





Reports

Ecology, 102(9), 2021, e03455
© 2021 by the Ecological Society of America

Differential impacts of alternate primary producers on carbon cycling

KHASHIFF K. MIRANDA ^{1,5} BROOKE L. WEIGEL ² SOPHIE J. MCCOY ³ AND CATHERINE A. PFISTER ^{2,4}

¹The College, University of Chicago, 1101 E 58th, Chicago, Illinois 60637, USA

²Committee on Evolutionary Biology, University of Chicago, 1025 E. 57th Street, Chicago, Illinois 60637, USA

³Department of Biological Sciences, Florida State University, 319 Stadium Drive, Tallahassee, Florida 32306, USA

⁴Department of Ecology & Evolution, University of Chicago, 1101 East 57th Street, Chicago, Illinois 60637, USA

Citation: Miranda, K. K., B. L. Weigel, S. J. McCoy, and C. A. Pfister. 2021. Differential impacts of alternate primary producers on carbon cycling. *Ecology* 102(9):e03455. 10.1002/ecy.3455

Abstract. Disturbance impacts the spatial distribution of primary producers, which can have cascading effects on ecosystem function. The lower-intertidal zone on the rocky shores of the Pacific Northwest is one such place where wave energy creates a mosaic-like distribution between two assemblages: surfgrass (*Phyllospadix scouleri*) meadows and macroalgal forests dominated by kelp. We simulated wave disturbance by experimentally removing patches of surfgrass monocultures, resulting in a macroalgal assemblage with increased diversity, biomass, and net primary productivity in the following year. Although surfgrass had a higher C:N compared to macroalgal assemblages, macroalgal assemblages achieved a higher biomass, fixed carbon at a faster rate, and released more dissolved organic carbon (DOC) during photosynthesis. Thus, despite similar standing amounts of carbon, macroalgal assemblages have increased carbon turnover—from fixation to DOC release. Comparative photophysiology indicated that surfgrasses have a competitive advantage over other macrophytes at low light levels, allowing them to persist when disturbance is reduced. Unexpectedly, disturbance in this system increased the potential for carbon sequestration when surfgrass monocultures were replaced by diverse macroalgae.

Key words: carbon sequestration; dissolved organic carbon; disturbance; ecosystem function; kelp forest; macroalgae; mosaic; *Phyllospadix scouleri*.

INTRODUCTION

Across ecosystems, photosynthetic primary producers are impacted by disturbance, including both physical disturbance (Sousa 1979, Power and Stewart 1987) and biotic disturbance in the form of herbivory (Dublin et al. 1990, Staver et al. 2011). Although there are key distinctions between biological and physical disturbance, including a lack of system feedbacks in the latter (Wootton et al. 2009), both types of disturbance can determine local species diversity (Connell 1978) and productivity (Reed et al. 2011, Tait and Schiel 2011), and can result in a patchy mosaic of distinct communities (Staver et al. 2011). Understanding the consequences of different primary producer assemblages is important, as global change has altered physical (e.g., heat waves) and

biological (e.g., grazer abundance) disturbances that favor distinct primary producers (Filbee-Dexter and Wernberg 2018, Carnell and Keough 2020). In this study, we simulated disturbance to quantify the ecosystem consequences of distinct assemblages of primary producers on rocky shores.

In aquatic ecosystems, hydrologic disturbances mediate autotrophic regime shifts in streams (Power and Stewart 1987) and in coral reefs (Jantzen et al. 2013). Menge et al. (2005) have suggested that wave disturbance controls the dominance of surfgrasses and macroalgal assemblages on marine rocky shores, where surfgrass dominate in wave-sheltered environments of the lower intertidal and canopy-forming macroalgae dominate in wave-exposed areas. In removal experiments by Turner (1983) and Stewart (1989), surfgrass took 3–4 yr to recover from disturbance through clonal growth, at which time they displaced macroalgal forests.

We investigated mosaics of phototrophs on rocky intertidal shores of the northeast Pacific, where surfgrass

Manuscript received 25 July 2020; revised 11 March 2021; accepted 2 June 2021. Corresponding Editor: Sergio A. Navarrete.

⁵E-mail: khashiffm@uchicago.edu

and macroalgae alternate in dominance over scales of one to tens of square meters. The marine angiosperm *Phyllospadix scouleri* (surfgrass) reproduces asexually and sexually, though it is slow to establish new meadow colonies through seed dispersal (Shelton 2010). Once surfgrass seedlings germinate, their clonal growth establishes a mat of rhizomes resulting in competitive dominance and a near monoculture in the lower intertidal (Menge et al. 2005). Though fast growing and productive (Shelton 2010), surfgrass colonies are susceptible to wave disturbance that dislodge them from rock substratum. Macroalgae similarly exhibit high growth rates (Mann 1973) and can attain a mass of 86 kg/m² annually (Paine 2002) in the mosaic areas we study here. Although the transition between both components of this mosaic have been noted and studied previously (Turner 1983, Menge et al. 2005, Shelton 2010), the photosynthetic potential and carbon and nitrogen dynamics of each component remains relatively unknown.

We evaluated how distinct phototroph assemblages dominated by surfgrass or macroalgae contributed to carbon dynamics in mosaics generated by experimental disturbances. Our experimental removal of patches of surfgrass resulted in rapid colonization by a species-rich assemblage of macroalgae. We show that although both vegetation states had an equivalent standing carbon content, macroalgal assemblages cycled carbon more rapidly, with greater photosynthetic rates, and a greater release of dissolved organic carbon (DOC) than equivalent plots of surfgrass. We tested a mechanism of dominance for surfgrass quantifying the photosynthetic potential of each primary producer species using PAM fluorometry. Surfgrasses have a competitive advantage at low irradiance levels, while macroalgae have higher maximum photosynthetic rates, providing a mechanism where each can dominate in different light environments.

METHODS

We experimentally removed 1-m² areas of surfgrass to simulate natural disturbance at a north-facing set of rocky benches in the intertidal zone on Tatoosh Island, Washington, United States (48.32° N, 124.74° W) referred to as Hedophyllum Cove (McCoy and Pfister 2014). The lower intertidal zone in this area contains a diverse set of phototrophs that are controlled by competitive interactions, wave disturbance, and herbivory (Paine 1984, 2002, Leigh et al. 1987, Wootton 1995, McCoy and Pfister 2014). Monocultures of surfgrass, spanning tens of meters, are interspersed with a diverse assemblage of kelp. In this area, we compared the nitrogen content, productivity, and carbon release of surfgrass patches to that of colonizing macroalgal stands following the removal of surfgrass in four 1 × 1 m plots. Four plots of identical dimensions where surfgrass was left intact served as control plots. Productivity dynamics of control (surfgrass) and removal (macroalgal assemblage) plots were compared after 2 months and 1 yr postremoval. The

removals occurred on 6 June 2016 along a rock bench at a tide height of −0.3 MLLW (mean lower low water). Upon removal, we recorded the proportional cover and wet mass of surfgrass in each plot. We assessed abundance as the proportional cover of kelp species on all control and removal plots after 2 months (2 August 2016) and 1 yr (21–23 July 2017) postremoval. After 1 yr, we harvested and quantified biomass from all eight plots to compare phototroph composition, biomass accumulation, and tissue carbon:nitrogen (C:N) content between surfgrass-dominated and macroalgal-dominated plots.

We compared the carbon dynamics of each phototroph assemblage by measuring (1) net primary production (NPP) of each species via oxygen evolution, (2) DOC release by surfgrass and macroalgal tissues, and (3) photosynthesis versus irradiance curves for the dominant species in all plots using pulse amplitude modulated (PAM) fluorometry in situ. NPP and DOC release per unit dry mass were quantified in 1-L chambers, and rates were extrapolated to the plot scale using the biomass from each treatment and control plot. We used the oxygen evolution method to determine carbon fixation rates, and DOC release was simultaneously quantified using changes in DOC concentration over time. We estimated total carbon contributions by relating carbon fixation rates to the C and N content of the phototrophs in each plot. Finally, we estimated ETR_{max} (maximum electron transport rate) and α (photosynthetic efficiency at low light) through PAM fluorometry to test the responses of surfgrass versus multiple species of macroalgae to differing light environments, a possible mechanism to maintain an intertidal mosaic. Methods are described in detail in Appendix S1.

RESULTS

Changes to species diversity and biomass over time

One year after the experimental removal of surfgrass, macroalgae covered the plots (Fig. 1), increasing the community diversity (Shannon–Wiener index) over that of control plots (Fig. 2a), and control plots remained dominated by surfgrass (Fig. 1a vs. 1b). Macroalgae colonized the newly exposed rock only 2 months after our removal of surfgrass. The kelp species *Laminaria setchellii*, *Nereocystis luetkeana*, *Alaria marginata*, and the green alga *Ulva* spp. were the first colonizers. One year later, surfgrass remained absent from the removal plots, which were dominated by the kelp *A. marginata* (48% cover), *L. setchellii* (11%), *N. luetkeana* (5%), and *Pleurophyucus gardneri* (1.5%), along with crustose coralline algae, articulated coralline algae, and foliose red algae (*Odonthalia floccosa*, *Neorhodomela larix*, *Calophyllum* spp., *Hymenaea* spp., *Mazella splendens*, *Chondracanthus exasperatus*; Fig. 1c). Although coralline and red algae contributed to proportional cover, kelp species (order *Laminariales*) made up almost 100% of the biomass 1 yr after surfgrass was removed (Fig. 1d).

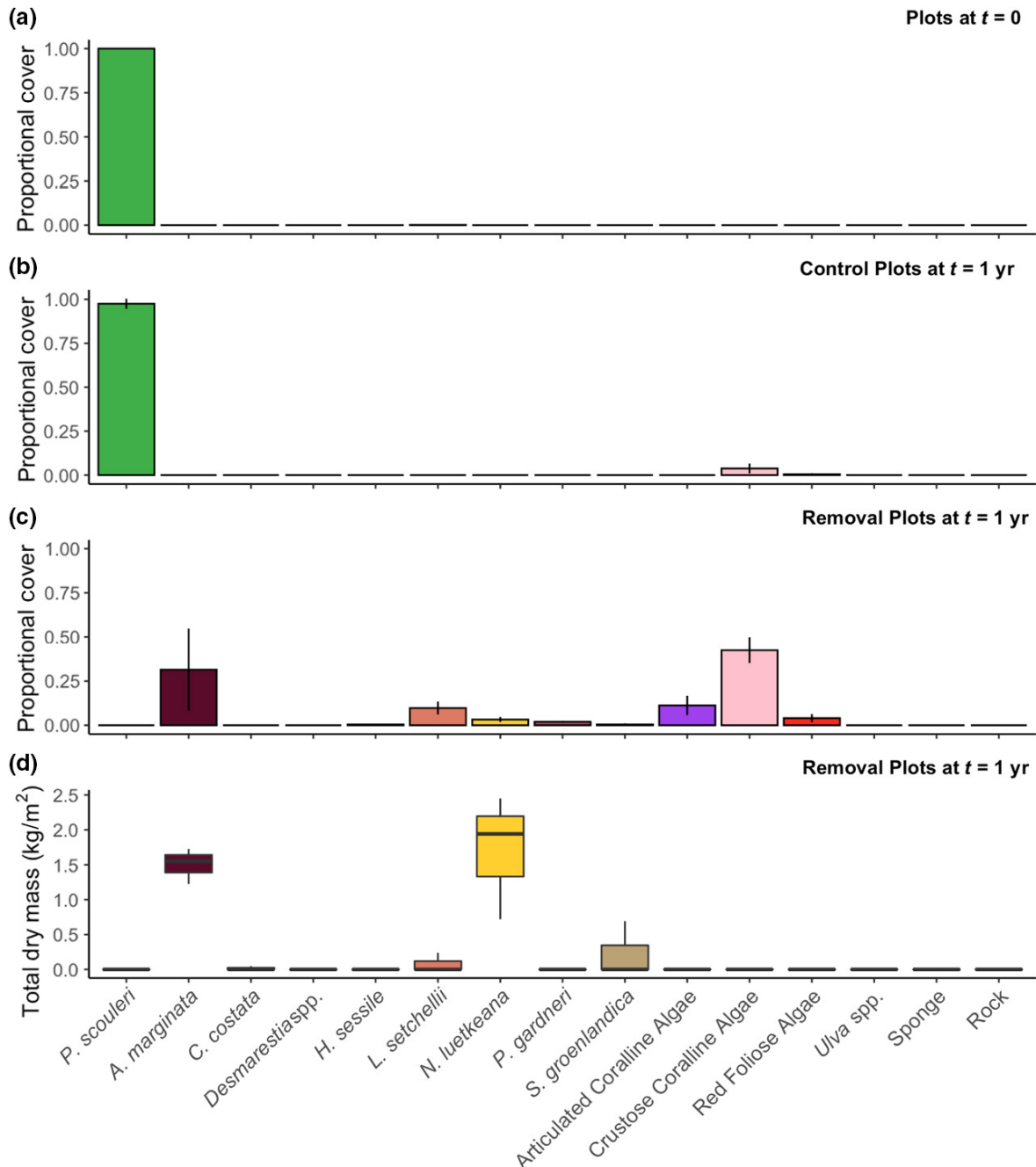


FIG. 1. Species abundance as proportional cover. (a) At $t = 0$, plots were surfgrass monocultures. After 1 yr, (b) control plots remained a surfgrass monoculture, and (c) removal plots were dominated by red algae and kelp. (d) The total dry mass (kg/m^2) in removal plots was composed primarily by the kelp species *Nereocystis luetkeana*, *Alaria marginata*, *Laminaria setchellii*, and *Saccharina groenlandica*, despite the high proportional cover of coralline algal species. Standard deviations are represented by error bars.

Productivity and carbon dynamics

After 1 yr, the surfgrass removal plots transitioned to a species-rich assemblage of macroalgae (Fig. 1c), which had a greater wet biomass and fixed carbon at a

faster rate than the surfgrass monocultures in control plots (Fig. 2c, g). Surfgrass removal increased primary producer diversity and richness (Shannon–Wiener index; Fig. 2a, b), and nearly doubled total plot wet mass through the rapid biomass

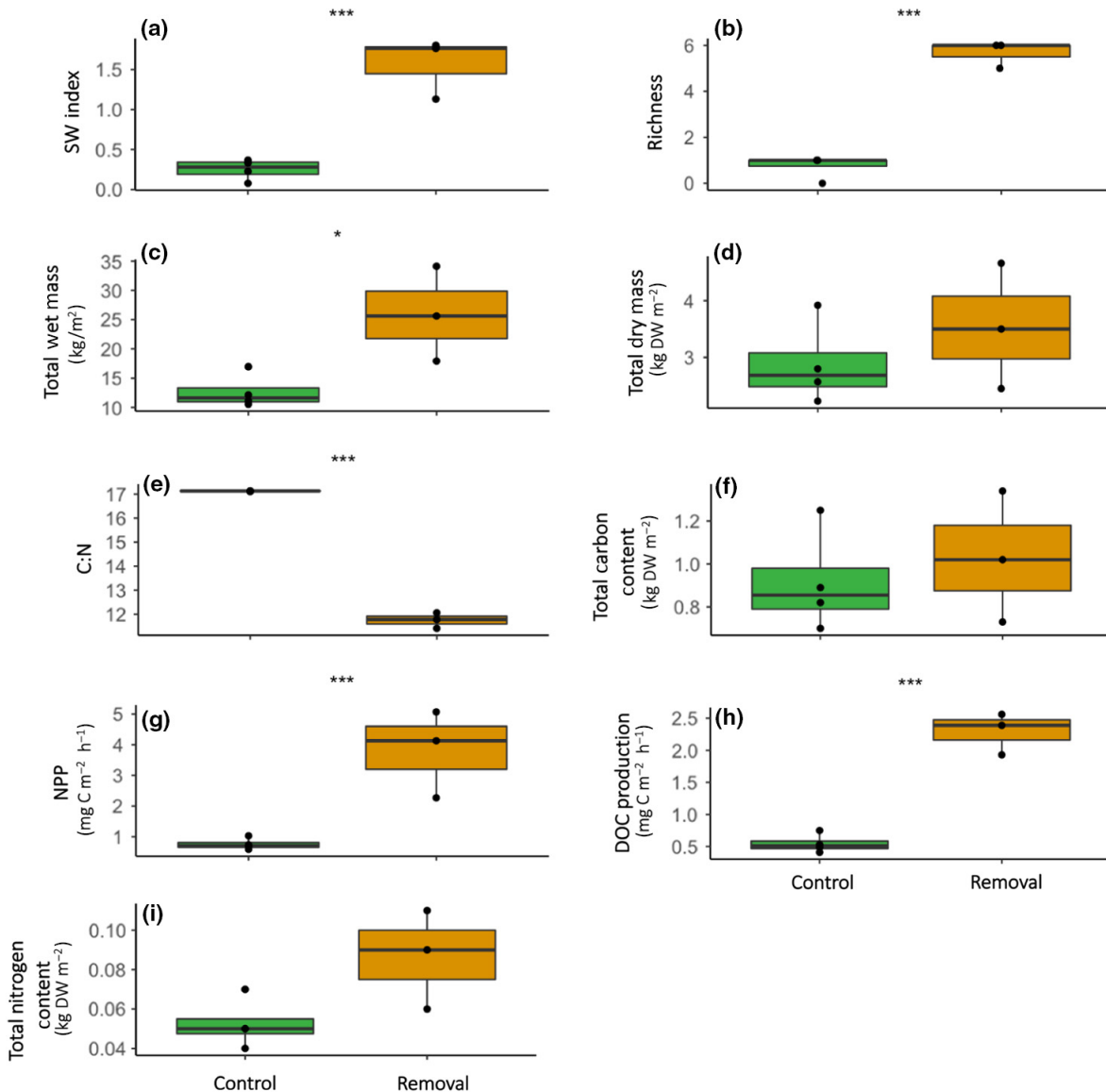


FIG. 2. A comparison of control (surfgrass monoculture) and removal plots (macroalgal assemblage) 1 yr after experimental surfgrass removal. (a) Shannon–Wiener (SW) diversity index was greater in removal plots; (b) algal species richness increased post-removal; (c) wet mass (kg/m²) was greater in the removal plots; (d) dry mass (kg/m²) across plots did not differ significantly; (e) C:N ratio was lower in the removal plots; (f) total carbon content (kg dry weight (DW)/m²) of the removal treatment did not significantly differ from the controls; (g), (h) net primary production (mg C h⁻¹ m⁻²) and dissolved oxygen concentration (DOC) production (mg DOC h⁻¹ m⁻²) rates were both greater in the removal plots; (i) total nitrogen content (kg DW/m²) was greater in removal plots. Asterisks at the top of each graph indicate significance level (**P* < 0.05, ***P* < 0.01, ****P* < 0.005); statistical tests in Table 1.

production of macroalgae over the first year (Fig. 2c; $t = 3.467$, $df = 5$, $P = 0.018$). NPP rates in the kelp-dominated removal plots were four times those in the control plots when we converted phototroph mass-specific oxygen production measurements conducted in chambers to plot-level productivity (Fig. 2g; $t = 5.887$, $df = 5$, $P = 0.002$). Further, the DOC release rate was 3.2 times greater for macroalgal-dominated plots compared to surfgrass monocultures (Fig. 2h; $t = 10.35$, $df = 5$, $P < 0.001$). Despite higher production rates

and greater DOC release of macroalgae, the higher C:N of surfgrass (Fig. 2e, $t = 27.7$, $df = 5$, $P < 0.001$) led to an equivalent dry mass (Fig. 2d, $t = -0.929$, $df = 5$, $P = 0.396$) and carbon content per unit area across treatments (Fig. 2f, $t = -0.553$, $df = 5$, $P = 0.604$). In addition to the greater accumulated biomass and NPP in macroalgal-dominated removal plots, the total nitrogen content was also greater in macroalgal plots than in surfgrass plots (Fig. 2i, $t = -2.402$, $df = 5$, $P = 0.061$).

Photophysiology comparisons between macroalgal assemblages and surfgrass

Physiological measurements of photosynthesis conducted using PAM fluorometry revealed that surfgrass had a significantly lower ETR_{max} (Fig. 3a; one-way ANOVA followed by Tukey tests) compared to kelp species, with the exception of *N. luetkeana* and *P. gardneri*, indicating that surfgrass have a lower maximum photosynthetic capacity compared to most kelp species. However, surfgrass had a higher α (Fig. 3b, one-way ANOVA and Tukey tests) and thus greater photosynthetic efficiency at low light levels than all kelp species (significantly greater α when compared with *A. marginata*, *C. costata*, and *H. sessile*).

DISCUSSION

Species composition

The disturbance of surfgrass monocultures enabled colonization by a diverse macroalgal assemblage, which increased the species richness of primary producers within a plot sevenfold. After 1 yr, removal plots were colonized by a kelp assemblage, with an understory of encrusting and turf-building algae. The complex layering of macroalgal assemblages is in stark contrast to the densely packed structure of surfgrass meadows extending from the rhizome through the canopy, allowing little niche space for co-occurring phototroph species.

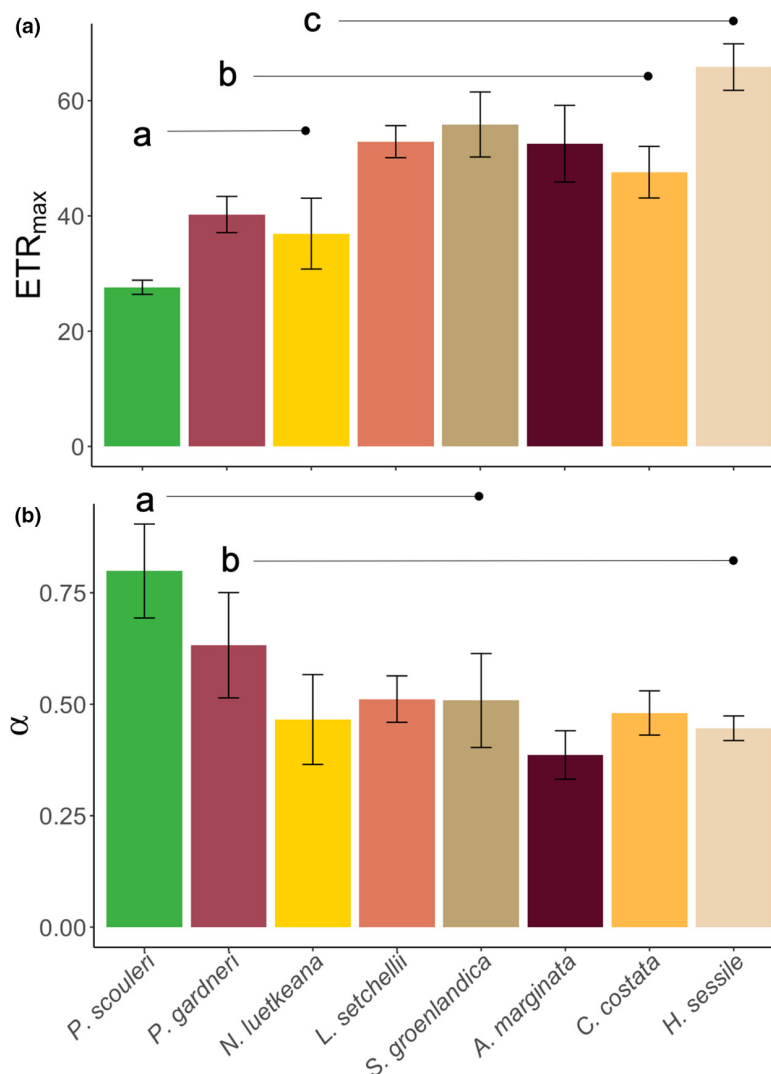


FIG. 3. Species-specific photophysiology results. (a) The maximum electron transport rate (ETR_{max} , \pm SE) for surfgrass had a significantly lower mean than all kelp species ($F_{7,88} = 9.483$, $P < 0.001$ and Tukey tests) while (b) also exhibiting the greatest α value ($F_{7,88} = 3.097$, $P < 0.01$ and Tukey tests), which is the slope indicating the increase in electron transport rate at low irradiance. Bars of the same letter indicate species were statistically indistinguishable with Tukey's honestly significant difference.

Implications for higher trophic levels

Primary producer biomass becomes available to the food web through herbivory and detrital pathways (Enríquez et al. 1993). The newly recruited macroalgal assemblage exhibited lower C:N ratios than surfgrass, providing a more nutritious target for herbivores. The detrital pathway is likely also enhanced in a macroalgal community as greater nitrogen content yields greater tissue quality and more efficient recycling (Zou et al. 2016). Macroalgal detrital pathways are also economically relevant to coastal fisheries, contributing an estimated 65–88% to salmon fry diet (Romanuk and Levings 2005). Further, we found that kelp assemblages released significantly more DOC than surfgrass, likely entering a bacterial-based food web.

Both seagrasses and macroalgae are ecosystem engineers that may impact higher trophic levels through habitat modification. Along rocky shores in the north Pacific, surfgrass enhances productivity and niche availability through this mosaic structure. By constructing a soft mat of rhizomes on an otherwise hard substrate, surfgrass meadows become refugia for invertebrate species that are unable to withstand the force of high wave energy (Moulton and Hacker 2011); with 70% of the invertebrate community in surfgrass rhizomes composed of scavengers, deposit feeders and suspension feeders that contribute to the detrital energy pathway in the food web. Kelp holdfasts also provision invertebrate refugia (Christie et al. 2003), though perhaps at a smaller scale. Here, we found that disturbance resulted in higher productivity and biomass accumulation by promoting the growth of macroalgae. However, by replacing surfgrass, macroalgal systems may lose the refugia in rhizomes that harbor detritivores and other microbial metabolisms.

Lessons from photophysiology

The differences we documented in photophysiology among rocky intertidal primary producers may enhance productivity by increasing the range of light conditions

that each species experiences (Tait et al. 2014). The rapid increase in photosynthesis at low irradiance seen in surfgrass (high α ; Fig. 3) suggests that they are adapted to low light levels that result from dense monocultures, and may be less affected by canopy shading effects from neighboring macroalgae. Possible competitive dominance at low light as well as clonal expansion and longevity (Shelton 2010) may be a reason why surfgrass is a dominant competitor in the lower intertidal. The ETR_{max} and α differed across macroalgae, with the highest electron transport rates at high light levels, suggesting complementary light resource use and providing a possible mechanism underlying the greater biomass of assemblages containing multiple species of kelp (Fig. 2).

Implications for carbon sequestration

Both surfgrass and macroalgae confer ecosystem functions that are of global importance for blue carbon sequestration (Smith 1981, Queirós et al. 2019). Through sediment burial and deep-sea export (where respiration and mineralization rates are low), macroalgae can sequester as much as ~173 Tg C/yr (Krause-Jensen and Duarte 2016), and seagrasses as much as ~104 Tg C/yr (Duarte and Krause-Jensen 2017), highlighting the importance of macrophytes as carbon sinks. The system we have described here does not have sediment burial because this nearshore ecosystem is built almost exclusively upon hard substrate, leaving deep sea export as the only viable mechanism for carbon sequestration. Based on our measurements of carbon content and fixation, surfgrass and macroalgae make different contributions to carbon cycling. Although the surfgrass monoculture had a significantly greater C:N, the macroalgal assemblage had higher productivity rates and significantly greater DOC production rates. Few studies have compared DOC fluxes from macroalgae and seagrasses, but Barrón et al. (2014) found that the DOC production from macroalgae was nearly twice that of seagrasses. Our estimates of carbon fixation and DOC release necessarily required us to enclose macrophytes; they thus may be lower than rates in natural

TABLE 1. Comparison of ecosystem parameters across plot treatments.

Ecosystem parameter		Control		Removal		P
		Mean	n	Mean	n	
Shannon–Wiener index***	Dimensionless	0.252	4	1.450	3	0.001
Algal species richness***	Count	0.75	4	5.25	3	0.001
Wet mass*	kg/m ²	12.69	4	25.89	3	0.018
Dry mass	kg dry weight (DW)/m ²	2.88	4	3.53	3	0.396
C:N ratio***	No units	16.96	4	11.75	3	<0.001
Total carbon content	kg DW/m ²	0.915	4	1.030	3	0.604
Net primary production***	mg C·h ⁻¹ ·m ⁻²	0.760	4	3.823	3	0.002
Dissolved oxygen content (DOC) production rate***	mg DOC·h ⁻¹ ·m ⁻²	0.545	4	2.293	3	<0.001
Total nitrogen content	kg DW/m ²	0.053	4	0.087	3	0.061

Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

water movement (Appendix S1, Section S2). However, if we assume the relative differences are unchanged, then DOC release by kelp assemblages was $\sim 5\times$ greater than that of the surfgrass *Phyllospadix*. Kelp release a significant proportion (14–16%) of primary productivity as DOC (Reed et al. 2015, Weigel and Pfister 2021), a potential energy source for heterotrophic microbial metabolisms. If the released DOC evades consumption, it may get exported to the deep sea. DOC is reported as the main pathway for carbon sequestration by macroalgae, with an estimated $\sim 8\%$ of macroalgal NPP making its way to the deep sea as DOC (Krause-Jensen and Duarte [2016: Fig. 3], 117 of 1,521 Tg C), and $\sim 2\%$ of seagrass NPP ending up in the deep sea as DOC (Duarte and Krause-Jensen [2017: Fig. 5], 11 of 490 Tg C). Although these published numbers pool across many species, our results show that, per unit area, seagrass and macroalgae have an equivalent amount of carbon biomass (Fig. 2f), but a greater turnover of carbon associated with kelp compared to seagrass, possibly leading to more DOC that is eventually sequestered. Although our NPP estimates in Table 1 for removal areas (scaled to $0.09\text{ g C}\cdot\text{d}^{-1}\cdot\text{m}^{-2}$) are an order of magnitude lower than those for canopy kelp forests in California Current system (North 1994), they are considerable and are comparable to other understory kelp systems (Smale et al. 2020), demonstrating the important contribution of understory kelp in high latitude oceans to blue carbon sequestration. Given the distribution of our study species across the rocky shores of the entire North Pacific (Turner 1983, Kuo et al. 1990, Menge et al. 2005), their role in cycling carbon may be generalizable across an extensive geographic range.

We found that disturbance increased the ecosystem-level carbon sequestration capacity, a result at odds with most other systems in which a phototroph assemblage following disturbance had a reduced capacity to sequester carbon. For example, fires convert forests to relatively unproductive savannahs (Staver et al. 2011), eutrophication reduces productivity in seagrass beds (van der Heide et al. 2011), and urchin grazing results in “barrens” with decreased kelp forest productivity (Steneck et al. 2002, Edwards et al. 2020). In one extreme case, the Alaskan Anaktuvuk River Fire of 2007 initiated large-scale changes in the land surface biophysical properties, converting a carbon sink to a carbon source (Rocha and Shaver 2011).

CONCLUSION

We found that disturbance on rocky shores changed the phototroph assemblage from the competitively dominant surfgrass to a more diverse kelp assemblage, *increasing* carbon sequestration in the ecosystem. Compared with surfgrass, macroalgal assemblages showed higher rates of NPP and DOC release, still relatively understudied components of the blue carbon cycle. As aquatic systems absorb more fossil fuel carbon,

comparative studies such as this are essential to understanding how benthic blue carbon sinks affect the carbon cycle.

ACKNOWLEDGMENTS

We are grateful to the Makah Tribe for access to Tatoosh Island, Washington, United States. Funding came from a University of Chicago E&E Fellowship (for KKM); National Science Foundation grant DEB 1556874 (to J.T. Wootton); and National Oceanic and Atmospheric Administration grant NOAA-COCA NA160AR431055 and Washington Department of Natural Resources grants 93099282 and 93100399 (to CAP). J. T. Wootton and T. Price provided invaluable advice and support; J. B. Wootton, A. M. Wootton, O. Cattau assisted during field work; G. Olack and C. Saucedo (University of Chicago) and A. Masterson (Northwestern University) assisted in CHN analysis. S. Navarrete and four anonymous reviewers improved the manuscript.

LITERATURE CITED

- Barrón, C., E. T. Apostolaki, and C. M. Duarte. 2014. Dissolved organic carbon fluxes by seagrass meadows and macroalgal beds. *Frontiers in Marine Science* 1:5–6.
- Carnell, P. E., and M. J. Keough. 2020. More severe disturbance regimes drive the shift of a kelp forest to a sea urchin barren in south-eastern Australia. *Scientific Reports* 10:11272.
- Christie, H., N. M. Jørgensen, K. M. Norderhaug, and E. Waage-Nielsen. 2003. Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian coast. *Journal of the Marine Biological Association of the United Kingdom* 83:687–699.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Duarte, C. M., and D. Krause-Jensen. 2017. Export from seagrass meadows contributes to marine carbon sequestration. *Frontiers in Marine Science*. <https://doi.org/10.3389/fmars.2017.00013>
- Dublin, H. T., A. R. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59:1147–1164.
- Edwards, M., B. Konar, J. H. Kim, S. Gabara, G. Sullaway, T. McHugh, M. Spector, and S. Small. 2020. Marine deforestation leads to widespread loss of ecosystem function. *PLoS One* 15:e0226173.
- Enriquez, S., C. M. Duarte, and K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content. *Oecologia* 94:457–471.
- Filbee-Dexter, K., and T. Wernberg. 2018. Rise of turfs: a new battleground for globally declining kelp forests. *BioScience* 68:64–76.
- Jantzen, C., G. M. Schmidt, C. Wild, C. Roder, S. Khokiattiwong, and C. Richter. 2013. Benthic reef primary production in response to large amplitude internal waves at the Similan islands (Andaman Sea, Thailand). *PLoS One* 8:e81834.
- Krause-Jensen, D., and C. M. Duarte. 2016. Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience* 9:737–742.
- Kuo, J., H. Iizumi, B. E. Nilsen, and K. Aioli. 1990. Fruit anatomy, seed germination and seedling development in the Japanese seagrass *Phyllospadix* (Zosteraceae). *Aquatic Botany* 37:229–245.
- Leigh, E. G., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave energy and intertidal productivity. *Proceedings of*

- the National Academy of Sciences of the United States of America 84:1314–1318.
- Mann, K. H. 1973. Seaweeds: their productivity and strategy for growth. *Science* 182:975–981.
- McCoy, S. J., and C. A. Pfister. 2014. Historical comparisons reveal altered competitive interactions in a guild of crustose coralline algae. *Ecology Letters* 17:475–483.
- Menge, B. A., G. W. Allison, C. A. Blanchette, T. M. Farrell, A. M. Olson, T. A. Turner, and P. V. Tamelen. 2005. Stasis or kinesis? Hidden dynamics of a rocky intertidal macrophyte mosaic revealed by a spatially explicit approach. *Journal of Experimental Marine Biology and Ecology* 314:3–39.
- Miranda, K., B. Weigel, S. McCoy, and C. Pfister. 2021. Differential impacts of alternate primary producers on carbon cycling. Dryad, data set. <https://doi.org/10.5061/dryad.mpg4f4r0g>
- Moulton, O., and S. D. Hacker. 2011. Congeneric variation in surfgrasses and ocean conditions influence macroinvertebrate community structure. *Marine Ecology Progress Series* 433:53–63.
- North, W. J. 1994. Review of *Macrocystis* biology. Pages 447–527 in I. Akatsuka, editor. *Biology of economic algae*. SPB Academic Publishing, The Hague, The Netherlands.
- Paine, R. T. 1984. Ecological determinism in the competition for space: the Robert H. MacArthur Award Lecture. *Ecology* 65:1339–1348.
- Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–739.
- Power, M. E., and A. J. Stewart. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist* 117:333–345.
- Queirós, A. M., et al. 2019. Connected macroalgal-sediment systems: blue carbon and food webs in the deep coastal ocean. *Ecological Monographs* 89:e01366.
- Reed, D. C., C. A. Carlson, E. R. Halewood, J. C. Nelson, S. L. Harrer, A. Rassweiler, and R. J. Miller. 2015. Patterns and controls of reef-scale production of dissolved organic carbon by giant kelp *Macrocystis pyrifera*. *Limnology and Oceanography* 60:1996–2008.
- Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone, and D. A. Siegel. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology* 92:2108–2116.
- Rocha, A. V., and G. R. Shaver. 2011. Burn severity influences postfire CO₂ exchange in arctic tundra. *Ecological Applications* 21:477–489.
- Romanuk, T. N., and C. D. Levings. 2005. Stable isotope analysis of trophic position and terrestrial vs. marine carbon sources for juvenile Pacific salmonids in nearshore marine habitats. *Fisheries Management and Ecology* 12:113–121.
- Shelton, A. O. 2010. The origin of female-biased sex ratios in intertidal seagrasses (*Phyllospadix* spp.). *Ecology* 91:1380–1390.
- Smale, D. A., A. Pessarrodona, N. King, M. T. Burrows, A. Yunnice, T. Vance, and P. Moore. 2020. Environmental factors influencing primary productivity of the forest-forming kelp *Laminaria hyperborea* in the northeast Atlantic. *Scientific Reports* 10:12161.
- Smith, S. V. 1981. Marine macrophytes as a global carbon sink. *Science* 211:838–840.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334:230–232.
- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation* 29:436–459.
- Stewart, J. G. 1989. Maintenance of a balanced, shifting boundary between the seagrass *Phyllospadix* and algal turf. *Aquatic Botany* 33:223–241.
- Tait, L. W., I. Hawes, and D. R. Schiel. 2014. Shining light on benthic macroalgae: Mechanisms of complementarity in layered macroalgal assemblages. *PLoS One* 9:e114146.
- Tait, L. W., and D. R. Schiel. 2011. Legacy effects of canopy disturbance on ecosystem functioning in macroalgal assemblages. *PLoS One* 6:e26986.
- Turner, T. 1983. Facilitation as a successional mechanism in a rocky intertidal community. *American Naturalist* 121:729–738.
- van der Heide, T., E. H. Nes, M. M. Katwijk, H. Olff, and A. J. Smolders. 2011. Positive feedbacks in seagrass ecosystems—Evidence from large-scale empirical data. *PLoS One* 6:e16504.
- Weigel, B. L., and C. A. Pfister. 2021. The dynamics and stoichiometry of dissolved organic carbon release by kelp. *Ecology* 102:e03221.
- Wootton, J. T. 1995. Effects of birds on sea urchins and algae: a lower intertidal trophic cascade. *Ecoscience* 2:321–328.
- Wootton, J. T., M. Cusson, S. A. Navarrete, and P. S. Petraitis. 2009. Disruptions, succession and stochasticity. Pages 201–212 in M. Wahl, editor. *Marine hard bottom communities. Patterns, dynamics, diversity, and change*. Springer-Verlag, Berlin, Germany.
- Zou, K., E. Thébault, G. Lacroix, and S. Barot. 2016. Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology* 30:1454–1465.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3455/supinfo>

OPEN RESEARCH

Data (Miranda et al. 2021) used in this study are publicly available on Dryad: <https://doi.org/10.5061/dryad.mpg4f4r0g>.