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Density of benthic macroalgae in the intertidal zone varies with surf zone hydrodynamics

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ABSTRACT
Surf zone hydrodynamics influence subsidies (larval settlers and phytoplankton food) to the intertidal zone; subsidies have been observed to be much higher at more dissipative shores compared to reflective shores. Benthic macroalgal populations may be favoured at more reflective surf zones due to slower water exchange with the coastal ocean, facilitating retention of spores. In addition, larval invertebrate settlers are far less abundant at more reflective surf zones, and benthic macroalgae may experience lower competition from sessile invertebrates for space. We used surf zone width as an indictor of surf zone hydrodynamics; surf zones are wider at more dissipative surf zones compared to reflective surf zones. We tested the hypothesis that as surf zone width increases, macroalgal density would decrease. We used aerial near-infrared and visible light images to calculate the normalised difference vegetation index (NDVI) at eight intertidal sites along the Oregon coast and compared NDVI with algal biomass (dry and wet weight per square metre) at each specific location; linear regressions between NDVI and dry and wet algal biomass were significant ($P < 0.01$); NDVI was an accurate indicator of macroalgal density. Surf zone width was measured using Google Earth images. NDVI and dry and wet algal biomass were significantly lower at wider surf zones ($P < 0.01$). Although the mechanism underlying this relationship is unknown, the intertidal macroalgal community clearly varied with surf zone hydrodynamics as indicated by surf zone width.

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Algal biomass; Benthic algae; Early life history; NDVI; Seaweed; Subsidies; Surf zone hydrodynamics

INTRODUCTION

At high tide, the water over the intertidal zone is the surf zone. Larvae of many benthic intertidal organisms develop in the coastal ocean and, at the completion of their development, the final barrier to onshore migration to settlement sites at the shore is the surf zone. Surf zone hydrodynamics vary from narrow, more reflective surf zones to wide, more dissipative surf zones. This variation in morphology is a function primarily of the steepness of the shore (Wright & Short 1984). More dissipative surf zones have more gradually sloping bottoms, with waves breaking far from shore, creating a wide surf zone. Bathymetric rip currents are often present (Shanks, Sheeley & Johnson 2017) and their presence increases the exchange of water between the offshore inner shelf and the surf zone (MacMachan *et al.* 2006). Surf zones with steeper slopes are considered more reflective. Waves break closer to the shore, producing a narrower surf zone, and the rate of water exchange is slower (Shanks *et al.* 2015). Recent research has demonstrated that subsidies (larval settlers and phytoplankton food) delivered to the intertidal zone from the coastal ocean vary directly with local surf zone hydrodynamics. Subsidies are much lower at narrow more reflective surf zones than at wider, more dissipative surf zones (Morgan *et al.* 2017; Shanks, Sheeley & Johnson 2017; Shanks *et al.* 2010; Shanks, Morgan, MacMahan & Reniers 2017; Shanks, Morgan, MacMahan, Reniers *et al.* 2017).

During studies on the variation in barnacle population structure with surf zone hydrodynamics, macroalgal densities were also observed to vary with surf zone width (Shanks *et al.* 2010; Shanks & Morgan, unpublished data). However, the sampling was designed primarily to study barnacles and did not adequately describe macroalgal abundance. The purpose of the study presented here was to rectify this sampling problem and to test whether macroalgal density varies with surf zone width, an indicator of surf zone hydrodynamics.

Using infrared and visible aerial images of Oregon intertidal zones, we calculated the normalised difference vegetation index (NDVI) for intertidal sample sites, physically sampled macroalgae at these exact locations (wet and dry weights), and compared macroalgal abundance as determined by these different methods to surf zone width as an indicator of surf zone hydrodynamics. NDVI was developed to quantify terrestrial vegetation density and health from aerial images (Kriegler *et al.* 1969; Rouse *et al.* 1974; Tucker 1979). Values of near-infrared (NIR; strongly reflected by vegetation) and red (absorbed by vegetation) in images are measured and used in the NDVI equation to produce an index of vegetation density. NDVI ranges from −1 to +1, with values around and below zero signifying relatively lower amounts of vegetation.

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Colour versions of one or more of the figures in the article can be found online at www.tandfonline.com/uphy.

MATERIAL AND METHODS

As an index of intertidal macroalgal density, we used the NDVI, an index of vegetation abundance in images, typically but not limited to images from remote sensing (Kriegler *et al.* 1969; Rouse *et al.* 1974; Tucker 1979). The NDVI is calculated as

$$NDVI = (R_{NIR} - R_R)/(R_{NIR} + R_R),$$

where R_{NIR} and R_{R} are the values in the NIR and red (from red, green, blue [RGB] values) at a location in an image.

NIR aerial images of the intertidal zone were taken in June 1993 by the Oregon Department of Fish and Wildlife (ODFW) as part of a study of Oregon's rocky shores. These NIR photographs were taken from an airplane and were used to analyse kelp stocks on the shore. Images were taken at low tide when the kelp canopy was exposed, but this meant that the rocky intertidal zone and associated benthic macroalgae were also exposed. The scale is 1:7200. The images are available at https://oregondigital.org/sets/rockyshore93. The NDVI for eight rocky intertidal sites was determined using the ODFW NIR image dataset for R_{NIR} values and images screen-grabbed from Google Earth for the R_{R} values (ImageJ, http://imagej.nih.gov/ij/). ImageJ was used to measure the R_{NIR} and R_{R} values at precisely the same locations in each image pair. For each location, a small area (approximately 100–200 m^2) was selected in the NIR images. The NIR images were taken during a low spring tide; the entire intertidal zone was exposed and photographed. Sample sites were selected in the middle of the intertidal zone such that samples were collected in the middle of the algal zone and at roughly 0 m mean low water. Sample sites were chosen based on their accessibility during low tide to allow for ground truth sampling of the algal community. Images were scaled in ImageJ by selecting distinctive landmarks within the image and measuring the distance between the landmarks in the Google Earth image using the Ruler tool; this distance between landmarks in each image (Google Earth and ODFW) was used as size scaling in the ImageJ analysis. An ImageJ plugin, Random ROI (Random Object of Interest), selected random individual pixels from the selected small areas in both the infrared ODFW and Google Earth images, and an ImageJ RGB plug-in measured the *R* values in these selected pixels.

The NDVI was calculated using images taken at different times; the NIR images were taken in June 1993 and the Google Earth images were taken in April 2013 and July 2012 during low tides such that the intertidal zone was exposed (Table 1). To test whether the NDVI calculated in this way was an accurate reflection of macroalgal density in the field, we collected physical samples at the exact location analysed within each image (see Table 1 for locations) and regressed the biomass in these samples against the NDVI. For each of the locations analysed for NDVI, a set of latitude and longitude coordinates was determined from Google Earth using the Placemark tool for the exact area of the image analysed. These coordinates and a Global Positioning System were used to locate the sample site in the field. A physical sample of macroalgae was taken at this Global Positioning System location and eight additional samples were collected at 1-m intervals surrounding this central sample. Macroalgae were cut, leaving holdfasts, from 0.125 × 0.25 m quadrats. Samples were blotted dry, weighed wet and then dried to a constant weight in a 50 °C oven. To test whether the NDVI was an accurate reflection of the density of macroalgae in the field, using the plotting programme Deltagraph 7 (Redrocksw.com), we calculated linear regressions between macroalgal biomass as wet and dry weights per square metre (independent variables) and the NDVI (dependent variable). Algae were not identified to species, but general descriptions and patterns were noted.

Average surf zone (Fig. 1) width was measured using the historical collection of images available in Google Earth (Figs 2, 3) at each location. Using the Ruler tool, surf zone width was measured directly offshore from each sample site as the distance from where the first wave broke at the outer edge of the surf zone to the highest extent of wave run up. A detailed description of the method of measuring surf zone width in Google Earth images can be found in Shanks, Sheeley & Johnson (2017) and Shanks, Morgan, MacMahan & Reniers (2017). Spring/summer images were available from 1994 to 2015 for each sample site. Depending on the sample location, between seven and nine images were available (Table 1; Fig. 1). To test whether algal biomass as wet and dry weights per square metre and NDVI (dependent variables) varied with surf zone width (independent variable) we calculated regressions and, because these relationships are clearly nonlinear (see below), we calculated nonlinear regressions. Using the plotting programme Deltagraph 7, we calculated exponential, logarithmic, and power curve regressions (all of which were significant at $P < 0.05$). We report the results of the logarithmic regressions.

Table 1. Sites with average surf zone width, geographic coordinates of the sample site along the Oregon coast, algal collection dates, and dates of Google Earth image used for the NDVI calculation.

Location name (m ± *s*, *n*)	Latitude, N	Longitude, W	Algal sample date in 2017	Google Earth image date
South Cove (6 ± 5, 7)	43°18.1015′	124°23.9945′	06 Aug.	03 Apr. 2013
Cape Arago (15 ± 8, 7)	43°18.4422′	124°24.1776′	08 Aug.	03 Apr. 2013
Pack Trail (36 ± 9, 7)	43°19.1614′	124°23.5473′	08 Aug.	03 Apr. 2013
Light House (87 ± 22, 8)	43°20.3433′	124°22.3343′	06 Aug.	03 Apr. 2013
Bastendorff (249 ± 68, 9)	43°20.5266′	124°21.4703′	06 Aug.	03 Apr. 2013
Stonefield Beach (131 ± 55, 9)	44°13.2888′	124°6.8499′	07 Aug.	22 July 2012
Bob Creek (57 ± 26, 9)	44°14.5885′	124°6.7705′	22 July.	22 July 2012
Strawberry Hill (123 ± 20, 9)	44°15.2808′	124°6.7792′	07 Aug.	22 July 2012

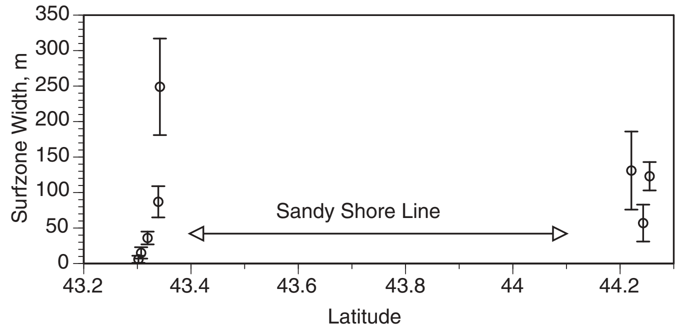


Fig. 1. Average surf zone widths (± SD, average of n = 7 to 9 images) as measured from Google Earth images taken in spring and summer plotted with latitude. Sites were centred around Cape Arago, Oregon (43°18′N) and Strawberry Hill, Oregon (44°12′N). Between the two sampled sections of coast there is a long (70 km) area of sandy beach shoreline. Sites were separated by about 100 km.

RESULTS

Algal communities at the more dissipative shores were sparse and consisted mainly of green algae such as *Ulva* and smaller brown algal species such as *Fucus*. Much to nearly all of the substrate was occupied by benthic filter feeders, primarily barnacles and mussels, which were sometimes densely packed and hummocked (Fig. 5). Much denser algal communities were observed at the more reflective shores and these communities were composed primarily of larger red and brown algal species (Fig. 4). Benthic filter feeders were much less dense when observed.

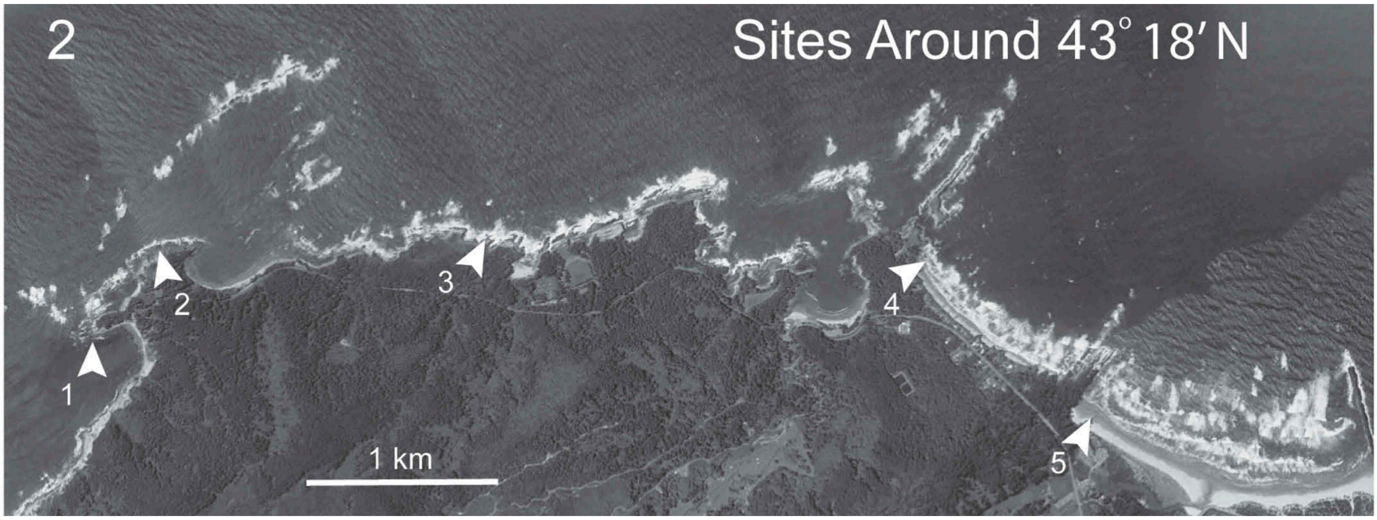
Despite the fact that NDVI was calculated using data from images taken in different years and the algal samples were collected 4 to 5 years later, NDVI is significantly related to both algal wet and dry biomass (g m^{-2}) with from > 80% to > 95% of the variability in NDVI explained by algal biomass (Figs 6, 7). Average spring/summer surf zone width at sample sites ranged from less than 10 to approximately 250 m (Fig. 1); three of the sites had narrow surf zones (< 50 m wide) and were considered more reflective (e.g. South Cove, Cape Arago, and Pack Trail; Fig. 2), four had wide surf zones (> 80 m wide) and were considered more dissipative (Light House, Strawberry Hill, Stonefield Beach, and Bastendorff; Figs 2, 3), and one, Bob Creek, was indeterminate (mean surf zone width 57 m; Fig. 3). We found significant negative nonlinear regressions between NDVI and macroalgal biomass as measured by wet and dry weights per square metre and surf zone width with surf zone width explaining from 85% to 95% of the variation (Figs 8, 9). We report the results from the logarithmic regressions, but calculated exponential and power curve regressions were significant, with similar r^2 values.

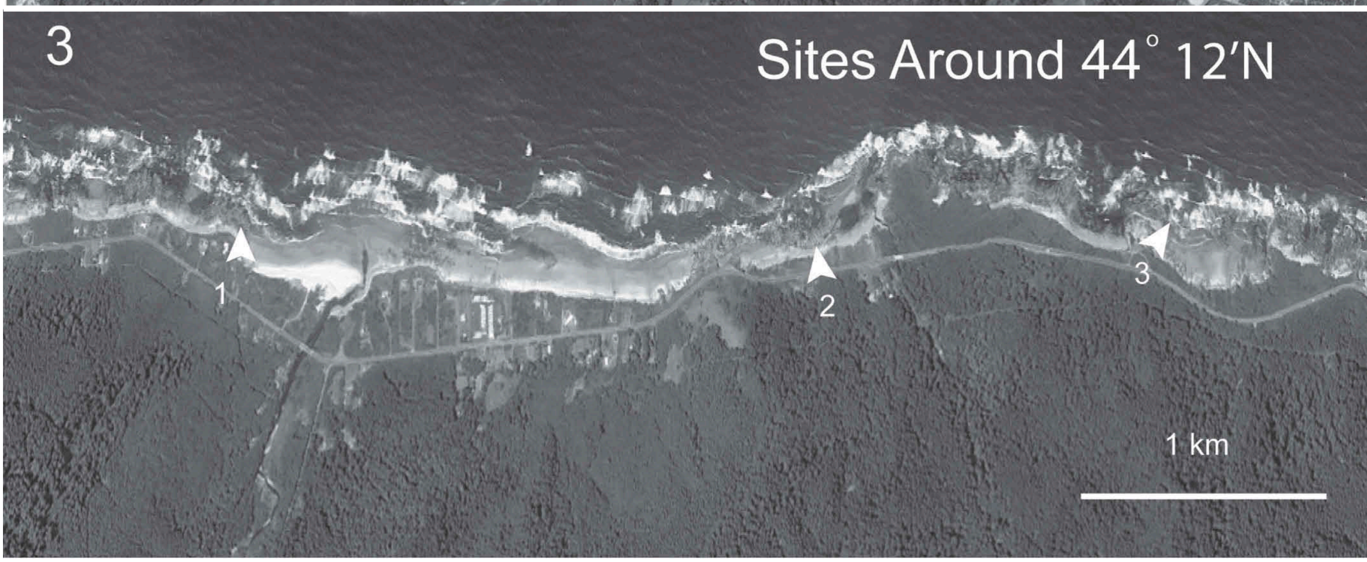
DISCUSSION

We found significant relationships between surf zone width and different measures of macroalgal abundance; macroalgal densities, as measured by NDVI and wet and dry biomass, were lower at wider more dissipative surf zones. These results are consistent with previous observations (Shanks *et al.* 2010).

The relationships observed between surf zone width, wet weight, dry weight, and NDVI were clearly nonlinear. At sites with wide surf zones, there was either no algae or very little. On the other end of the spectrum, sites with much wider surf zones had a greater abundance of algae. Clearly, the data are nonlinear and the regressions were fit as such.

From our sampling, we cannot define a mechanism by which surf zone hydrodynamics might affect macroalgal density; we can only describe the differences in macroalgal density in relation to surf zone width. However, given what is known about surf zones, in relation to other studies, we can suggest some hypothetical mechanisms. Subsidies of larval settlers (e.g. barnacles) are significantly higher — often an order of magnitude higher — at more dissipative surf zones (Shanks, Morgan, MacMahan & Reniers 2017). These populations of filter feeders are supported by significantly higher subsidies of phytoplankton food in more dissipative surf zones (Shanks, Morgan, MacMahan & Reniers 2017). At these more dissipative sites the rocky intertidal zone is often completely covered by a densely packed community of filter feeders, often dominated by barnacles. For example, at sites sampled by Shanks, Morgan, MacMahan & Reniers (2017) with surf zones < 50 m wide, average barnacle densities were 339 per 100 cm^2 (s = 266 100 cm^2), and at sites with wider more dissipative surf zones average barnacle densities were 1613 100 cm^2 (s = 1118 100 cm^2). The difference in the density of barnacles < 1.5 mm, new recruits, is even more striking; at narrow, more reflective surf zones, average new recruit densities were 16 per 100 cm^2 (s = 15 per 100 cm^2), and at sites with wider, more dissipative surf zones, average new recruit densities were 824 per 100 cm^2 (s = 797 per 100 cm^2). Low density of macroalgae at more dissipative shores may be due to intense competition for space with populations of sessile filter feeders. This could lead to lower densities of macroalgae and, hence, lower abundance of macroalgal spores being released and, as a consequence, lower densities of settling algal spores (negative feedback). Alternatively, high abundance of macroalgae at more reflective sites may be a direct consequence of hydrodynamics, in which the exchange of water within a reflective surf zone with that offshore is slower than in more dissipative surf zones (MacMahan *et al.* 2010). This may allow algal spores released from the intertidal zone to remain close to shore, leading to higher spore settlement. This process would lead to positive feedback; more settlers should lead to more adults, which in turn produce more spores. Determination of the underlying mechanisms will require more observation and experimentation.

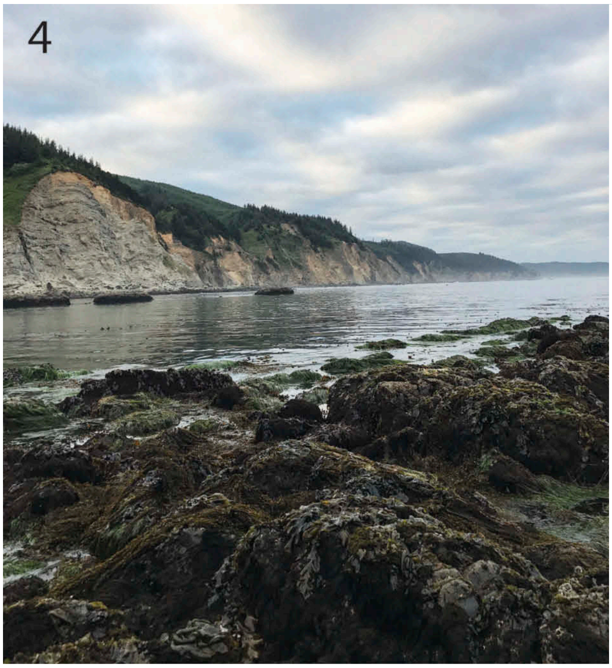




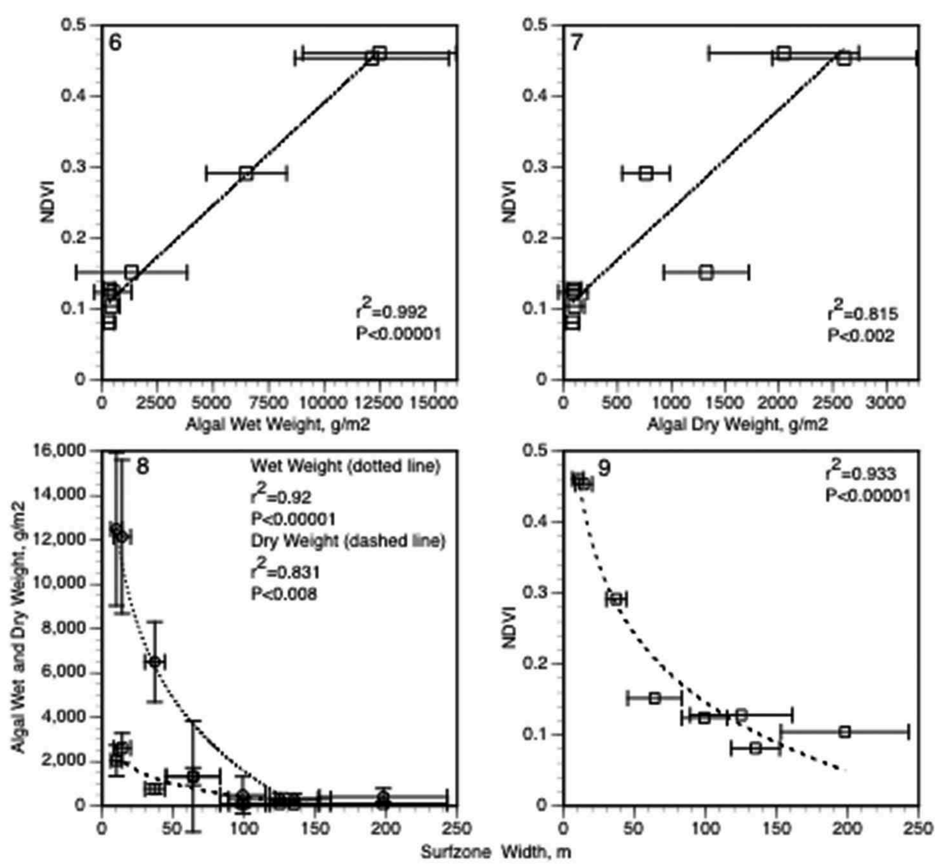
Figs 2,3. Study sites.
Fig. 2. Sites around Cape Arago. South Cove (1), Cape Arago (2), Pack Trail (3), Light House (4), and Bastendorff (5).
Fig. 3. Sites around Strawberry Hill. Stonefield Beach (1), Bob Creek (2), and Strawberry Hill (3). In 2 and 3, north is to the right in each image.

Since its development in the early 1970s, NDVI has been used extensively in terrestrial environments (Kriegler *et al.* 1969; Rouse *et al.* 1974; Tucker 1979); however, its application in benthic marine ecosystems has been less extensive. NDVI was used in salt marsh ecosystems (Green *et al.* 1998) and to quantify macroalgal densities on rocky shores and in kelp beds (Guichard *et al.* 2000; Guillaumont *et al.* 1993; Meulstee *et al.* 1988). Most studies of macroalgae in rocky intertidal areas are done using time-consuming field surveys. Remote censusing to monitor rocky intertidal areas may ease monitoring of these important and sensitive habitats (Bryson *et al.* 2013). To test whether NDVI provides useful information on the density of intertidal macroalgae, we regressed NDVI against physical samples of algae collected at exactly the same intertidal locations at which NDVI was calculated and found that over 80% of variation in NDVI is explained by macroalgal biomass (g m^{-2}).

The ODFW photographs, which provided the R_{NIR} data, were taken in 1993; the Google Earth images, which provided the R_{R}, were taken between 2012 and 2013; and the physical macroalgal samples from the field were collected in 2017. Surprisingly, despite the fact that samples were collected from different years, we found a very strong relationship between the calculated NDVI and macroalgal biomass. This suggests that relative amount of macroalgal cover on the sampled rocky shores may display limited variation in seasonal abundance between years. Sites with low or high standing stock of macroalgae in a season tend to have low or high standing stocks year after year. The relative abundance of adult barnacles, new recruits, and daily barnacle settlement at multiple sites has also remained consistent over multiple years and varies directly with surf zone width, that is, with higher densities and settlement where surf zones are wider and more dissipative (Shanks, Morgan, MacMahan & Reniers 2017). For example, one of the authors (ALS) has visited both South Cover and Strawberry Hill (Figs 2, 3) annually for at least two decades and observed that the algal and benthic filter-feeder communities remained, at least within a season, similar over time, and communities have appeared consistent over time. From year to year,



Figs. 4,5. Representative study sites. [Note the width of the surf zones visible in Figs 4 and 5; narrow at South Cove (Fig. 4), wide at Strawberry Hill (Fig. 5).]
Fig. 4. General overview of a representative more reflective site (South Cove, Fig. 2 site 1).
Fig. 5. General overview of a representative more dissipative site (Strawberry Hill, Fig. 3, site 3).



Figs. 6-9.
Figs 6,7. Relationship between macroalgal abundance as determined from an NDVI analysis of aerial images and mean algal biomass (error bars SE) as measured by wet and dry weights of algae collected at the locations where the NDVI analysis was made. Statistical results are from linear regressions fit to the data.
Fig. 8. Relationship between mean algal biomass (error bars SE) as wet and dry weights. Statistical results are from logarithmic regressions fit to the data. Equations for the curves are dry weight, $-839.8\ln x + 4281$, wet weight $-4763\ln x + 23{,}497$, and NDVI $-0.1397\ln x + 0.789$.
Fig. 9. Macroalgal abundance as determined from the NDVI analysis regressed with average spring/summer surf zone width (error bars SE) at the sample sites. Statistical results are from logarithmic regressions fit to the data. Equations for the curves are: dry weight, $-839.8\ln x + 4281$, wet weight $-4763\ln x + 23{,}497$, and NDVI $-0.1397\ln x + 0.789$.

suitable rocky substrate at a site has been relatively unchanged; however, sites with similar amounts of rocky shore did not produce similar amounts of algae or filter feeders. Instead, similarities in community structure varied with the width of the surf zones.

Menge *et al.* (1997) compared community structure and ecology of two intertidal sites on the Oregon coast, Strawberry Hill and Boiler Bay. The intertidal zone at Strawberry Hill was dominated by sessile filter feeders, chiefly mussels and barnacles, with low densities of macroalgae. Boiler Bay, on the other hand, was dominated by macroalgae and their associated herbivores. These differences were thought to result from differing coastal hydrodynamic conditions on the continental shelf. We offer an alternative explanation. The rock platform at Strawberry Hill is situated within a more dissipative surf zone (average surf zone width 123 ± 20 m SD); whereas, Boiler Bay is a more reflective site with a narrow surf zone (average surf zone width 13 m, 9 m SD). Given the hydrodynamics of the surf zone at Strawberry Hill, the intertidal community is sustained by high subsidies of settling larvae and phytoplankton food; the community structure is set by the very local hydrodynamics of the adjacent surf zone. Here, the densities of macroalgae and herbivores are low and the densities of filter feeders are high (Menge *et al.* 1997). In contrast, research on the effect of surf zone type on subsidies to the intertidal zone (Morgan *et al.* 2017; Shanks, Sheeley & Johnson 2017; Shanks, Morgan, MacMahan & Reniers 2017) suggests that Boiler Bay, due to the hydrodynamics of the adjacent more reflective surf zone, has much lower subsidies of larval settlers and phytoplankton food. By mechanisms that we do not yet understand, but appear to be related to surf zone hydrodynamics, the density of macroalgae at Boiler Bay is high supporting a community of herbivorous grazers.

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