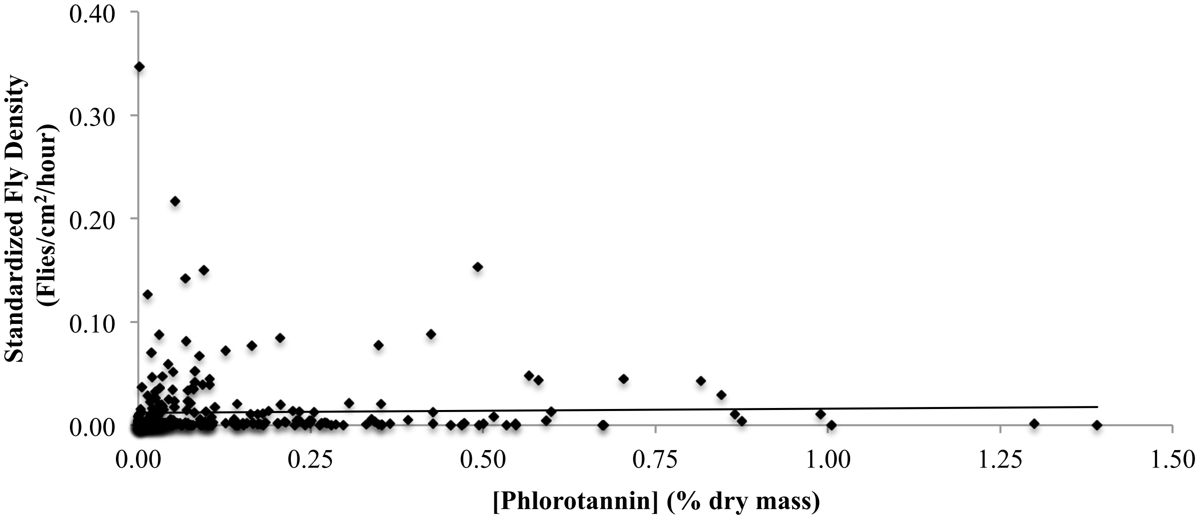
Appendix 21. Relationship between phlorotannin concentration and bacterial colony density at beaches and the rocky intertidal seasonally from July 2013 to April 2014. Regression: peak density -370.64 (±41.559)* phlorotannin concentration + 201.6 (±197.140), $r^2 = 0.037$, $P = 0.063$, $F_{1,96} = 3.535$.



Appendix 22. Relationship between phlorotannin concentration and total bacterial density at beaches and the rocky intertidal seasonally from July 2013 and January 2014. Regression: peak density -8E+7 (±26159780.7)* phlorotannin concentration + 5E+7 (±102708428), r^2 = 0.013, P = 0.439, $F_{1,49}$ = 0.608.



Appendix 23. Relationship between phlorotannin concentration and kelp fly density at beaches and the rocky intertidal seasonally from May 2013 to June 2014. Regression: peak density -0.004 (±0.001)* phlorotannin concentration + 0.012 (0.005), $r^2 = 0.018$, P = 0.232, $F_{1,301} = 1.448$.



Appendix 24. Relationship between bacterial density and fly density on beaches and the rocky intertidal seasonally from July 2013 and January 2014. Regression: peak fly density 9E-12 (±0.001)* bacterial density 0.0034 (±0.000), $r^2 = 0.025$, P = 0.235, $F_{1,57} = 1.441$.