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Surfzone hydrodynamics alter phytoplankton subsidies affecting reproductive output and growth of tidal filter feeders

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ABSTRACT

Surf zones, classified from reflective to dissipative, separate the ocean from shore and subsidies from the coastal ocean must pass through surf zones to reach the shore. We have observed that variations in phytoplankton concentrations in the water over the intertidal zone varied with surfzone hydrodynamics and we hypothesized that this variation would alter growth rates, population structure, and reproductive output of *Mytilus californianus* and *Balanus glandula*.

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From May 2016-April 2017, along 7 km of Cape Arago, Oregon, surfzone phytoplankton concentrations were determined weekly at nine sites with varying surfzone hydrodynamics as indicated by surfzone widths. Throughout the year concentrations of phytoplankton in wider, more dissipative surf zones were, on average, 16x higher than in narrow, more reflective surf zones. Similar to previous observations, surfzone-width explained >90% of the variability in phytoplankton concentrations in the surf zone. On average, ~83% of *B. glandula* had egg lamellae at more dissipative shores compared to only 8% at more reflective. An index of potential reproductive output by barnacle populations as measured by ash free dry weight (AFDW) of egg lamellae was ~243x larger at more dissipative than reflective shores and surfzone phytoplankton concentrations and surfzone width explained ~96 and 92% of the variability in this index. On average, density of *M. californianus* was ~2x higher at more reflective shores, but 60% of these individuals were smaller and non-reproductive compared to only 24% at the more dissipative sites. The gonad tissue weight/m² of medium sized mussels was ~5x greater at more dissipative than reflective shores. Surfzone phytoplankton concentrations and surfzone width explained ~80 and 65% of the variability in individual mussel gonad mass and ~69 and 56% of the variability in mussel population gonad mass, respectively. *M. californianus* were out-planted to assess growth rates and, after 5 months, average body mass was ~3x greater at more dissipative than reflective shores. Surfzone phytoplankton concentrations and width explained ~85 and 92% of the mass increase, respectively. Phytoplankton subsidies varied with surfzone hydrodynamics altering the growth and reproductive output of two ecologically important intertidal filter feeders.

Keywords: dissipative, reflective, chlorophyll-*a*, growth rates, reproductive output, upwelling, IUH, intermittent upwelling hypothesis

INTRODUCTION

Intertidal communities are, at least in part, sustained by resources from the coastal ocean (Polis et al. 1997, Krenz et al. 2011). The coastal ocean is separated from the shore by surf zones and subsidies from the coastal ocean must pass through the surf zone to reach intertidal communities. Variations in surfzone hydrodynamics can significantly alter the delivery of subsidies, larval settlers and phytoplankton food, to intertidal communities (Rilov et al. 2008, Shanks et al. 2010, Shanks et al. 2017a, Shanks et al. 2017c). While past research concluded that variations in subsidies were due to hydrodynamics over the continental shelf (Bustamante et al. 1995, Menge et al. 1997b, Connolly et al. 2001, Menge et al. 2003, Blanchette et al. 2007b), recent findings reveal surfzone hydrodynamics to be just as, if not more, important in influencing subsidies to intertidal communities (Morgan et al. 2017b, Shanks et al. 2017a, Shanks et al. 2017b, Shanks et al. 2017c).

Surfzone hydrodynamics vary due to coastal morphology (Wright and Short 1984, Lippmann and Holman 1990, Woodroffe 2002) and surf zones range along a continuum from dissipative to reflective shores (Wright and Short 1984). More dissipative shores are characterized by wider surf zones, gradual beach/shore slopes, fine-grain sand on beaches, and, often, the presence of bathymetric rip currents. Bathymetric rip currents carry water out of the surf zone onto the inner shelf and waves push water back into the surf zone over the shoals between rip current channels (MacMahan et al. 2010), creating eddies within the surf zone (Reniers et al. 2010). Rip currents strengthen with larger waves and during low tide (MacMahan et al. 2006). Shanks et al. (2017b) found that at a more dissipative surf zone site, Sand City, concentrations of coastal phytoplankton taxa were not only higher within the surf zone compared to offshore samples, but concentrations were highest in rip current samples. Coastal phytoplankton can be caught by rising bubbles (Krichnavaruk et al. 2007) and at Sand City high phytoplankton concentrations were associated with foam; the authors hypothesized that at more dissipative shores with bathymetric rip currents,

coastal phytoplankton attached to bubbles become concentrated within the rip current circulation system, similar to what has been observed with surfzone diatoms, taxa adapted to living within more dissipative surf zones (Talbot and Bate 1987b, a) and buoyant particles (Fujimura et al. 2014).

Bathymetric rip currents, present in more dissipative surf zone, is likely a key element of surfzone hydrodynamics in aiding delivery of both zoo and phytoplankton subsidies from the coast ocean to shore communities.

At the opposite end of the continuum are reflective shores characterized by narrow surf zones, steep beach/shore slopes, and coarse-grain sand if the shore is a beach. Due to shore steepness, wave energy is reflected seaward and bathymetric rip currents are unlikely to form, however, topographic and transient rip currents may be present. Topographic rip currents form due to the interruption of alongshore currents by topographic barriers (e.g., points and headlands), creating a seaward current (Castelle and Coco 2013). Transient rips form due to turbulent eddies in the surf zone (Suanda and Feddersen 2015). Unlike bathymetric rip current systems, topographic and transient rip currents do not set up persistent eddy systems and tend to permanently eject floating objects (e.g., bubble attached phytoplankton) out of the surf zone (Castelle and Coco 2013). At reflective shores, there is surface flow landward at the breaker line, and offshore undertow pushing water seaward through the remainder of the water column within the surf zone (Shanks et al. 2015). Shanks et al. (2017a, b) found that phytoplankton concentrations within the more reflective surfzone at Carmel State River beach were at least 10x lower than in the water just offshore, as little as 20 m offshore, despite the fact that water within the surf zone was exchanged with offshore onshore water. The authors found chlorophyll-*a* concentrations were significantly lower in surface waters, the water entering the surfzone, and that this low concentration in the water entering the surf zone from the inner shelf likely accounted for the low concentration of phytoplankton subsidies within the surf zone.

Hydrodynamics directly affect the growth of intertidal filter feeders (Leigh and Paine 1987, Brown and Quinn 1988, McQuaid and Lindsay 2000, Steffani and Branch 2003). Detailed hydrographic and biological studies of a more reflective and more dissipative surf zone found that coastal phytoplankton taxa concentrations within the surf zone, food subsidies, were significantly and around an order of magnitude lower than just offshore at the reflective surf zone and the reverse was true at the more dissipative surf zone (Shanks et al. 2017b). By altering phytoplankton food subsidies to the shore, hydrodynamics may also indirectly alter reproductive output and growth rates of filter feeders in intertidal communities. Along the Oregon coast, larval barnacle production and barnacle growth rates were higher in areas with higher food concentrations (Leslie et al. 2005) and mussel populations at shores that received higher phytoplankton subsidies grew faster (Bracken et al. 2012). Phytoplankton subsidies in reflective surf zones around Cape Arago, Oregon were found to be an order of magnitude lower than in adjacent dissipative surf zones (Shanks et al. 2017c). Hence, where surfzone are wide and more dissipative, we hypothesized that growth and reproductive output of intertidal filter feeders should be higher than at narrower more reflective surf zones. To test this hypothesis, we measured phytoplankton concentrations within surf zones at nine sites around Cape Arago, Oregon with varying surfzone hydrodynamics as indicated by surfzone width and the reproductive output, growth, and population structure of *Balanus glandula* and *Mytilus californianus* at these sites.

METHODS

We sampled nine sites with surfzone widths varying from 10 to 300 m (e.g., more reflective to more dissipative), spanning ~7 km of shore around Cape Arago, Oregon (Figure 1). By sampling closely spaced stations we hoped to minimize the effect of offshore hydrographic conditions (e.g., variation in upwelling and wave climate) and offshore variation in phytoplankton. We avoided sampling sites within bays and coves due to the altered hydrodynamics at these sites (Shanks and

McCulloch 2003). One of the key characteristics of surf zones is their width, more reflective surf zones are narrow while more dissipative are wider (Wright and Short 1984), hence, surfzone width can be used as a proxy to characterize the surfzone hydrodynamics present at a site (Shanks et al. 2017a, Shanks et al. 2017c). Surfzone width was measured in Google Earth images. Nine to ten images of the study area were available from 1994-2015 (Figure 1; Appendix S1 Table S2, Figure S4). Surfzone width was measured as the distance from the most seaward breaking wave to the swash line (Shanks et al. 2017a, Shanks et al. 2017c). While some sites were sandy beaches with rock outcrops, the majority of sites were rocky shores, sites typically studied by intertidal ecologists. Imagery of the shoreline was sufficient to estimate our independent variable. Fieldwork was conducted weekly over a year (see below) and it was observed that, although there was a range in the surfzone widths at each site due to daily weather conditions and time of year, on average, surfzone widths remained close to the averages shown in Figure 1 obtained from the Google Earth images; sites with narrow surf zones remained narrow and wide surf zones remained wide. Sites with average surfzone widths >50 m, sites with bathymetric rip currents, were considered more dissipative while sites with narrower surf zones were considered more reflective.

To determine phytoplankton concentrations, water within the surfzone was sampled ~weekly from May 2016 to April 2017. Three replicate water samples (~500-550 ml) were collected by casting a well-bailer attached to a rope into the surf within 10 m of shore. The well-bailer, an acrylic tube with a small hole at one end and a one-way valve at the other, traps water when submerged and retains the water during retrieval. Samples were collected at low-tide as some sites were inaccessible at higher tides. A 100 ml subsample was used to determine chlorophyll-*a* (chl-*a*) concentration using standard techniques (Parsons et al. 1993). The remaining ~400 ml was preserved with acid Lugol's for cell counts. Phytoplankton samples were concentrated on a 25 μ m sieve and transferred to a beaker. Samples were homogenized by random stirring and a subsample placed on a Sedgewick-rafter slide. Diatoms were identified (Tomas 1997) and enumerated using

standard methods (Sournia 1978). Using the data collected from May-August 2016, linear regressions were calculated between average surfzone width (independent variable) and average concentrations of chl-*a*, total phytoplankton cell concentration in the surfzone (sum of all cells), and total cell concentrations of *Chaetoceros* spp., *Pseudo-nitzschia* spp., *Thalassiosira* spp., and *Skeletonema* spp. (dependent variables). A Bonferroni correction was used to account for the pairwise comparisons between the four phytoplankton taxa ($\alpha = 0.01$). Phytoplankton cell concentrations were not log transformed prior to analysis. To determine if there was a difference between phytoplankton concentrations within the surf zone and seaward on the inner shelf, three replicate water samples were collected using the well-bailer from within surfzones and seaward of the surfzone at 8 of the 9 sites on September 2 and 23, 2016 (Figure 1; Appendix S1 Table S1). Phytoplankton concentrations were determined as described above. Using a two-way ANOVA, we tested if phytoplankton surfzone concentrations and offshore were similar and if they varied with surfzone hydrodynamics as measured by surfzone width. Phytoplankton data were log transformed prior to analysis and a Shapiro-Wilk test was used to test for normality.

To determine size distributions of *M. californianus* at each site, in July 2016 a 20 m transect was laid parallel to the water and through mussel populations at 1.6 ± 0.2 m above mean low low water (MLLW). Tidal elevation was determined used standard clinometer techniques. An observer with a sighting level stood where the transect line was laid at each site and a second person holding a surveyor's rod stood at the water line. Using the sighting level, the observer measured height on the surveyor's rod. Knowing the tidal height at the time the measurement was taken and using standard trigonometry, the tidal height of the transect line was determined. Four 0.33 x 0.33 m quadrats were randomly placed along the transect from which all mussels were collected. The length (umbo to posterior shell edge) was measured with Vernier calipers to the nearest 0.1 mm. Mussels were sorted into six size classes: 40-50, 51-60, 61-70, 71-80, 81-90, and 91-100 mm. Reproductive state was determined (see below). Differences in size-frequency distributions between dissipative

and reflective sites were tested with a Kolmogorov-Smirnov test. To examine the effect of surfzone width and phytoplankton abundance on *M. californianus* reproductive output we examined mussels from the 61-70 mm size class; only this size class was examined as it was the only size class present at all sites from which gonad tissue could almost always be sampled. 61-70 mm mussels were collected from an additional three 0.33 x 0.33 m quadrats randomly placed on the transects. The mantle and associated gonad tissue were dissected from the body of at least 25 mussels from each site. Mantle and associated gonad tissue which had some thickening or coloration were deemed reproductive (Dittman & Robles, 1991; Phillips, 2007). Sexes were not separated as sex was difficult to ascertain visually. Tissue samples were dried at 70°C for 48 hr., weighed, dried at 450°C overnight, and then weighed to obtain the Ash-Free Dry Weight (AFDW). We calculated an index of reproductive potential by multiply the average AFDW of gonad from 61-70 mm mussels times their density in the field. This index (dependent variable) was regressed against surfzone width and phytoplankton cell concentrations (independent variables).

Growth of *M. californianus* was followed at the 9 sites for ~5 months. In March 2016, 800 ~3 cm long mussels were collected from Yoakam Pt (Site 3, Figure 1). Mussels were marked with Floy Tags® attached with Splash Zone Epoxy® and by filing a groove (<1 mm) into the posterior shell edge (Dehnel 1956, Seed 1976, Blanchette et al. 2007a). Length from the umbo to the groove and from the umbo to the top of the shell at the posterior end was measured to 0.1 mm with Vernier calipers. Weight, including epoxy and tag, was measured to the nearest gram. If tags were lost, shell growth, but not weight could be determined. Five days after collection, 80 mussels were transplanted to each site at 1.4 ± 0.1 m above MLLW. Animals were placed within cages made from PVC tubes covered with 1 cm plastic mesh. Cages were held to the rock by Splash Zone Epoxy®. Average spacing between cages was ~10 m. This design allowed mussels to move beneath the mesh during high tide, encouraging byssal thread attachment. After four weeks, mussels had attached to the rock

and cages were removed. In September 2016, after ~5 months, mussels were collected and mass, length, height, and width were measured. Changes in size (dependent variable) were correlated with both surfzone width and phytoplankton cell concentrations (independent variables).

We estimated the size-specific reproductive output of *B. glandula* populations at the sites. In July 2016 at each site a 20 m transect was laid parallel to the water and inside the barnacle zone at 1.7 ± 0.3 m above MLLW. Four 100 cm² quadrats were randomly placed along the transect from which all barnacles were collected. Individuals from these samples were used to determine shell volume, reproductive state, and egg lamellae AFDW. Barnacles from dense populations tended to have cylindrical shells while those from lower density populations were more conical (Figure 4). For cylindrical shells, shell length and basal diameter (BD) were measured and for conical shells opercular diameter (OD) was also measured. Volume was calculated depending on whether an individual was conical or cylindrical. Egg lamellae were dissected from at least 25 randomly selected individuals with BD > 2 mm (smaller individuals were not reproductive). Egg lamellae were dried at 70°C for 48 hr., weighed, dried at 450°C overnight, and then weighed to obtain the AFDW. These samples provided egg lamellae AFDW and percentage of the population that were reproductive. At eight, randomly placed 100 cm² quadrats along each transect, a picture was taken using a Canon EOS-7D camera with a 50 mm macro lens. A ruler in the photograph provided scale. These photographs were used to determine density and percent cover of barnacles following techniques used by Shanks et al. (Shanks et al. 2017a). Average egg lamellae mass and shell volume (dependent variables) were regressed against surfzone width and phytoplankton cell concentrations (independent variables). Average egg lamellae mass per barnacle was multiplied by population density and the percentage of the individuals that were reproductive to obtain the average total egg lamellae AFDW/100 cm² at each site. This was used as an index of potential population reproductive

output. The potential reproductive output (dependent variable) was regressed against both surfzone width and phytoplankton concentrations (independent variables).

RESULTS

There were 9-10 dates (5/1994, 8/2000, 6/2003, 4/2004, 8/2005, 6/2007, 11/2011, 8/2012, 5/2013, 5/2015) with Google Earth images in which surfzone width could be accurately measured. Images were available from high and low tides and a range of sea states. The majority of the images were from spring and summer so obtaining average seasonal surfzone widths was not possible; average surfzone width was calculated using all dates. The widths of the surfzone varied depending on the conditions at the time the photographs were taken (Figure 2), but surfzone width of narrow more reflective surfzone consistently stayed below 50 m while wider more dissipative surf zones remained wider than 50 m. Shanks et al. (2017a) found that bathymetric rip currents were absent at surf zone narrower than 50 m. Bastendorff N., Bastendorff S., Yoakam Pt., and Lighthouse (Figure 1; Appendix S1 Table S1) were characterized by wide surf zones (average width $235 \pm \text{SE } 26$ m) with bathymetric rip currents; these sites were considered more dissipative. At Mussel Pt., Shore Acres, Pack Trail, Cape Arago, and Middle Cove surf zones were narrow (average width 21 ± 4 m) and there were no bathymetric rip currents; these sites were considered more reflective.

During May-August 2016, phytoplankton cell concentrations within the surf zone were $\sim 14\times$ higher at more dissipative than reflective shores (Figure 2). During September-December 2016, phytoplankton concentrations at all shores decreased dramatically, but concentrations were still $\sim 15\times$ higher at more dissipative shores. By January and through April 2017, cell concentrations dropped even lower with concentrations about $10\times$ lower than during the summer at all nine sites, however, concentrations within more reflective surf zones were still much lower than within more dissipative surf zones. Due to large week-to-week variation in cell concentrations at more dissipative

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sites, differences were not, however, significant during the winter months. Regressions between average surfzone width and average total phytoplankton surfzone concentrations from each sample period were significant and explain 89-94% of the variability (Figure 2). Surfzone Chl-*a* concentrations in more dissipative surf zones were around 6 µg/L in the spring and early summer, peaked to 8 µg/L in August and decreased during the remainder of the year to as low as 2 µg/L. At more reflective sites, spring/early summer concentrations were between 2 and 3 µg/L, peaked in August at around 4 µg/L, and dropped to 2 µg/L for the remainder of the study. Chl-*a* concentrations were ~2x higher at more dissipative than reflective shores in all seasons (Figure 2), but as concentrations in more dissipative surf zones fell through winter (December-April 2017), the significant difference between more dissipative and reflective surf zones disappeared. The regressions between seasonal Chl-*a* concentration and surfzone width were significant and explain 60-87% of the variability (Figure 2). Some diatom taxa are surfzone specialists and inhabit more dissipative surf zones (Lewin and Schaefer 1983). *Asterionellopsis* spp., a surfzone specialist, was present, however, it accounted for only ~7% of phytoplankton in more dissipative surf zones in May-August 2016, ~2% in September-December 2016, and was absent in January-April 2017. Four genera (*Chaetoceros* spp., *Pseudo-nitzschia* spp., *Thalassiosira* spp., and *Skeletonema* spp.), typical coastal phytoplankters, accounted for ~88% of the phytoplankton counted from May-August 2016, ~96% from September-December 2016, and ~90% from January-April 2017. These taxa were positively correlated with surfzone width from May-August (Supplement Figure 2); surfzone width explained 91, 87, 92, and 95% of the variability in the surfzone concentration of *Chaetoceros* spp., *Pseudo-nitzschia* spp., *Thalassiosira* spp., and *Skeletonema* spp., respectively.

On two days, phytoplankton populations were sampled concurrently seaward on the inner shelf and within the surfzone. The average distance from the offshore sample site to the breaker line was 0.5 ± 0.1 and 0.5 ± 0.04 km at dissipative and reflective sites, respectively, and the difference in offshore distance from the different types of surf zones was not significant ($F = 0.28$, $df = 1$, $p =$

0.602) (Figure 1). There was no alongshore variation in offshore phytoplankton concentrations between dissipative and reflective sites on either date ($F = 1.66$, $df = 3$, $p = 0.23$). On September 2 and 23, 2016 phytoplankton concentrations were ~5x and ~2x higher *inside* the surfzone at more dissipative shores and ~7x and ~3x higher *outside* the surfzone at more reflective shores, respectively (Figure 1). On September 2, phytoplankton concentrations were significantly different by site (e.g., reflective vs. dissipative) ($F_{(6, 42)} = 292.96$, $p < 0.0005$), location (e.g., in vs. seaward of the surf zone) ($F_{(1, 42)} = 100.652$, $p < 0.0005$), and there was a significant interaction effect ($F_{(6, 42)} = 167.789$, $p < 0.0005$). The Shapiro-Wilk test of normality revealed three of the seven sites had significantly different variances. On September 23, the effect of site and location on phytoplankton concentrations was significant for site ($F_{(6, 42)} = 66.461$, $p < 0.0005$), location ($F_{(1, 42)} = 126.946$, $p < 0.0005$), and there was a significant interaction effect ($F_{(6, 42)} = 47.574$, $p < 0.0005$). The Shapiro-Wilk test of normality revealed four of seven sites had significantly different variances. Surfzone phytoplankton concentrations were higher than in the offshore ocean at more dissipative sites while at reflective sites surfzone concentrations were lower than offshore.

Mussel density at more reflective shores was almost twice that at dissipative, but these mussels were generally smaller than mussels at more dissipative shores (Smirnov-Kolmogorov: $D(900) = 0.364$, $p < 0.0001$) (Figure 3). At sites with more reflective surf zones, on average 60% of mussels were smaller, non-reproductive individuals (40 to 50 mm size class) while at more dissipative surf zones only 24% of the mussel population was smaller, non-reproductive individuals. Average mussel gonad and body mass at more dissipative shores were ~6x and ~2x higher, respectively, than at more reflective shores (Figure 4 and 5). The population level potential reproductive output of just the 61-70 mm size class was 12x higher at more dissipative than reflective shores (Figure 5). Given that a larger percentage of the populations at more reflective sites were small, non-reproductive individuals than at the more dissipative sites, this estimate of the

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difference in population level reproductive output is conservative and under represents the true difference; if a sample of all the size classes were to be taken, and not just the 61-70 mm as was done in this study, the true difference would be larger. The regressions between average surfzone width and gonad mass, body mass, and population potential reproductive output were significant and explain 65, 58, and 56% of the variability, respectively (Appendix S1 Figure S2). Regressions between average phytoplankton concentration and average mussel gonad mass, mussel body mass, and the index of population level potential reproductive output were also significant and explain 80, 71, and 69% of the variability, respectively (Figure 5). On average, 47% of mussels survived at reflective sites compared to 18% at more dissipative sites. Mussels that did not “survive” were simply absent at the end of the experiment. Mussel shell growth did not vary significantly between the dissipative and reflective sites, however, growth as increase in weight was significantly different; mussels at more dissipative shores added ~3x more body mass than mussels at more reflective shores (Figure 5). The average mussel mass increase was positively correlated with surfzone width and phytoplankton concentrations (Appendix S1 Figure S2 and Figure S3, respectively) explaining 92% and 85% of the variability, respectively.

Average *Balanus glandula* shell volume was ~2x larger at more dissipative than reflective shores and was positively correlated with surfzone width and phytoplankton concentration (Appendix S1 Figure S3 and Figure S6, respectively), which explained 45 and 63% of the variability, respectively. Average AFDW of barnacle egg lamellae was ~3x larger at more dissipative than reflective shores and positively correlated with surfzone width and phytoplankton concentration (Appendix S1 Figure S3 and Figure S6, respectively), explaining 79 and 85% of the variability, respectively. Percent barnacle cover, percent reproductive, and density of barnacles with BD > 2mm were 6, 10, and 5x higher at more dissipative than more reflective shores, respectively (Appendix S1 Figure S3). At more reflective sites, only ~8 % of the population were reproductive while at more

dissipative sites 83% were. The population level potential reproductive output was ~13x higher at dissipative shores (Appendix S1 Figure S3). At more reflective sites, the average barnacle population level reproductive output as measured as AFDW of egg lamellae was only 0.004 g/100 cm² compared to 1.42 g/100 cm² at more dissipative sites. The regressions between average phytoplankton concentration and these dependent variables were significant and explain 83, 77, 92, and 96% of the variability, respectively (Figure 6). The regressions between average surfzone width and barnacle percent cover, density, percent reproductive, and population potential reproductive output were significant and explain 78, 73, 93, and 92% of the variability, respectively (Appendix S1 Figure S3).

DISCUSSION

Using Google Earth imagery, we successfully measured one of the key characteristics of surf zones, surfzone width (Shanks et al., 2017a, Shanks et al., 2017c). Surfzone width is primarily set by two variables, the wave climate and shore slope. By sampling closely spaced stations (ave spacing 0.88 km) with similar geographic orientation we controlled for wave climate. Shore slope, especially at rocky shores, changes slowly to very slowly (i.e., over geologic time scales), hence, due to the local slope of the shore, the surf zone associated with a shore will tend to remain fairly to very constant for extended periods.

We found that phytoplankton cell and Chl-*a* concentrations within surf zones were significantly higher at more dissipative than reflective shores, a pattern that persisted for eight months of a year-long, weekly sampling regime and was observed in an earlier study, which sampled most of the same sites (Shanks et al. 2017c). Two locations (Yoakam Pt., more dissipative and Mussel Pt., more reflective) were spaced only ~50 m apart (Figure 1 and Supplemental, Table 1) yet there was on average an order of magnitude higher phytoplankton concentration within the Yoakam Pt. dissipative surf zone. Concurrent offshore and onshore samples were taken on two days about three

weeks apart in September. At more dissipative shores, phytoplankton cell concentrations were significantly higher within the surfzone than offshore while the reverse was true at more reflective shores; this relationship between surfzone hydrodynamics of the relative concentration of phytoplankton in the surf zone compared to just offshore was also observed in Shanks et al. (Shanks et al. 2017b). Phytoplankton subsidies are freely exchanged at more dissipative shores while at more reflective shores the surf zone acts as a semi-permeable barrier limiting subsidies.

Phytoplankton subsidies from the coastal ocean increased from spring into summer. In August we observed an increase in both phytoplankton abundance and Chl-*a* concentrations, which was due to an increase in *Pseudo-nitzschia* spp.. Concentrations decreased through the fall and winter. During the spring, summer, and fall there were significant differences between surfzone phytoplankton cell concentrations at dissipative and reflective shores, but this significant difference vanished in winter. Variance at both reflective and dissipative sites increased during winter sampling, which could have led to the observed non-significant difference. Perhaps the higher variance in winter is due to an increase in wave energy caused by winter storms. A similar pattern was seen for Chl-*a* concentrations, but the significant difference between dissipative and reflective shores disappeared earlier in the year than for phytoplankton cell abundance.

Variation in mussel growth rates have been attributed to alongshore variations in upwelling strength and persistence leading to variation in phytoplankton subsidies to the shore (Menge et al. 1997a, Menge et al. 1997b, Menge et al. 2003, Phillips 2007). By sampling closely spaced stations around Cape Arago we attempted to control for variation in the concentration of phytoplankton in the coastal ocean and on the two dates on which we sampled the waters seaward of our sample sites there was no significant and little alongshore variation in phytoplankton concentration. In the

offshore samples, cell concentration varied by at most a factor of <2.5, but between the surfzone samples concentration varied by from 133 to >800 times (2 and 23 Sept., respectively). Reproductive output and growth of *Mytilus californianus* varied directly with both surfzone width and phytoplankton cell concentrations. Where phytoplankton subsidies were larger, i.e., more dissipative shores, mussel growth and gonad size were larger than at reflective shores where subsidies were much smaller; the magnitude of phytoplankton subsidies to the intertidal zone, as regulated by surfzone hydrodynamics, appears to be a determining factor in mussel growth and gonad development. At the completion of the 5-month growth rate experiment, more mussels remained (attached and alive) at more reflective shores. Mussel population densities were also higher at reflective shores albeit, small, non-reproductive mussels compared to dissipative mussel populations. We did not measure mussel recruitment, settlement, or settler survival at our sites so we can only speculate about these results. Overall, our index of reproductive potential and the percentage of mussels that were small and non-reproductive suggest that larval production at more dissipative shores is much higher than at reflective.

Barnacles at more dissipative shores were more cylindrical shaped, frequently tightly packed with secondary barnacles settling on the primary barnacle population (i.e., those attached to the rock), individuals were often easily dislodged, and percent cover was higher than at more reflective shores (Figure 4); these characteristics are typical of barnacles in dense populations (Bertness et al. 1998, Shanks et al. 2017a). Conversely, barnacles at more reflective shores were cone shaped and seldom tightly packed (Figure 4). New recruits settled on older individuals were rare. Variation in barnacle density due to surfzone hydrodynamics suggests variation in larval subsidies may also be due to surfzone hydrodynamics as, in fact, has been observed (Morgan et al. 2016, Morgan et al. 2017a, Morgan et al. 2017b, Shanks et al. 2017a). Shanks et al. (2017a) found that new-recruit barnacle densities, weekly recruitment and daily settlement were significantly higher at more

dissipative shores. Daily barnacle settlement was tracked at two of our study sites (Pack Trail, reflective and Bastendorff, dissipative) and daily settlement at Pack Trail was found to be orders of magnitude lower than at Bastendorff (Shanks et al. 2017a). Variation in food and larval subsidies is driven in part by surfzone hydrodynamics and both influence barnacle populations. *Balanus glandula* density (individuals with BD > 2mm), percent cover, individual volume, percentage of barnacles with egg lamellae, average egg lamellae mass per individual, and population reproductive output were all positively correlated with phytoplankton cell concentrations and these subsidies varied with surfzone hydrodynamics. Our index of potential barnacle population reproductive output was significantly higher at more dissipative shores. To place this in a physical context, Bastendorff S. is a ~400 m² rock platform densely populated by barnacles. This population of barnacles is subsidized by phytoplankton passing through and likely concentrated by a more dissipative surf zone and their index of population reproductive output was 1.36 g/100 cm². Cape Arago is typical of the more reflective sites with an index of population reproductive output of 0.006 g/100 cm² (Cape Arago, Site #9 in Figure 1). The difference between these sites in our index of population reproductive output suggests that the barnacle population on the tiny rock platform at Bastendorff produces about 7 times more larvae than the barnacle population in the entire intertidal zone at the tip of Cape Arago (Figure 7).

Bottom-up subsidies from the coastal ocean affect the structure of rocky shore communities (Menge et al. 1997a, Menge et al. 1997b, Menge et al. 2003). Research on surfzone hydrodynamics has shown that the surf zone itself is fundamental in actually regulating these coastal bottom-up subsidies to both rocky and sandy shore communities (Morgan et al. 2016, Morgan et al. 2017b, Shanks et al. 2017a, Shanks et al. 2017b, Shanks et al. 2017c); variation in population structure, reproductive output and growth rates of intertidal mussels and barnacles is due to larval and phytoplankton subsidies from the coastal ocean, but the magnitude of these subsidies varies with surfzone hydrodynamics.

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FIGURE LEGENDS

Figure 1. Map) Locations of surf zones sampled around Cape Arago, Oregon. The average distance between sites was 0.83 km and the distance between the northernmost and southernmost site was 7 km. Asterisks represent locations of cruise samples taken outside the surf zone on September 2 and 23, 2016. See Supplemental Table 1 for coordinates of onshore and offshore locations. Bastendorff N. (1), Bastendorff S. (2), Yoakam Pt. (3), Mussel Pt. (4), Lighthouse (5), Shore Acres (6), Pack Trail (7), Cape Arago (8), Middle Cove (MD). A) Average (\pm SE) surfzone widths from Google Earth images take between May 1994-May 2015 (n=9-10 pictures were used depending on image quality). Sites ordered from north to south. Dissipative and reflective surf zones are indicated by shaded and open bars, respectively. Surf zones narrower than 50 m did not contain bathymetric rip currents. B and C) Average (\pm SE) phytoplankton concentrations on (B) September 2, 2016 and (C) 23, 2016 from samples taken offshore (unshaded bars) and within the surf zones (shaded bars) at eight of the nine sample sites (n=3 phytoplankton samples). Plus symbols indicate a significant difference ($p < 0.05$, t-test) between offshore and surf zone phytoplankton concentrations. Middle Cove could not be sampled on September 23.

Figure 2. (A) Average (\pm SE) surfzone phytoplankton cell and (B) chlorophyll-a concentrations in sampled surf zones, from May 2016-April 2017. Samples were taken approximately weekly. Bastendorff N., Bastendorff S., Yoakam Pt., and Lighthouse, sites with wide surf zone and bathymetric rip currents, have been grouped as more dissipative shores (solid line with light grey \pm SE confidence bands) while Mussel Pt., Shore Acres, Pack Trail, Cape Arago, Middle Cove were sites with narrow surf zones and no bathymetric rip currents, have been grouped as more reflective surf zones (dotted line with dark grey \pm SE confidence bands). (C, E, G) Average (\pm SE) surfzone width

plotted against average phytoplankton cell concentrations and (D, F, H) average surfzone chl-*a* concentrations from May 2016-August 2016.

Figure 3. (A) Size distributions of *Mytilus californianus* sampled in July 2016. Sites are arranged from widest surf zone (top left) to narrowest (bottom right). Shaded and open bars indicate more dissipative and reflective shores, respectively. (B) Size distribution for sites grouped into more dissipative and reflective surf zones (shaded and open bars, respectively).

Figure 4. Photographs of typical barnacle populations at (A) dissipative and (B) reflective shores. (C) Mantel and gonads of 61-70 mm mussels from a dissipative (left) and reflective (right) shore.

Figure 5. Average (\pm SE) surfzone phytoplankton cell concentrations plotted against 61-70 mm sized *Mytilus californianus* average (A) AFDW gonad and (B) AFDW body per individual and (C) average *M. californianus* population reproductive potential AFDW gonad (g/m^2) of this size class of the populations. (D) Average surfzone phytoplankton cell concentration plotted against average growth (mass change, g) after five months (March to September 2016) of out-planted *Mytilus californianus* individuals.

Figure 6. Surfzone phytoplankton cell concentration plotted against *Balanus glandula* (A) percent cover, (B) density of adults (BD > 2 mm), (C) shell volume per individual, (D) AFDW of egg lamellae per individual, (E) average percentage of adults with egg lamellae, (F) and average population reproductive potential (average total AFDW of egg lamellae/100 cm^2). Values are averages (\pm SE).

Figure 7. Google Earth image of the intertidal zone at the tip of Cape Arago, Oregon (Site #8 in Figure 1). The white box is $\sim 400 \text{ m}^2$ and represents the area of the rock platform sampled at Bastendorff S (Site #2 in Figure 1). The total area of the intertidal zone at Cape Arago is $\sim 13,000 \text{ m}^2$. Bastendorff S was located within a dissipative surf zone and the barnacle population was typical of the dissipative sites sampled; the population was dense ($157/100 \text{ cm}^2$), a large percentage were reproductive (88%) and potential reproductive output was high ($1.36\text{g}/100 \text{ cm}^2$). Cape Arago is associated with a more reflective surf zone and the barnacle population was similar to those sampled at other more reflective sites; the population was sparse ($13/100 \text{ cm}^2$), a small percentage were reproductive (25%) and potential reproductive output was much lower ($0.006 \text{ g}/100 \text{ cm}^2$). Our index of potential reproductive output suggests that larval production by barnacles at Bastendorff S, a population that would occupy the white box in the figure, would produce 7 times more larvae than the entire population occupying the Cape Arago intertidal zone.

FIGURES

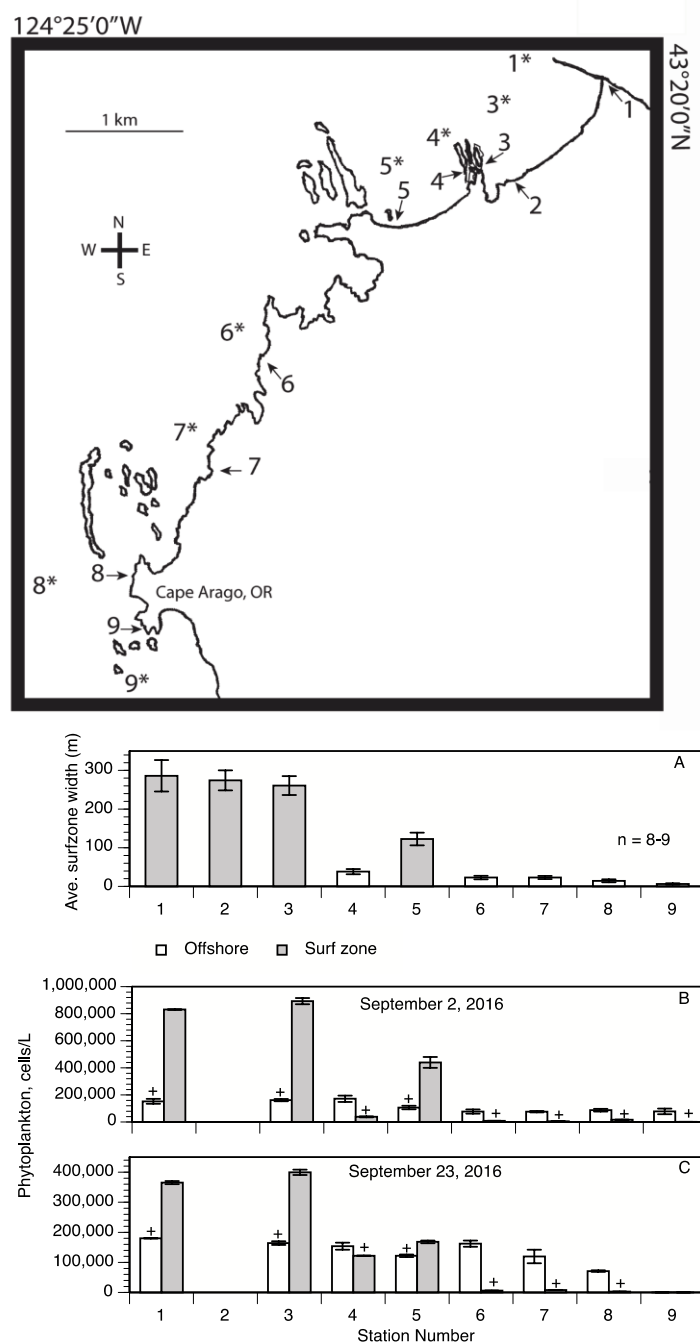


Figure 1.

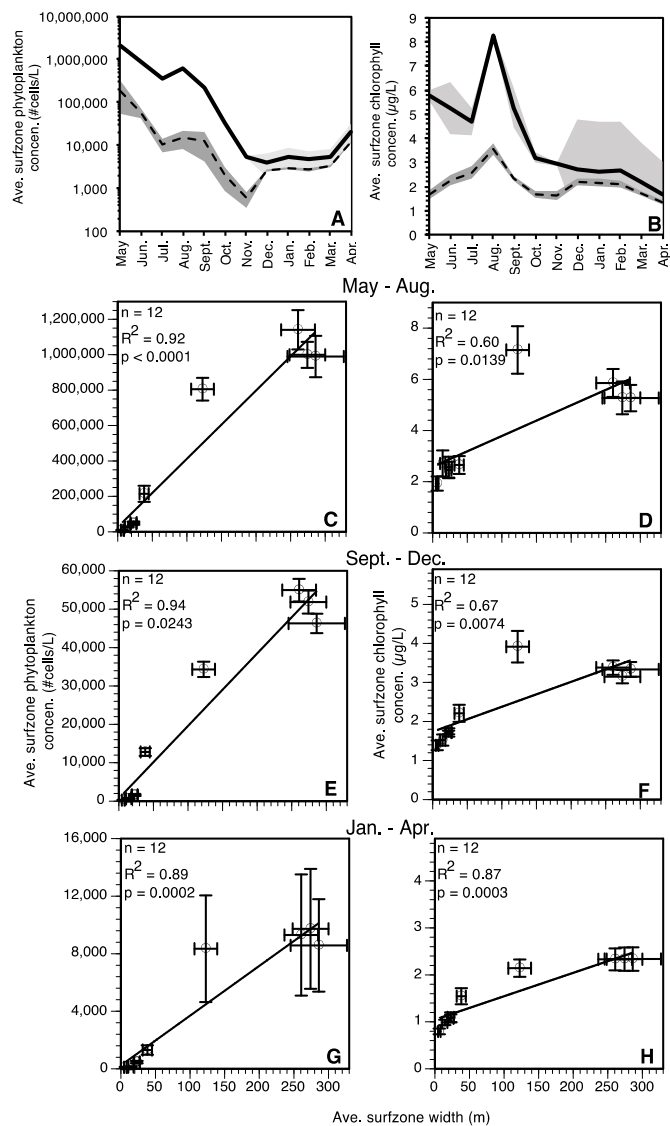


Figure 2

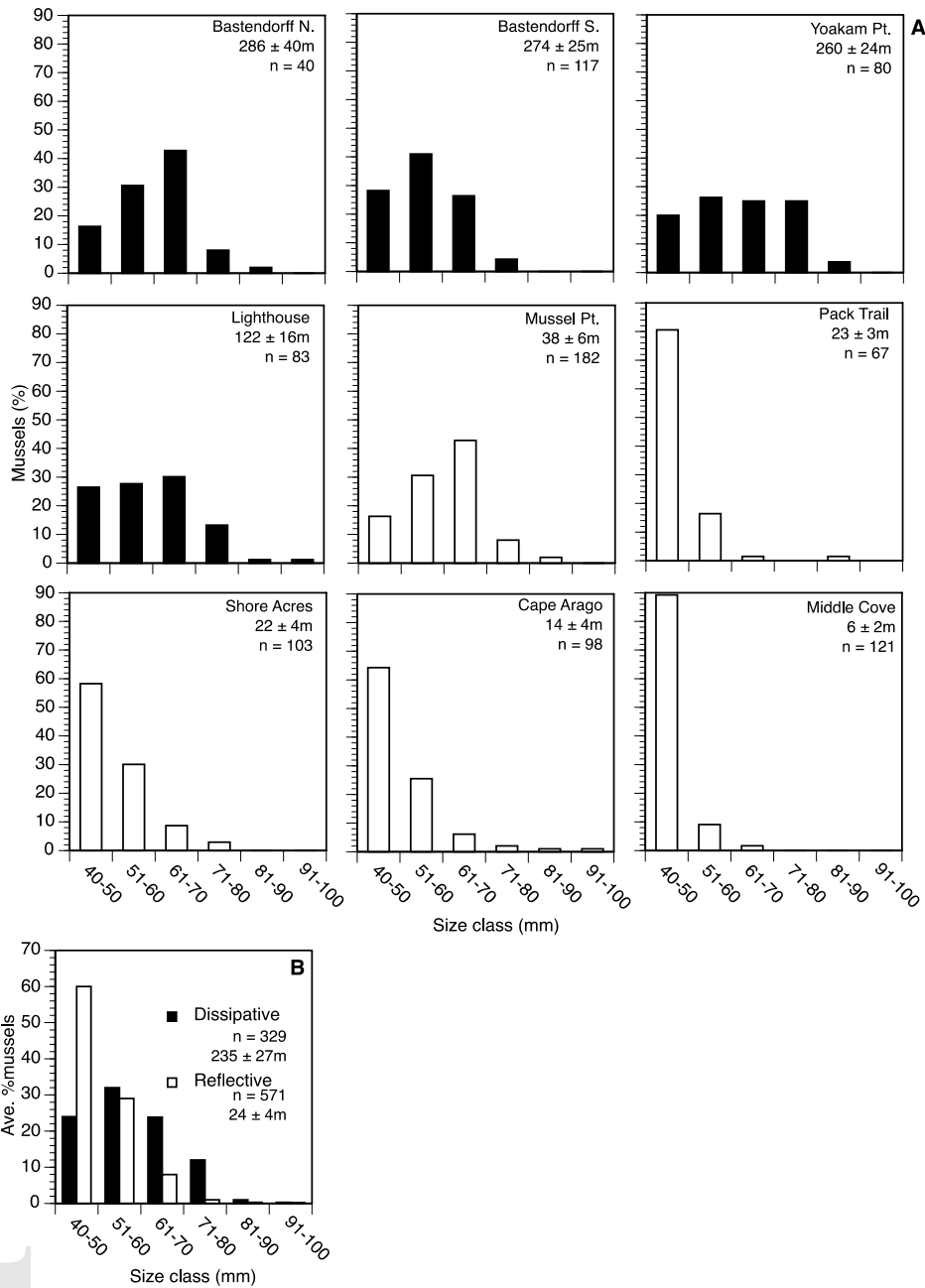


Figure 3

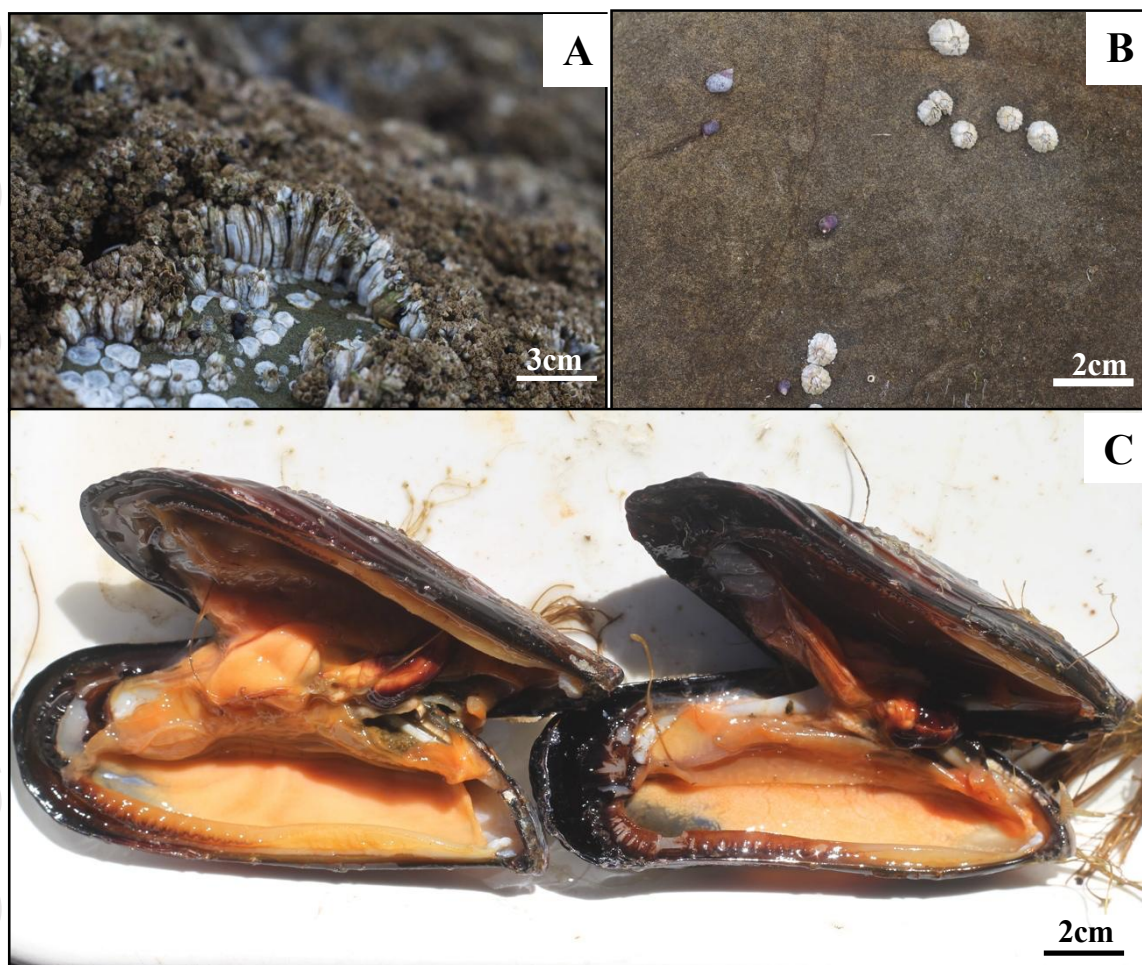


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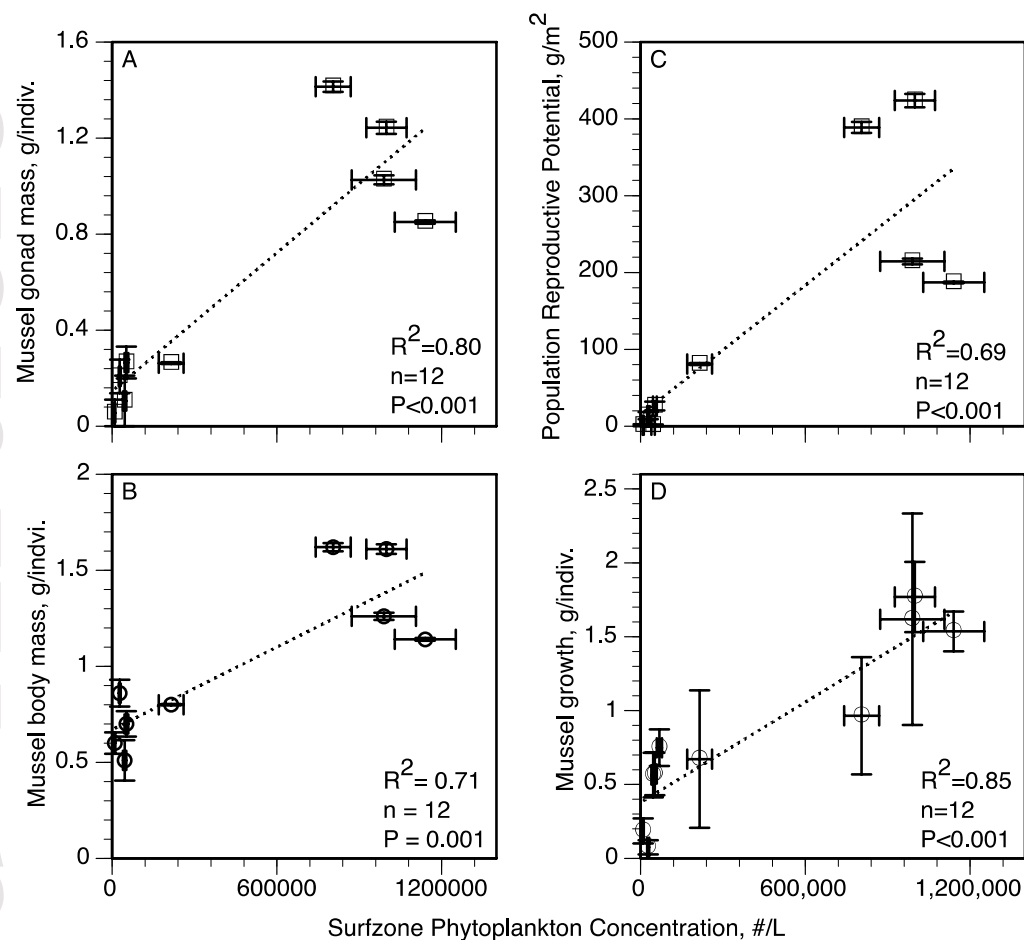


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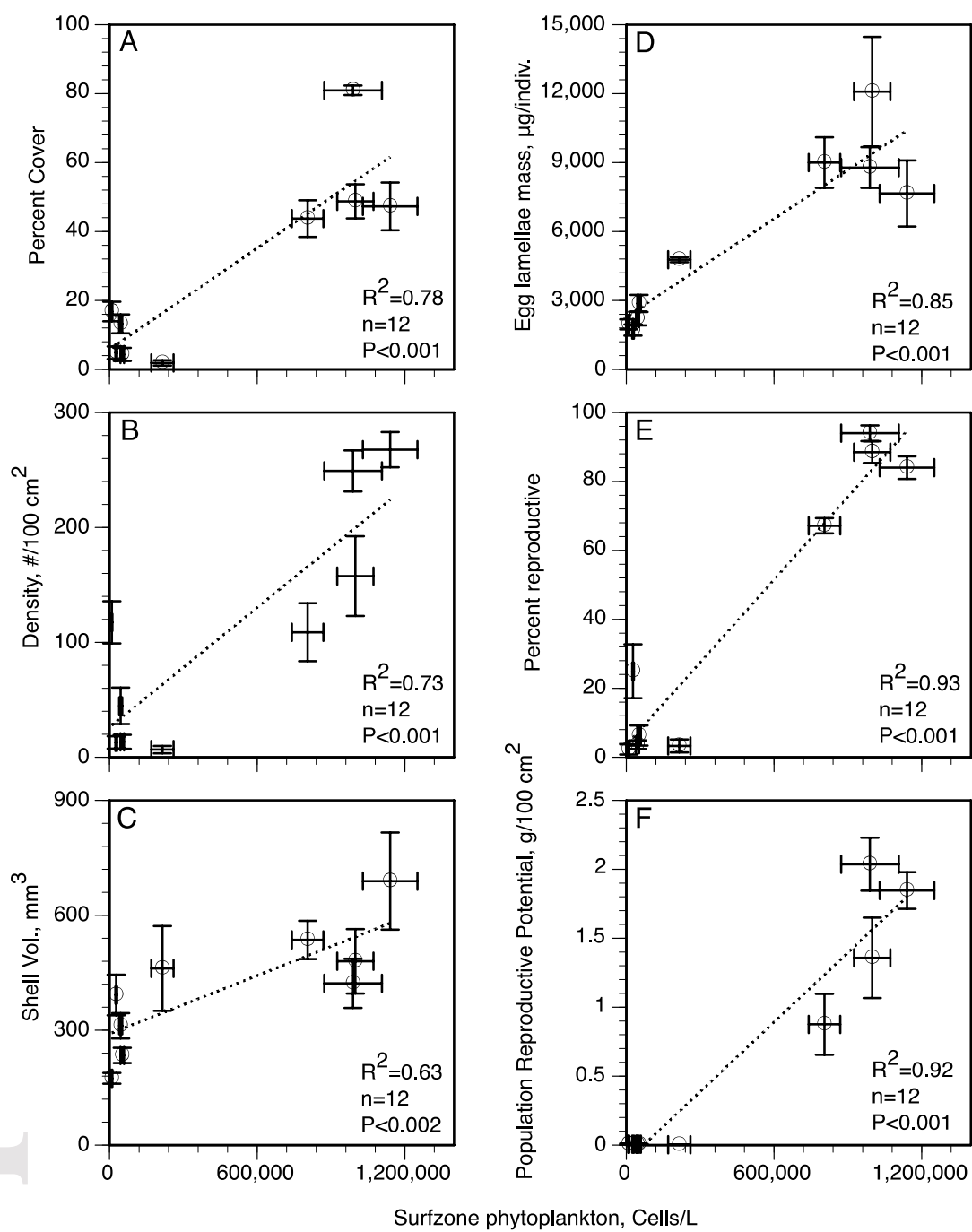


Figure 6.

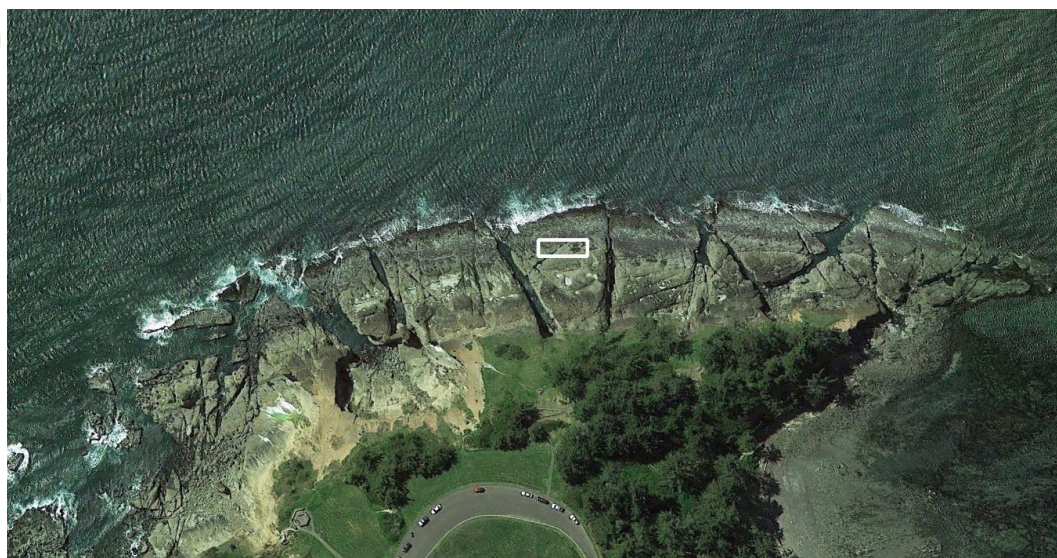


Figure 7.