Variability of macroalgal dissolved organic carbon dynamics: Insights for social-ecology beyond Blue Carbon

大型藻類由来の溶存有機炭素動態の変動性：ブルーカーボンを超える社会生態学的洞察

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Dedication

for the seaweed of Oshoro Bay

and beyond

and for their Peoples

may the future be abundant

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(1) **Carlson, A. K.** (2025). Geoscience Obligations to Decolonization: An ʻŌiwi Methodology of "Makahanalimukaikeea" in Ainu Mosir. In L. A. Jacobs (Ed.), *Indigenous Voices: Critical Reflections on Traditional Ecological Knowledge*, forthcoming Spring 2025. Corvallis: **Oregon State University Press**.

(2) Jacobs, L. A., Yamane, C. Y. E. W., Hernandez, J., McAllister, T., **Carlson, A. K.,** Fisk, J., Milligan-McClellan, K., Gazing Wolf, J., Jennings, L. L., Grenz, J., & Avery, C. B. (2025). A Critical Declaration of Decolonization and Indigenization for Scientific Research and the Academy. In L. A. Jacobs (Ed.), *Indigenous Voices: Critical Reflections on Traditional Ecological Knowledge*, forthcoming Spring 2025. Corvallis: **Oregon State University Press**.

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(4) **Carlson, A. K.**, Yoshimura, T., & Kudo, I. (2024). Kelp dissolved organic carbon release is seasonal and annually enhanced during senescence. ***Journal of Phycology***, *60*(4), 980–1000. https://doi.org/10.1111/jpy.13483

(5) Okazaki, R., Teramoto, N., **Carlson, A. K.**, Nakanishi, K., & Kudo, I. (2022). Application of chemostat culture to nutrient uptake rate measurements by the macroalgae *Saccharina japonica* var. *religiosa* (Phaeophyceae) and *Ulva australis* (Ulvophyceae). ***Phycological Research***, *70*(3), 142–150. https://doi.org/10.1111/pre.12483

Conference Presentations

(1) **Carlson, A. K.** Variability of Macroalgal Dissolved Organic Carbon Dynamics: Insights from a Diasporic Kanaka ʻŌiwi Research Methodology in Ainu Mosir. Oral presentation at the **Asian Pacific Phycological Forum**, 15 April 2024.

(2) **Carlson, A. K.** Understanding variable macroalgal dissolved organic carbon dynamics through a diasporic ʻŌiwi research methodology. Oral presentation at the **University of Hawaiʻi at Hilo TCBES Symposium**, 30 March 2023.

(3) **Carlson, A. K.** Geoscience Obligations to Decolonization. Virtual oral presentation at the **American Association of Geographers**, 26 March 2023.

(4) **Carlson, A. K.**, Yoshimura, T., & Kudo, I. Kelp dissolved organic carbon release is variable, passive, and decoupled from photosynthetically active radiation. Virtual oral presentation at the **International Seaweed Symposium**, 23 February 2023.

(5) **Carlson, A. K.** Blue Carbon Science for Indigenous Sovereignty. Virtual oral presentation at the **International Seaweed Symposium**, 21 February 2023.

(6) **Carlson, A. K.**, Yoshimura, T., & Kudo, I. Seasonal kelp dissolved organic carbon release at Oshoro Bay: Insights for Blue Carbon through an ʻupena of pilina framework. Virtual oral presentation at the **Ocean Sciences Meeting**, 28 February 2022.

(7) **Carlson, A. K.**, Yoshimura, T., & Kudo, I. Microbial decay conditions in a Hokkaido kelp bed stimulate refractory dissolved organic carbon production. Virtual oral presentation at the **Aquatic Sciences Meeting**, 26 June 2021.

Abstract

Globally, macroalgae are foundational to the social-ecological systems of many Indigenous Peoples (Sterling et al., 2017; Winter et al., 2020; Reid et al., 2022), inclusive of Ainu People in Ainu Mosir, where this study was conducted (Kawai et al., 2012; Kaminaga, 2018). Modern Indigenous science methodologies have also focused on improved understanding of macroalgae through systematic observation and analysis (Kobluk et al., 2021; Puniwai & Goin, 2021) and Indigenous scientists and stewards have stated interests in improved seaweed biogeochemistry knowledge (Kuaʻāina Ulu ʻAuamo, 2021; Hahn et al., 2022; Spillias et al., 2022). However, data on the mechanisms of active exudation and passive leakage of macroalgal dissolved organic carbon (DOC) are sparse and contradictory (e.g., Weigel & Pfister, 2021; Paine et al., 2021) and the lability and traceability of macroalgal DOC is understudied (Wada et al., 2008; Gao et al., 2021). Multi-year, year-round, and multi-species studies are particularly lacking, resulting in high levels of uncertainty at multiple scales. These experiments aim to improve understanding of the variability of macroalgal DOC release, bioavailability, and fluorescence characteristics, with a particular focus on the effects of photosynthetically active radiation (PAR), seasonal variability related to growth stage, individual macroalgal tissue condition and stress exposure, and species variability through long-term studies. By developing and applying a decolonial research methodology from a diasporic Kanaka ʻŌiwi (Native Hawaiian) standpoint, these insights could allow macroalgal DOC to serve as a proxy for ecological health and be useful to Indigenous cultivation from Hawaiʻi to Ainu Mosir and beyond.

The primary subject is the prostrate annual kelp *Saccharina japonica* var. *religiosa* (order Laminariales) from Oshoro Bay, Ainu Mosir (Hokkaido). Individual biomass is at a minimum in

winter, with growth up to two meters from spring to summer, followed by declines due to grazing, erosion, and senescence in autumn (Abe et al., 1985). Additional experiments were conducted on orders Fucales (*Sargassum thunbergii*, *Sargassum confusum*), Gelidiales (*Gelidium elegans*), Gigartinales (*Mazzaella japonica*, *Neodilsea yendoana*), Laminariales (*Costaria costata*), and Ulvales (*Ulva australis*, *Ulva linza*). Whole macroalgae were collected approximately bi-monthly from January 2020 to November 2023. In situ seawater was collected throughout the macroalgal ecosystem, as well as at reference points inside and beyond the bay. Tanks with macroalgae and control tanks with only reference seawater (3-L each) were incubated ex situ, subject to different PAR treatments (e.g., 200 and 400 or 200 and 1200 µmol photons PAR $m^{-2} \cdot s^{-1}$), and sampled at least daily. After incubation, the macroalgae were removed and dried to a constant weight. A 150-d bioavailability experiment then quantified the degradation rate of macroalgal DOC due to microbial activity, with the remaining portion considered to be recalcitrant. All seawater samples were filtered with pre-combusted 0.7 µm glass fiber filters and stored below −20 °C until analysis by a total organic carbon analyzer. Selected samples were analyzed by 3D fluorescence spectroscopy to characterize DOC lability.

There were significant intra-annual differences (two-way ANOVA and Tukey's HSD tests, $p < 0.05$) in mean kelp DOC release rates (mg $C \cdot g^{-1}$ $DW \cdot d^{-1}$) (± standard error between *n* kelp) with higher rates during the autumn "late decay" period (0.71 ± 0.10, $n = 27$) compared to the winter "early growth" period (0.14 ± 0.025, $n = 10$) and summer "early decay" period (0.25 ± 0.050, $n = 24$). Due to the high individual variability in DOC release rates in this and previous studies, methods recommendations include (1) to verify linearity of DOC release and report least squares mean rates where appropriate, and (2) to quantify individual macroalgal "replicate" variability with coefficients of variation to facilitate comparisons between studies.

Mean seasonal recalcitrant DOC (RDOC) % results were 3% ± 9% in the winter, 15% ± 2% in the spring, 14% ± 1% in the summer, and 22% ± 2% in the autumn. Fluorescence kinetics were variable but outperformed elevated RDOC concentrations in traceability. Mean results across seasons showed substantial degradation of protein-like "peak T", partial degradation of UV humic-like "peak A" (except when enhanced in autumn), enhancement of visible humic-like "peak C", and conservation of visible marine humic-like "peak M" by the end of the 150-d kelp DOC bioavailability experiments. When comparing red, green, and brown macroalgae, red macroalgae were the primary contributors of DOC and fluorescence in winter and summer, but green macroalgae were dominant in spring. Excluding results from bleaching and heatwave stress, the highest recalcitrant DOC proportions were from *S. confusum* (36% ± 0.57%, $n = 3$) and *S. thunbergii* (49%, composite $n = 3$) in autumn, while the highest recalcitrant DOC production rates were from *U. australis* (0.20 mg C · g^{-1} DW · d^{-1}, composite $n = 2$) in spring. However, these differences were significantly outweighed by the typically order of magnitude enhancement effect of bleached tissue (for *U. australis* and *M. japonica*) and heatwave stress (for *S. japonica* var. *religiosa* and *N. yendoana*) on DOC and fluorescence recalcitrance. In contrast, results from *U. australis* during the summer heatwave were several times lower than in spring. Significant linear proportionality was established between fluorescence peak intensities and DOC concentrations, but were season-, species-, sample time-, and fluorescence type-specific. Proportionality between "peak T" and DOC concentrations at the end of the bioavailability experiments was the best predictor of in situ DOC concentrations. By using mean seaweed community results, seasonal macroalgal contributions were estimated as 24%–44% (23–37 μM) of in situ DOC.

These insights into the variability of macroalgal DOC release and bioavailability at the scales of seasons, species, and individual tissue conditions can help clarify the dynamics of macroalgal DOC in coastal ecosystems. In particular, studies addressing ecophysiological stress are essential to constraining macroalgal DOC and fluorescence contributions, yet certain species may be significantly more resilient or have contrasting responses to these stresses and must also be studied. Indigenous stewards and scientists may particularly benefit from incorporating these insights into their monitoring and management methodologies. Overall, most macroalgal species demonstrated low DOC recalcitrant proportionality (5–15%) relative to assumptions in global estimates (30%). The results of these studies provide initial steps to predict in situ macroalgal DOC contributions at the local scale, but significant work remains as the proposed prediction model is highly context-specific. The variability at the scales of season, species, life history, and stress factors even within a single sampling site indicates the inherent difficulties in confidently monitoring, reporting, and verifying carbon sequestration contributions for the purpose of Blue Carbon credits.

Beyond the technical difficulties highlighted in the biogeochemical results of the preceding experiments, this dissertation also reviews the broader literature on technical and social challenges facing Blue Carbon as a climate change mitigation strategy. This review indicated that narrow ecosystem services accounting leads to perverse prioritization of carbon dioxide removal (CDR) over holistic social-ecological health, carbon offsets provide cover for the continuation of extractive corporate and colonial operations, industrial-scale interventions result in negative social-ecological disruptions, and even small-scale non-Indigenous projects exacerbate the loss of Indigenous coastal sovereignty. Therefore, funding and labor toward colonial Blue Carbon projects is ultimately counterproductive to holistic social-ecological

vitality and should be re-directed toward the full-scale restoration of Indigenous aquaculture and coastal cultivation practices (within sovereign social-ecological systems). Moreover, since Blue Carbon and other ecosystem services should be considered a co-benefit of Indigenous stewardship and restoration, their funding should not be dictated by colonial monitoring, reporting, and verification requirements. Ultimately, existing and practical Indigenous alternatives to Blue Carbon and climate coloniality must be urgently prioritized to achieve a decarbonized and decolonized world.

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Preface: Introduction of Objectives and Outline

Objectives

The original motivation for researching macroalgal dissolved organic carbon (DOC) dynamics was for its potential contribution to Blue Carbon as a climate change mitigation strategy (e.g., Krause-Jensen & Duarte, 2016)—this was the basic framing used for my Master's thesis. However, doctoral and post-doctoral work should clearly articulate research methodologies that move beyond shallow considerations of "basic" scientific results. In other words, it is imperative to understand the broader impacts and context of the science being done. Therefore, after beginning a review of the literature on how epistemology, ontology, and axiology inform research standpoints and methodologies (e.g., Smith, [1999] 2021; Meyer, 2008; Wilson, 2008; Oliveira & Wright, 2016; Walter & Andersen, 2016), and after further prompting by Professor Rosie Alegado, I began the process of articulating this foundation and its implications—resulting in Chapter 1 of this dissertation. In brief, this showed that my standpoint-based methodology would be to conduct "basic" biogeochemical experiments on macroalgal DOC dynamics as an ecophysiological response and to discuss the implications of these results in the broader context of social-ecology and Blue Carbon—explicitly through an Indigenous lens (as a diasporic Kanaka ʻŌiwi/Native Hawaiian in Ainu Mosir/Hokkaido). This clarified that, going forward, the core motivation for this research would be to understand how macroalgal DOC dynamics might provide relevant insights for Indigenous social-ecology, potentially including but not limited to Blue Carbon credits.

For some basic biogeochemical context, macroalgal DOC release is an ecophysiological response (Hurd et al., 2014) and serves many biogeochemical roles that can impact microbial activity, oxygen concentrations, pH values, or contribute to carbon sequestration (Carlson &

Carlson, 1984; Wada & Hama, 2013; Carlson & Hansell, 2015; Watanabe et al., 2020; Edworthy et al., 2023). Macroalgae can function as ecosystem engineers (Bellgrove et al., 2017), and Indigenous scientists and coastal stewards are particularly interested in macroalgal research for the insights it can provide toward supporting thriving ecosystems and productive aquaculture (Kua‘āina Ulu ‘Auamo, 2021; Hahn et al., 2022; Spillias et al., 2022). Understanding trends in macroalgal DOC dynamics may therefore be useful to Indigenous stewards when considering selective harvesting strategies or adjusting coastal engineering controls. For example, Indigenous integrated multi-trophic aquaculture such as loko i‘a (fishponds that integrate seaweed cultivation) in Hawai‘i are engineered to adjust water exchange (Keala et al., 2007) within the context of broader systems of social-ecological resource governance (Winter et al., 2018). Therefore, monitoring the relationship between macroalgal DOC dynamics and factors such as environmental parameters or seasonal growth stage may be one relevant metric for decision making.

The orientation of these macroalgal ecophysiology and biogeochemistry experiments toward empowering sovereign Indigenous seaweed cultivation is based on my research standpoint and is therefore intrinsic to this research. This application is consistent with the broader obligations of geoscience to advance decolonization (i.e., Black and Indigenous sovereign liberation) (Yusoff, 2018; Liboiron, 2021a; Sultana, 2022a; Carlson, 2025). This discussion is also critically relevant to this field of research because Indigenous coastal stewardship and biocultural restoration are essential for social-ecological health (Morishige et al., 2018; Bennett et al., 2021; Jacobs et al., 2022). To be clear, this also applies to Ainu People throughout Ainu Mosir (Grunow et al., 2019; Ishihara, 2020; Uzawa, 2020), inclusive of this study’s sampling location of Oshoro Bay. However, there are no established mechanisms for

Indigenous community peer-review, consent, or partnerships in Hokkaido as exist elsewhere for geoscience research (e.g., Liboiron et al., 2018; Alegado et al., 2023).

Since these studies are focused on macroalgal DOC dynamics as an ecophysiological mechanism (and how these insights might be relevant to Indigenous monitoring and stewardship), Indigenous Knowledge of seaweed is not the subject of investigation and is not discussed here in detail. However, it is important to briefly comment on the cultural relevance of kelp to Ainu People. First, the historical harvesting of kelp by Ainu People is not disputed (Kawai et al., 2012). Moreover, the Japanese word konbu derives from the (southern regional) Ainu word kompu, giving some indication of its prominent societal role. Currently, kelp continues to be culturally relevant, for example, in cuisine such as kompusito (Kaminaga, 2018). While settler-colonialism continues to disrupt modern Ainu kelp cultivation from being practiced at larger scales, Ainu People and culture persist. Therefore, Ainu People interested in seaweed cultivation may find these results on variable macroalgal DOC dynamics relevant to current or future stewardship and harvesting practices.

While these studies on macroalgal DOC dynamics will have the greatest place-based relevance to Oshoro Bay and Ainu Mosir, they may also provide insights to Indigenous Peoples globally. However, the insights discussed here are only meant to supplement place-based Indigenous Knowledge of seaweed cultivation, which has persisted for millennia and continues to evolve (Abbott & Williamson, 1974; Kobluk et al., 2021; Reid et al., 2022). Nevertheless, settler-colonialism has disrupted Indigenous Knowledge and systems of governance in many places (Whyte, 2018). Therefore, general insights from this dissertation may be relevant to the processes of rebuilding more nuanced place-based stewardship practices globally.

Outline

This dissertation begins with Chapter 1 in order to address three key questions, namely: (1) What is a research standpoint and methodology?; (2) Are they important to this field?; and (3) If so, what is the research standpoint and methodology of this dissertation? Chapters 2–5 focus on the fundamental science underlying variable macroalgal DOC dynamics. Key questions in Chapter 2 include: (1) Is kelp DOC release seasonal?; (2) What are the mechanisms underlying DOC release rate variability?; and (3) Can we constrain kelp DOC release rate variability? Chapter 3 shifts the focus to the bioavailability of kelp DOC. Therefore, associated fluorescence characteristics of this dissolved organic matter (DOM) were also studied to gain insights into the origins and development of protein-like (typically labile) and humic-like (typically recalcitrant) fluorescence signatures. The key questions of Chapter 3 include: (1) What proportion of kelp DOC is recalcitrant?; (2) What do the recalcitrance kinetics of fluorescence signatures reveal about origins and traceability?; and (3) Is kelp-derived fluorescence recalcitrant enough and distinct enough to potentially trace? Chapter 4 expands beyond a single kelp species to explore variability between species as well as the impact of in situ heatwave and bleaching stress on DOC dynamics. The key questions of this chapter are: (1) Do macroalgal DOC and fluorescence dynamics vary by species?; (2) How does in situ heatwave and bleached tissue stress impact these dynamics by species?; and (3) Do these additional considerations conflict with or add nuance to the previous single species results? Another purpose of studying the relationship between fluorescence and macroalgal DOC under various contexts was to attempt to build a preliminary predictive model correlating macroalgal-derived DOC to in situ fluorescence peak intensities (Chapter 5). An original motivation for this was to help quantify macroalgal contributions of recalcitrant DOC in terms of estimating a potential carbon sequestration budget.

However, the immediate value of empirical correlations between fluorescence peak intensities and DOC concentrations may primarily be in reducing analytical labor. This value may be exponentially enhanced if technologies for in situ and remote sensing of fluorescent DOM continue to improve. Therefore, the key questions of Chapter 5 were: (1) Is fluorescence and DOC proportionality significant?; (2) If so, does controlling for specific contexts (e.g., season, sample time, species assemblage) improve correlation values?; and (3) Can variably distinct proportionalities between fluorescence and DOC provide insights for in situ tracing of macroalgal DOC? Nevertheless, even if technical barriers to quantifying macroalgal DOC contributions to carbon sequestration are overcome, it is critical to ask whether there are fundamental ethical flaws related to Blue Carbon credit accounting. Therefore, Chapter 6 focuses on reviewing the known social and technical issues with Blue Carbon (and the longer history with terrestrial carbon offsets) as a climate change mitigation strategy. Chapter 6 ultimately concludes that re-directing funds to sovereign Indigenous coastal stewardship would be more effective and ethical.

As demonstrated here, articulating my methodology had profound effects: it informed the structure of this dissertation, modified the goals, and clarified the broader value of the empirical results. In particular, it highlighted the need to consider the broader impacts of my research in the contexts of climate coloniality and environmental justice. These critical impacts are evidence of the importance of research standpoints and methodologies more broadly. Based on the results of Chapters 2–5 and the review in Chapter 6, the primary benefit of monitoring macroalgal DOC dynamics is to understand social-ecological health—any carbon sequestration role must be viewed as an ancillary benefit. Therefore, the Summary discusses key findings in the applied context of Indigenous stewardship. These insights aim to help Indigenous coastal stewards

anticipate variable local DOC accumulation and plan for ecological implications.

"Ka manu kāhea i ka waʻa e holo"

(The bird that calls to the canoe to sail) (Pukui, 1983, ʻŌlelo Noʻeau 1478)

CHAPTER ONE

Geoscience Obligations to Decolonization: An ʻŌiwi Methodology of "Makahanalimukaikeea" in Ainu Mosir

A version of this chapter is accepted for publication (In Press) as Chapter 8 of an Oregon State University Press peer-reviewed book:

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Part One: Kuleana and Kūlana in Geoscience Research

Conventional geoscience research operates within and upholds the ongoing settler-colonial systems of oppression at the root of the climate and planetary crises and must be confronted. Therefore, researchers must rigorously investigate their roles in advancing decolonization and sovereign liberation, even through laboratory-based and so-called basic science, or else remain complicit. To do so, geoscientists should articulate and re-orient their research methodologies to address their standpoint-derived (positional) obligations to the local Black and Indigenous Peoples, communities, and environments impacted by their research. This will allow for critical examination of the worldviews, ways of Knowing, ways of Being, value systems, background, and motivations researchers have for doing science. This is essential for meaningful and ethical science, especially within the context of settler-colonial governments and institutions. Ultimately, ethical and sustainable science requires a decolonized future, so our scientific objectives must be aligned with Black and Indigenous sovereign liberation.

In this chapter, I share my attempt to develop a decolonial research methodology as a diasporic Kanaka ʻŌiwi (Native Hawaiian, person of the bone) environmental scientist and transient settler/outsider in Ainu Mosir (the Indigenous homeland of Ainu People). To do this, I investigate my kūlana (position, station, situation)-derived kuleana (rights, responsibilities, authorities, obligations) as a case study. Rooted in ʻŌiwi scholarship, this methodology uses an ʻupena of pilina (fishing net of social-ecological relationships) worldview, my moʻokūʻauhau (genealogies), and ʻōlelo Hawaiʻi (Hawaiian language) concepts and values. While this methodology remains flawed and is case-specific, it may provide some guidance for other scientists to engage with their own standpoint-derived research obligations to decolonization.

As a starting point, it is imperative that scientists more critically engage with reflective

questions such as, “What is my kuleana here?” (The Mauna Kea Syllabus, 2021). Kānaka ʻŌiwi (Native Hawaiian, people of the bone) scholars and activists explain that in ʻōlelo Hawaiʻi (Hawaiian language, translations from Pukui & Elbert, 1986), kuleana evokes the rights, privileges, and responsibilities one has to people and place as well as the authority and justification to act in different contexts (Goodyear-Kaʻōpua et al., 2014; Aikau et al., 2016). Kuleana is also central to Kanaka ʻŌiwi research methodologies broadly (Oliveira & Wright, 2016). In this chapter, I critically examine my kuleana and kūlana (station, position, situation) while engaged in noiʻi (Knowledge seeking, research) by articulating my research methodology and standpoint.

From an ʻŌiwi perspective, understanding kuleana requires understanding kūlana and our relationality to our places of research, especially in the context of outsider identities and local familiarity. For example, one ʻōlelo noʻeau (wise saying) related to kuleana instructs “E mālama i ka ʻōlelo, i kuleana e kipa mai ai” (“remember the invitation, for it gives you the privilege of coming here”) (Pukui, 1983). Moreover, even with an invitation, one’s place-based experience and expertise (and therefore, rights to conduct research) may be limited. This is illustrated by the ʻōlelo noʻeau “No nehinei aʻe nei nō; he aha ka ʻike?” (“[You] just arrived yesterday; what do [you] know?”) (Pukui, 1983). With these values in mind, the Kūlana Noiʻi Working Group was formed through broad community input to provide guidance for “how an individual carries themselves as they seek knowledge or information”, particularly in the place-based context of community engaged scientific research in Hawaiʻi. These guidelines are fundamentally concerned with building and nurturing strong, mutual pilina (relationships) between researchers and community members, in addition to sharing ʻike (Knowledge, awareness, understanding, vision) and aloha (love, affection, compassion) (Kūlana Noiʻi Working Group, 2021). This

shows that the Kūlana Noiʻi are primarily focused on kūlana in terms of how individual researchers physically and socially conduct themselves, particularly in relation to the local community and place.

Here, I focus on kūlana in the more abstract sense of standpoint. Taking this step back makes kūlana relevant to research objectives, framing, and applications, even for primarily laboratory-based or so-called basic (i.e., not applied) science. A focus on kūlana as standpoint and how it relates to kuleana as responsibility allows for a more critical assessment of researcher motivations, justifications, and obligations beyond conventional standards for research ethics. This framing also aligns with other Indigenous research methodologies, such as those described by Smith (Ngāti Awa, Ngāti Porou), Wilson (Cree), Walter (Trawlwoolway), and Andersen (Métis) (Smith, [1999] 2021; Wilson, 2008; Walter & Andersen, 2016). Essentially, if a researcher does not understand their own standpoint (including their ways of Knowing, ways of Being, value systems, and social position), they cannot assess whether they have the authority to conduct the research or how to ensure their research is relevant. This is why articulating a research methodology and standpoint is critical.

Ultimately, decolonial research methodologies require objectives aligned with material outcomes (Deloria Jr., [1969] 1988; Tuck & Yang, 2012; la paperson, 2017). While defining specific visions of decolonization and Indigenous sovereignty is beyond the scope here, it is essential to emphasize a few key points. First, Eve Tuck (Unangax̂) and K. Wayne Yang (settler/trespasser) emphasize that decolonization must mean material land back, with restoration and empowerment of Indigenous self-sufficiency and sovereignty in our homelands (Tuck & Yang, 2012). In the geosciences, examples include Indigenous scientists working in the context of restoring Indigenous sovereignty over parks and protected areas (Fisk et al., 2021), biocultural

restoration, food sovereignty, and community-based management in Hawai‘i (Delevaux et al., 2018; Montgomery & Vaughan, 2018), as well as conservation management and ecological restoration that centers Indigenous value systems (Grenz, 2020; Jacobs et al., 2022). The abundance of Indigenous-led science oriented toward sovereignty makes it clear that the path forward is already being forged.

Next, joint and overlapping solidarity between Black, Indigenous, and Afro-Indigenous Peoples, as well as other oppressed and colonized Peoples is essential (Fanon, [1961] 2004; Freire, [1968] 2018; Lorde, [1984] 2012; hooks, [1994] 2014; King, 2019; Mays, 2021) and must be considered in decolonial geoscience methodologies. From the classic work of Walter Rodney (Guyanese) to contemporary work by Andrews (British African-Caribbean), it is well established how the structures of colonial oppression are intimately dependent on the ongoing oppressive effects of the colonization of the African continent (Rodney, [1972] 2018; Andrews, 2021). Black authors in the U.S.A. have shown how historical (structural) enslavement is not a relic of the past but lives on in the ongoing systems of caste (Wilkerson, 2020), mass incarceration (Alexander, [2010] 2020), and Afropessimism’s theory of Black social death (Wilderson III, 2020).

Since 1979, Robert D. Bullard’s scholarship on the racist impacts of pollution on Black communities in the southern U.S.A. and his now classic book, *Dumping In Dixie* (Bullard, [1990] 2018) paved the way for the fields of environmental and climate justice, leaving no room for doubt that environmental science must consider and address anti-Black racism. Meztli Yoalli Rodríguez Aguilera (Mestiza Mexicana) also provides a relevant example of how ecological grief and environmental racism impacts Black and Indigenous Peoples in Oaxaca, Mexico (Rodríguez Aguilera, 2022). Therefore, geoscience methodologies that aspire to be decolonial

but only consider a narrow conception of Indigenous sovereignty will ultimately fail if they still perpetuate environmental injustice and anti-Black racism.

With this context, the research methodology described here establishes the standpoint-derived obligations for my research project. While Liboiron (Métis) has previously explained the importance of standpoint, obligations, and decolonization within the realm of basic geoscience research (Liboiron, 2021a; Liboiron, 2021b), this chapter develops those ideas into a specific and explicit research methodology that is firmly grounded in ʻŌiwi methodologies, values, and language. The additional context of my Indigenous upbringing in diaspora and current displacement in Ainu Mosir also create complications that may offer insights for others navigating and disrupting settler-colonial science. Therefore, I share my methodology and standpoint as a case study and call for all geoscientists, even those conducting basic research, to investigate their standpoint-derived obligations and re-frame how they discuss their data and results in terms of those obligations. From the successes and flaws of this case study, as well as the broad decolonial scholarship it stands on, I hope that the path forward for other geoscientists may be made clearer.

Case Study: Research Kuleana of a Kanaka ʻŌiwi in Ainu Mosir

Even as a Kanaka ʻŌiwi well versed in the importance of kuleana, I had not fully engaged in questioning my kūlana-derived kuleana as a researcher before embarking on a five-year Ph.D. program at Hokkaido University. Yet, the history of diasporic kuleana is well documented (Chang, 2019) and cannot be overlooked since "resistance to settler-colonialism is a responsibility for both Kanaka ʻŌiwi in Hawaiʻi, as well as those in the diaspora" (Vaughn, 2019). Therefore, I have had to critically examine the limitations of my positionality as an

invited guest of the Japanese government (MEXT Scholar), while also being an uninvited outsider/transient settler from the perspective of the Indigenous Ainu People.

Parallels with Parachute Science

Given this context, I discuss how my background informed my initial and evolving motivations for pursuing a Ph.D. in Environmental Science at Hokkaido University specifically. More personal motivations included a life-long interest in Japan and Japanese culture, having grown up with both genealogical and place-based Japanese cultural influences, and taking my first Japanese language class when I was 11 years old. In terms of education and research opportunities, Hokkaido specifically was of interest due to its well-known wild and commercial kelp, combined with the relevant resources and experts at Hokkaido University for researching kelp carbon dynamics.

Yet, despite these ties and interests, I am still of course an outsider and so it is important to investigate the similarities and differences between my positionality and the extractive practice of "parachute science" (Asase et al., 2021; de Vos, 2022). Conducting research as an outsider is often fundamentally flawed (Said, [1979] 2014) and even Indigenous researchers operating from the diaspora face many ethical obstacles (Aikau, 2019; Mwampamba et al., 2021). In my case, as an outsider with kuleana outside of my current residence, my research objectives are inherently extractive and center an outsider's perspective. Despite this, my situation is critically distinct from typical parachute science due to my context of working in an all-Japanese lab at a public Japanese university, without exerting power structures to dominate local Japanese People, places, and Knowledges.

Perpetuating Ainu Colonization

However, this narrative is disrupted by the fact that while Japanese People can be considered Indigenous to the main island of Honshu, they are indisputably settler-colonizers in Ainu Mosir (Hokkaido), which is the Indigenous homeland of Ainu People. Uzawa (Ainu), explains that the Japanese government first recognized Ainu People as a minority ethnic group in a 1991 report to the United Nations, then as an Indigenous People by a 2008 resolution, and most recently as an Indigenous People by a 2019 law. Yet, Ainu People still do not have legal rights to self-determination or sovereignty (Uzawa, 2020). Even though the area where I collect seawater and macroalgal samples (within Oshoro Bay) has been affiliated with a Hokkaido University marine station since 1908 (Yotsukura, 2021), it is still part of the Ainu homeland. In fact, conducting conventional research anywhere in Hokkaido is a form of perpetuating settler-colonialism as there is no legal requirement to consider the rights of Ainu People or communities to manage the use of their ancestral and modern homelands for research purposes.

Unfortunately, historical and ongoing settler-colonial violence has oppressed open identification as Ainu People, which also complicates issues surrounding ethical accessibility and community engagement. For example, Ishihara describes herself as an "Ainu Liminar"—her term for those of Ainu heritage who have had their Ainu voices stolen from them by Japanese settler-colonialism and do not feel that they can identify as Ainu People (Grunow et al., 2019; Ishihara, 2019). Ishihara also uses the term "Silent Ainu" for People who may identify as Ainu but do not feel comfortable publicly identifying their Ainu ethnicity due to issues of discrimination and pressures of assimilation (Ishihara, 2018; Ishihara, 2020). These issues complicate the validity of government demographic surveys on the Ainu population in Japan (Uzawa, 2020). Therefore, while it might be expected that the survey result of zero Ainu

respondents in the Shiribeshi region where Oshoro Bay is located (Uzawa, 2020) is an underestimate, it is an indication that there isn't a publicly active local Ainu community in the broader region with whom I can engage.

Despite these issues, it would be unethical to dismiss the relevance of Ainu sovereignty in Hokkaido as too complicated a topic for this research project. Indeed, Ainu People elsewhere in Hokkaido may have their own genealogical and personal relationships to Oshoro Bay maintained diasporically throughout and beyond Hokkaido. Therefore, regardless of the apparent absence of Ainu People living near Oshoro Bay, this research must engage with the broader Ainu community and ensure its relevance to them.

My standpoint, therefore, includes both my identity as an invited guest and researcher (MEXT Scholar) of the Japanese government, and as an uninvited transient settler from the perspective of Indigenous Ainu People to whom Hokkaido is their present and ancestral homeland. As an outsider, reconciling these identities with a kuleana to not conduct extractive research is inherently complicated. For example, it would generally not be appropriate for me to attempt to use or discuss Ainu Knowledge without the co-production of that Knowledge (Lock et al., 2022). Also, attempting to re-center my research toward primarily benefitting Ainu People would likely be disingenuous and fundamentally flawed due to my positionality.

However, this positionality should not be used as an excuse to engage in the "moves to innocence" (Mawhinney, 1998; Tuck & Yang, 2012) that are characteristic of resistance to anti-racist and anti-oppression activities. Instead, I have to look to my standpoint-derived kuleana and investigate how I can have a positive impact while centering my Indigenous positionality in my research. I, therefore, have kuleana to ensure that the insights generated by my scientific research are advancing a restoration of Indigenous sovereign management of these macroalgal

ecosystems, most especially for the Ainu People and communities on whose land and waters this research is based.

In other words, based on this kūlana, I have kuleana to advance decolonization and Indigenous sovereignty through my research on macroalgal biogeochemistry and Blue Carbon, with particular attention to ʻŌiwi and Ainu Peoples. As Figure 1.1 shows, my kuleana, kūlana, and moʻokūʻauhau are all linked and collectively informed by an ʻŌiwi/Indigenous relational worldview. This methodology is therefore born from the complex identities and contexts of my standpoint and represents a flawed starting point for my research; nevertheless, this case study may provide useful insights to others.

Summary and Objectives

Explicitly stating a research methodology according to one's own cultural and place-based contexts is critical for engaging in one's positionality relative to the various places one has relationships and responsibilities to (standpoint-derived kuleana). Even geoscientists conducting basic research must investigate how their positionality and their research impact Black and Indigenous Peoples, communities, and environments, and whether oppressive systems are upheld or decolonization objectives are advanced. Therefore, I offer three primary objectives for this chapter, as follows:

1. To situate my research on macroalgal dissolved organic carbon dynamics and implications for Blue Carbon strategies in the context of my responsibilities and limitations;
2. To encourage other Kanaka ʻŌiwi as well as other Indigenous scientists to confidently and explicitly incorporate our Indigenous-based methodologies into our research to

benefit and center Indigenous Peoples, communities, environments, and sovereignty; and

3. To encourage geoscientists broadly to engage in their methodologies and standpoints to investigate how their science perpetuates settler-colonial systems or advances decolonization.

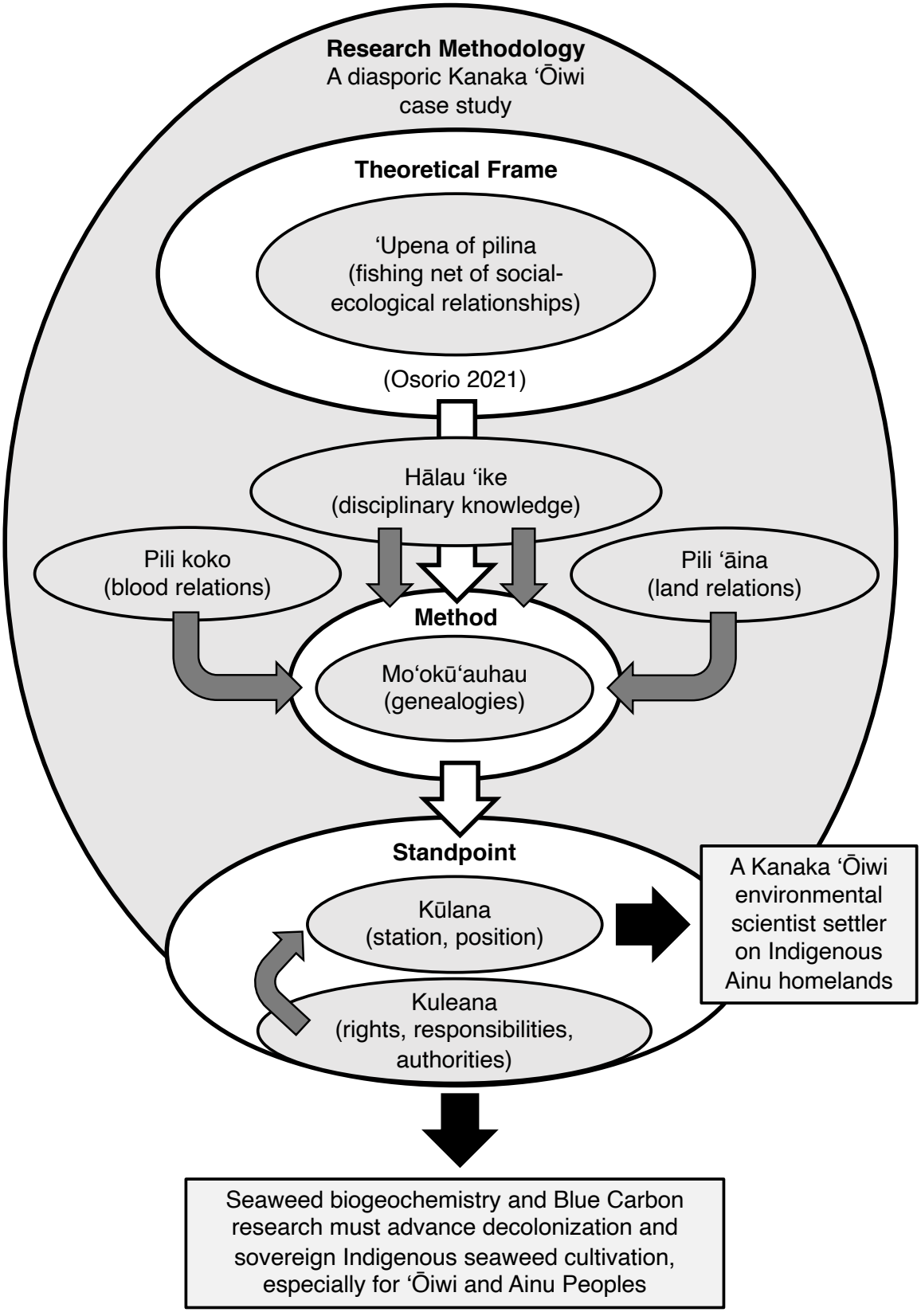
Research Methodology
A diasporic Kanaka ʻŌiwi case study
Theoretical Frame
ʻUpena of pilina (fishing net of social-ecological relationships)
(Osorio 2021)
Hālau ʻike (disciplinary knowledge)
Pili koko (blood relations)
Pili ʻāina (land relations)
Method
Moʻokūʻauhau (genealogies)
Standpoint
Kūlana (station, position)
Kuleana (rights, responsibilities, authorities)
A Kanaka ʻŌiwi environmental scientist settler on Indigenous Ainu homelands
Seaweed biogeochemistry and Blue Carbon research must advance decolonization and sovereign Indigenous seaweed cultivation, especially for ʻŌiwi and Ainu Peoples

Figure 1.1: Components and outcomes of this diasporic Kanaka ʻŌiwi research methodology. This methodology is guided by an ʻupena of pilina worldview as its theoretical frame and foundation for shaping the other methodological components. Various moʻokūʻauhau (genealogies) inform my kūlana (standpoint) as a Kanaka ʻŌiwi environmental scientist settler on Indigenous Ainu homelands. This positionality informs my kuleana (rights and responsibilities), which are framed through the broader social-ecological worldview. Ultimately, this framing indicates that my macroalgal biogeochemistry research should advance Indigenous sovereignty, especially for ʻŌiwi and Ainu Peoples. Specifically, my macroalgal biogeochemistry research must be oriented toward and made useful for sovereign Indigenous seaweed cultivation, stewardship, and social-ecological health.

Part Two: Methodologies of Moʻokūʻauhau

One meaning of "I ka wā ma mua, ka wā ma hope" is that the past informs and secures the future (Kameʻeleihiwa, 1992; Wilson-Hokowhitu, 2019). Through moʻokūʻauhau (genealogies), we can therefore better understand kūlana and ultimately kuleana, even in the context of research objectives and outcomes (Figure 1.1). First, the cultural centrality of moʻokūʻauhau to Kānaka ʻŌiwi can be illustrated by the genealogical nature of the various Kumulipo (cosmogonic creation chants), which are primary kumu (sources, teachers) for understanding where all living entities come from and their context in the world (Kanahele, 2011; Nuʻuhiwa, 2019).

Looking to modern ʻŌiwi scholarship, moʻokūʻauhau and the Kumulipo are also central to research methodologies and broader ʻŌiwi ways of Knowing and Being (Wilson-Hokowhitu, 2019). Notably, they serve as the foundation for Papakū Makawalu (Kanahele, 2011), which describes a "methodology and pedagogy for understanding the Hawaiian Universe" from multiple perspectives (Nuʻuhiwa, 2019). Papakū Makawalu is particularly relevant to decolonial geoscience because of how it has been combined with grounded theory to construct land stewardship policy (Kanahele-Mossman & Karides, 2021) in the context of Kānaka ʻŌiwi opposition to the proposed Thirty Meter Telescope on Mauna Kea (Alegado, 2019; Kahanamoku et al., 2020). Personal moʻokūʻauhau have also been critically applied across disciplines (e.g., Kurashima, 2018; hoʻomanawanui, 2019; Osorio, 2021), including in the context of sustainability science (Kealiikanakaolehaililani et al., 2018).

Ultimately, how much and in what ways personal moʻokūʻauhau are shared methodologically, if at all, will vary based on the nuances of each situation, and should never be coerced or required as a standardized practice. This is especially important to emphasize given

the context of colonial violence, trauma, and blood quantum (Kauanui, 2008). Therefore, this methodology refers to my moʻokūʻauhau as a starting point to center kuleana and pilina without explicitly reciting my moʻokūʻauhau pili koko (blood relation genealogy).

ʻŌiwi methodologies of moʻokūʻauhau also incorporate moʻokūʻauhau pili ʻāina (genealogy of land connections) and moʻokūʻauhau hālau ʻike (disciplinary genealogy). Considering these moʻokūʻauhau together in a research methodology, therefore, informs kūlana. In addition, clarifying research-relevant social position informs what or how research questions are asked and answered. For Kānaka ʻŌiwi scientists, using moʻokūʻauhau as methodology, including their relationships to ʻŌiwi worldviews of kuleana and pilina, can provide a powerful way to investigate how pono (righteous, good, correct) one's research concept, conduct, and impacts may be.

Case Study: Moʻokūʻauhau

Moʻokūʻauhau Pili Koko

Based on moʻokūʻauhau pili koko and cultural upbringing, I am a Kanaka ʻŌiwi with a multi-racial heritage raised in the international diaspora. Before both my birth and my mother's birth in the diaspora, the one hānau (sands of birth) of our kūpuna (grandparent generation, Elders, ancestors) were most recently in the ahupuaʻa (community-level land division) of Waiākea in the moku (district) of Hilo on Hawaiʻi Island, while those of previous generations included the ahupuaʻa of Niuliʻi and Makapala (Moku o Kohala) and Honuʻapo (Moku o Kaʻū) on Hawaiʻi Island, as well as the ahupuaʻa of Waiheʻe and Wailuku (Moku o Pūʻali Komohana) and the ahupuaʻa of Kanahena (Moku o Honuaʻula) on the Island of Maui. It is also worth remembering that some of my living kūpuna still have memories of their kūpuna who were born,

even became mākua (parents), in the internationally-recognized Kingdom of Hawai‘i. This time of Indigenous sovereignty and period when ‘ōlelo Hawai‘i was the primary language has therefore not been forgotten and may yet be reclaimed.

In terms of our many kulāiwi (ancestral lands, where bones are buried), Niuli‘i in particular is home to additional kuleana and pilina for our ‘ohana. This is one place we know our kūpuna signed the 1897 Kū‘ē petitions—the democratically and legally successful protest against annexation to the United States of America (Silva, 2004; Goodyear-Ka‘ōpua et al., 2014). Today, ‘ohana from the Hussey line in Niuli‘i continue to steward kuleana land that was distributed in the Great Māhele (mid-1800s land division policy of the Kingdom of Hawai‘i). In addition, Niuli‘i is a piko (umbilical cord, navel, focal point) for connecting both the Malakaua and Hussey lines to the Maui kūpuna who can be traced all the way back to Papahānaumoku and Wākea (Earth Mother and Sky Father).

Briefly summarizing my genealogy, by the time of my upbringing, my Hawai‘i-based Kanaka ‘Ōiwi mo‘okū‘auhau had largely assimilated and integrated aspects of English (beyond 5 generations) and Okinawan (within 5 generations) cultural identities. Additional ancestors within 5 generations (with English, German, Irish, and West African ethnocultural identities) from separate genealogies were largely assimilated into the white majority culture of the U.S.A. Therefore, my standpoint is primarily influenced by Kanaka ‘Ōiwi and white-U.S.A. cultures, both mediated in the context of an international diaspora, as I describe below.

Mo‘okū‘auhau Pili ‘Āina and Hālau ‘Ike

Here, I briefly summarize mo‘okū‘auhau pili ‘āina (genealogy of land connections) and mo‘okū‘auhau hālau ‘ike (disciplinary genealogy). I was born on the homelands of the Patwin

and Miwok Peoples (in the area currently referred to as Davis, California, U.S.A.) with my upbringing and grade-school education beginning there at César Chávez Spanish Immersion School. My grade-school education then continued at the North American-curriculum international schools where my parents taught: International School Bangkok, which is on land first settled by the Tai People (Nonthaburi, Thailand); Colegio Internacional Puerto la Cruz, which is on/neighbors lands of the Kalina/Kariña, Waikerí, and Taíno Peoples (Barcelona, Venezuela); and American School of Doha, which is on land of the Indigenous Arab Peoples (Doha, Qatar). I then earned a B.S. in Environmental Engineering from Northwestern University, which is situated on lands of the Peoria, Bodwéwadmi (Potawatomi), Myaamia, Očhéthi Šakówiŋ, Hoocąk, and Kiikaapoi (Kickapoo) Peoples (Evanston, Illinois, U.S.A.). After graduating, I lived and worked as an environmental engineer on lands of the Tséstho'e (Cheyenne), Očhéthi Šakówiŋ, hinono'eino' biito'owu' (Arapaho), Núu-agha-tʉvʉ-pʉ̲ (Ute), and Ndé Kónitsąąíí Gokíyaa (Lipan Apache) Peoples (Denver and Aurora, Colorado, U.S.A.). Now, I am currently earning a Ph.D. in Environmental Science from Hokkaido University (Sapporo, Japan), which is within Ainu Mosir, the homelands of Ainu People. From these moʻokūʻauhau I establish my kuleana and kūlana as a diasporic (displaced and transient settler) Kanaka ʻŌiwi environmental scientist.

These moʻokūʻauhau clarify the combination of my experience in conventional science and engineering with sources of Indigenous Knowledges, ways of Knowing, and ways of Being. For me, these sources include kūpuna, ʻōlelo noʻeau, the unique worldview understood through ʻōlelo Hawaiʻi, oral histories and recordings, environmental observations, naʻau (intestines, mind, heart), ʻike ʻohana (family Knowledge), Traditional Ecological Knowledges, and so on.

These various moʻokūʻauhau-derived ways of Knowing and Being are therefore integrated into this trans-disciplinary academic and cultural methodology.

Moʻokūʻauhau Limu: Macroalgal Research Motivations

Next, I discuss how my moʻokūʻauhau motivated my interest in pursuing a Ph.D. degree program in which I investigate macroalgal biogeochemistry and Blue Carbon more specifically. Because of my moʻokūʻauhau, I have had a life-long relationship with coastal environments, with an awareness of and concern for the impacts of climate change since early childhood. It is also relevant that through an ʻŌiwi worldview, the environment and sea are not resources for extraction but rather living ʻāina and akua (elemental gods) that feed and sustain people. According to this worldview, they must be respected and cared for within sustainable, mutual relationships (McGregor et al., 2003). This context provided my broad motivation for initially studying environmental engineering and then narrowing my interests to marine biogeochemistry for a graduate degree.

Regarding macroalgae specifically, limu (seaweed, as well as other submerged plants or algae) are an important part of ʻāina in Hawaiʻi and provide an example of how ʻāina sustains Kānaka both nutritionally and culturally (Abbott, 1978). Even in the diaspora, my upbringing has always included seaweed as a food source. Various limu species (e.g., limu kohu, līpoa, paheʻe, and līpalu) are also featured in mele (songs) such as "Ka Uluwehi O Ke Kai" by Aunty Edith Kanakaʻole, popularly performed during kanikapila (impromptu music playing sessions) including in my ʻohana. Other important cultural roles include limu kala in hoʻoponopono (family conferences to set relationships right) and the food kapu (restriction, consecration) on pakaiea (a particular limu) for ʻohana with a manō (shark) ʻaumakua (deified ancestor).

In the Kalākaua version of the Kumulipo ("He Kumulipo"), the importance of limu is also established from a moʻokūʻauhau perspective by appearing in the first era, long before Kānaka, and only after coral polyps, earthworms, sea urchins, and shellfish are born (Keaulumoku, 1700; Liliʻuokalani, 1897; Kanahele, 2011). All told, "He Kumulipo" explicitly names the birth of the following limu in the sea, along with their respective inland forest kiaʻi (protectors): ʻēkaha, ʻakiʻaki, manauea, kōʻeleʻele, puakī, kīkala moa, limu kele, limu kala, līpuʻupuʻu, loloa, nē, and hulu waena. In fact, there are up to 149 documented traditional names for various limu in ʻōlelo Hawaiʻi, with more names likely known historically (Abbott & Williamson, 1974).

Taken together, limu have a strong importance to Kānaka ʻŌiwi in general, and also to me personally. This also motivates my deeper connection to and interest in macroalgal cultivation specifically, compared to other climate change mitigation strategies such as geological sequestration. Even other Blue Carbon ecosystems such as mangroves, which are an invasive and harmful species in Hawaiʻi (Möhlenkamp et al., 2018), cannot hold the same cultural meaning to me as macroalgae. This reality that mangroves may have Blue Carbon value yet be ecologically damaging in Hawaiʻi underscores the fact that social-ecological health can be better understood through place-based genealogies and culture rather than a narrow fixation on accounting services such as Blue Carbon.

Summary

This case study reflects on and honors my moʻokūʻauhau as a way to understand my research kūlana and kuleana, so this framing and process is most relevant to other Kānaka ʻŌiwi researchers. Other Indigenous scientists will have their own Traditions and methodologies that

similarly incorporate genealogies but should be sure to root their work in the specific values of their own cultures. Likewise, non-Indigenous geoscientists can turn to the social sciences for more general methodologies, such as auto-ethnography. Broadly, these genealogical relationships and histories are critically relevant to geoscientists because they inform the rights a researcher has to conduct research and the responsibilities that a researcher has to the local land.

In my case, based on my cultural worldview and genealogies, combined with formal experience (academic and professional) as an environmental engineer, I developed a motivation for pursuing research on macroalgal dissolved organic carbon in relation to its Blue Carbon potential (i.e., its potential to meaningfully contribute to climate change mitigation through carbon sequestration). Despite the many potential research areas with as great or greater potential to contribute to climate change mitigation or other positive contributions to society, my moʻokūʻauhau were essential to motivating (through cultural values) my engagement in this specific field and will continue to shape my motivations going forward.

These genealogies give me the rights and obligations to do this research in a way that empowers Indigenous sovereignty. However, they also limit how and where I can responsibly do research—an aspect that conventional geoscience commonly overlooks. Conventional geoscientists too often assume that their academic degrees give them the right to conduct any kind of science anywhere. Instead, we must look back to where we came from to see where we are allowed to go.

Part Three: An ʻUpena of Pilina Worldview

The intrinsic relationship between moʻokūʻauhau and key ʻŌiwi ethics means moʻokūʻauhau are of primary importance in understanding one's kuleana within an ʻupena of pilina (fishing net of social-ecological relationships; Osorio, 2021). In Osorio's conceptualization, each intimate cord that connects Kānaka to each other and to ʻāina needs nurturing to keep our social-ecological systems healthy. This relational worldview is also reflected in modern ʻŌiwi science by integrating written and oral histories of Traditional Ecological Knowledge in marine (Puniwai, 2020) and terrestrial (Kamelamela et al., 2022) ecosystem restoration toward the goal of ʻāina momona—"thriving and productive communities of people, place, and natural resources" (Andrade et al., 2022). New Indigenous Knowledge is also generated through rigorous and intimate observation (Puniwai et al., 2016; Morishige et al., 2018; Andrade & Morishige, 2022). More broadly, the worldview of lōkāhi refers to the balance between humans, ʻāina, and spirits, but again, this balance is dependent on the agency of the kuaʻāina (backbone of the land) who cultivate land and culture in the countryside (McGregor, 2007). Unfortunately, modern imbalances have resulted in a period of hulihua (upheaval, turning), manifestly visible through the hōʻailona (signs) of climate change and other global crises (McGregor et al., 2020).

This ʻŌiwi relational view of social-ecological balance is wholly distinct from the worldview of modern "western" environmentalism that separates humans and the natural environment (McGregor, 2007) and so the distinction deserves explicit emphasis. The European concept of nature espoused by conventional conservationists is genealogically linked to the ideas of Alexander van Humboldt (1769–1859). While van Humbodlt critiqued Spanish colonization in South America and expressed some sympathy and respect toward Indigenous Peoples, he and

those who were inspired by him (including Charles Darwin, Henry David Thoreau, George Perkins Marsh, and John Muir) championed ideas of conserving or preserving a "wilderness" that was isolated from inherently negative human impacts (Wulf, 2015). Ultimately, this idea of nature as an isolated recreational space was far from benign and was weaponized in the violent displacement of Indigenous Peoples from their homelands—all in the names of conservation and preservation (Dunbar-Ortiz, 2014; Bennett et al., 2021; Xego & Obioha, 2021).

However, from many Indigenous perspectives, one cannot visit nature because nature is not and cannot be separate from society, and this is reflected in our languages. Actually, in ʻōlelo Hawaiʻi there is no word for nature in the sense of an outdoor environment (Pukui & Elbert, 1986). The closest word to nature or the environment is ʻāina, which again literally means those who sustain or feed, a definition that requires mutual relationships between Indigenous Peoples, non-human beings, and the lands, air, and waters. These relationships are not trivial given that 80% of the world's biodiversity is protected by Indigenous Peoples (Garnett et al., 2018) and that environmental stewardship by Indigenous Peoples is quantifiably more effective than other conservation strategies (Dawson et al., 2021).

In fact, in ʻŌiwi Indigenous statecraft, social-ecological systems were defined by a deep and complex pilina between humans and ʻāina that sustainably supported intense populations (up to 1 million people, comparable to modern numbers) for at least hundreds of years (Beamer, 2014; Osorio, 2021). For example, within an ahupuaʻa (social-ecological community, with boundaries organizing resource access and kuleana) there was productive equilibrium between loko iʻa (multi-trophic fishponds cultivating fish, shellfish, and limu), loʻi kalo (taro fields), and areas kapu (forbidden, sacred, protected) to resource use (Keala et al., 2007, Beamer, 2014; Winter et al., 2018). Moreover, the complexities of the biocultural resource management systems

extended to the scale of moku (social-ecological region or district) within an island (Winter et al., 2018). This shows why it is useful to look to our histories of Indigenous sovereignty to envision future decolonization.

When considering these social-ecological relationships and systems, it is also important to be clear that the Kingdom of Hawai‘i was a multi-ethnic sovereign Indigenous Nation. Therefore, a future Indigenous government of Hawai‘i can and should be multi-ethnic while still centering Kānaka ‘Ōiwi sovereignty and social-ecological relationships, Value systems, and worldviews. More specifically, Nitasha Tamar Sharma (Hawai‘i-born Indian-Jewish settler) discusses the ways Hawai‘i has been a haven for Black People (including Black Kānaka ‘Ōiwi) as well as the ways anti-Black racism still needs to be confronted (Sharma, 2021). Such havens are not only compatible with, but necessary for the joint struggle toward Black and Indigenous sovereign liberation and are critical threads in this vision of an ‘upena of pilina. The expansive concept of an ‘upena of pilina forces us to understand how the biocultural and social-ecological elements of an ahupua‘a or moku system conceptually and meta-physically form a decolonial future that is co-created.

Case Study: Macroalgal Blue Carbon in An ‘Upena of Pilina

In this research methodology, I focus on ‘Ōiwi ethics as articulated through an ‘upena of pilina because it focuses on the importance of deep relationships between and amongst Indigenous Peoples and the land within a complex fishing net whose cords need constant tending. This interconnected and multi-faceted framing helps bring together many ‘Ōiwi Values into a more integrated and holistic worldview. This conceptualization also helps serve as a reminder of the various cords that must be tended. This framing emphasizes that all projects, no

matter how well or ethically executed, are simply one piece in a greater collaborative effort. Understanding and articulating one's positionality within an ʻupena of pilina is therefore important for being an effective and ethical part of greater efforts and communities.

Indeed, this positionality of centering ʻŌiwi ethics has specific implications for macroalgal Blue Carbon research. For example, much discussion surrounding macroalgal Blue Carbon includes large-scale projects either for biofuels, off-shore kelp forests, or even deep-sea biomass sinking, all of which have a substantially weaker or non-existent social-ecological relationship between people and macroalgae. Such projects are generally antithetical to a Kanaka ʻŌiwi worldview, at least as they are currently articulated by non-Indigenous people. Some of their specific limitations and negative consequences, as well as broader questions surrounding carbon dioxide removal (CDR) projects, have also been highlighted in the scientific literature (e.g., Morrow et al., 2020; Boyd et al., 2022; Ricart et al., 2022).

Despite the need for greater funding and empowerment for sovereign Indigenous cultivation of macroalgae, monetization of Blue Carbon credits could result in perverse outcomes. I critique the coloniality of the broader Blue Carbon credit market in greater depth in Chapter 6 of this dissertation but highlight a few key points here. Cautionary examples can be seen in the history of terrestrial carbon offset projects, with tensions between the government and Indigenous control (Asiyanbi, 2016), as well as uneven benefits (Poudyal et al., 2016). More fundamentally, there is increasing recognition of the need to move beyond the transactional context of ecosystem services accounting (Pascua et al., 2017). By looking to the successful social-ecological systems of Hawaiʻi, it becomes clear that macroalgal Blue Carbon must exist within a sustainable and productive context of an ʻupena of pilina and not simply a narrow fixation on sequestering carbon at the expense of all else.

This conceptualization is also helpful for conveying that if the pilina connecting macroalgal cultivation to the rest of the ʻupena are frayed or broken, or if macroalgal cultivation is attempted outside the ʻupena—outside the boundaries of the ahupuaʻa—then such activities are not contributing to the long-term, sustainable health of the social-ecological system. Therefore, ʻŌiwi sustainable aquaculture and agriculture systems serve as important examples of ecomimicry (Winter et al., 2020) and a circular economy (Beamer et al., 2021) for not only re-establishing a social-ecological equilibrium but also for achieving far greater productivity and independence than the present-day colonial system has been able to provide.

Indigenous cultivation of macroalgae is also important beyond Hawaiʻi, as demonstrated by modern and historical accounts. However, I do not have the positionality or relationality to discuss the specifics of other Indigenous social-ecological systems. While I am engaging in discussions with local and Ainu People, it is not within my authority to be specific regarding historical or current efforts by or prioritized interest of Ainu People to engage in macroalgal cultivation. However, my efforts to bridge knowledge gaps regarding macroalgal dissolved organic carbon dynamics and its potential Blue Carbon role, may offer some value to macroalgal cultivation by Ainu People. For example, macroalgal dissolved organic carbon could be considered a culturally-relevant proxy for coastal social-ecological health and quantitative data insights could help guide Indigenous coastal management and monitoring. Therefore, it will be important to communicate relevant results to Ainu communities and maintain an active role to ensure that any Blue Carbon funding is re-directed to Ainu People in Hokkaido over larger-scale industrial and commercial interests. This also represents an opportunity to grow relationships between ʻŌiwi and Ainu Peoples that will persist far beyond the scope of my research project. Building solidarity amongst sovereign Indigenous Peoples by sharing Traditional Ecological

Knowledges of seaweed cultivation can be an important component of the global Land Back movement.

Summary

I have kuleana to these places and environments because my research is based in, related to, and has benefitted from them. Therefore, I must be active in providing relevant Knowledge and advocacy for sovereign Indigenous cultivation of social-ecological systems and their contributions to Blue Carbon. However, this relational framing also confronts the value of transactional carbon offsets and ecosystem services accounting. Instead, the central objective should be Indigenous social-ecological health, with Blue Carbon only acting as a supporting tool, if at all.

The result of articulating my standpoint through ʻŌiwi methodologies and re-centering macroalgal biogeochemistry toward decolonization can also be expressed in a new ʻōlelo noʻeau that will guide my research: "Makahanalimukaikeea". Consistent with other ʻōlelo noʻeau, there are various kaona (hidden meanings) embedded in the phrase, but one translation offered here is as follows: "There is life and sovereignty in the work of seaweed". This kuleana must not only benefit Kānaka ʻŌiwi in Hawaiʻi but also other Indigenous Peoples worldwide in their efforts for sovereign coastal management and cultivation.

Part Four: Conclusions and Recommendations

My methodology is informed by both various personal moʻokūʻauhau (pili koko, pili ʻāina, and hālau ʻike) and "He Kumulipo" more broadly. My ways of Knowing are guided by extensive ʻŌiwi scholarship on research methodology, culture, Values, Traditional Ecological Knowledges, and environmental science, combined with ʻike naʻau and ʻōlelo noʻeau. My hālau ʻike also includes academic and professional experience in conventional environmental science and engineering. These various sources of Knowledges, Values, and ways of Being, provide me with the motivation to research macroalgal biogeochemistry and Blue Carbon sequestration potential, within a framework that centers research objectives and outcomes around Indigenous Peoples and sovereignty. In particular, greater consideration of social-ecological ethics (as expressed here through an ʻupena of pilina worldview) and systems (as evidenced by the moku and ahupuaʻa systems of Hawaiʻi) can lead to a deeper awareness of whether and how one's research advances a sustainable and just future or maintains conventional settler-colonial systems of extraction, oppression, and the separation of humans from "nature". From an ʻŌiwi perspective, just as research is ceremony (Wilson, 2008), research is—and must be—aloha ʻāina.

To guide other geoscientists, I offer three reflective questions. For one, geoscientists should continuously address the question "What are my obligations, rights, and responsibilities here?". Understanding one's research standpoint clarifies responsibilities to and authority within scientific, social, and environmental communities. We must also ask "How does my research perpetuate settler-colonialism?" and "How can my research advance Black and Indigenous sovereign liberation?".

In fact, the answers to these questions can and should be embedded in published research manuscripts as they are particularly relevant to the introduction (objectives and motivations) as

well as the discussion (applications, implications, and conclusions). Just as it is now conventional to frame the relevance of geoscientific results within the context of climate change, sustainability, or other global environmental crises, so too should basic research be framed within the trans-disciplinary context of ongoing colonialism.

For geoscientists broadly, we not only can, but must ensure our research is advancing decolonization. Colonialism is inseparable from the climate crisis (Táíwò & Cibralic, 2020; Ghosh, 2021; Sultana, 2022a; Sultana, 2022b) as well as issues of environmental justice and racism (Bullard, [1990] 2018; Whyte, 2018; Gilio-Whitaker, 2019). Research attempting to solve or mitigate these issues as strictly geophysical or environmental is deeply incomplete without a concurrent effort toward decolonization. Colonialism is not sustainable.

To conclude, this process of articulating a research methodology facilitated deeper investigations of my moʻokūʻauhau, kūlana, kuleana, and pilina, thereby re-orienting my research toward deliberately advancing decolonization and sovereign Indigenous cultivation of seaweed through aloha ʻāina. In doing so, this chapter hopes to help more Indigenous scientists conduct science in a way that is true to themselves and their communities. If all geoscientists apply these concepts according to their unique contexts and their own standpoint-derived obligations, we can make truer progress toward the inseparable objectives of decolonization, Black and Indigenous sovereign liberation, and a thriving planet.

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CHAPTER TWO

Kelp dissolved organic carbon release is seasonal and annually enhanced during senescence

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Abstract

Macroalgae influence local and global biogeochemical cycles through their production of dissolved organic carbon (DOC). Yet, data remain scarce and annualized estimates are typically based on high growth periods without considering seasonal variability. While the mechanisms of active exudation and passive leakage need clarifying, ecophysiological stress is known to enhance DOC release. Therefore, DOC leakage from seasonally senescent macroalgae may be overlooked. This study focuses on the annual kelp *Saccharina japonica* var. *religiosa* (class Phaeophyceae) from Oshoro Bay, Hokkaido, Japan. Three years (2020–2022) of seasonal data were collected and analyzed, with least squares mean DOC release rates established for kelp (n = 88) across 16 incubation experiments ($t \geq 4$ d, DOC samples ≥ 1 d^{-1}) under different photosynthetically active radiation (PAR) treatments (200, 400, 1200, or 1500 µmol photons · m^{-2} · s^{-1}). Differences in PAR, dry weight biomass (g DW), sea surface temperature, or salinity could not explain DOC release rate variability, which was high between individual kelp. Instead, there were significant intra-annual differences, with mean DOC release rates (mg C · g^{-1} DW · d^{-1}) (± standard error between n kelp) higher during the autumn "late decay" period (0.71 ± 0.10, n = 27) compared to the winter "early growth" period (0.14 ± 0.025, n = 10) and summer "early decay" period (0.25 ± 0.050, n = 24). This relationship between seasonal senescence and macroalgal DOC release is further evidence that long-term, place-based studies of DOC dynamics are essential and that global extrapolations are premature.

Introduction

Macroalgal dissolved organic carbon (DOC) has important roles in local and global biogeochemistry (Wada & Hama, 2013; Powers et al., 2019; Lønborg et al., 2020). Locally, kelp can elevate seawater DOC concentrations by nearly 50% within kelp forests (Pfister et al., 2019). In general, DOC can physically alter the marine environment by absorbing ultraviolet (UV) radiation (Blough & Del Vecchio, 2002) and interacting with chemical pollutants (Sánchez-Marín et al., 2010). DOC reactivity varies across a spectrum from labile to recalcitrant (including semi-labile, semi-refractory, refractory, and ultra-refractory) (Hansell, 2013) that depends on biotic and abiotic processes (Wada et al., 2015, Powers et al., 2020). If DOC is bioavailable and consumed by microheterotrophs within days or weeks, it can stimulate local bacterial activity—thereby increasing respired carbon dioxide (CO_2) and decreasing oxygen concentrations (Newell & Lucas, 1981; Azam et al., 1994; Halewood et al., 2012). On the other hand, macroalgal-derived recalcitrant DOC (Wada et al., 2008; Watanabe et al., 2020; Buck-Wiese et al., 2023) may contribute to global carbon sequestration via the microbial carbon pump (Jiao et al., 2010). However, this potential role is still uncertain (Gallagher et al., 2022; Xiong et al., 2024) and difficult to account (Hurd et al., 2022; Pessarrodona et al., 2023; Hurd et al., 2024). Nevertheless, DOC outwelling by coastal vegetated ecosystems does contribute to ocean DOC reservoirs (Santos et al., 2021), which are significant components of the global carbon cycle (Carlson & Hansell, 2015). Overall, macroalgal DOC is a key parameter to understanding marine biogeochemistry at multiple scales.

Macroalgal DOC release is an ecophysiological response (Hurd et al., 2014) that is variably stimulated as an active exudation or passive leakage process (Weigel & Pfister, 2021), with conflicting and complex interactions reported by mechanistic studies, and substantial

reliance on phytoplankton models (e.g., Fogg et al., 1965) as discussed in Paine et al. (2021). The "overflow hypothesis" posits that DOC exudation is enhanced when photosynthesis outpaces growth requirements (Fogg, 1983; Nagata, 2000). Alternatively, macroalgal DOC release has been correlated with a variety of environmental factors including desiccation (Wyatt et al., 2014), salinity fluctuations (Pregnall, 1983; Kirst, 1996; Hurd et al., 2014; Zhao et al., 2023), distal tissue erosion and fragmentation (Johnston et al., 1977; Newell et al., 1980), UV exposure (Viñegla et al., 2006; Rothäusler et al., 2011; Laturnus et al., 2010), tissue photobleaching (Aguilera et al., 1999; Bischof & Rautenberger, 2012), variable irradiance (Reed et al., 2015), saturating irradiance (Powers et al., 2019), high CO_2 concentrations (Iñiguez et al., 2016a; Diaz-Pulido & Barrón, 2020), heat stress (Iñiguez et al., 2016b; Egea et al., 2023), nitrogen limitation (Mizuta et al., 1994; Weigel & Pfister, 2021; Paine et al., 2023a), and iron limitation (Paine et al., 2023b). Passive leakage can occur throughout all growth stages, but may be enhanced during cell lysis, fragmentation, or senescence, as well as osmotic stress (García-Robledo et al., 2008; Agustí & Duarte, 2013; Hurd et al., 2014). Variable in situ exposure to these interactive stress factors may explain high individual variability in reported DOC release rates even under the same experimental conditions. For example, Abdullah and Fredriksen (2004) comment that the incubations that had a relatively weaker correlation between DOC release rate and biomass illustrated "the variable 'condition' of the plant". Disentangling these variables remains difficult, and one alternative may be to broadly assess seasonal patterns in DOC release as they relate to an annual life-cycle of growth and senescence.

In fact, the seasonal relationship between dissolved organic matter (DOM) extracellular leakage from "mature and distal tissue" has long been known in macroalgae such as *Laminaria* sp. (Johnston et al., 1977), but the lack of seasonal replication and bias toward perennial species

remain key data gaps. While macroalgal DOC studies have been published since the 1960s (Khailov & Burlakova, 1969; Sieburth, 1969), few are based on more than one or two sampling events, and only a handful have collected multi-year seasonal data (e.g., Abdullah & Fredriksen, 2004; Wada et al., 2007; Reed et al., 2015; Paine et al., 2023a). The proposed drivers of kelp DOC release seasonality include primary production for *Laminaria hyperborea* (Abdullah & Fredriksen, 2004) and *Ecklonia cava* (Wada et al., 2007), and nitrogen availability for *Ecklonia radiata* (Paine et al., 2023a), but statistical significance was not established. Reed et al. (2015) reported no seasonality or difference between growing, mature, and senescent *Macrocystis pyrifera* blades. However, because these studies were on perennial kelp these results may not be generalizable to annual kelp. Even so, in situ seasonal patterns in seawater DOC concentrations have been broadly linked to annual *Saccharina japonica* growth and decay stages in large-scale integrated multi-trophic aquaculture systems in China (Mahmood et al., 2017; Li et al., 2018). Quantitative seasonal attribution remains speculative since most incubation experiments have been single events aimed at studying microbial bioavailability and recalcitrant characteristics of DOC for carbon sequestration estimations (Zhang & Wang, 2017; Li et al., 2022; Zhang et al., 2022). Only Gao et al. (2021) has conducted seasonal (winter and spring) incubation experiments in the context of DOC release by kelp in large-scale mariculture. This overall scarcity of empirical data has resulted in synthesis papers making annualized generalizations based on few or no seasonal data (e.g., Barrón et al., 2014). Estimates based on limited data therefore critically overlook essential seasonal, environmental, and biological variations, including senescent passive leakage.

Beyond uncertainties in kelp DOC release rates at the seasonal and individual scales, there remains little certainty regarding the linearity of kelp DOC release or the validity of

calculating release rates from an initial and final value as is the case in most studies. Potential non-linearity was reported by Wada et al. (2007) whose incubation experiments were 54–102 h but standardized release rate calculations to 30 h due to an apparent saturating effect. Zhang and Wang (2017) conducted a 20 d incubation experiment on *Ulva prolifera* (Ulvophyceae) in the summer that demonstrated potential non-linearity similar to Wada et al. (2007). Pregnall (1983) established linearity of DOC release from *U. prolifera*, but only for 3 h incubations. In earlier short-term experiments (< 6 h), Moebus and Johnson (1974) attributed non-linearity of DOC release from *Ascophyllum nodosum* (Phaeophyceae) and *Fucus vesiculosus* (Phaeophyceae) to natural wounds or damage induced during collection and handling. While non-linearity may be a consequence of the incubation method and needs to be distinguished from non-linearity that would occur in situ (Brylinsky, 1977; Carlson & Carlson, 1984), artificially stressed DOC release rates can still provide useful insights. Yet, Wada et al. (2007) and Zhang and Wang (2017) reported DOC release rates based only on the initial and final values, thus discounting the internal non-linearity. All other reviewed studies on DOC release from macroalgae in the Phaeophyceae class only collected initial and final DOC samples and could not comment on the linearity of release. This represents a significant knowledge gap and uncertainty in reported rates.

To address this need for kelp DOC release studies that investigate release rate variability at the scales of inter-annual, seasonal, individual kelp, and incubation period linearity, this study conducted 16 sampling events and incubation experiments ($t \geq 4$ d, sample frequency ≥ 1 d^{-1}) seasonally (4 to 6 times per year) over three years (2020–2022). The subject of this study was the kelp *Saccharina japonica* var. *religiosa* (class Phaeophyceae), collected from Oshoro Bay. *S. japonica* var. *religiosa* is a prostrate kelp that has a primarily annual life history, with some biennial exceptions observed at Oshoro Bay (Funano, 1983). Briefly, sorus formation peaks in

autumn, embryonal sporophytes can be observed in late autumn or early winter, maximum biomass and lengths of 1–2 m are attained by early summer, and then biomass declines due to grazing, erosion, and natural senescence in autumn (Funano, 1983; Abe et al., 1985; Agatsuma et al., 2000; Yotsukura et al., 2019). This kelp forms dense beds in Oshoro Bay that are mainly monospecific, with some *Costaria costata* (class Phaeophyceae) and *Undaria pinnatifida* (class Phaeophyceae) interspersed, and cover approximately 500 m^2 along the northeastern shelf edge as well as 1000 m^2 in the southeastern portion of the surveyed area (Figure 2.1). Previous and concurrent data analyzed by our laboratory indicate that *S. japonica* var. *religiosa* C:N ratios are typically between 8–11 (maximum of 13) at Oshoro Bay, without significant seasonal differences (Kudo, unpublished). For context, a C:N ratio less than 10 generally indicates nitrogen sufficiency and above 20 indicates nitrogen limitation (Hurd et al., 2014). The global mean molar ratio of seaweed C:N is 20 based on 495 species (Sheppard et al., 2023). Given the lack of seasonal variability in nitrogen content, any seasonal variations in DOC release are likely due to other seasonally variable environmental parameters (e.g., in situ temperature, salinity, or photoperiod) or the seasonal cycle of growth, senescence, and reproduction.

Because mechanistic attributions of seasonal patterns in DOC release to specific drivers is highly complex, the objective here was to instead determine whether 3 years of seasonal data was sufficient to reveal significant seasonal patterns in DOC release that have remained obscured by high individual variability and insufficient seasonal replication in the existing literature. Based on the preceding background information, this study therefore assesses the following six hypotheses, in order of importance:

- Hypothesis 1: Kelp DOC release varies seasonally in an annual pattern;
- Hypothesis 2: After controlling for seasonality, kelp DOC release rate variability is partly

explained by PAR stress above saturation irradiance;

- Hypothesis 3: Variable kelp biomass between or within sampling events will partly explain DOC release rate variability;
- Hypothesis 4: Individual kelp DOC release rate variability is high within a single sampling event;
- Hypothesis 5: Kelp incubated for at least 4 d will exhibit an initial "healthy" DOC release rate, a later "stressed" DOC release rate, and a significantly elevated DOC release rate if death occurs;
- Hypothesis 6: Seasonal extremes in environmental parameters such as salinity, temperature, or photoperiod will partly explain DOC release rate variability.

Materials and Methods

Place-based research standpoint and methodology

Well-defined research methodologies (which are informed by epistemology, ontology, and axiology) are foundational to meaningful and ethical science, particularly in terms of understanding objectives and broader impacts (Smith, [1999] 2021; Wilson, 2008; Oliveira & Wright, 2016; Walter & Andersen, 2016). There is also growing precedent in the marine and environmental sciences for scientists to be clear about their place-based and standpoint-derived obligations to the peoples and lands their science impacts (Liboiron et al., 2018; Alegado et al., 2023). This includes the broader and coupled obligations of science to advance decolonization (i.e., Black and Indigenous sovereign liberation) and confront climate coloniality (Yusoff, 2018; Liboiron, 2021a; Sultana, 2022a, 2024; Carlson, 2025; Jacobs et al., 2025). The place-based (e.g., Kawai et al., 2012; Kaminaga, 2018; Grunow et al., 2019; Ishihara, 2020; Uzawa, 2020)

standpoint and methodology underlying this research is therefore an intrinsic and essential component of this study and is described in Chapter 1 of this dissertation (Carlson, 2025).

In brief, the lead author's research standpoint in this study is as a Kanaka ʻŌiwi (Native Hawaiian) environmental scientist in Ainu Mosir (the Indigenous homeland of Ainu people). Based on this, the methodology of this research program is to conduct macroalgal biogeochemistry experiments that increase basic scientific knowledge toward relevant insights for Indigenous stewards globally. For example, a key motivation of this study is to provide insights into the factors underlying seasonal macroalgal DOC release variability to help Indigenous coastal stewards anticipate variable local DOC accumulation and plan for ecological implications. The explicit implications of this study's findings within the context of Indigenous science and social–ecological stewardship (e.g., Morishige et al., 2018; Winter et al., 2018; Bennett et al., 2021; Jacobs et al., 2022) will be discussed in Chapter 6 (Carlson, 2024) and the Summary of this dissertation.

Field site

Oshoro Bay is home to Hokkaido University's Oshoro Marine Biological Station and offers several advantages in terms of year-round field sampling and relevance to this study's objectives. Located on the west coast of the Shakotan Peninsula (Figure 2.1), it is largely protected from wind and waves due to rocky cliffs, with an inlet facing northwest. Tidal level differences on the Sea of Japan coast are also relatively small, creating good habitat for marine flora and fauna as well as facilitating collection and measurement activities. Due to the shallow habitat (less than 1 m of seawater) and warm Tsushima current, annual sea surface temperatures have a strong seasonal pattern and fluctuate significantly from 5 °C in the winter to above 20 °C

in the summer (Motoda, 1971; Motoda et al., 1987; Yotsukura, 2021; Figure 2.2). The shallow, sub-tidal ecosystem along the southwestern portion of Oshoro Bay is home to dense kelp beds of *S. japonica* var. *religiosa* in the spring and summer, with other macroalgae and sea urchins dominating in late autumn and winter. Habitats as shallow as this are not uncommon for *S. japonica*, but *S. japonica* var. *religiosa* and other variants can also commonly be found at depths up to 10 m (Yotsukura et al., 2019; Kawai & Sugawara, 2020). The surveyed area is delimited by the temperature and salinity sampling points shown in Figure 2.1.

Field sampling

Field surveys to collect whole kelp individuals for ex situ incubation were completed 16 times. This included three surveys in winter (January 2020, early March 2020, and January 2021), four surveys in spring (late March 2020, March 2021, April 2021, and May 2022), four surveys in summer (June 2020, August 2020, July 2021, and July 2022), and five surveys in autumn (October 2020, October 2021, November 2021, October 2022, and November 2022). Kelp samples were detached from the underlying rocky substrate (typical holdfast depth of 30–50 cm) along the northeastern shelf edge (Figure 2.1). Tidal motion was seasonally variable, typically 5–10 cm $\cdot$ s^{-1} in the spring and summer before increasing to a maximum of up to 30–40 cm $\cdot$ s^{-1} in the winter. Care was taken to minimize damage to the holdfast and kelp samples were transported in a polyethylene bag with in situ seawater to our laboratory on the Hokkaido University campus in Sapporo within a few hours of collection (42 km drive). Each sampling event incubated $n = 6$ kelp in separate incubation tanks, except the winter events due to minimal biomass (January 2020: $n = 2$, January 2021: $n = 4$, and early March 2020: $n = 4$). In the October 2021 sampling event, death occurred in $n = 3$ kelp, and only data from the $n = 3$ live kelp are

included in the primary datasets and figures (Table 2.1, Table S2.1, Figure S2.1).

In situ sea surface temperature and salinity field probe measurements were taken at eight locations within the macroalgal bed area and one reference location within the bay (Figure 2.1). Acid-washed 18-L polyethylene tanks were filled with pre-screened (100 μm mesh) seawater collected from the reference location within the bay. The reference location was a pier on the northeast side of Oshoro Bay about 100 m from the kelp bed sampling location (Figure 2.1) for all sampling events except August 2020, October 2020, and July 2022, when seawater was collected in the bay by a small fishing boat (Figure 2.1). The 18-L holding tanks of reference seawater served as the stock for the 3-L tanks used in the laboratory incubation experiments.

Incubation experiment

After returning to our laboratory in Sapporo, kelp samples were gently rinsed with seawater from the reference point outside the macroalgal bed area. Rinsing was done to reduce the effect of DOC released during transportation and to reduce epibiota such as attached microalgae or grazers, while minimizing disruptions to the kelp microbiome. The kelp samples were then placed in clear polystyrene tanks filled with approximately three liters of the same reference seawater, fully submerging the kelp while leaving approximately two liters of headspace. The top of each tank was covered in a plastic wrap. Tank seawater volumes were confirmed by weight.

Kelp and control tanks of reference seawater were incubated at the in situ sea surface temperature for t = 4–9 d and sampled at least once per day, with the rationale for the different incubation periods provided as follows and summarized in Table 2.1 and Table S2.1. To account for the variable sampling frequency and length, kelp DOC release rates were calculated as least

squares means of all samples collected throughout an incubation period. Table S2.1 provides the statistical information and variable incubation method parameters (incubation duration *t* and PAR treatment level) for each linear regression (n = 88 kelp incubation experiments). The release rates therefore are daily rates that represent average DOC dynamics between day and night and should be distinguished from results from shorter term incubations that report hourly day-time or night-time release rates separately. Further details on these calculations are provided in the section on DOC calculations.

In general, the relatively long incubation periods were chosen to assess the linearity of kelp DOC release rates, with the understanding that potential nutrient depletion (Okazaki et al., 2022) or other stress conditions might reveal an early "healthy" or "nutrient sufficient" rate and a later "stressed" or "nutrient depleted" rate (Weigel & Pfister, 2021; Paine et al., 2023a). In the first experiment, the longest incubation time (t = 9 d) in January 2020 was chosen due to the minimal biomass and the expected low DOC release rate. Second, the incubation period of t = 7 days was applied from early March 2020 through January 2021 to discern potential non-linearity, as previously described. Third, the incubation period was reduced to t = 5–6 d for March 2021 through July 2021 when separate phases were not discernible from previous data. Fourth, the reduction to t = 4 d was based on the expectation that the higher PAR treatment (1200 µmol photons · m^{-2} · s^{-1}) in the October 2021 through November 2022 experiments might lead to higher DOC release rates and oversaturation.

The potential effect of irradiance on DOC release rates was tested in each of the sampling events (n = 16 events) by treating half of the incubated kelp to a lower irradiance treatment and half to a higher irradiance treatment. The lower irradiance exposure was 200 µmol photons · m^{-2} · s^{-1} from artificial LED sources for all sampling events. The higher irradiance exposures varied

and were 400 (incubation experiments from January 2020 to July 2021) or 1200 (incubation experiments from May 2022 through November 2022) µmol photons · m^{-2} · s^{-1} from artificial LED. The increase in the higher PAR treatment for the 2022 experiments was done to verify whether the lack of a significant difference in DOC release rates according to the previous PAR treatment values (200 and 400 µmol photons · m^{-2} · s^{-1}) was due to an insufficiently high PAR. The artificial cool white LED light sources were controlled by a light/dark timer set according to the actual daylight hours (photoperiod) (Figure 2.2b). Incubation experiments on the rooftop of the laboratory building were conducted in October and November 2021 to test the effect of natural irradiance relative to concurrent indoor artificial LED incubation experiments. Average measurements (Biospherical Instruments Quantum Scalar Irradiance Meter) of outdoor rooftop irradiance levels were 2000 (October 2021) and 1500 (November 2021) µmol photons · m^{-2} · s^{-1}.

Because the *S. japonica* var. *religiosa* bed was shallow (less than 50 cm depth), dense, and subject to tidal motion, in situ sub-surface irradiance was variable and certain in situ kelp would be periodically exposed to direct irradiance. Therefore, the 200 µmol photons · m^{-2} · s^{-1} irradiance was representative of kelp subject to dense community shading, 400 µmol photons · m^{-2} · s^{-1} was representative of submerged kelp not subject to community shading, and 1200 µmol photons m^{-2} s^{-1} was an upper limit representative of kelp periodically exposed by tidal motion to direct irradiance on a sunny day. Maximum above water irradiance on sunny summer days was approximately 2500 µmol photons · m^{-2} · s^{-1}. It is also noted that, while kelp typically remained submerged in situ and were not subject to prolonged direct air exposure, even minor desiccation could stimulate enhanced DOC release (Paine et al., 2021).

Two 3-L control tanks of filtered reference seawater were also incubated, one on each

tier. These control samples assessed the potential for DOC contamination from the incubator environment or during the sampling process, as well as any detectable DOC trends due to plankton activity or free-living bacteria in the seawater. Incubated control seawater DOC concentrations showed no evidence of accumulation, despite some fluctuations within the incubation periods that were considered to be within the analytical variability or heterogeneity of the incubation tank (Figure S2.1).

At the end of the incubation, kelp wet weight was measured by weighing the incubation tank before and after removing the kelp sample, in addition to confirming the wet weight on aluminum foil before drying. The removed kelp samples were then dried at 60 °C on aluminum foil until a constant dry weight was achieved, typically after 4 to 5 d. DOC release results for each kelp were normalized by their respective dry weight.

Seawater sample storage and DOC analysis

In general, seawater sample storage and DOC analysis followed best practices consistent with Halewood et al. (2022). Seawater samples from the incubation tanks were taken with a 25-mL syringe and immediately filtered through a pre-combusted (450 °C for 5 hours) 0.7 µm Whatman glass-fiber filter (GF/F). The syringes were rinsed with 4-mL seawater samples three times before taking a 50-mL sample. The decreasing volume in the tank was accounted for to normalize the increasing DOC concentrations throughout the incubation period, and the final seawater volume was confirmed by weight at the end of the incubation. The seawater samples were frozen at −30 °C in 60-mL amber borosilicate glass sample bottles until analysis. The bottles were cleaned before use, first in a 2% neutral detergent bath (Wako Contaminon N), followed by a 1.2 M HCl bath, then pre-combusted at 550 °C for 5 hours.

All seawater samples were analyzed for DOC by a total organic carbon analyzer (Shimadzu TOC-5000A or TOC-V) according to the high-temperature combustion method. DOC samples were acidified by adding 100 µL of 2 M HCl to ensure the pH was lower than 3 and that dissolved inorganic carbon (DIC) would be removed after sparging for 10 minutes. Each sample was injected into the combustion column at least 3 times with a coefficient of variation (CV) within 2%.

Potassium hydrogen phthalate was used to make a standard stock solution of 8.3×10^4 µmol · L^{-1} (1000 mg · L^{-1}) DOC. The standard stock solution was typically diluted to concentrations between 42 and 2.7×10^3 µmol · L^{-1} DOC (0.5–32 mg · L^{-1}) to calibrate the analyzer with a five or six point linear regression model (100 µL analytical injections). For higher concentrations, standard stocks up to 3.3×10^4 µmol · L^{-1} DOC (400 mg · L^{-1}) were used to calibrate separate five point linear regression models (13 µL analytical injections). In general, the analyzer was initially conditioned with Milli-Q, standard potassium hydrogen phthalate samples, and seawater standards. Subsequently, Milli-Q and standard samples were checked after analyzing five seawater samples. Other methods of ensuring replicability included re-analyzing samples within or between analysis runs. CV greater than 2% or significant deviations between standard sub-samples triggered re-conditioning or maintenance before proceeding. To assess spatial heterogeneity of DOC within the incubation tanks, triplicate DOC samples were collected from each of the (n = 6) kelp tanks at the end (t = 4 d) of the November 2021, May 2022, July 2022, October 2022, and November 2022 incubation experiments (Figure S2.2).

DOC calculations

Kelp-derived DOC inventory (mg C · g^{-1} DW) refers to the mass of DOC (mg C) in the

incubation tanks attributable to the kelp holobiont (i.e., relative to the corresponding control tank DOC inventory and inclusive of kelp microbiome DOC dynamics [Bengtsson et al., 2011]) at an elapsed incubation time *t* and normalized by the kelp dry-weight biomass (g DW). It is calculated as follows:

$$\text{Kelp-derived DOC inventory}_t = \frac{(C_{\text{kelp},\,t} - C_{\text{control},\,t}) \times V_t}{\text{Kelp biomass}}$$

where C_t is the concentration of DOC (mg · L^{-1}) in the seawater sample collected at an elapsed incubation time *t* and *V* is the volume of seawater in the kelp incubation tank at time *t* (i.e., the seawater volume decreased 62 mL after every collected sample).

Mean kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) (± *SE* between kelp replicates) were calculated as least squares means from linear regressions of elapsed incubation time and the corresponding kelp-derived DOC inventory (mg C · g^{-1} DW). To address the potential of variable incubation times to impact DOC release rate calculations, the least squares means method and simple moving average method were graphically and statistically compared (Figure S2.3, Figure S2.4, Appendix S2.1). All calculated rates and supporting statistical parameters are summarized in Table S2.1.

Statistical analyses

A two-way fixed factor analysis of variance (ANOVA) tested the effect of season and qualitative irradiance level (low, medium, or high) on DOC release rates using Type-II sums of squares for an unbalanced design (Appendix S2.1, Appendix S2.2, Appendix S2.3). Statistical significance (ANOVA, $p < 0.05$) of individual linear regressions between bulk DOC release rates (mg C · d^{-1}) and biomass (g DW), as well as between normalized DOC release rates (mg C · g^{-1} DW · d^{-1}) and individual environmental parameters (PAR, photoperiod, sea surface temperature,

or salinity) were determined for the four seasonal groupings. PAR was experimentally manipulated with two treatment levels within each incubation experiment, so linear regressions were also tested (ANOVA, $p < 0.05$) between normalized DOC release rates and quantitative irradiance levels (200, 400, 1200, or 1500 µmol photons · m^{-2} · s^{-1}) within each sampling event. A two-way fixed factor ANOVA tested the effect of using a standardized simple moving average (e.g., standardizing to a 4 d incubation length) or the least squares method on DOC release rates, with season as an interactive effect using Type-I sums of squares for a balanced design (Appendix S2.1, Figure S2.4). Code for the statistical analyses performed in the software program R (version 4.3.1) are included in the supplemental materials.

Results

Seasonal DOC release

To quantitatively test significant intra-annual differences, the aggregated data was separated according to the four boreal seasons (based on equinox dates). In terms of overall biomass trends and peak biomass being reached between June and July (Figure 2.2a), the four seasonal categories can also be ascribed qualitative "growth stage" labels, as follows: winter (early growth), spring (late growth), summer (early decay), and autumn (late decay). Mean (± *SE* between *n* kelp) DOC release rates (mg C · g^{-1} DW · d^{-1}) were also determined for eight bi-seasonal periods for additional insights, as follows: early winter ($n = 6$ kelp), late winter ($n = 4$), early spring ($n = 12$), late spring ($n = 12$), early summer ($n = 18$), late summer ($n = 6$), early autumn ($n = 15$), and late autumn ($n = 12$) (Figure 2.3).

The two-way ANOVA results indicated that irradiance treatment (low, medium, or high) was not a significant factor ($df = 2$, error $df = 79$, $F = 0.098$, $p = 0.90$) while season was a

significant factor ($df = 3$, error $df = 79$, $F = 6.14$, $p = 0.00083$). Tukey's Honest Significant Differences (HSD) pairwise tests then confirmed the significant differences ($p < 0.05$) were between the autumn "late decay" (0.71 ± 0.10 mg C · g^{-1} DW · d^{-1}) seasonal period and the winter "early growth" (0.14 ± 0.025 mg C · g^{-1} DW · d^{-1}, $p = 0.0050$) and summer "early decay" (0.25 ± 0.050 mg C · g^{-1} DW · d^{-1}, $p = 0.0017$) seasonal periods (Figure 2.3, Figure S2.1, Appendix S2.2). Conducting the same two-way ANOVA test with eight bi-seasonal groupings indicated bi-seasonal grouping was also a significant factor ($df = 7$, error $df = 75$, $F = 2.97$, $p = 0.0083$). Tukey HSD pairwise tests confirmed the differences were between late autumn and early winter (t value = 3.15, $p = 0.044$), late autumn and early summer (t value = 3.13, $p = 0.046$), and late autumn and late summer (t value = 3.34, $p = 0.026$) (Appendix S2.3).

Intra-annual variation was also assessed by comparing the percent difference between an individual sampling event's mean DOC release rate and the weighted annualized mean (0.36 mg C · g^{-1} DW · d^{-1}). This percent difference was as high as $215\% \pm 64\%$ (November 2022, $n = 6$) and the DOC release rate from a single kelp sample was up to 529% higher (March 2021, "high light kelp 1") than the weighted annualized mean (Figure S2.5). Based on seasonal averages, mean DOC release rates from multiple sampling events only conducted during a single seasonal period would have deviated from the weighted annualized mean by $-62\% \pm 7\%$ in winter "early growth" ($n = 10$), $+11\% \pm 27\%$ in spring "late growth" ($n = 24$), $-32\% \pm 14\%$ in summer "early decay" ($n = 24$), or $+95\% \pm 28\%$ in autumn "late decay" ($n = 27$) (Figure S2.5).

DOC release and irradiance

When controlling for the confounding impact of season, there were no statistically significant (ANOVA, $p < 0.05$) linear relationships between photoperiod (hours) and kelp DOC

release rates (mg C · g^{-1} DW · d^{-1}) in winter ($p = 0.34$, $df = 1$, error $df = 8$, $F = 1.05$), spring ($p = 0.45$, $df = 1$, error $df = 22$, $F = 0.58$), summer ($p = 0.10$, $df = 1$, error $df = 22$, $F = 2.95$), or autumn ($p = 0.30$, $df = 1$, error $df = 25$, $F = 1.11$) results (Figure S2.6).

Overall, there were no significant (ANOVA, $p < 0.05$) linear relationships between PAR levels (i.e., 200, 400, 1200, or 1500 µmol photons · m^{-2} · s^{-1}) and DOC release rates when analyzing results from winter ($p = 0.78$, $df = 1$, error $df = 8$, $F = 0.083$), spring ($p = 0.95$, $df = 1$, error $df = 22$, $F = 0.0046$), summer ($p = 0.11$, $df = 1$, error $df = 22$, $F = 2.77$), and autumn ($p = 0.87$, $df = 1$, error $df = 25$, $F = 0.026$) separately (Figure 2.4a) or within any of the individual sampling events (Figure 2.4b). This included the November 2021 experiment, which compared the effect of 200 µmol photons · m^{-2} · s^{-1} from artificial LED sources to natural, roof-top irradiance of 1500 µmol photons · m^{-2} · s^{-1} ($p = 0.44$, $df = 1$, error $df = 4$, $F = 0.73$).

DOC release and kelp biomass

Mean biomass (grams dry weight per individual) of the incubated kelp varied consistent with its annual life cycle (± *SE* between *n* kelp replicates), reaching an inter-annual mean peak biomass in early summer of 8.2 ± 0.89 g DW · ind^{-1} ($n = 18$) (Figure 2.2a). Individual linear regressions between DOC release rates (mg C · ind^{-1} · d^{-1}) and biomass (g DW · ind^{-1}) within each sampling event were significant (ANOVA, $p < 0.05$) in four of the 16 experiments: March 2021 ($p = 0.030$, $R^2 = 0.73$, $df = 1$, error $df = 4$, $F = 10.94$), July 2021 ($p = 0.048$, $R^2 = 0.66$, $df = 1$, error $df = 4$, $F = 7.93$), November 2021 ($p = 0.0011$, $R^2 = 0.95$, $df = 1$, error $df = 4$, $F = 70.34$), and May 2022 ($p = 0.041$, $R^2 = 0.69$, $df = 1$, error $df = 4$, $F = 8.89$) (Table S2.2). When aggregating results seasonally, linear regressions were significant (ANOVA, $p < 0.05$) in winter ($p = 0.0023$, $R^2 = 0.73$, $df = 1$, error $df = 8$, $F = 19.36$), spring ($p = 0.016$, $R^2 = 0.73$, $df = 1$, error

df = 22, *F* = 6.84), summer (*p* = 0.020, R^2 = 0.73, *df* = 1, error *df* = 22, *F* = 6.30), and autumn (*p* = 0.032, R^2 = 0.73, *df* = 1, error *df* = 25, *F* = 5.13) results (Figure 2.5).

Variability of DOC release between individual kelp

Mean DOC release rates varied from a low of 0.075 ± 0.023 mg C · g^{-1} DW · d^{-1} (*n* = 6) in August 2020 to a high of 1.1 ± 0.23 mg C · g^{-1} DW · d^{-1} (*n* = 6) in November 2022 (Figure 2.6a). Variability in DOC release rates between individual kelp was quantified as coefficients of variation (CV) for each sampling event. November 2021 (late autumn, *n* = 6) results showed the least variation between kelp DOC release rates with a CV of 26%. March 2021 (early spring, *n* = 6) results had the highest CV of 148%. Calculating a mean CV for each bi-seasonal category indicated that early spring had the highest average variability (± *SE* between *n* = 3 events) of 103% ± 22% and late autumn had the lowest average variability (± *SE* between *n* = 2 events) of 38% ± 12% (Figure S2.7). Each sampling event CV was also aggregated into four seasonal averages (± *SE* between *n* events) as follows, winter: 62% ± 9% (*n* = 3 events), spring: 93% ± 19% (*n* = 4 events), summer: 77% ± 15% (*n* = 4 events), and autumn: 61% ± 15% (*n* = 5 events) (Figure 2.6b).

Linearity of kelp DOC release rates

All kelp samples enhanced the DOC inventory relative to the initial inventory and to the concurrent control inventories (Figure 2.6a and Figure S2.1). Triplicate DOC samples were collected at the end (*t* = 4 d) of the November 2021–November 2022 kelp incubation experiments and the CV of each set of triplicates represents the spatial heterogeneity of DOC within the corresponding incubation tank. Mean CV (± *SE* between *n* = 6 sets of triplicates) were

4.3% ± 0.89% (November 2021), 3.5% ± 0.75% (May 2022), 5.0% ± 3.0% (July 2022), 2.1% ± 0.46% (October 2022), and 3.3% ± 0.80% (November 2022) (Figure S2.2).

Regressions of DOC accumulation over the corresponding incubation period for each individual kelp (n = 88) were significantly (ANOVA, $p < 0.05$) linear for 80 of the 88 kelp incubations (Table S2.1). DOC release from the dead kelp in October 2021 followed three phases. In the first phase (t = 0–1 d), DOC release rates were comparable to other autumn results (1.8 ± 0.37 mg C · g^{-1} DW · d^{-1} , n = 3). In the second phase (t = 1–2 d), DOC release was unprecedentedly high (88 ± 24 mg C · g^{-1} DW · d^{-1} , n = 3). In the third phase (t = 2–4 d), DOC release was negative or stable (−4.6 ± 3.8 mg C · g^{-1} DW · d^{-1} , n = 3) (Figure S2.1). The extremely high DOC release upon death was more than an order of magnitude higher than the highest individual DOC release rate recorded from live kelp (2.3 mg C · g^{-1} DW · d^{-1}, March 2021) (Table S2.1, Figure S2.1).

Variability of ambient seawater parameters

Sea surface temperature varied from 5.1 ± 0.17 °C in January 2020 to 23.5 ± 0.17 °C in August 2020 (Figure 2.2c). When controlling for the confounding impact of season, there were no significant linear relationships (ANOVA, $p < 0.05$) between sea surface temperature (°C) and kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) in winter (p = 0.37, R^2 = 0.10, df = 1, error df = 4, F = 0.90), spring (p = 0.79, R^2 = 0.0034, df = 1, error df = 4, F = 0.074), summer (p = 0.10, R^2 = 0.12, df = 1, error df = 4, F = 3.03), or autumn (p = 0.35, R^2 = 0.034, df = 1, error df = 4, F = 0.89) results (Figure S2.8).

Salinity varied from 28.9 ± 0.3 in late March 2020 to 33.7 ± 0.09 in July 2021 (Figure 2.2d). When controlling for the confounding impact of season, there were no significant linear

relationships (ANOVA, $p < 0.05$) between salinity and kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) in winter ($p = 0.29$, $R^2 = 0.14$, $df = 1$, error $df = 4$, $F = 1.31$), spring ($p = 0.96$, $R^2 = 1\times10^{-4}$, $df = 1$, error $df = 4$, $F = 0.0029$), summer ($p = 0.97$, $R^2 = 7\times10^{-5}$, $df = 1$, error $df = 4$, $F = 0.0016$), or autumn ($p = 0.46$, $R^2 = 0.022$, $df = 1$, error $df = 4$, $F = 0.57$) results (Figure S2.9).

Mean incubated in situ seawater DOC concentrations (± *SE* of *n* samples during the given incubation) varied from a low of 66 ± 3.7 µmol · L^{-1} ($n = 8$) in January 2020 to a high of 87 ± 1.0 µmol · L^{-1} ($n = 12$) in July 2022. There were no significant paired differences (two-tail paired *t*-tests) in mean DOC concentrations between control seawater incubated at lower or higher irradiances in winter ($p = 0.61$, $df = 1$, two-tail critical $t = 12.71$), spring ($p = 0.43$, $df = 3$, two-tail critical $t = 3.18$), summer ($p = 0.17$, $df = 3$, two-tail critical $t = 3.18$), or autumn ($p = 0.13$, $df = 4$, two-tail critical $t = 2.78$). The mean CV (± *SE*) over the course of the incubation experiments were 6.5% ± 1.0% ($n = 16$ events) for DOC concentrations in control tanks treated to lower irradiance, 5.3% ± 0.65% ($n = 15$ events) for higher irradiance treatments, and 5.9% ± 0.62% ($n = 31$) overall. These fluctuations were likely due to a combination of minor spatial heterogeneities within the incubated control seawater and phytoplankton and bacterial DOC dynamics.

Discussion

Seasonal DOC release

The primary hypothesis that kelp DOC release would vary seasonally was confirmed by significantly higher autumn rates during senescence across three annual cycles (Figure 2.3). Seasonally variable parameters such as kelp biomass or in situ temperature, salinity, and photoperiod were not primary factors in explaining variability. Seasonal nitrogen limitation is a

significant factor in DOC release from some kelp (Weigel & Pfister, 2021; Paine et al., 2023a), with reported exceptions (Reed et al., 2015), but *S. japonica* var. *religiosa* from Oshoro Bay had year-round nitrogen sufficiency in concurrent analyses (Kudo, unpublished). Active exudation mechanisms such as herbivory defense (Abdullah & Fredriksen, 2004), desiccation prevention (Wyatt et al., 2014), and UV protection (Swanson & Druehl, 2002) are not expected to be enhanced in autumn. However, sorus formation in *S. japonica* var. *religiosa* peaks in October at Oshoro Bay (Abe et al., 1982) and the release of gametes and zoospores has been linked to enhanced DOC release in other kelp (Brawley et al., 1999; Swanson & Druehl, 2002; Li et al., 2018). While the following discussion of the literature indicates a stronger link between DOC release and senescence or tissue stress, this remains an important ecophysiological relationship.

Autumn senescence is considered the strongest explanatory factor based on the theory of DOC leakage by cell lysis or senescence being a primary mechanism of DOC release in phytoplankton (Agustí & Duarte, 2013) and likely parallel mechanisms in macroalgae (Paine et al., 2021). Macroalgal specific studies on substantial DOC leakage as mucilage during distal decay and tissue fragmentation (Johnston et al., 1977; Newell et al., 1980; García-Robledo et al., 2008; Leclerc et al., 2013), from "withered" (Kubo & Tanaka, 2023) or "rotting" kelp (Li et al., 2018), from detritus or wrack (Ramshaw et al., 2017; Perkins et al., 2022), as well as from microbially-mediated degradation of kelp-derived particulate organic carbon (POC) releasing additional DOC (Dyer et al., 2019; Feng et al., 2022; Li et al., 2023) generally support this theory. However, precise methods do not exist for differentiating between active and passive processes (Paine et al., 2021). In our study, kelp tissue was physically weakened, eroding, and fragmenting due to grazing and senescence in the autumn, indicating the relevance of the preceding studies in explaining enhanced DOC release.

Alternatively, several seasonal studies did not find higher DOC release in the autumn, during non-growth months, or for senescent tissue. Reed et al. (2015) did not find a significant relationship between growing, mature, and senescent kelp tissue and DOC release rates. However, they note that perennial *Macrocystis* "blades are short-lived (~50–100 d) and rapidly transition through growth, maturation, and senescence" (Reed et al., 2015; Rodriguez et al., 2016). Paine et al. (2023a) collected juvenile sporophytes of the perennial kelp *E. radiata* (Wernberg et al., 2019) across seasons. This was based on a previous finding that DOC release was not significantly different between juvenile and mature sporophytes (Paine et al., 2023c), but they did not assess senescent tissue. *E. cava* is also a perennial species (Serisawa et al., 2001), but Wada et al. (2007) indicate that the "release rate of POC was highest in October when the biomass of *E. cava* considerably declines in Oura Bay (Yokohama et al., 1987)". Most kelp may have been senescent in the autumn, yet only one kelp was incubated for the autumn DOC release experiment (Wada et al., 2007), limiting conclusions. Based on our results, senescence is a confounding variable that should not be overlooked in perennial kelp DOC release.

DOC release and irradiance

While light regulates photosynthesis and therefore macroalgal growth (Raven & Hurd, 2012), there are conflicting reports regarding its role in macroalgal DOC release. Several studies have demonstrated higher day-time compared to night-time DOC release (Sieburth, 1969; Haas et al., 2011; Reed et al., 2015; Weigel & Pfister, 2021). Coastal darkening due to turbidity can also reduce DOC production (Blain et al., 2021). On the other hand, there was no difference in DOC release by *Nereocystis luetkeana* (Phaeophyceae) under low or high light levels (Weigel & Pfister, 2021). Mueller et al. (2016) found that low light reduced DOC release by Caribbean turf

algae in ambient but not nutrient enriched seawater. DOC release rates from *Sargassum thunbergii* (Phaeophyceae) increased under short-term step-wise increases in PAR (0, 20, 40, 80, 160, 320, 640 and 1500 μmol photons · m^{-2} · s^{-1}), but were only significantly different between the two lowest and two highest levels (Zhao et al., 2023). These results indicate that, under nutrient sufficiency, macroalgal DOC release may increase up to the saturation irradiance level, after which DOC release is stable until a potential stress threshold is reached.

Contrary to the expectations of the second hypothesis, there were no relationships between PAR level and DOC release (Figure 2.4). This conclusion is based on no overall linear relationship after controlling for season (Figure 2.4a), on paired comparisons from 15 sampling events (excluding October 2021) (Figure 2.4b), and no paired effect of natural irradiance relative to artificial irradiance in the November 2021 experiment (Figure 2.4b). Based on photosynthesis-irradiance curves for *S. japonica* from Borlongan et al. (2020), photosynthesis was likely saturated at 200 μmol photons · m^{-2} · s^{-1} and additional active exudation of DOC due to photosynthate overflow at higher irradiances was not expected (Iñiguez et al., 2016a; Diaz-Pulido & Barrón, 2020). The lack of the expected stress response (enhanced passive leakage of DOC) may be attributable to the shallow habitat and apparent acclimatization to higher irradiance (Gerard, 1988). In contrast, kelp at greater depths (e.g., *M. pyrifera*) have highly spatially varied light environments (Gerard, 1984) and 13% of the variability in their DOC production has been statistically attributed to sea surface irradiance (Reed et al., 2015). Therefore, our finding of no stress induced DOC release at irradiance levels an order of magnitude beyond saturation irradiance (but still representative of potential in situ exposure) may only be characteristic of shallow, light adapted kelp.

DOC release and kelp biomass

The assumption of approximate proportionality between biomass and DOC release is reflected in the standard use of biomass normalized DOC release rates. However, high variability in biomass normalized DOC release rates as reported in previous studies indicates that "DOC release changes independently of the variation of their biomass" (Wada et al., 2007). Other studies have likewise concluded that seasonal macroalgal physiology is a more relevant factor than biomass in explaining DOC release variability (Paine et al., 2023a). Individual *S. japonica* var. *religiosa* may vary in terms of reproductive stage, holdfast weight, and stipe length (Abe et al., 1985). However, the macroalgal blade is the primary source of DOC release, and variably degraded blade tissue condition has been associated with variable DOC release in the context of iron limitation (Paine et al., 2023b). Therefore, individual biomass should explain a portion of DOC release rate variability, with deviations suggesting an ecophysiological response.

Partially meeting the expectations of the third hypothesis, linear regressions between kelp biomass (g DW) and individual kelp DOC release (mg C $\cdot$ ind^{-1} $\cdot$ d^{-1}) were significant across seasons, but only explained 24% and 22% of the individual DOC release rate variability in spring and summer, respectively, and only 14% of the variability in autumn (Figure 2.5). This indicates that the mechanism driving elevated autumn DOC release was a variable condition independent of biomass between individual kelp, such as stage of senescence (Rodriguez et al., 2016), and not a uniform factor such as ambient seawater temperature, salinity, or nutrient availability. In addition, only four of the 16 sampling event data sets demonstrated a significant linear relationship between biomass and DOC release rate (Table S2.2), although this may be attributed to the relatively small sample sizes.

Variability of DOC release between individual kelp

Confidence in previously reported seasonal trends of macroalgal DOC release is undermined by moderate to high individual DOC release rate variability. Fundamentally, higher coefficients of variation (CV) for biological replicates obscure what might otherwise be significant differences in experimental variables. While CV have not been directly reported or discussed by other studies for macroalgal DOC release rates, it is broadly understood as a relevant evaluation metric in aquatic ecosystem experiments (Conquest, 1983). In broad ecological applications, CV values within 30% have been discussed as acceptable or normal (Isensee, 1976; Giddings & Eddlemon, 1979). CV values above this indicate that additional replication may be necessary to discern significant differences. We determined CV values for previous studies where this back calculation was readily possible and found most to be above the 30% threshold. CV between reported *E. cava* DOC release rates within a single incubation event were high in August (78%) and May (77%), but low in April (17%) and December (8%) (Wada et al., 2007). The CV for average day and night results (across spring, summer, and autumn) from *L. hyperborea* were 83% and 80%, respectively (Abdullah & Fredriksen, 2004). Individual variability in *Sargassum horneri* DOC release was moderately high in February (CV = 34%) and March (CV = 42%) (Watanabe et al., 2020). Individual variability in *S. japonica* DOC release was also moderately high in January (CV = 43%) and April (CV = 32%) (Gao et al., 2021). Until the factors driving high individual DOC release rate variability can be disentangled, it may be advisable to increase replications at multiple scales.

Consistent with the expectations of the fourth hypothesis and the results of previous studies (Johnston et al., 1977; Abdullah & Fredriksen, 2004; Wada et al., 2007; Reed et al., 2015; Gao et al., 2021; Weigel & Pfister, 2021), individual variability between kelp was

particularly high for certain incubation experiments in this study. Spring, summer, and autumn each had a sampling event with a CV over 100% (March 2021: 148%, June 2020: 111%, and October 2020: 112%). Similarly to Wada et al. (2007), variability appeared to be independent of season (e.g., their spring results varied from 17%–77%), and seasonal differences in mean CV were not significant in our study (Figure 2.6b). The relatively high seasonal averages between 61%–93% in this study, indicate that individual variability is a year-round phenomenon not attributable to seasonal factors. In addition, this high variability means that multi-year seasonal data remains critical to determining significant patterns in macroalgal DOC dynamics.

Linearity of kelp DOC release rates

We first considered potential confounding factors in assessing linearity of release. Analytical variability was constrained to CV within 2%, so CV in replicate DOC samples represent the spatial heterogeneity of DOC within the incubation tank. Mean CV (± *SE*) for a given incubation experiment were at most 5.0% ± 3.0% (July 2022) and otherwise about 2–4% (Figure S2.2). This is considered acceptable as Wada et al. (2007) reported a CV in triplicate DOC samples of 7.5 ± 6.5% from their kelp incubation experiments. Therefore, any non-linear release should be reflective of the actual DOC dynamics and not of analytical or spatial variability.

Contrary to the expectations of the fifth hypothesis, nearly all incubation experiments demonstrated statistically significant linear relationships in terms of DOC accumulation as a function of elapsed incubation time. The eight non-linear results are attributed to (1) the minimal biomass in early winter, (2) two negligibly low DOC release rates in March 2021, and (3) to a saturation-like effect in three incubations (one each from late March 2020, March 2021, and

November 2022) (Figure S2.1). Graphical analyses showed that, across seasons, rates tended to be biased high in the initial incubation period ($t < 1$ d) and stable afterwards (Figure S2.3). To assess the effect of variable incubation periods on calculated rates, a two-way ANOVA with season as an interactive effect compared a simple moving average standardized to a $t = 4$ d incubation period for all experiments to the least squares means method. There were no significant differences between methods (ANOVA, $p = 0.20$, $df = 1$, error $df = 162$, $F = 1.64$) (Appendix S2.1). The use of DOC release rates calculated from a simple 4 d average rate did not alter the conclusions regarding significant seasonal variability. The two-way ANOVA results using the simple average rates indicated that irradiance treatment (low, medium, or high) was not a significant factor ($df = 2$, error $df = 79$, $F = 0.21$, $p = 0.81$) while season was a significant factor ($df = 3$, error $df = 79$, $F = 4.11$, $p = 0.0092$) (Appendix S2.1). Therefore, results using the least squares means method are reported as they are not as susceptible to biases as a simple moving average from a single incubation time (Drobnitch et al., 2017; Martin et al., 2018). The potential for non-linear outliers and scarcity of experiments assessing linearity (Wada et al., 2007) for other species or environments suggests that mean DOC release rates should not solely be calculated from an initial and final value.

In addition, the extremely high DOC release from dead kelp was consistent with the fifth hypothesis. Fragmented, detrital, and senescent kelp are important sources of DOC (Newell et al., 1980; Krumhansl & Scheibling, 2012; Pedersen et al., 2020; Kubo & Tanaka, 2023) that can facilitate transport beyond continental shelfs (van der Mheen et al., 2024). However, it is not known how DOC release rates from whole kelp may change at the moment of death. Our results clarify this knowledge gap and show three distinct phases in DOC release (Figure S2.1), described as follows:

1. Stressed Phase (t = 0–1 d): The kelp were likely still alive but stressed, releasing relatively high rates of DOC that were still comparable to other autumn results (1.8 ± 0.37 mg C · g^{-1} DW · d^{-1} , n = 3);
2. Initial Death Response Phase (t = 1–2 d): The extreme DOC release during the following period was a short-term response upon death. The nearly two orders of magnitude in difference between DOC release from naturally decaying (but otherwise healthy) kelp and dead kelp in October 2021 is also an indication that tissue death had not unknowingly occurred in samples from other sampling events (88 ± 24 mg C · g^{-1} DW · d^{-1} , n = 3);
3. Post-Death Phase (t = 2–4 d): There was a negative DOC rate indicating net consumption. If DOC continued to be passively exuded from the dead kelp, it was apparently outweighed by the likely substantially enhanced (although unquantified) microbial consumption of DOC (−4.6 ± 3.8 mg C · g^{-1} DW · d^{-1} , n = 3).

Other reported values of kelp DOC release rates (± *SE*) comparable to this extreme rate of 88 ± 24 mg C · g^{-1} DW · d^{-1} from dead kelp include the June 2004 result of 30 ± 6.2 mg C · g^{-1} DW · d^{-1} in Wada et al. (2007). Wada et al. (2007) explained this order of magnitude higher result as being due to the "leakage of the intracellular organic constituents" and that it was "likely that the algae were weakened by the confinement by the experimental bag". The review by Paine et al. (2021) notes that the highest macroalgal DOC release rates are from desiccated seaweed. Specifically, *Cladophora glomerata* (class Chlorophyceae) was reported to release DOC at 292 ± 14 mg C · g^{-1} DW · d^{-1} after 6 hours of desiccation compared to 41 ± 6.2 mg C · g^{-1} DW · d^{-1} when continuously wet (Wyatt et al., 2014). This notably indicates that what is considered a healthy DOC release from some Chlorophyceae is comparable to multiple reported

rates from extremely stressed Phaeophyceae species.

DOC release and ambient temperature or salinity stress

Contrary to the expectations of the sixth hypothesis, linear regressions of ambient sea surface temperature and salinity with DOC release rates in our study were not significant in any season. We expected a potential summer stress response because the August 2020 temperature (23.5 °C) represents an exceedance of the historically typical maximum temperature (22 °C) at Oshoro Bay (Motoda, 1971; Motoda et al., 1987; Yotsukura, 2021), although it is not unprecedented (e.g., 24.3 °C in August 2018) (Fujii et al., 2021). Experiments on the effect of elevated temperatures have had mixed results including significantly higher DOC release for *Laminaria solidungula* (Iñiguez et al., 2016b), a summer shift to a negative DOC flux in *Caulerpa prolifera* (Egea et al., 2023), no effect on *S. thunbergii* (Zhao et al., 2023), no effect on *Saccharina latissima* (Iñiguez et al., 2016b), and no winter effect in *C. prolifera* (Egea et al., 2023). Ecophysiological responses to ocean warming (Pessarrodona et al., 2018) are also fundamentally different from those to marine heatwaves (and analogous short term experimental manipulations). The conflicting effects of higher temperatures should be given additional attention and disentangled from confounding variables such as depleted seawater nutrients in late summer (Nakata et al, 2001; McPhee-Shaw et al., 2007).

While no intra-seasonal relationships were found for salinity and DOC release, this may be because the greatest salinity differential was from 31.0 in early March 2020 to 28.9 in late March 2020. In contrast, a previous study at Oshoro Bay associated a drop in seawater salinity (30 to 12 within one week) and concurrent seawater temperature increase in the spring of 1999 with increased susceptibility for bacterial infection resulting in severe lesions and thallus

bleaching on *S. japonica* var. *religiosa* (Vairappan et al., 2001). Salinity values of about 20–25 are typically associated with spring snow melt runoff and infiltration at Oshoro Bay, with lower values linked to short-term responses (e.g., salinity 10.8 after a large autumn storm event) (Fujii et al., 2021). Other studies generally report higher DOC release with decreasing salinity, with species-specific or salinity range exceptions. Zhao et al. (2023) reported enhanced DOC release from *S. thunbergii* when salinity dropped from 30 to 20 (but not from 35 to 30), while Pregnall (1983) reported a linear regression between salinity values (5, 10, 20, 25, and 30) and DOC release from *U.* (*Enteromorpha) prolifera*. Chen et al. (2023) found a significant difference in DOC release rates between salinity values of 5 and 30 for *Gracilaria lemaneiformis*, *S. thunbergii*, and *Ulva lactucta*, but no significant difference for *U.* (*E.) prolifera* or *Pyropia haitanensis*. From these results, a relative (e.g., ≥ 5) drop in salinity or fluctuation below a threshold (e.g., 25) does not universally induce a significant DOC response in marine macroalgae. Yet, there is also value in the increased confidence that smaller fluctuations than these, such as in our study (28.9–33.7), have not been shown to constitute sufficient osmotic stress in terms of DOC release.

Conclusion

This study showed statistically significant seasonal differences in kelp DOC release rates between the autumn "late decay" period and the winter "early growth" and summer "early decay" periods that were not attributable to variations in individual kelp biomass; ambient salinity, sea surface temperature, or photoperiod; or experimental irradiance treatments. The role of ecophysiological stress in stimulating DOC release was demonstrated by an order of magnitude higher result from dead kelp. Based on these results and existing knowledge of kelp

DOC release mechanisms, annual senescence is considered the most likely driver of the significant variability in this study. We also make two methods recommendations: (1) to verify linearity of DOC release and report least squares mean rates where appropriate, and (2) to quantify individual macroalgal "replicate" variability with coefficients of variation to facilitate comparisons between studies. Annualizing non-seasonal data or extrapolating DOC release from primary production remains a fundamentally flawed approach, particularly when the role of passive senescent leakage is overlooked. Instead, the complex variability of macroalgal DOC release highlights the need for year-round, long-term, place-based studies.

Acknowledgements

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Tables and Figures

Table 2.1. Summary of variable incubation experimental conditions.

Incubation period (d)	**Paired PAR treatments (μmol photons · m^{-2} · s^{-1})**	**Incubated kelp**
$t = 4$ October 2021– November 2022	200 (artificial LED) and 400 (artificial LED) January 2020–July 2021	$n = 2$ January 2020
$t = 5$ March 2021	200 (artificial LED) and 1200 (artificial LED) May 2022–November 2022	$n = 4$ Early March 2020, January 2021
$t = 6$ April 2021, July 2021	200 (artificial LED) and 2000 (natural) October 2021	$n = 6$ All other sampling events (October 2021 incubated $n = 3$ live kelp and $n = 3$ dead kelp)
$t = 7$ Early March 2020– January 2021	200 (artificial LED) and 1500 (natural) November 2021	
$t = 9$ January 2020		

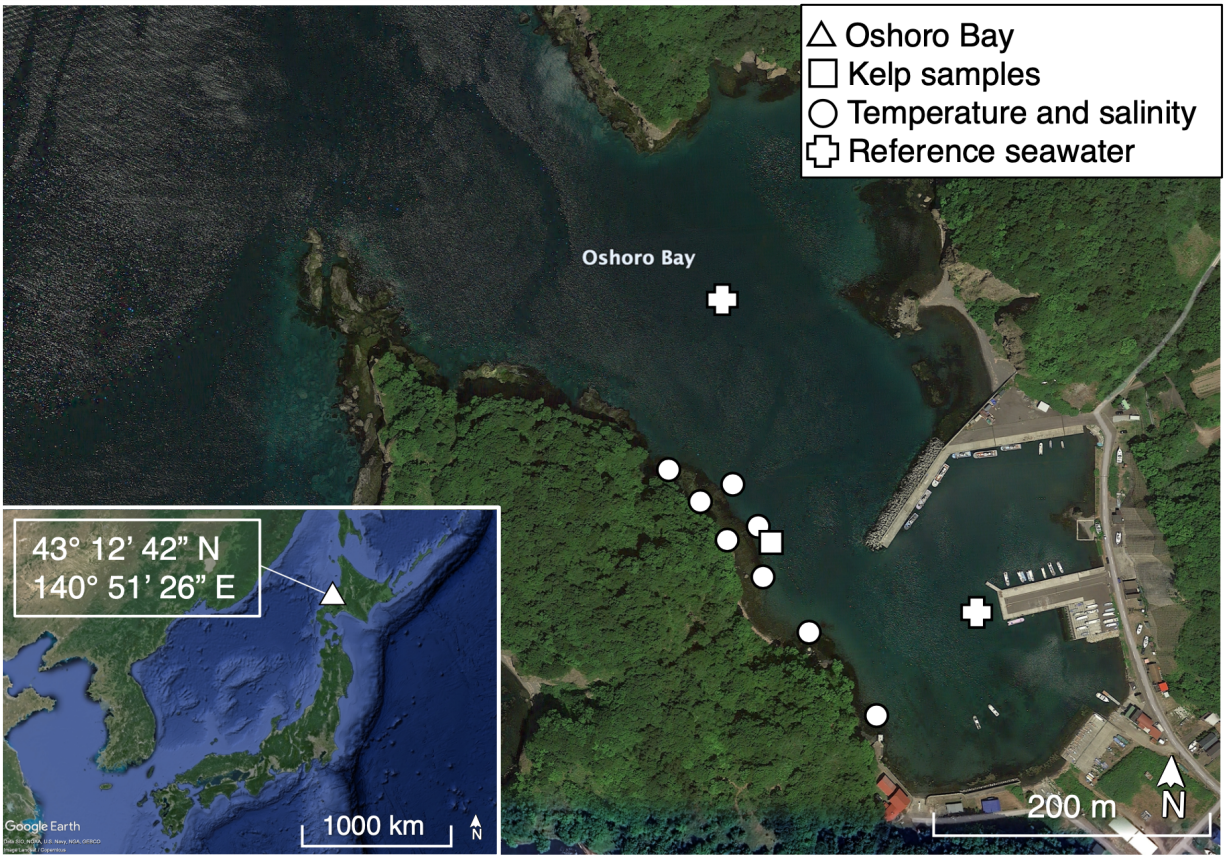


Figure 2.1. July 2021 aerial images showing an overview of Oshoro Bay, the kelp sampling location, temperature and salinity measurement locations, and reference seawater sampling locations. An inset of the relative location of Oshoro Bay on the Shakotan peninsula in Hokkaido is also provided (Google Earth 2021).

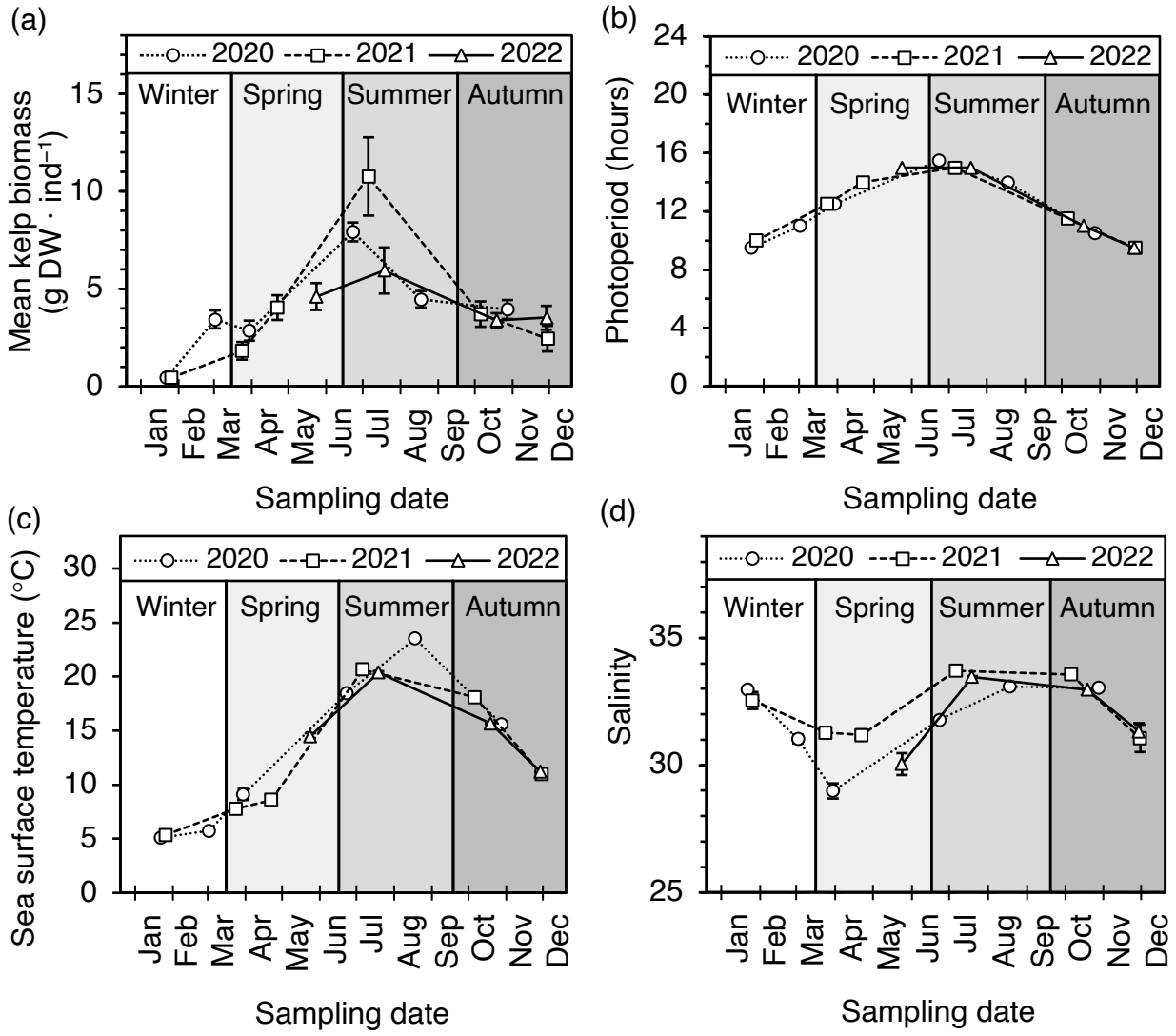


Figure 2.2. Annual cycles of biomass and environmental parameters. Data are (a) means (± *SE* between kelp, n = 2–6) of individual kelp dry weight biomasses (g DW · ind^{-1}), (b) photoperiod hours used for the incubation experiments, (c) means (± *SE* between sampling locations, n = 9) of in situ sea surface temperature (°C), and (d) means (± *SE* between sampling locations, n = 9) of salinity values. In situ sampling locations are shown in Figure 2.1. Some error bars are smaller than the data symbol.

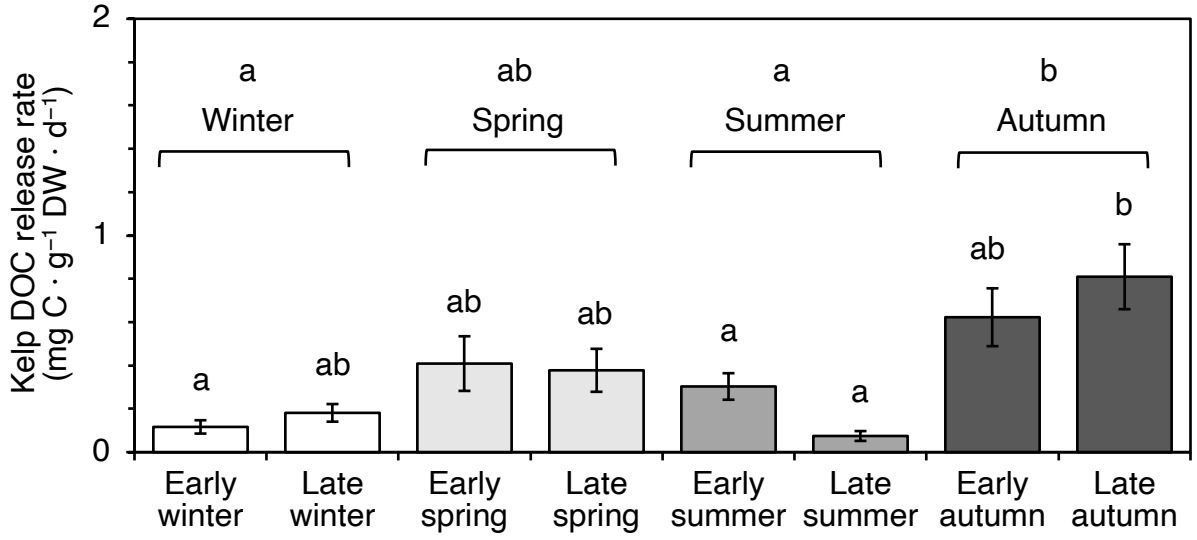


Figure 2.3. Mean DOC release rates by season. Data are least squares means of kelp DOC release rates represented as biomass normalized rates (mg C · g^{-1} DW · d^{-1}), with results aggregated according to eight bi-seasonal categories (± *SE* between kelp). Shading effects visually differentiate results by the four seasons. Letters indicate significant seasonal differences ($p < 0.05$) in kelp DOC release rates based on two-way ANOVA tests on the effect of either season (winter, spring, summer, or autumn) or bi-seasonal period (subdivided into early and late seasonal periods), combined with qualitative irradiance treatment levels (low, medium, or high), on kelp DOC release rates.

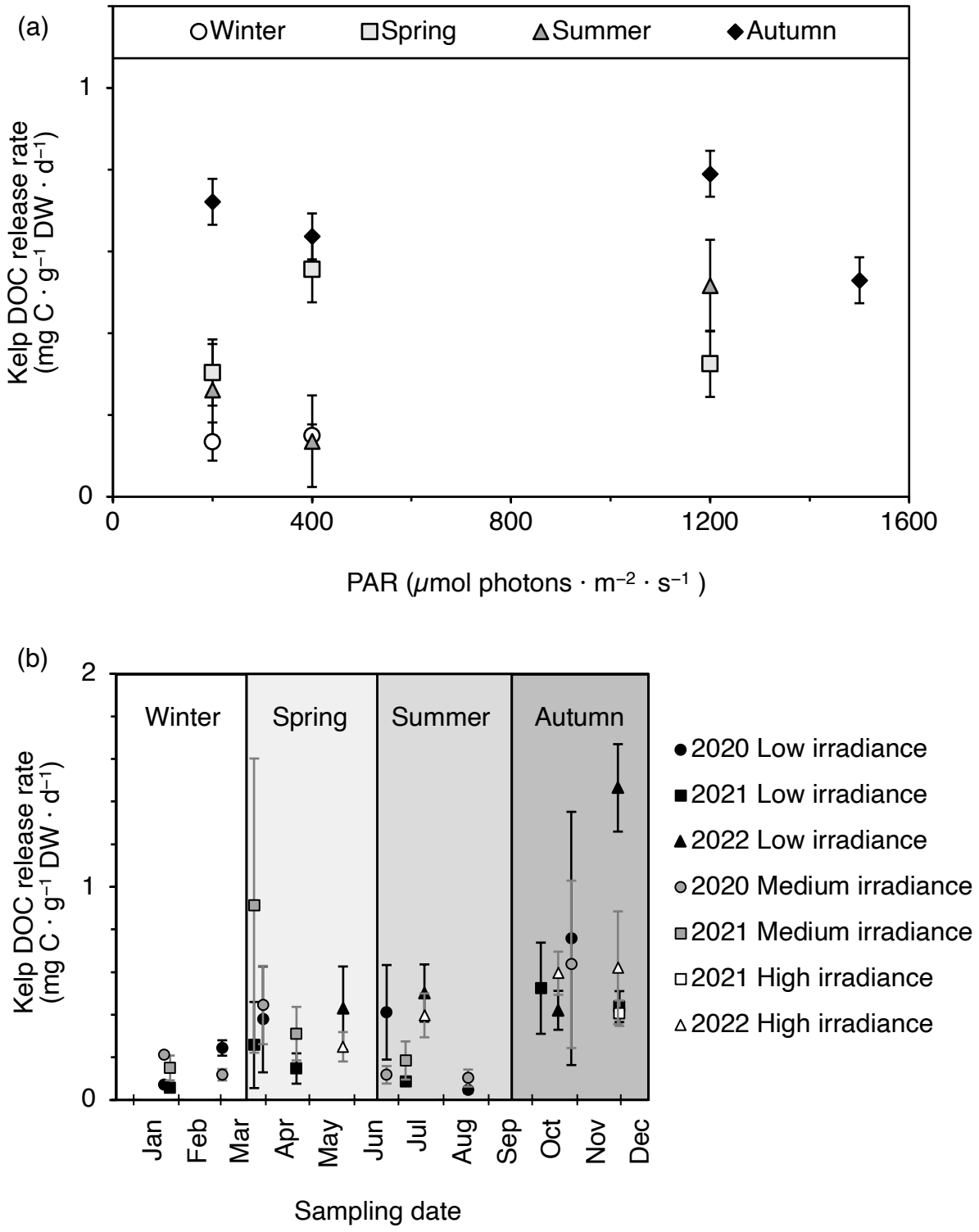


Figure 2.4. Irradiance and DOC release rates. Data are (a) seasonally categorized mean kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) (± *SE*) as a function of their corresponding irradiance

treatment (200, 400, 1200, or 1500 µmol photons · m^{-2} · s^{-1}) and (b) comparisons of mean DOC release rates (± *SE*) from paired irradiance treatments within each sampling event. Irradiance designations indicate exposure to 200 (low), 400 (medium), or 1200 (high) µmol photons · m^{-2} · s^{-1} from artificial LED sources. High irradiance in November 2021 averaged 1500 µmol photons · m^{-2} · s^{-1} from natural irradiance. There were no significant (ANOVA, $p < 0.05$) linear regressions between irradiance levels and DOC release rates seasonally or within any of the sampling events.

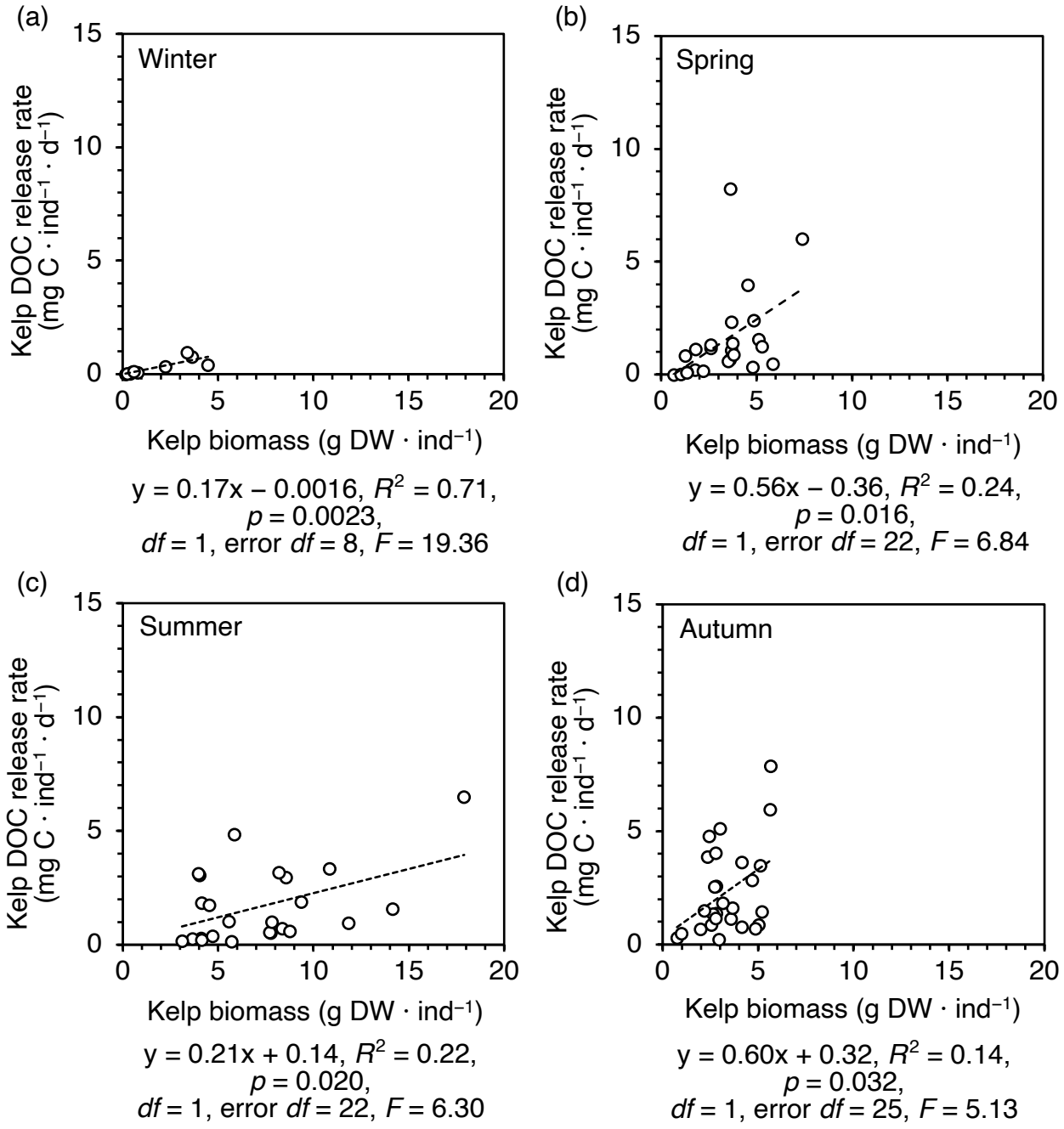


Figure 2.5. DOC release rates and kelp biomass. Linear regressions (ANOVA, $p < 0.05$) between individual kelp DOC release rates (mg C · ind^{-1} · d^{-1}) and corresponding individual kelp biomass (g DW · ind^{-1}), in (a) winter, (b) spring, (c) summer, and (d) autumn results. DOC release rates are least squares means for each individual kelp (n = 85) across the 16 sampling events.

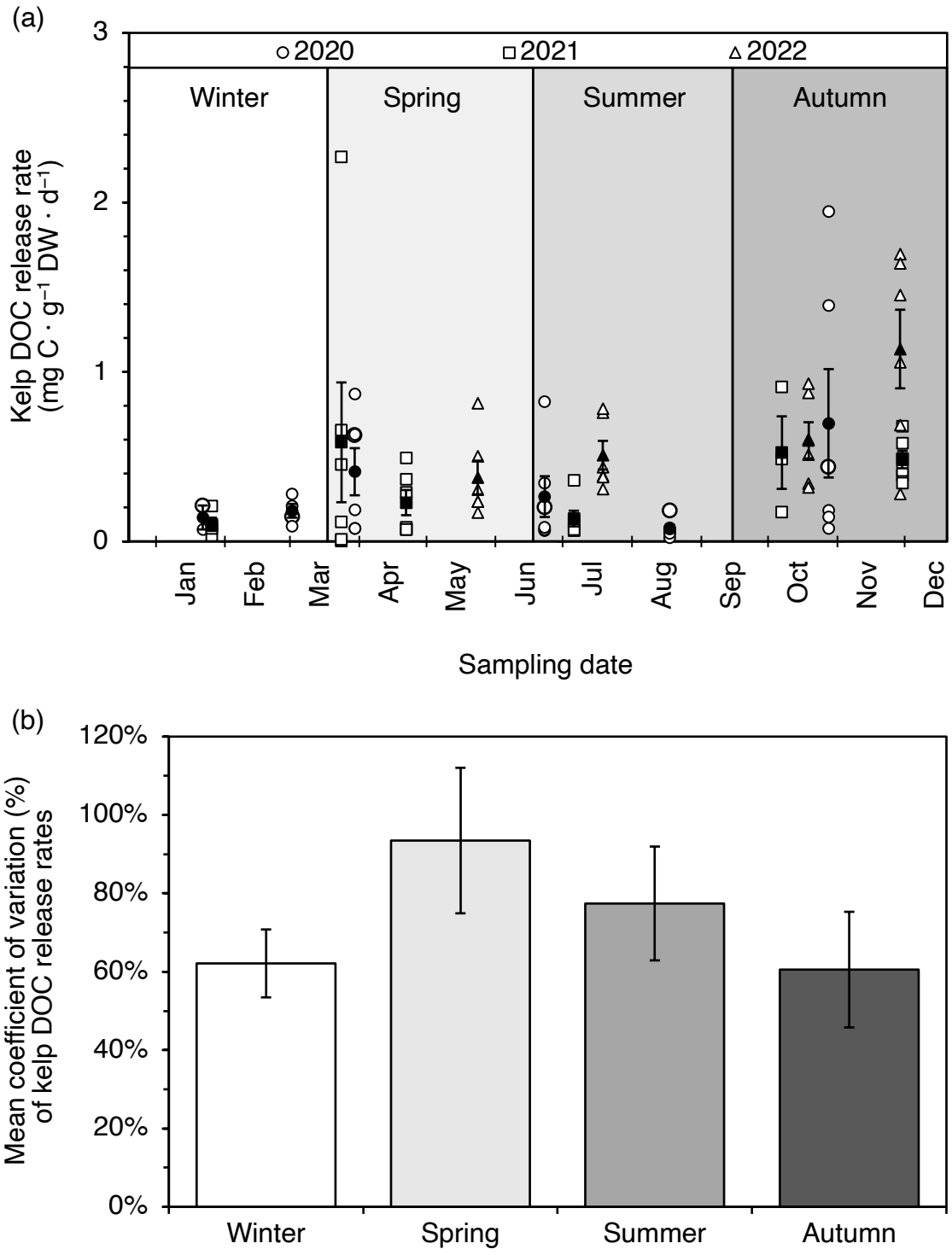
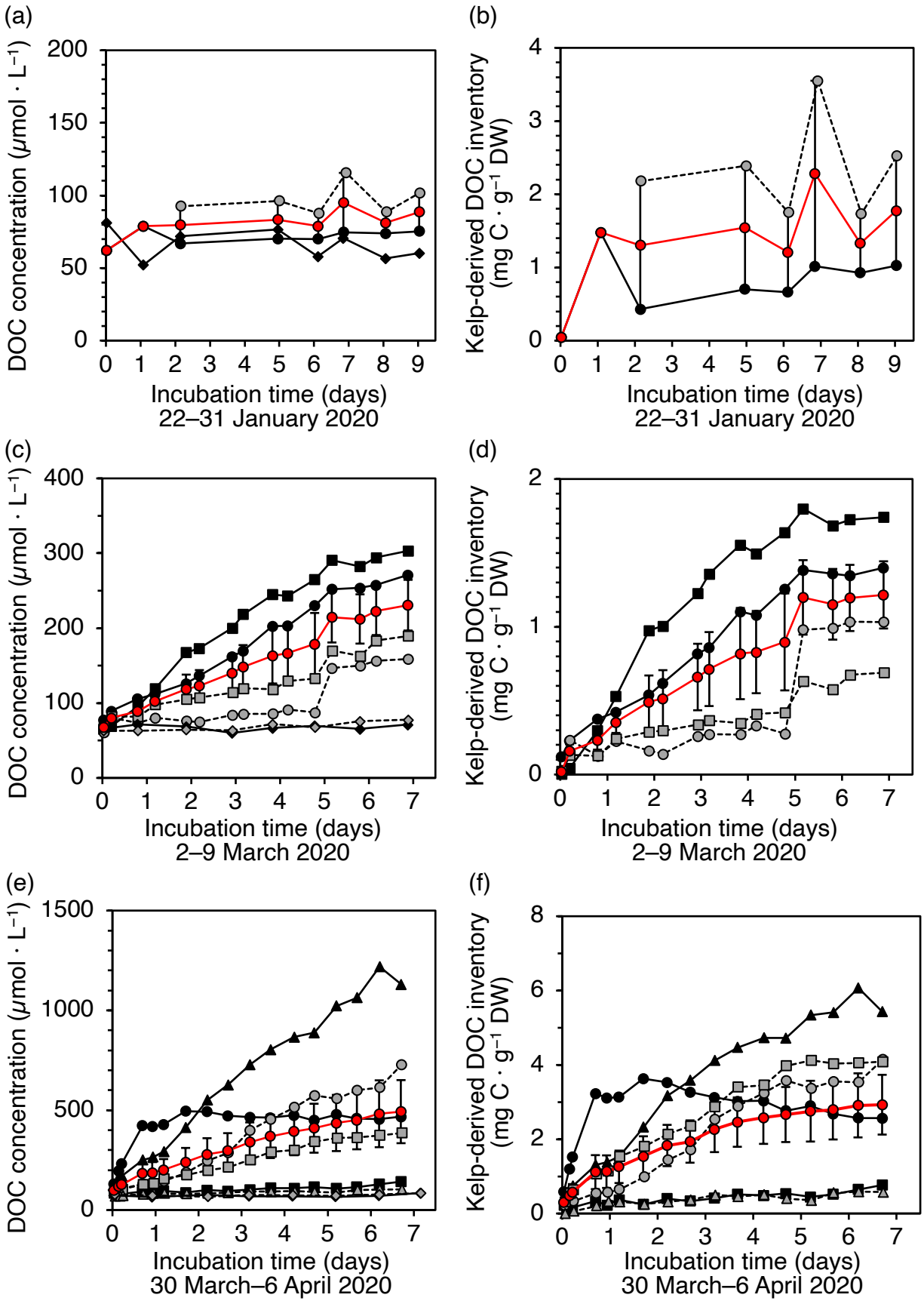
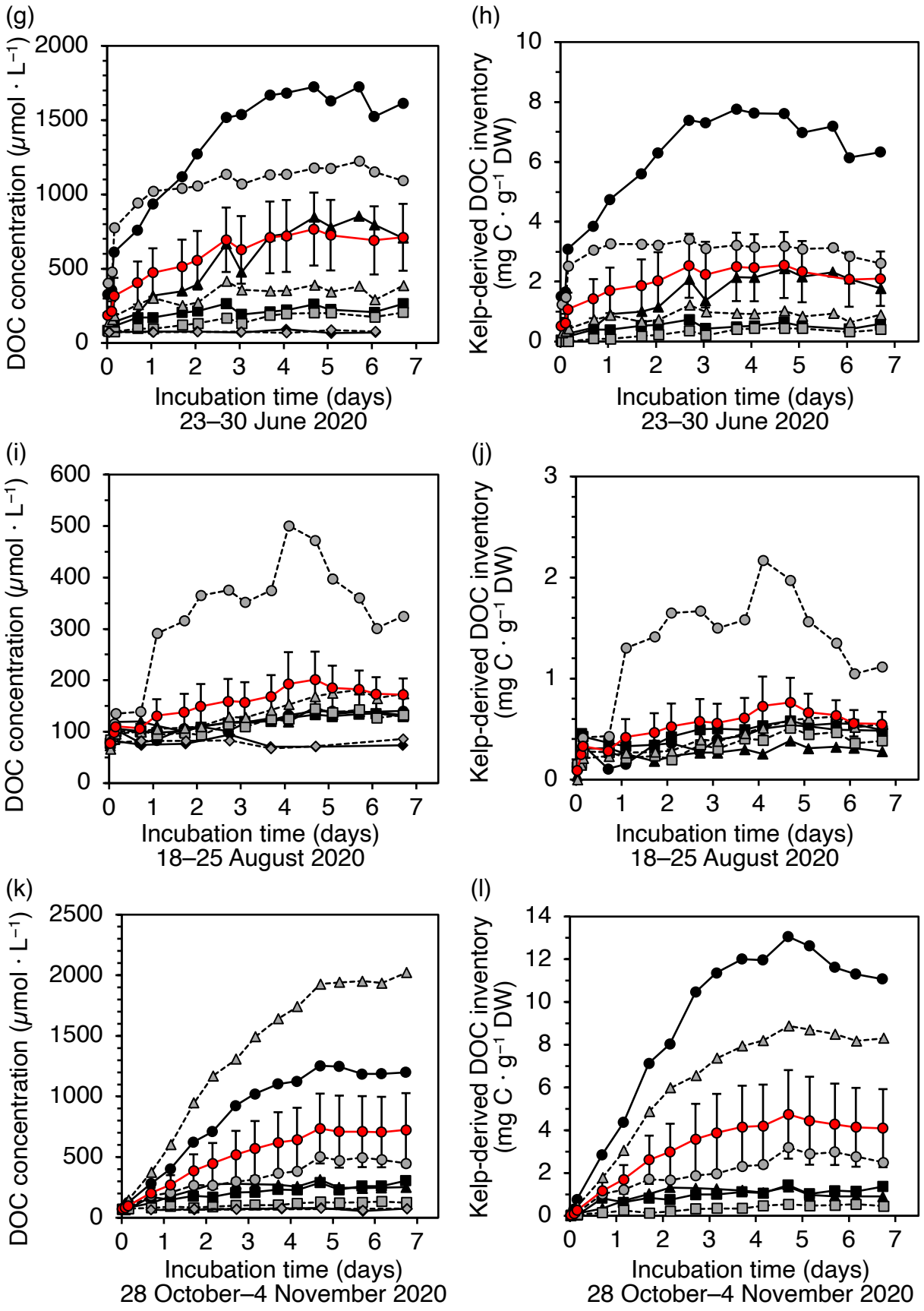
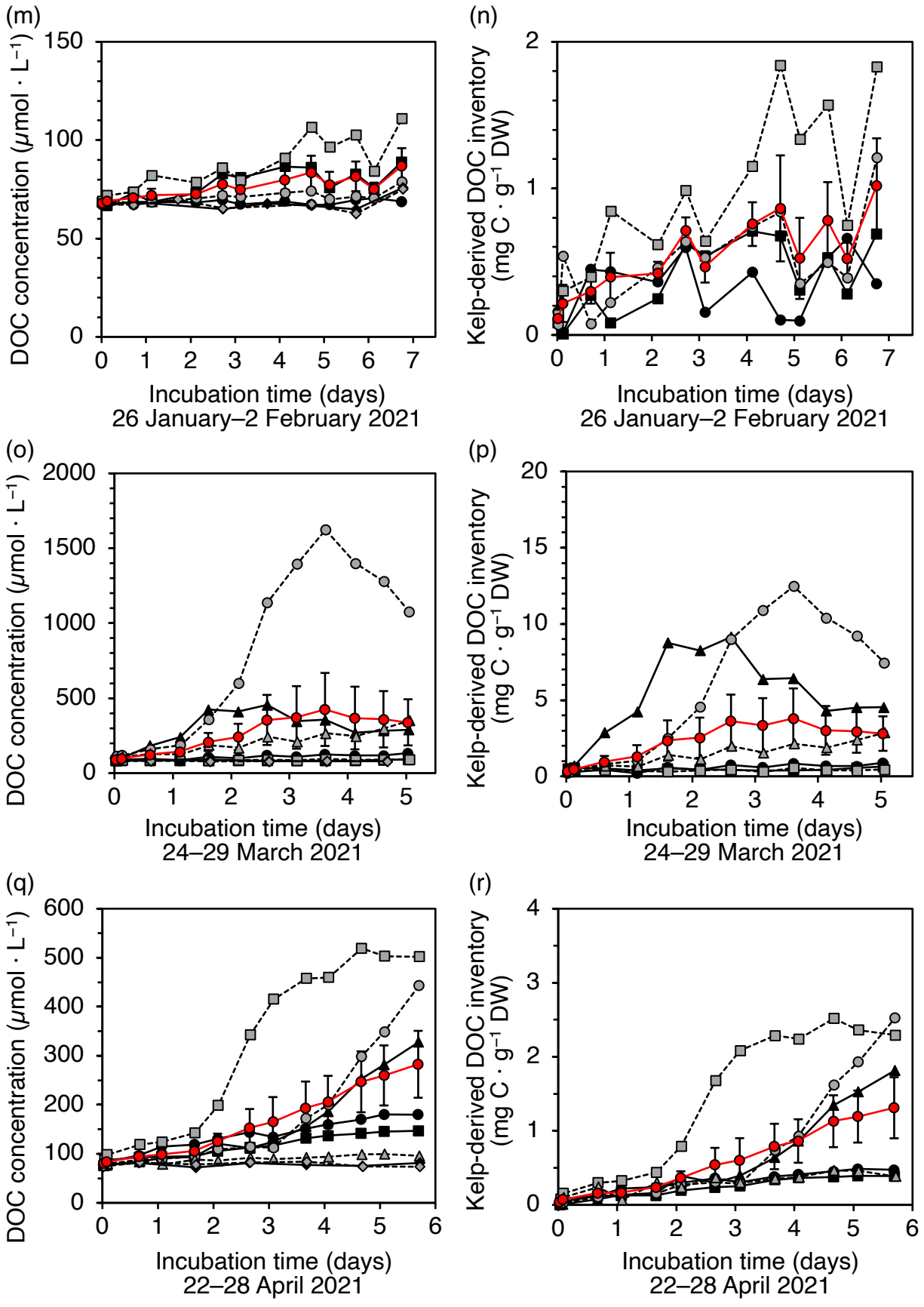


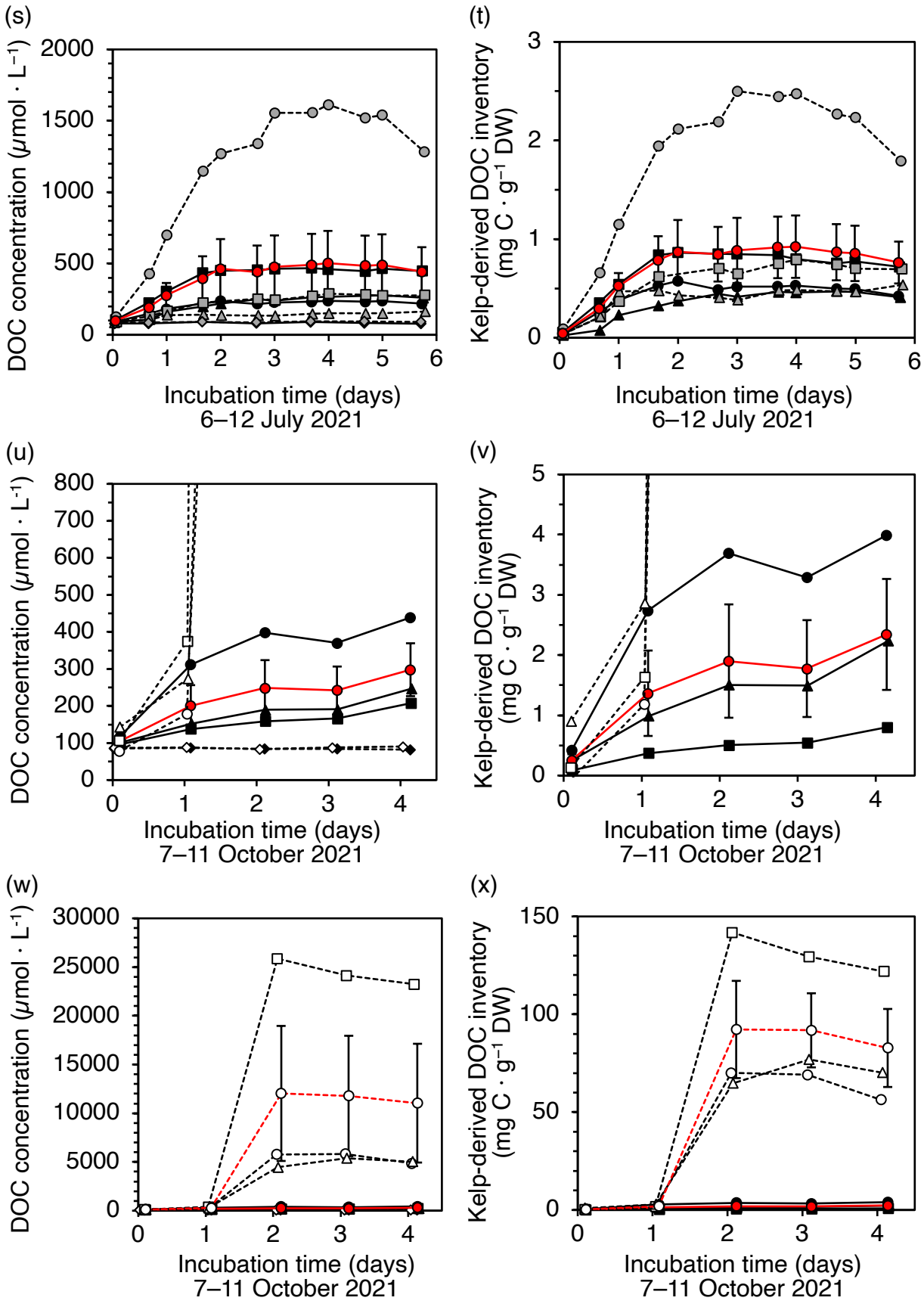
Figure 2.6. Variability of individual kelp DOC release rates. (a) Black data points are arithmetic means (± *SE* between kelp) of the individual kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) within each sampling event. Some error bars are smaller than the data symbol. White data points

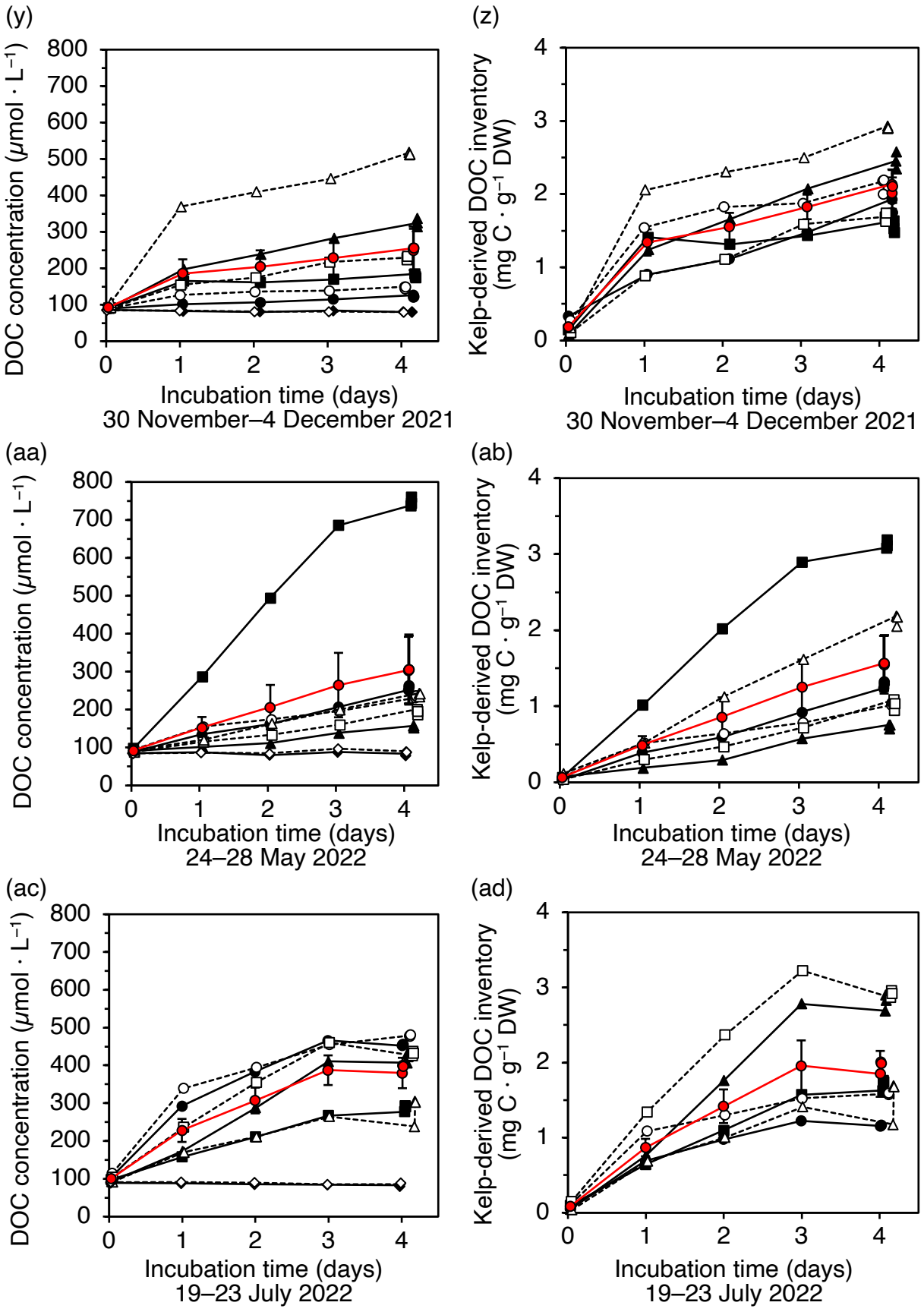
represent the individual kelp DOC release rates calculated as least squares means from linear regressions of DOC concentrations (n = 5–17 samples per incubation) at regular intervals during the incubation period (t = 4–9 d). Each sampling event incubated n = 6 kelp except January 2020 (n = 2), January 2021 (n = 4), early March 2020 (n = 4), and October 2021 (n = 3). (b) Individual variability of kelp DOC release rates quantified as coefficients of variation. CV were calculated for each sampling event and then aggregated to determine four seasonal mean CV values (± *SE* between events [winter: n = 3, spring: n = 4, summer: n = 4, autumn: n = 5]).

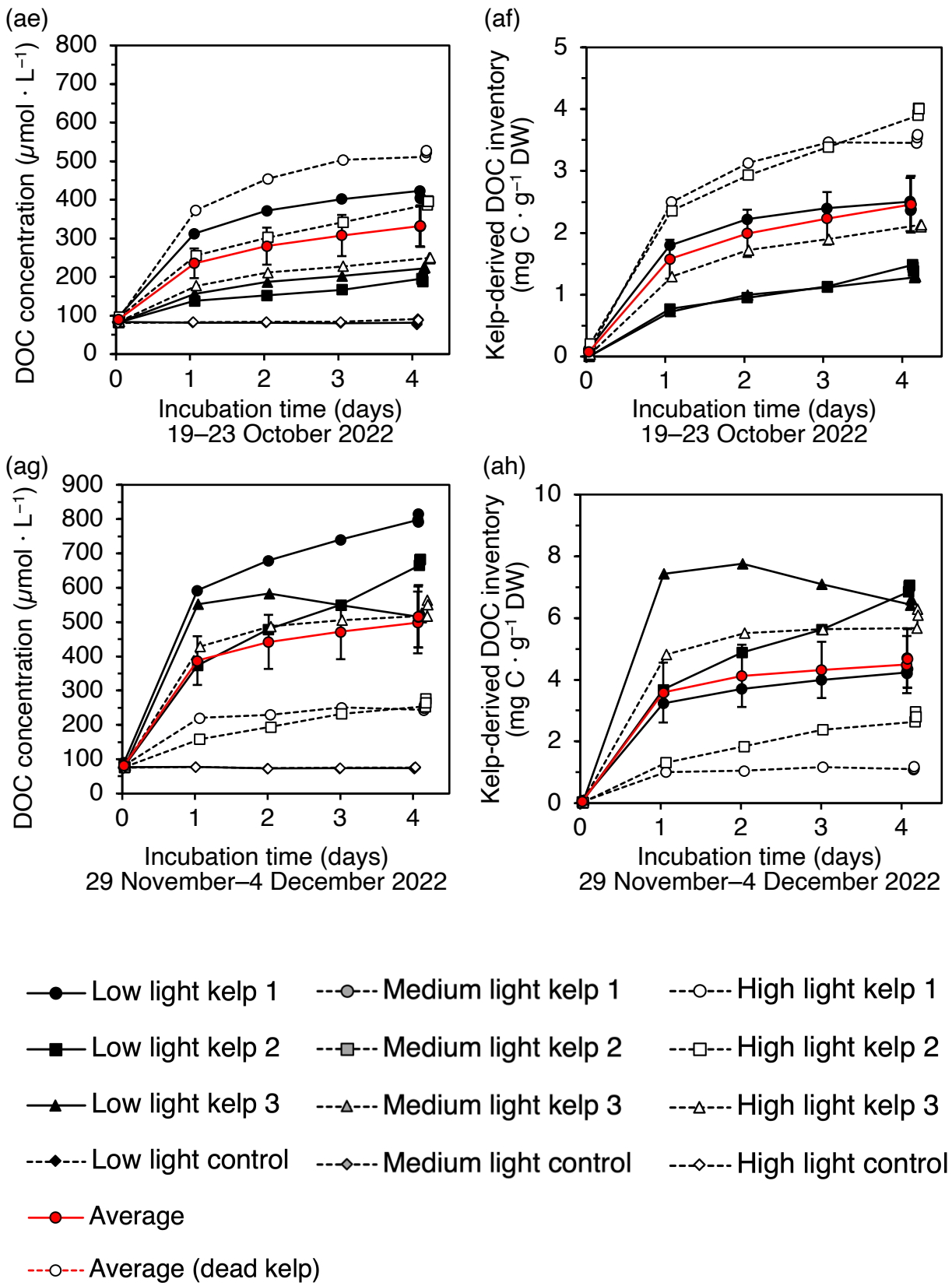

(a)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
22–31 January 2020
(b)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
22–31 January 2020
(c)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
2–9 March 2020
(d)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
2–9 March 2020
(e)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
30 March–6 April 2020
(f)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
30 March–6 April 2020


(g)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
23–30 June 2020
(h)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
23–30 June 2020
(i)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
18–25 August 2020
(j)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
18–25 August 2020
(k)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
28 October–4 November 2020
(l)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
28 October–4 November 2020


(m)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
26 January–2 February 2021
(n)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
26 January–2 February 2021
(o)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
24–29 March 2021
(p)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
24–29 March 2021
(q)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
22–28 April 2021
(r)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
22–28 April 2021


(s)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
6–12 July 2021
(t)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
6–12 July 2021
(u)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
7–11 October 2021
(v)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
7–11 October 2021
(w)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
7–11 October 2021
(x)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
7–11 October 2021


(y)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
30 November–4 December 2021
(z)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
30 November–4 December 2021
(aa)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
24–28 May 2022
(ab)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
24–28 May 2022
(ac)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
19–23 July 2022
(ad)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
19–23 July 2022


(ae)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
19–23 October 2022
(af)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
19–23 October 2022
(ag)
DOC concentration (μmol · L⁻¹)
Incubation time (days)
29 November–4 December 2022
(ah)
Kelp-derived DOC inventory (mg C · g⁻¹ DW)
Incubation time (days)
29 November–4 December 2022
Low light kelp 1
Medium light kelp 1
High light kelp 1
Low light kelp 2
Medium light kelp 2
High light kelp 2
Low light kelp 3
Medium light kelp 3
High light kelp 3
Low light control
Medium light control
High light control
Average
Average (dead kelp)

.

Figure S2.1. Incubation time-series of volume-corrected DOC concentrations (μmol · L^{-1}) and biomass-normalized kelp-derived DOC inventories (mg C · g^{-1} DW) for all incubated kelp (*n* = 88) and control seawater (*n* = 31). Average kelp-derived DOC results (± *SE* between *n* kelp) are also included for each sampling event. Low light designations indicate exposure to photosynthetically active radiation (PAR) of 200 μmol photons · m^{-2} · s^{-1} from artificial LED sources. Medium light designations (incubation experiments from January 2020 to July 2021) indicate exposure to 400 μmol photons · m^{-2} · s^{-1} from artificial LED sources. High light designations indicate exposure to 1200 μmol photons · m^{-2} · s^{-1} from artificial LED sources (incubation experiments from May 2022 through November 2022), or 1500 (November 2021) or 2000 (October 2021) μmol photons · m^{-2} · s^{-1} from natural irradiance. Each pair of graphs correspond to the 16 incubation experiments conducted in (a)–(b) January 2020, (c)–(d) early March 2020, (e)–(f) late March 2020, (g)–(h) June 2020, (i)–(j) August 2020, (k)–(l) October 2020, (m)–(n) January 2021, (o)–(p) March 2021, (q)–(r) April 2021, (s)–(t) July 2021, (u)–(v) October 2021 (live kelp), (w)–(x) October 2021 (dead kelp), (y)–(z) November 2021, (aa)–(ab) May 2022, (ac)–(ad) July 2022, (ae)–(af) October 2022, and (ag)–(ah) November 2022.

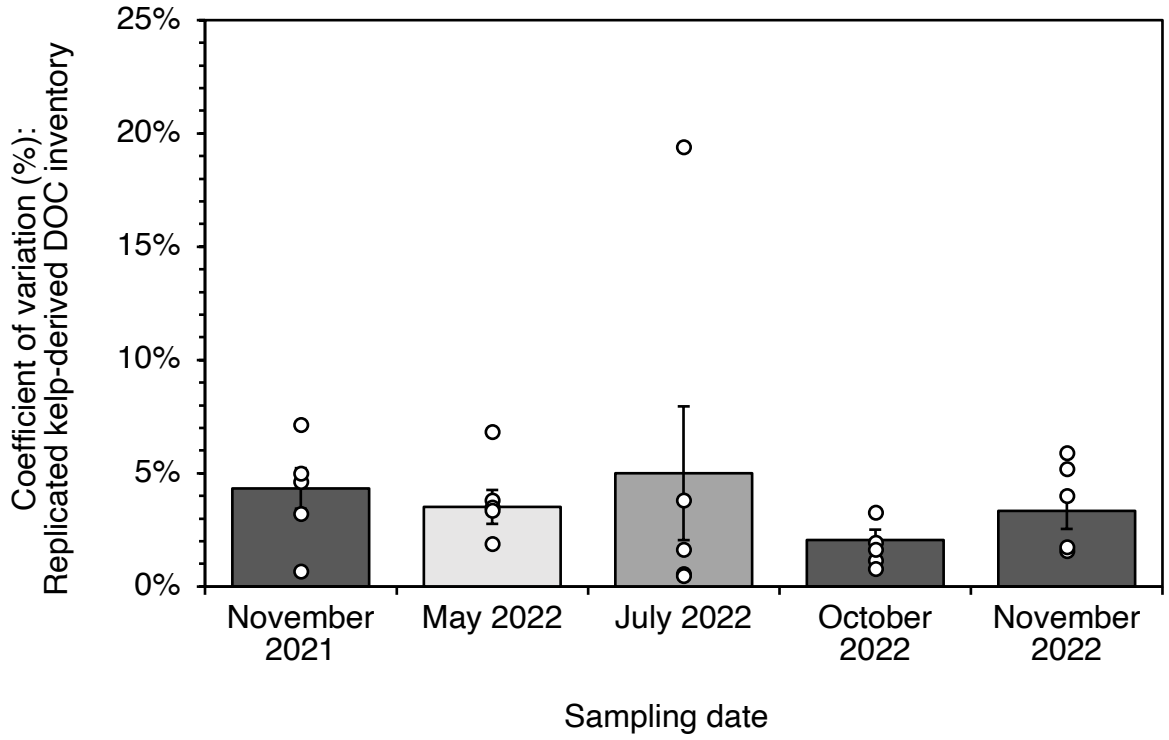
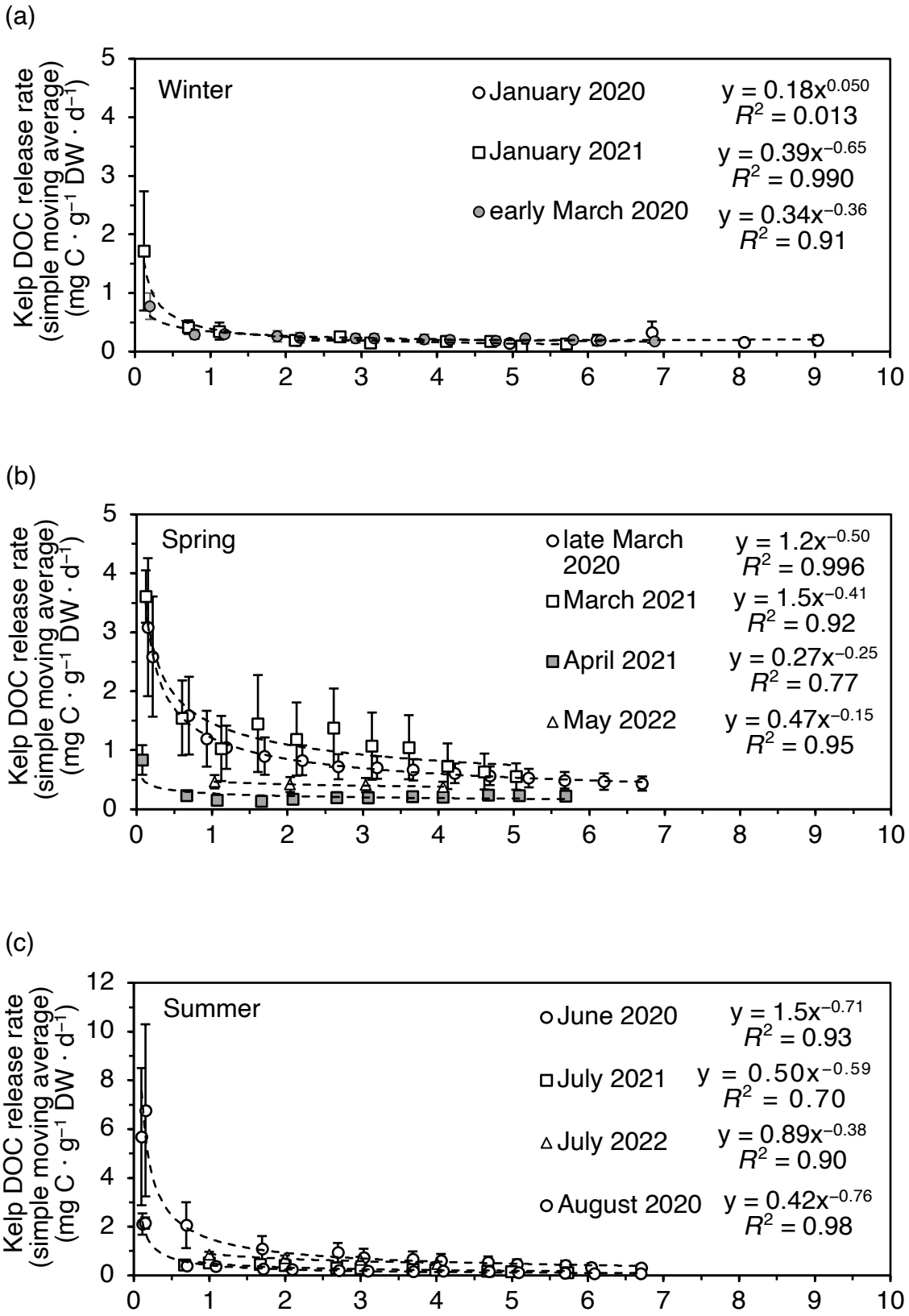


Figure S2.2. Coefficients of variation (%) for replicated kelp-derived DOC inventories (mg C · g^{-1} DW). Data points are individual CV of triplicate DOC samples at the end of each kelp incubation experiment (n = 6 kelp incubations) in November 2021, May 2022, July 2022, October 2022, and November 2022. Columns are mean CV (± *SE* between n = 6 sets of individual CV). Results represent the spatial heterogeneity of DOC within the kelp incubation tanks. Shading effects visually differentiate results by season.


(a)
Winter
January 2020
y = 0.18x^0.050
R2 = 0.013
January 2021
y = 0.39x^−0.65
R2 = 0.990
early March 2020
y = 0.34x^−0.36
R2 = 0.91
Kelp DOC release rate (simple moving average) (mg C · g−1 DW · d−1)
(b)
Spring
late March 2020
y = 1.2x^−0.50
R2 = 0.996
March 2021
y = 1.5x^−0.41
R2 = 0.92
April 2021
y = 0.27x^−0.25
R2 = 0.77
May 2022
y = 0.47x^−0.15
R2 = 0.95
Kelp DOC release rate (simple moving average) (mg C · g−1 DW · d−1)
(c)
Summer
June 2020
y = 1.5x^−0.71
R2 = 0.93
July 2021
y = 0.50x^−0.59
R2 = 0.70
July 2022
y = 0.89x^−0.38
R2 = 0.90
August 2020
y = 0.42x^−0.76
R2 = 0.98
Kelp DOC release rate (simple moving average) (mg C · g−1 DW · d−1)

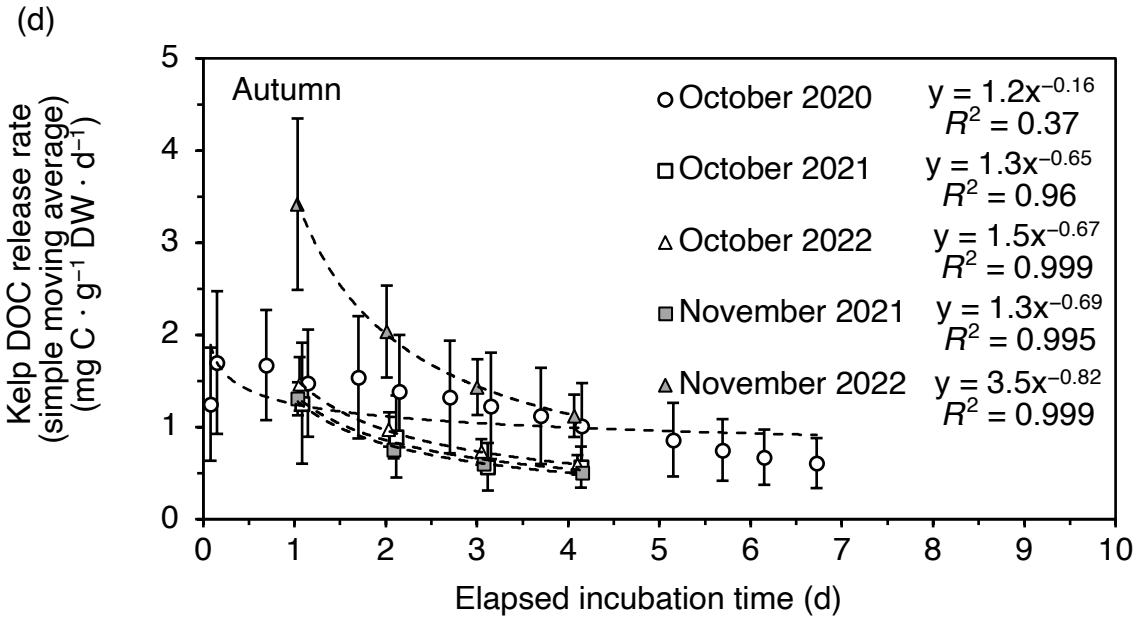


Figure S2.3. DOC release rates as a function of variable incubation time. Time-series showing effect of elapsed incubation time (d) on calculating DOC release rates (mg C · g^{-1} DW · d^{-1}) as simple moving averages (± *SE* between *n* kelp) for (a) winter, (b) spring, (c) summer, and (d) autumn results. Best-fit curves shown are power relationships.

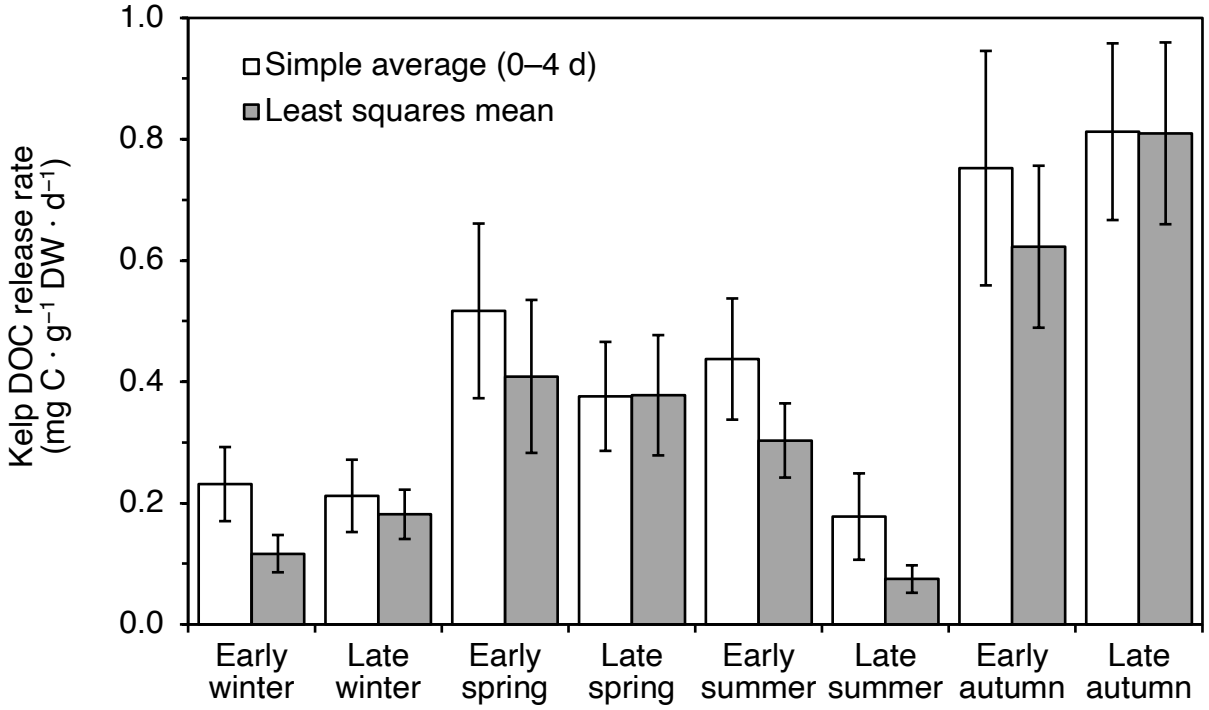


Figure S2.4. Seasonal effect of DOC release rate calculation method. Data are means (± *SE*) of kelp DOC release rates represented as biomass normalized rates (mg C · g^{-1} DW · d^{-1}), with results aggregated according to eight bi-seasonal categories. White shading corresponds to results calculated as a simple average between samples at $t = 0$ and $t = 4$ d. Gray shading corresponds to results calculated as least squares means of all collected samples throughout the respective incubation period.

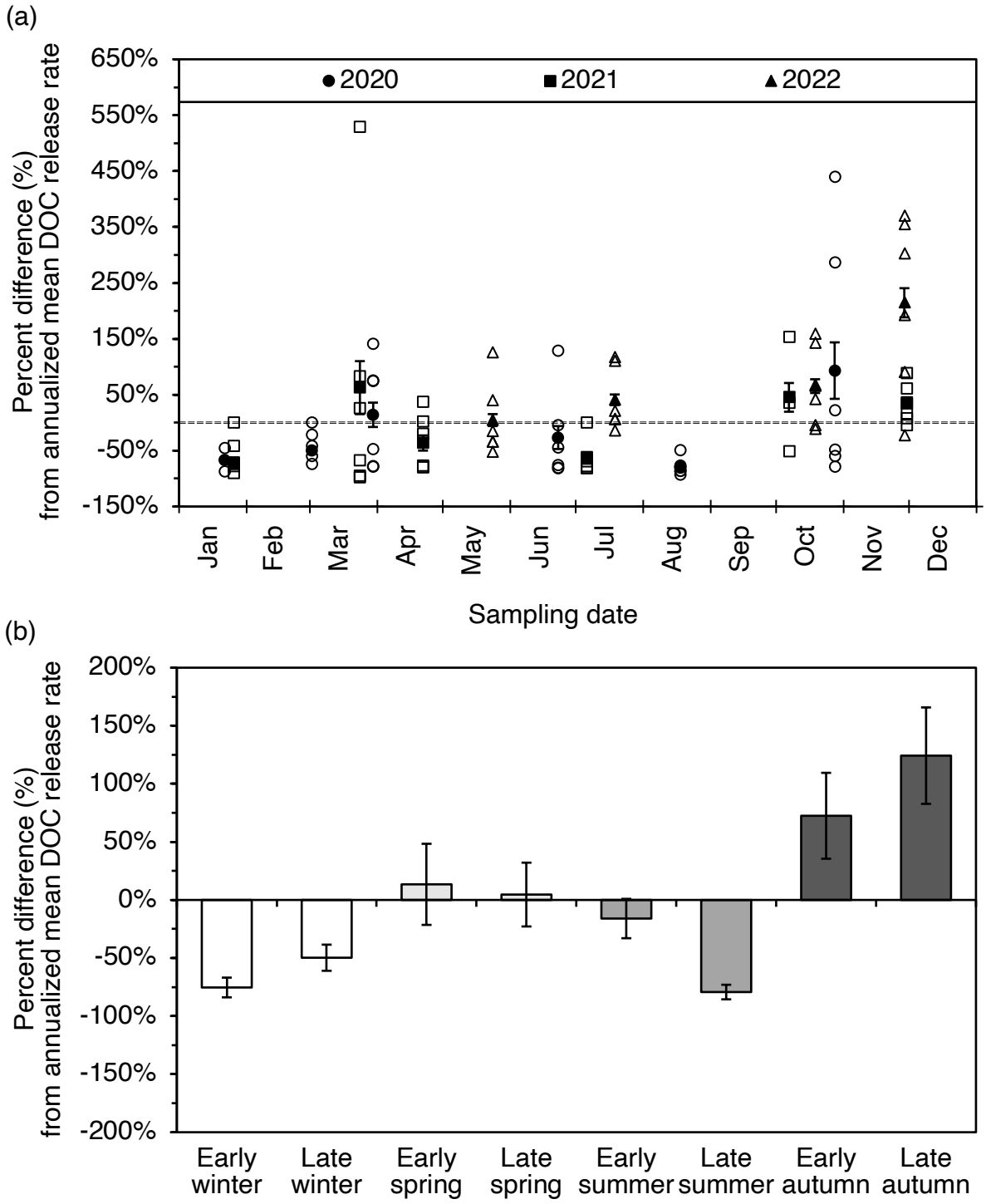


Figure S2.5. Percent difference (%) of experimental DOC release rates from weighted annualized mean DOC release rate. Data are (a) means (± *SE*) of the percent differences (%) for each sampling event in black, with individual kelp results in white or (b) means (± *SE*) of the %

differences for each sampling event aggregated according to bi-seasonal period. The annualized mean DOC release rate of 0.36 mg C · g^{-1} DW · d^{-1} was calculated from bi-seasonal weighted averages.

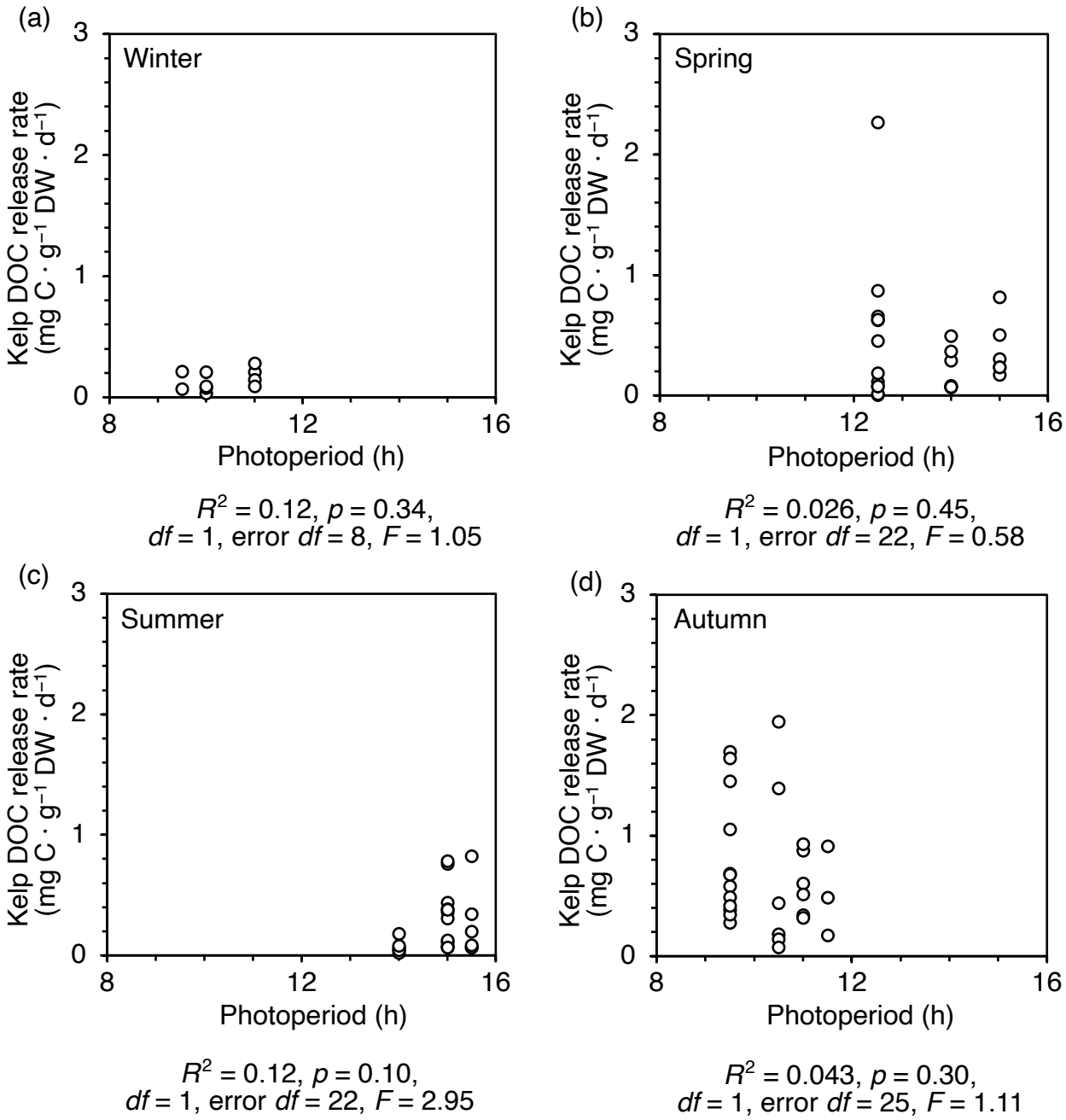


Figure S2.6. DOC release rates and photoperiod. Seasonal relationships between kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) and ambient photoperiod (h) for (a) winter, (b) spring, (c) summer, and (d) autumn results. DOC release rates are least squares means for each individual kelp (n = 85) across the 16 sampling events. Linear regressions were not significant (ANOVA, p > 0.05).

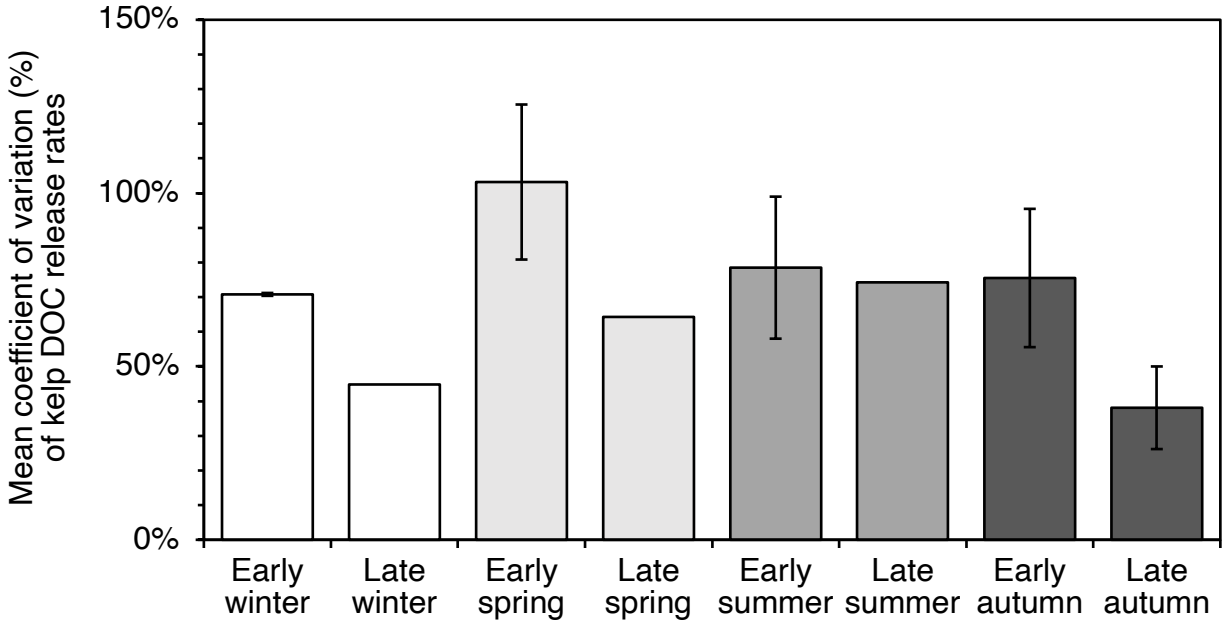


Figure S2.7. Bi-seasonal mean coefficients of variation of DOC release rates. Individual variability of kelp DOC release rates quantified as coefficients of variation. CV were calculated for each sampling event and then aggregated to determine eight bi-seasonal mean CV values (± *SE* between events [early winter: $n = 2$, late winter: $n = 1$, early spring: $n = 3$, late spring: $n = 1$; early summer: $n = 3$, late summer: $n = 1$; early autumn: $n = 3$; late autumn: $n = 2$]).

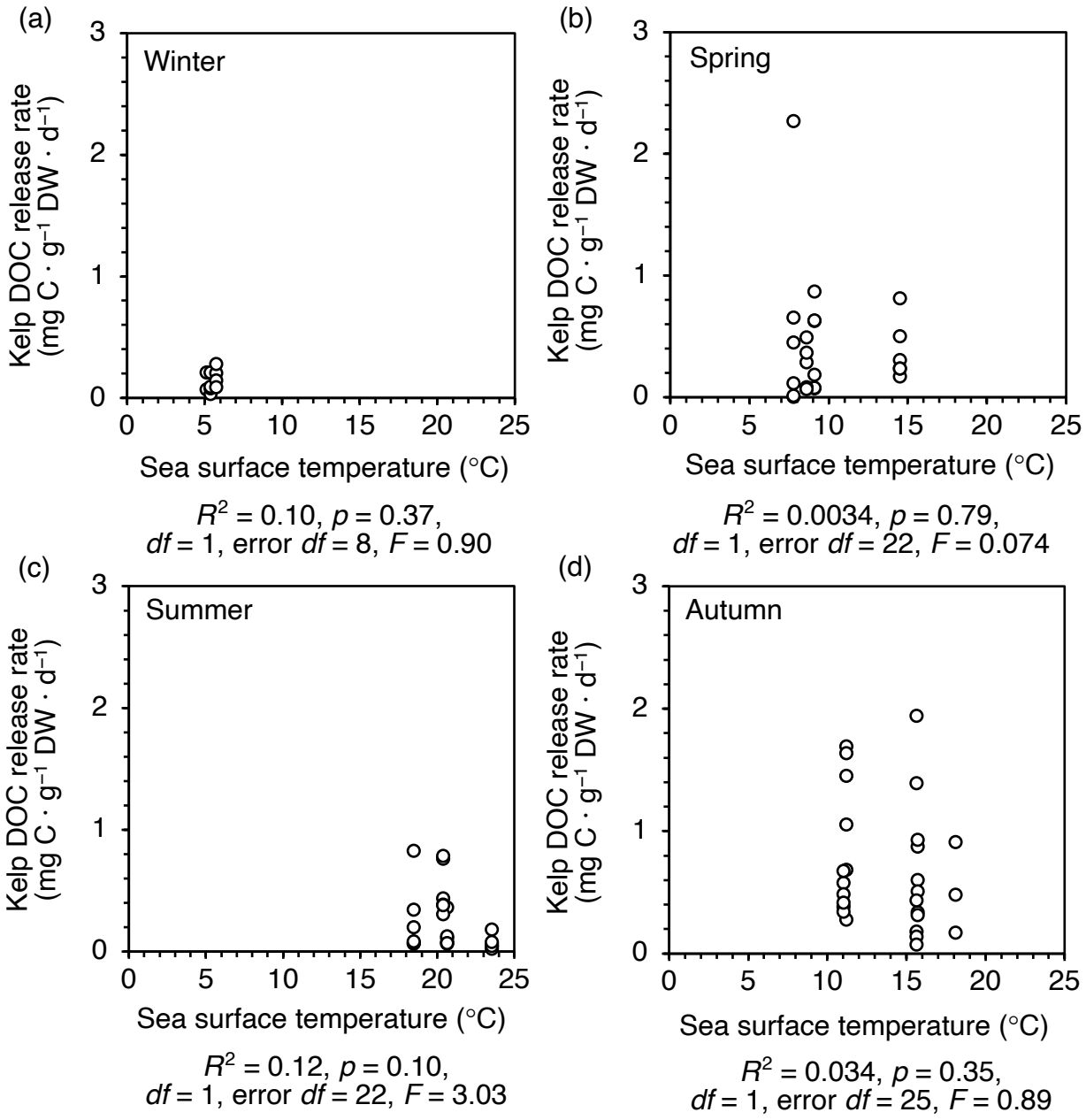


Figure S2.8. DOC release rates and ambient sea surface temperature. Seasonal relationships between kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) and mean in situ sea surface temperature (°C) for (a) winter, (b) spring, (c) summer, and (d) autumn results. DOC release rates are least squares means for each individual kelp (n = 85) across the 16 sampling events. Linear regressions were not significant (ANOVA, $p > 0.05$).

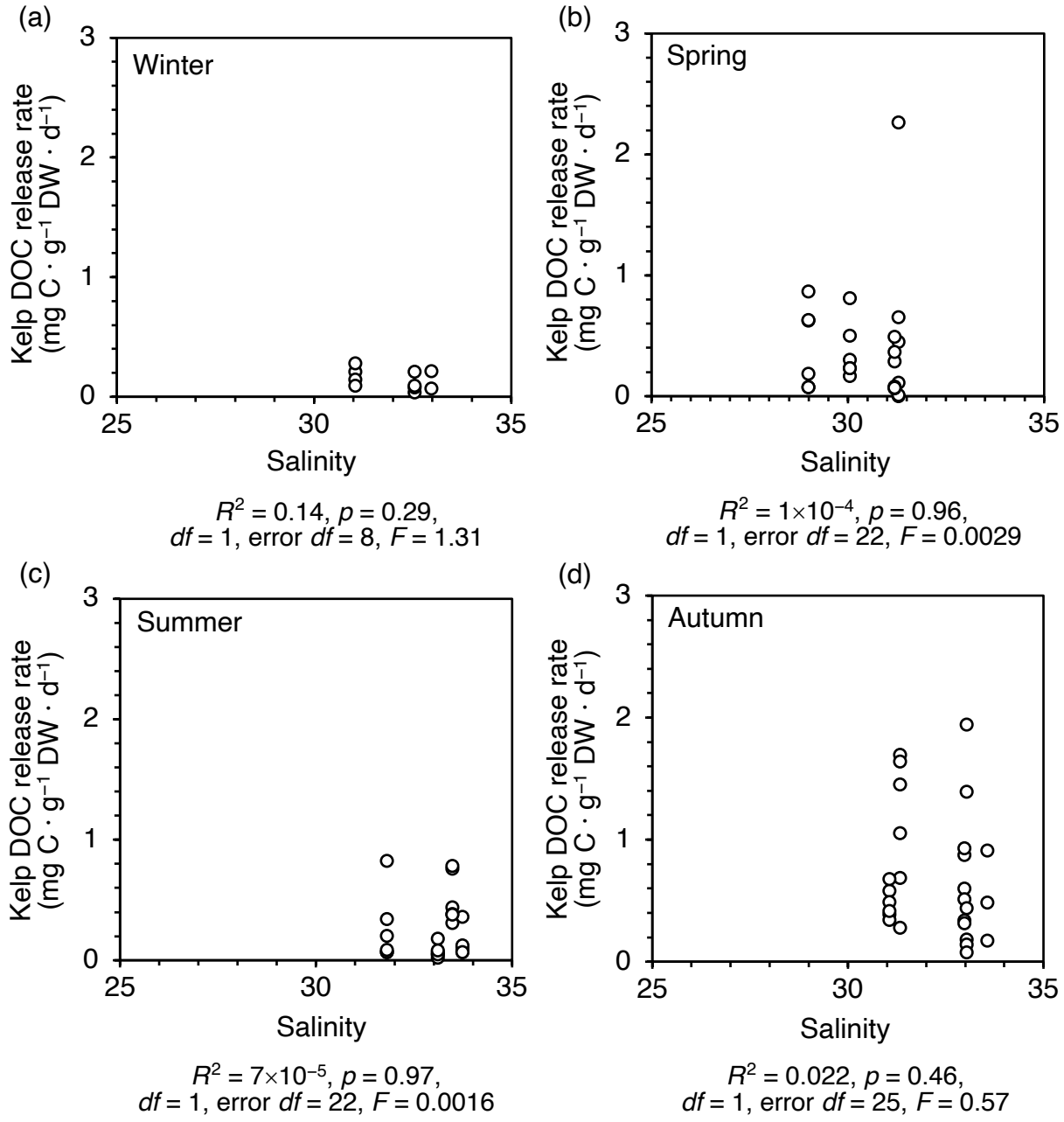


Figure S2.9. DOC release rates and ambient salinity. Seasonal relationships between kelp DOC release rates (mg C · g^{-1} DW · d^{-1}) and mean in situ salinity for (a) winter, (b) spring, (c) summer, and (d) autumn results. DOC release rates are least squares means for each individual kelp (n = 85) across the 16 sampling events. Linear regressions were not significant (ANOVA, p > 0.05).

Table S2.1. Linearity of kelp DOC release rates. DOC release rates (mg C · g^{-1} DW · d^{-1}) are least squares means from linear regressions of elapsed incubation time and the corresponding kelp-derived DOC inventory (mg C · g^{-1} DW). Incubation seawater samples were taken at regular intervals throughout each incubation period ($t \geq 4$ d, DOC samples ≥ 1 d^{-1}) and analyzed for DOC. Kelp DOC release was significantly (ANOVA, $p < 0.05$) linear with time for 80 of the 88 kelp incubations.

Least squares mean kelp DOC release rate (mg C · g^{-1} DW · d^{-1}) ANOVA statistics		Low light kelp 1	Low light kelp 2	Low light kelp 3	High light kelp 1	High light kelp 2	High light kelp 3
January 2020	Mean	0.071	NA	NA	0.21	NA	NA
	R^2	0.27			0.41		
	df	1			1		
	error *df*	7			5		
	F	2.59			3.46		
	p	0.15			0.12		
	Incubation period (d)	0–9			0–9		
	PAR (µmol photons · m^{-2} · s^{-1})	200			400		
Early March 2020	Mean	0.21	0.28	NA	0.15	0.092	NA
	R^2	0.96	0.90		0.76	0.94	
	df	1	1		1	1	
	error *df*	14	14		14	14	
	F	347.87	125.09		43.37	226.16	
	p	3×10^{-11}	2×10^{-8}		1×10^{-5}	5×10^{-10}	
	Incubation period (d)	0–7	0–7		0–7	0–7	
	PAR (µmol photons · m^{-2} · s^{-1})	200	200		400	400	
Late March 2020	Mean	0.19	0.076	0.87	0.63	0.63	0.078
	R^2	0.17	0.84	0.95	0.96	0.95	0.78
	df	1	1	1	1	1	1
	error *df*	16	16	16	16	16	16
	F	3.36	84.55	307.47	423.67	294.37	57.15
	p	0.085	9×10^{-8}	7×10^{-12}	6×10^{-13}	1×10^{-11}	1×10^{-6}
		0–7	0–7	0–7	0–7	0–7	0–7

	Incubation period (d)	200	200	200	400	400	400
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)						
June 2020	Mean	0.83	0.066	0.34	0.20	0.070	0.085
	R^2	0.59	0.47	0.80	0.25	0.80	0.39
	df	1	1	1	1	1	1
	error *df*	15	14	15	15	14	15
	F	21.68	12.22	58.49	4.93	56.66	9.56
	p	3×10^{-4}	4×10^{-3}	1×10^{-6}	0.042	3×10^{-6}	7×10^{-3}
	Incubation period (d)	0–7	0–7	0–7	0–7	0–7	0–7
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	400	400	400
August 2020	Mean	0.067	0.0049	0.024	0.18	0.048	0.081
	R^2	0.74	0.51	0.31	0.39	0.67	0.87
	df	1	1	1	1	1	1
	error *df*	14	15	15	15	15	15
	F	40.77	15.64	6.63	9.72	30.97	96.13
	p	2×10^{-5}	1×10^{-3}	0.021	7×10^{-3}	5×10^{-5}	6×10^{-8}
	Incubation period (d)	0–7	0–7	0–7	0–7	0–7	0–7
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	400	400	400
October 2020	Mean	1.9	0.18	0.14	0.44	0.077	1.4
	R^2	0.80	0.76	0.45	0.86	0.89	0.85
	df	1	1	1	1	1	1
	error *df*	15	15	15	15	15	15
	F	59.21	47.36	12.28	90.11	119.55	86.18
	p	1×10^{-6}	5×10^{-6}	3×10^{-3}	1×10^{-7}	2×10^{-8}	1×10^{-7}
	Incubation period (d)	0–7	0–7	0–7	0–7	0–7	0–7
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	400	400	400
January 2021	Mean	0.036	0.079	NA	0.093	0.21	NA
	R^2	0.15	0.52		0.46	0.71	
	df	1	1		1	1	
	error *df*	12	12		12	12	
	F	2.18	13.17		10.24	29.77	
	p	0.17	3×10^{-3}		8×10^{-3}	1×10^{-4}	

	Incubation period (d)	0–7	0–7		0–7	0–7	
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200		400	400	
March 2021	Mean	0.11	0.0026	0.66	2.3	0.014	0.45
	R^2	0.74	0.0028	0.16	0.73	0.13	0.92
	df	1	1	1	1	1	1
	error *df*	10	10	10	10	9	10
	F	28.47	0.028	1.85	26.69	1.31	110.78
	p	3×10^{-4}	0.87	0.20	4×10^{-4}	0.28	1×10^{-6}
	Incubation period (d)	0–5	0–5	0–5	0–5	0–5	0–5
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	400	400	400
April 2021	Mean	0.083	0.070	0.29	0.37	0.49	0.071
	R^2	0.93	0.95	0.88	0.80	0.90	0.80
	df	1	1	1	1	1	1
	error *df*	12	12	12	12	12	12
	F	154.44	229.69	86.32	48.79	112.21	48.18
	p	3×10^{-8}	3×10^{-9}	8×10^{-7}	1×10^{-5}	2×10^{-7}	2×10^{-5}
	Incubation period (d)	0–6	0–6	0–6	0–6	0–6	0–6
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	400	400	400
July 2021	Mean	0.066	0.11	0.080	0.36	0.13	0.070
	R^2	0.45	0.48	0.74	0.59	0.74	0.58
	df	1	1	1	1	1	1
	error *df*	11	11	11	11	10	11
	F	8.94	10.35	31.05	15.89	29.16	15.19
	p	0.012	8×10^{-3}	2×10^{-4}	2×10^{-3}	3×10^{-4}	2×10^{-3}
	Incubation period (d)	0–6	0–6	0–6	0–6	0–6	0–6
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	400	400	400
October 2021	Mean	0.91	0.17	0.49	18	37	21
	R^2	0.79	0.94	0.94	0.71	0.74	0.84
	df	1	1	1	1	1	1
	error *df*	4	4	4	4	4	4
	F	14.74	64.87	57.86	9.84	11.28	20.49
	p	0.018	1×10^{-3}	2×10^{-3}	0.035	0.028	0.011

	Incubation period (d)	0–4	0–4	0–4	0–4	0–4	0–4
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	2000 (natural) death induced	2000 (natural) death induced	2000 (natural) death induced
November 2021	Mean	0.39	0.34	0.58	0.49	0.42	0.68
	R^2	0.94	0.69	0.94	0.79	0.93	0.81
	df	1	1	1	1	1	1
	error *df*	4	4	4	4	4	4
	F	61.79	8.79	58.66	15.13	50.96	17.33
	p	1×10^{-3}	0.041	2×10^{-3}	0.018	2×10^{-3}	0.014
	Incubation period (d)	0–4	0–4	0–4	0–4	0–4	0–4
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	1500 (natural)	1500 (natural)	1500 (natural)
May 2022	Mean	0.31	0.81	0.17	0.24	0.24	0.50
	R^2	0.995	0.97	0.98	0.94	0.996	0.997
	df	1	1	1	1	1	1
	error *df*	4	4	4	4	4	4
	F	756.65	130.93	166.62	67.42	940.88	1166.04
	p	1×10^{-5}	3×10^{-4}	2×10^{-4}	1×10^{-3}	7×10^{-6}	4×10^{-6}
	Incubation period (d)	0–4	0–4	0–4	0–4	0–4	0–4
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	1200	1200	1200
July 2022	Mean	0.31	0.44	0.76	0.39	0.78	0.38
	R^2	0.86	0.97	0.96	0.83	0.88	0.94
	df	1	1	1	1	1	1
	error *df*	4	4	4	4	4	4
	F	24.76	120.71	87.49	19.12	29.97	64.19
	p	8×10^{-3}	4×10^{-4}	7×10^{-4}	0.012	5×10^{-3}	1×10^{-3}
	Incubation period (d)	0–4	0–4	0–4	0–4	0–4	0–4
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	1200	1200	1200
October 2022	Mean	0.60	0.34	0.32	0.88	0.93	0.51
	R^2	0.78	0.92	0.89	0.80	0.89	0.86
	df	1	1	1	1	1	1
	error *df*	4	4	4	4	4	4
	F	14.35	45.49	32.40	16.28	31.87	24.27

	p	0.019	3×10^{-3}	5×10^{-3}	0.016	5×10^{-3}	8×10^{-3}
	Incubation period (d)	0–4	0–4	0–4	0–4	0–4	0–4
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	1200	1200	1200
November 2022	Mean	1.1	1.7	1.6	0.28	0.69	1.5
	R^2	0.78	0.92	0.53	0.71	0.95	0.74
	df	1	1	1	1	1	1
	error *df*	4	4	4	4	4	4
	F	14.09	44.57	4.51	9.65	74.08	11.44
	p	0.020	3×10^{-3}	0.10	0.036	1×10^{-3}	0.028
	Incubation period (d)	0–4	0–4	0–4	0–4	0–4	0–4
	PAR (µmol photons · $m^{-2} \cdot s^{-1}$)	200	200	200	1200	1200	1200

Table S2.2. Linear regressions of kelp biomass and DOC release rate by sampling event. Kelp biomass (g DW · ind^{-1}) is individual dry weight and DOC release rates are least squares means (mg C · ind^{-1} · d^{-1}) calculated from linear regressions of volume-corrected DOC concentrations throughout the incubation period ($t \geq 4$ d, DOC samples ≥ 1 d^{-1}). Each sampling event conducted six kelp incubations, except for January 2020 ($n = 2$), early March 2020 ($n = 4$), January 2021 ($n = 4$), and October 2021 ($n = 3$). Significant (ANOVA, $p < 0.05$) linear regressions were determined for March 2021, July 2021, November 2021, and May 2022.

Sampling event	**Linear coefficient**	R^2	*df*	**error *df***	*F*	***p* value**
January 2020	0.78	1	1	0	NA	NA
early March 2020	0.057	0.032	1	2	0.065	0.82
late March 2020	0.96	0.65	1	4	7.48	0.052
June 2020	−0.78	0.28	1	4	1.58	0.28
August 2020	0.16	0.25	1	4	1.32	0.31
October 2020	0.89	0.12	1	4	0.56	0.50
January 2021	0.13	0.51	1	2	2.11	0.28
March 2021	2.5	0.73	1	4	10.94	0.030
April 2021	0.17	0.093	1	4	0.41	0.56
July 2021	0.39	0.66	1	4	7.93	0.048
October 2021	−0.49	0.51	1	1	1.04	0.49
November 2021	0.72	0.95	1	4	70.34	0.0011
May 2022	1.0	0.69	1	4	8.89	0.041
July 2022	0.13	0.29	1	4	1.61	0.27
October 2022	0.80	0.43	1	4	3.01	0.16
November 2022	0.25	0.040	1	4	0.17	0.70

Appendix S2.1. Interactive effect of DOC release rate calculation method and season on DOC release rate values and significant seasonal differences: two-way ANOVA (Type I and II) test results with R code

two-way ANOVA (Type I) on whether the calculation method has a significant effect on DOC release rate results:

```
> str(DOC_rate_method)
'data.frame':        170 obs. of  5 variables:
 $ Season: Factor w/ 4 levels "Winter","Spring",..: 1 1 1 1 1 1 2 2 2 2 ...
 $ Date  : chr  "2020/01/22" "2020/01/22" "2020/03/02" "2020/03/02" ...
 $ Sample: chr  "HK1-HI" "HK1-LI" "HK1-HI" "HK1-LI" ...
 $ Method: Factor w/ 2 levels "LSM","Simple_4d": 1 1 1 1 1 1 1 1 1 1 ...
 $ Rate  : num  0.2127 0.0714 0.1456 0.2082 0.0918 ...

> anova(lm(Rate ~ Method * Season, data = DOC_rate_method))

Analysis of Variance Table

Response: Rate
              Df Sum Sq Mean Sq F value    Pr(>F)
Method         1  0.351 0.35103  1.6433    0.2017
Season         3  6.971 2.32371 10.8780 1.505e-06 ***
Method:Season  3  0.022 0.00724  0.0339    0.9916
Residuals    162 34.606 0.21362
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

two-way ANOVA (Type II) on significant seasonal differences in DOC release rates when using the simple 4 d rate values:

```
> str(simpleDOC_release_data)
'data.frame':    85 obs. of  6 variables:
 $ ID          : chr  "43852-HK1-HI" "43852-HK1-LI" "43892-HK1-HI" "43892-HK1-LI" ...
 $ simplerateDOC: num  0.5127 0.1418 0.0791 0.2584 0.0979 ...
 $ Season      : Factor w/ 4 levels "Winter","Spring",..: 1 1 1 1 1 1 2 2 2 2 ...
 $ Bi_Season   : Factor w/ 8 levels "Early winter",..: 1 1 5 5 5 5 2 2 2 2 ...
 $ PAR         : Factor w/ 3 levels "low","med","high": 2 1 2 1 2 1 2 1 2 1 ...
 $ Date        : chr  "2020/01/22" "2020/01/22" "2020/03/02" "2020/03/02" ...
```

```
> SeasonalDOC.lm <- lm(simplerateDOC ~ Season + PAR, data = simpleDOC_release_data)
> SeasonalDOC.II.aov <- car::Anova(SeasonalDOC.lm, type = 2)
> SeasonalDOC.II.aov
Anova Table (Type II tests)

Response: simplerateDOC
          Sum Sq Df F value   Pr(>F)
Season     3.2687  3  4.1126 0.009156 **
PAR        0.1088  2  0.2053 0.814821
Residuals 20.9303 79
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> glht.Tukey <- glht(SeasonalDOC.lm,linfct=mcp(Season="Tukey"))
> summary(glht.Tukey)

           Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts

Fit: lm(formula = simplerateDOC ~ Season + PAR, data = simpleDOC_release_data)

Linear Hypotheses:
                  Estimate Std. Error t value Pr(>|t|)
Spring - Winter == 0   0.2778     0.1950   1.424   0.4836
Summer - Winter == 0   0.1687     0.1950   0.865   0.8203
Autumn - Winter == 0   0.6022     0.2010   2.996   0.0183 *
Summer - Spring == 0  -0.1091     0.1486  -0.734   0.8814
Autumn - Spring == 0   0.3244     0.1503   2.159   0.1410
Autumn - Summer == 0   0.4335     0.1503   2.885   0.0249 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Appendix S2.2. Effect of bi-seasonal period and PAR on DOC release: two-way ANOVA (Type II) and Tukey's HSD test results with R code

```
> str(DOC_release_data)
'data.frame':        85 obs. of  5 variables:
 $ ID       : chr  "43852-HK1" "43852-HK2" "43892-HK1" "43892-HK2" ...
 $ normDOC  : num  0.0714 0.2128 0.2082 0.2804 0.1456 ...
 $ Season   : Factor w/ 4 levels "Winter","Spring",..: 1 1 1 1 1 1 2 2 2 2 ...
 $ Bi_Season: Factor w/ 8 levels "Early winter",..: 1 1 5 5 5 5 2 2 2 2 ...
 $ PAR      : Factor w/ 3 levels "low","med","high": 1 2 1 1 2 2 1 1 1 2 ...

> Bi_SeasonalDOC.lm <- lm(normDOC ~ Bi_Season + PAR, data = DOC_release_data)
> Bi_SeasonalDOC.II.aov <- car::Anova(Bi_SeasonalDOC.lm, type = 2)
> Bi_SeasonalDOC.II.aov

Anova Table (Type II tests)

Response: normDOC
          Sum Sq Df F value   Pr(>F)
Bi_Season  3.6241  7  2.9735 0.008303 **
PAR        0.0253  2  0.0726 0.930083
Residuals 13.0588 75
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

> glht.Tukey <- glht(Bi_SeasonalDOC.lm,linfct=mcp(Bi_Season="Tukey"))
> summary(glht.Tukey)

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts

Fit: lm(formula = normDOC ~ Bi_Season + PAR, data = DOC_release_data)

Linear Hypotheses:
                                Estimate Std. Error t value Pr(>|t|)
Early spring - Early winter == 0  0.29226    0.19670   1.486   0.8017
Early summer - Early winter == 0  0.19083    0.19858   0.961   0.9765
Early autumn - Early winter == 0  0.51527    0.20545   2.508   0.1976
Late winter - Early winter == 0   0.06482    0.26935   0.241   1.0000
Late spring - Early winter == 0   0.27382    0.25440   1.076   0.9565
Late summer - Early winter == 0  -0.04190    0.24091  -0.174   1.0000
Late autumn - Early winter == 0   0.70571    0.22407   3.149   0.0435 *
Early summer - Early spring == 0 -0.10143    0.14173  -0.716   0.9959
Early autumn - Early spring == 0  0.22301    0.15121   1.475   0.8074
```

```
Late winter - Early spring == 0  -0.22744    0.23066  -0.986   0.9729
Late spring - Early spring == 0  -0.01844    0.21301  -0.087   1.0000
Late summer - Early spring == 0  -0.33416    0.19670  -1.699   0.6734
Late autumn - Early spring == 0   0.41346    0.17568   2.353   0.2662
Early autumn - Early summer == 0  0.32443    0.14661   2.213   0.3410
Late winter - Early summer == 0  -0.12601    0.23226  -0.543   0.9993
Late spring - Early summer == 0   0.08299    0.20411   0.407   0.9999
Late summer - Early summer == 0  -0.23273    0.19858  -1.172   0.9326
Late autumn - Early summer == 0   0.51488    0.16478   3.125   0.0458 *
Late winter - Early autumn == 0  -0.45044    0.23816  -1.891   0.5448
Late spring - Early autumn == 0  -0.24144    0.20630  -1.170   0.9330
Late summer - Early autumn == 0  -0.55716    0.20545  -2.712   0.1275
Late autumn - Early autumn == 0   0.19045    0.16748   1.137   0.9421
Late spring - Late winter == 0    0.20900    0.28148   0.743   0.9949
Late summer - Late winter == 0   -0.10672    0.26935  -0.396   0.9999
Late autumn - Late winter == 0    0.64089    0.25440   2.519   0.1929
Late summer - Late spring == 0   -0.31572    0.25440  -1.241   0.9108
Late autumn - Late spring == 0    0.43189    0.20864   2.070   0.4278
Late autumn - Late summer == 0    0.74761    0.22407   3.336   0.0258 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Appendix S2.3. Effect of seasonal period and PAR on DOC release: two-way ANOVA (Type II) and Tukey's HSD test results with R code

```
> str(DOC_release_data)
'data.frame':	85 obs. of  5 variables:
 $ ID       : chr  "43852-HK1" "43852-HK2" "43892-HK1" "43892-HK2" ...
 $ normDOC  : num  0.0714 0.2128 0.2082 0.2804 0.1456 ...
 $ Season   : Factor w/ 4 levels "Winter","Spring",..: 1 1 1 1 1 1 2 2 2 2 ...
 $ Bi_Season: Factor w/ 8 levels "Early winter",..: 1 1 5 5 5 5 2 2 2 2 ...
 $ PAR      : Factor w/ 3 levels "low","med","high": 1 2 1 1 2 2 1 1 1 2 ...

> SeasonalDOC.lm <- lm(normDOC ~ Season + PAR, data = DOC_release_data)
> SeasonalDOC.II.aov <- car::Anova(SeasonalDOC.lm, type = 2)
> SeasonalDOC.II.aov

Anova Table (Type II tests)

Response: normDOC
          Sum Sq Df F value    Pr(>F)
Season     3.1541  3  6.1394 0.0008309 ***
PAR        0.0377  2  0.1102 0.8957993
Residuals 13.5288 79
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

> glht.Tukey <- glht(SeasonalDOC.lm,linfct=mcp(Season="Tukey"))
> summary(glht.Tukey)

	 Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts

Fit: lm(formula = normDOC ~ Season + PAR, data = DOC_release_data)

Linear Hypotheses:
                   Estimate Std. Error t value Pr(>|t|)
Spring - Winter == 0  0.25464    0.15680   1.624  0.36681
Summer - Winter == 0  0.09964    0.15680   0.635  0.91899
Autumn - Winter == 0  0.55424    0.16157   3.430  0.00501 **
Summer - Spring == 0 -0.15500    0.11946  -1.298  0.56287
Autumn - Spring == 0  0.29960    0.12082   2.480  0.06948 .
Autumn - Summer == 0  0.45460    0.12082   3.763  0.00169 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Adjusted p values reported -- single-step method)
```

CHAPTER THREE

Recalcitrant kinetics of kelp dissolved organic carbon and fluorescence peaks reveal distinct pathways

Abstract

Improved understanding of the recalcitrance of macroalgal dissolved organic carbon (DOC) and associated fluorescence characteristics are important for clarifying local and global roles in carbon cycles. However, empirical results from months-long macroalgal DOC bioavailability experiments remain scarce and none have assessed multi-year, year-round data. Therefore, current estimates of macroalgal DOC recalcitrance are highly uncertain, yet increasingly being used to quantify the global carbon sequestration potential of macroalgae. This study addresses these uncertainties by analyzing three years (2020–2022) of seasonal data from 150-d bioavailability experiments on DOC derived from the kelp *Saccharina japonica* var. *religiosa* (class Phaeophyceae) from Oshoro Bay, Hokkaido, Japan. Results indicate that fluorescence peak intensities (one protein-like and three humic-like peaks) and DOC produced during the preceding kelp incubation experiments followed different degradation or enhancement pathways during the bioavailability experiments. Specifically, while DOC concentrations and the protein-like "peak T" were consistently degraded, the humic-like "peak A" was degraded in winter, spring, and summer, but enhanced in autumn, while the humic-like "peak C" and "peak M" maintained or enhanced intensities. These relationships indicate that kelp-derived fluorescence signatures are more persistent than DOC concentrations. The relatively low seasonal recalcitrance of DOC (10–20%) after the ex situ 150-d experiments is an indication that contributions to the global DOC pool are overstated. Overall, these variable, yet significant relationships indicate that year-round, robust datasets are critical to understanding coastal biogeochemistry.

Introduction

Improved understanding of the bioavailability of macroalgal dissolved organic carbon (DOC) and fluorescent dissolved organic matter (FDOM) is important for clarifying local and global roles in carbon cycles (Wada et al., 2008; Wada & Hama, 2013; Carlson & Hansell, 2015; Watanabe et al., 2020; Watanabe et al., 2024). Macroalgal DOC has typically been assumed to be primarily labile and consumed by bacterial activity or degraded by physical processes (e.g., UV exposure) on short time-scales. However, even relatively low proportions of recalcitrant DOC have been shown to contribute to the global DOC pool. Microbial activity itself can also produce or enhance recalcitrant DOC (Brophy & Carlson, 1989; Ogawa et al., 2001; Jiao et al., 2010) or facilitate export via the microbial carbon pump (Jiao et al., 2011). In the context of accounting potential carbon sequestration services, there has been increased interest in quantifying the reactivity (Hansell, 2013; Benner & Amon, 2015) of macroalgal DOC (Li et al., 2022). The potential Blue Carbon role of macroalgae and various proposals for its use as a climate change mitigation strategy remain controversial in terms of basic scientific mechanisms and social impacts (Boyd et al., 2022; Ricart et al., 2022; Williamson & Gattuso, 2022; Carlson, 2024).

While global methods for monitoring, verifying, and reporting (MRV) refractory DOC derived from macroalgae for the purpose of carbon accounting or credits are preliminary and potentially unfeasible (Dolliver & O'Connor, 2022; Hurd et al., 2022; Hurd et al., 2024), the basic biogeochemistry of macroalgal DOC recalcitrance can still provide useful insights in terms of monitoring ecosystem health and water quality at local coastal scales (Yamashita & Tanoue, 2004; Wada & Hama, 2013; Zhang et al., 2017; Paine et al., 2021; Hall et al., 2022). Humic-like fluorophores in FDOM are associated with recalcitrant characteristics and studying the dynamics

of fluorescence peak intensities can reveal insights into the origins and fate of DOM at local and global scales (Yamashita et al., 2007, 2020, 2021a).

However, empirical results from macroalgal DOC bioavailability experiments remain scarce. For example, only Wada et al. (2008) assessed seasonal data collected over at least a year, but bioavailability experiments were limited to 30–60 d in duration. In contrast, Watanabe et al. (2020) demonstrated the importance of using a 150-d bioavailability experiment to differentiate between the degradation kinetics during the labile, semi-labile, and semi-refractory stages. Yet, in that study, only two experiments were conducted (Watanabe et al., 2020). Long-term (120–150 d) bioavailability experiments on DOC from *Saccharina japonica* have been limited to one (Zhang et al., 2023) or two (Gao et al., 2021) sampling events. Zhang and Wang (2017) assessed the bioavailability of DOC from *Ulva prolifera*. Kubo and Tanaka (2023) determined recalcitrance of DOC from withered *Ecklonia cava* based on leached humic-like fluorescence during long-term (30 d) incubations. Hulatt et al. (2009) assessed the recalcitrance of macroalgal dissolved organic matter (DOM) in terms of chromophoric DOM (CDOM) from 11 species but did not quantify DOC. Large variabilities in results between studies are therefore difficult to attribute to internal or external factors such as differences in geography, species, experimental method, sampling season. Assessing a comprehensive dataset from a singular sampling location and species is therefore useful for establishing a robust baseline for internally variable factors. While quantifying refractory DOC fluxes for the purpose of global carbon sequestration and carbon credit accounting remains fraught, approximate estimates of at least semi-recalcitrant DOC proportions for local ecosystems at annual scales can be useful in terms of predicting patterns, monitoring, and management strategies.

The objective of this study was to assess multi-year, year-round data on kelp DOC

bioavailability kinetics and fluorescence signatures to gain insights into significant patterns or relationships between factors. To guide this objective, the following three hypotheses were tested:

- Hypothesis 1: Kelp-derived DOC recalcitrant proportions are seasonally variable (because seasonally enhanced kelp DOC release is primarily labile);
- Hypothesis 2: Protein-like fluorescence signatures will be less recalcitrant than DOC (i.e., a proxy for solely labile characteristics);
- Hypothesis 3: Humic-like fluorescence signatures can be differentiated by origin (e.g., solely kelp-derived or mixed kelp- and microbially-derived).

Materials and Methods

Place-based research standpoint and methodology

The place-based research standpoint and methodology underlying this study is developed in Chapter 1 of this dissertation (Carlson, 2025), and previously applied to empirical macroalgal biogeochemistry in Chapter 2 of this dissertation (Carlson et al., 2024), as well as discussions of the broader social-ecological impacts of Blue Carbon as a climate change mitigation strategy in Chapter 6 of this dissertation (Carlson, 2024). The importance and relevance of explicit research methodologies and standpoints is well-established (e.g., Smith, [1999] 2021; Wilson, 2008; Oliveira & Wright, 2016; Walter & Andersen, 2016), including for empirical environmental science (Liboiron et al., 2018; Alegado et al., 2023). In brief, the place-based (e.g., Kawai et al., 2012; Kaminaga, 2018; Grunow et al., 2019; Ishihara, 2020; Uzawa, 2020) standpoint defining this research means the results will be most relevant to Ainu People and Ainu Mosir (Hokkaido) and that globalized insights will be primarily appropriate in the context of Indigenous science

and social-ecological stewardship (e.g., Morishige et al., 2018; Winter et al., 2018; Bennett et al., 2021; Jacobs et al., 2022).

Seawater sample collection, storage, and DOC analysis

The basic process of seawater sample collection, filtration, bottle storage, bottle cleaning, DOC analysis, and assessing analytical replicability was previously described in Chapter 2 of this dissertation (Carlson et al., 2024) and consistent with best practices established by Halewood et al. (2022). Chapter 2 (Carlson et al., 2024) also described the process of kelp collection and incubation used to establish the initial concentrations of kelp-derived DOC used in this study's bioavailability experiment. Bioavailability experiments were conducted for 15 sampling events from early March 2020 through November 2022 (sampling details provided in Chapter 2), with the final bioavailability experiment concluding in April 2023.

Fluorescence and absorbance analysis

Seawater samples were thawed overnight at about 4 °C and then allowed to reach room temperature immediately prior to the three-dimensional excitation-emission matrix (EEM) spectra measurements. EEM spectra were measured using a spectrofluorometer (Horiba FluoroMax-4) according to the analytical procedure described by Yamashita et al. (2017). Emissions scans from 290 nm to 600 nm at 2-nm intervals were acquired at excitation wavelengths between 250 nm and 450 nm at 5-nm intervals. The bandpass widths were 5 nm for both excitation and emission monochromators. Fluorescence spectra were scanned with an integration time of 0.25 s and were acquired in S/R mode. Samples were measured in a 1-cm quartz cuvette and Milli-Q was used as the blank. Corrections according to Murphy et al. (2010)

were made, including subtracting daily Milli-Q water blank of the EEM spectrum to eliminate the water Raman scatter peaks. The inner filter effect was also corrected for with the corresponding absorbance results. Absorbance analysis of DOM was conducted with a spectrophotometer (Shimadzu UV-1800) with a 1 cm cuvette according to the analytical procedure described by Yamashita et al. (2021b). The absorbance spectrum was determined from 250 to 800 nm at 0.5 nm intervals under a medium scan speed. Fluorescence intensities were finally calibrated for cross-instrument comparisons by dividing by the integral of the Raman peak according to Lawaetz and Stedmon (2009). These corrected intensity values are reported as Raman Units (RU) consistent with other studies on macroalgal FDOM (e.g., Kubo & Tanaka, 2023). They can also be simply converted to Quinine Sulfate (QS)-equivalents by the equation QS = RU/0.0767 (Lawaetz & Stedmon, 2009) for direct comparison to additional studies on macroalgal FDOM using such units (e.g., Wada et al., 2008). The resulting fluorescence intensity peak locations were consistent with known peaks and excitation/emission ranges described by Coble (1996) for comparison to other macroalgal DOC and fluorescence studies (e.g., Wada et al., 2008). However, this study performs an additional calculation (described in the following section) to determine the fluorescence intensity values attributable to the kelp holobiont, consistent with standard practice for kelp-derived DOC calculations. We recommend future studies on macroalgal FDOM and DOC adopt this practice.

Kelp-derived DOC and fluorescence calculations

Modified from Chapter 2 of this dissertation (Carlson et al., 2024) and Paine et al. (2023a), kelp-derived DOC inventory (mg C $\cdot$ g^{-1} DW) refers to the mass of DOC attributable to the kelp holobiont (i.e., relative to the corresponding control tank DOC inventory and inclusive

of kelp microbiome DOC dynamics [Bengtsson et al., 2011]) and normalized by the kelp dry-weight biomass (g DW). It is calculated as follows:

$$\text{Kelp-derived DOC inventory}_t = \frac{\left(C_{\text{kelp, t}} - C_{\text{control, }t}\right) \times V}{\text{Kelp biomass}}$$

where $C_{\text{kelp, }t}$ is the concentration of DOC (mg C · L^{-1}) in the seawater sample collected at an elapsed time t after kelp removal from the incubation tank (i.e., the start of the bioavailability experiment), $C_{\text{control, }t}$ is the concentration of DOC (mg C · L^{-1}) in the seawater sample collected from the corresponding control seawater incubation tank at an elapsed time t after the start of the bioavailability experiment, and V is the volume of seawater in the kelp-derived DOC incubation tank at the start of the bioavailability experiment.

Likewise, the kelp-derived fluorescence intensity inventory (RU · L · g^{-1} DW) refers to the volumetric amount of intensity attributable to the kelp holobiont and normalized by the kelp dry-weight biomass (g DW). It is calculated as follows:

$$\text{Kelp-derived fluorescence intensity inventory}_t = \frac{\left(I_{\text{kelp, }t} - I_{\text{control, }t}\right) \times V}{\text{Kelp biomass}}$$

where $I_{\text{kelp, }t}$ is the intensity of fluorescence (RU) in the seawater sample collected at an elapsed time t after the start of the bioavailability experiment and $I_{\text{control, }t}$ is the intensity of fluorescence (RU) in the seawater sample collected from the corresponding control seawater incubation tank at an elapsed time t after the start of the bioavailability experiment.

Therefore, at t = 0 d, the kelp-derived inventories represent the total amounts of DOC (mg C · g^{-1} DW) and fluorescence intensity (RU · L · g^{-1} DW) produced during the initial incubation experiment to be used in the subsequent bioavailability experiment. At t = 150 d, the kelp-derived inventories represent the amounts that were recalcitrant to degradation by the end of the bioavailability experiment. Recalcitrant proportions (%) are therefore calculated as the ratio

of kelp-derived inventories at t = 150 d and t = 0 d.

Results

Kelp DOC and fluorescence relative recalcitrance

Three distinct fluorescence peaks were generated during kelp incubation and persisted during the bioavailability experiments. The following characterization of the peaks is based on Coble (1996). The first peak consistently corresponded with "peak T", a tryptophan- or protein-like peak at 275/340. The second peak consistently corresponded with "peak A", a UV humic-like peak at 260/400–460. The third peak alternately corresponded with two neighboring peaks: "peak C", a visible humic-like peak at 320–360/420–460 or "peak M", a visible marine humic-like peak at 290–310/370–410. Therefore, while results for all four peaks are reported, "peak C" and "peak M" were generally not distinguishable in the EEM diagrams.

DOC concentrations consistently degraded during the bioavailability experiment across seasons (winter: 7% ± 9%, spring: 15% ± 2%, summer: 29% ± 8%, autumn: 21% ± 3% of initial concentrations) (Figure 3.1a). Protein-like "peak T" intensities degraded across all seasons (winter: 28% ± 15%, spring: 31% ± 8%, summer: 38% ± 6%, and autumn: 31% ± 3% of initial intensity values) (Figure 3.2a). Humic-like "peak A" intensity degraded in winter (69% ± 18%), spring (63% ± 10%), and summer (70% ± 8%) but was enhanced in autumn (119% ± 14%) (Figure 3.3a). Humic-like "peak C" intensities were not significantly different from their initial values in winter (112% ± 33%) and summer (92% ± 7%), but were significantly enhanced in spring (119% ± 14%) and autumn (155% ± 15%) (Figure 3.4a). Humic-like "peak M" intensities were not significantly different from their initial values in any season (Figure 3.5a). Annualized mean protein-like "peak T" intensities were significantly different from those for the humic-like

peaks. Annualized mean humic-like "peak A" intensities were significantly different from those for "peak C" and "peak M".

Seasonal kelp DOC and fluorescence production rates

As reported in Chapter 2 of this dissertation (Carlson et al., 2024), kelp-derived total DOC production rates were significantly enhanced in autumn (0.71 ± 0.10 mg C · g^{-1} DW · d^{-1}) relative to winter (0.14 ± 0.025 mg C · g^{-1} DW · d^{-1}) and summer (0.25 ± 0.050 mg C · g^{-1} DW · d^{-1}), but not significantly different from spring results (0.40 ± 0.10 mg C · g^{-1} DW · d^{-1}) (Figure 3.1b). Newly reported effective kelp-derived recalcitrant DOC production rates were higher in autumn (0.15 ± 0.014 mg C · g^{-1} DW · d^{-1}) and spring (0.12 ± 0.036 mg C · g^{-1} DW · d^{-1}) relative to winter (0.035 ± 0.028 mg C · g^{-1} DW · d^{-1}) and summer (0.085 ± 0.030 mg C · g^{-1} DW · d^{-1}).

Initial (t = 0 d) fluorescence peak intensity production rates were highest in spring for all four fluorescence signatures. Protein-like "peak T" had the highest intensity production rates of all signatures in winter (0.019 ± 0.0021 RU · L · g^{-1} DW · d^{-1}), spring (0.032 ± 0.0050 RU · g^{-1} DW · d^{-1}), and autumn (0.038 ± 0.0088 RU · L · g^{-1} DW · d^{-1}), while humic-like "peak A" had the highest overall intensity production rate in summer (0.012 ± 0.0021 RU · L · g^{-1} DW · d^{-1}) (Table 3.1). Recalcitrant (t = 150 d) fluorescence intensity production rates were similarly high in spring and autumn relative to winter and summer for all four fluorescence signatures. Humic-like "peak A", "peak C", and "peak M" were similarly higher than protein-like "peak T" in winter and spring. Humic-like "peak A" was uniquely higher than the other fluorescence signatures in summer and autumn (Table 3.1).

Discussion

Seasonality of recalcitrant kelp DOC

Hypothesis 1 expected that the final (biomass normalized) kelp-derived DOC contributions would be similar across seasons. According to this hypothesis, any seasonality in the initial DOC concentrations established in Chapter 2 of this dissertation (Carlson et al., 2024) would be primarily due to enhanced labile DOC release that would be largely degraded by the end of the 150-d bioavailability experiment. In other words, the seasonally elevated total kelp DOC release during autumn senescence found by Carlson et al. (2024) would be proportionally more labile. In Gao et al. (2021) there were no significant differences between the total, labile (bioavailable), or recalcitrant DOC production rates in winter (January) and spring (April). In contrast, Watanabe et al. (2020) reported both higher total and recalcitrant DOC production rates in winter (February) compared to spring (March). However, seasonal trends cannot be confidently concluded on the basis of two sampling events.

In our study, Hypothesis 1 was partially confirmed as the recalcitrant DOC contributions in autumn results were not significantly higher than spring or summer results despite the significantly higher autumn DOC release reported by Carlson et al. (2024). The winter results in this study indicated negligible recalcitrant DOC (no significant difference from zero), which is consistent with the finding in Carlson et al. (2024) of minimal to negligible DOC release in winter results. These findings indicate that enhanced DOC release during stress (such as autumn senescence) is proportionally more labile and does not enhance recalcitrant DOC contributions.

Kelp-derived protein-like fluorescence kinetics

Hypothesis 2 expected that protein-like fluorescence peak intensities would be degraded

and would be less recalcitrant than DOC. Supporting this, protein-like "peak T" was consistently degraded during the bioavailability experiments, but contrary to expectations was significantly more recalcitrant than DOC. However, this result is not unprecedented as Wada et al. (2008) reported that protein-like "peak T" was stable in spring and autumn, slightly degraded in winter, and exponentially degraded in summer. Protein-like "peak T" production rates were significantly variable with significantly lower rates in the summer. Spring rates were also significantly higher than winter rates but not significantly different from autumn rates. Overall, this indicates that spring and autumn are the primary seasons for labile production.

Distinct humic-like fluorescence pathways

Hypothesis 3 expected that the humic-like fluorescence signatures would have distinct kinetic pathways providing insights into their origins as either solely kelp-derived or a mixture of kelp- and microbially-derived fluorescence. Highly recalcitrant macroalgal-derived humic-like material is likely associated with the production of phenolic compounds which are a defense mechanism against herbivory (Van Alstyne, 1988; Paul et al., 2006) and UV exposure (Sieburth & Jensen, 1969; Swanson & Druehl, 2002).

Humic-like "peak A"

Humic-like "peak A" was degraded in winter, spring, and summer, and enhanced in autumn. This may be due to "peak A" being associated with kelp-derived detritus or POM, in which case persistent kelp POM after kelp removal in the autumn experiments may have continued to generate "peak A" fluorescence. In Wada et al. (2008), humic-like "peak A" was significantly degraded in the summer (June), enhanced in early spring (April), and not

significantly different in autumn (October), late spring (May), or winter (December). Seasonally, initial "peak A" production was an order of magnitude higher in summer (June) compared to other seasons, with autumn (October) and early spring (April) higher than winter (December) and late spring (May) (Wada et al., 2008).

Humic-like "peak C"

Humic-like "peak C" was significantly enhanced relative to initial values in spring and autumn, indicating the potential role of microbial transformations and generations of recalcitrance continuing throughout the bioavailability experiment. This enhancement of "peak C" is consistent with the results of other kelp bioavailability experiments (Wada et al., 2008). In Wada et al. (2008), humic-like "peak C" was also relatively higher compared to other peaks in natural seawater from macroalgal beds across seasons and decoupled from the order of magnitude higher fluorescence and DOC production reported in summer (June) (Wada et al., 2008). This indicates that "peak C" may be generated directly by microorganisms in natural seawater (i.e., heterotrophic bacteria or microalgae) and that this activity may be enhanced in the presence of kelp-derived DOC. It is not clear if the enhancement of humic-like "peak C" is derived from the simultaneous degradation of protein-like "peak T" and humic-like "peak A" and this should be investigated further.

Humic-like "peak M"

In our results, humic-like "peak M" did not significantly change between the beginning and end of the bioavailability experiment. However, in Wada et al. (2008), humic-like "peak M" was enhanced in spring (April and May), exponentially degraded in summer (June), and

unchanged in autumn (October) and winter (December). This indicates that the recalcitrance of kelp-derived humic-like fluorescence types is highly context dependent. Seasonally, initial "peak M" production was an order of magnitude higher in summer (June) compared to other season, with autumn (October) and early spring (April) higher than winter (December) and late spring (May) (Wada et al., 2008).

Conclusion

In this multi-year study, kelp DOC recalcitrance was generally lower than previously cited global estimates, with a few exceptions at the scales of season and individual kelp. We also clarified several key aspects of the relationships between kelp DOC and fluorescence produced during incubation experiments and subsequently degraded, conserved, or enhanced during bioavailability experiments. Protein-like "peak T" and humic-like "peak M" were attributable to live kelp production, while humic-like "peak A" is suspected to be derived from kelp POM, and humic-like "peak C" is likely generated by both short- and long-term microbial activity during the incubation and bioavailability experiments. These insights indicate that protein-like "peak T" may be a suitable semi-quantitative proxy for tracing local kelp-derived DOC concentrations, while humic-like "peak C" could be a qualitative signature of kelp-derived DOM at the global scale.

Tables and Figures

Table 3.1. Seasonal fluorescence peak intensity production rates.

		Fluorescence peak intensity production rates ($RU \cdot L \cdot g^{-1}\ DW \cdot d^{-1}$)			
Fluorescence signature		Winter	Spring	Summer	Autumn
protein-like	Initial	0.019 ±	0.032 ±	0.010 ±	0.024 ±
"peak T"	(t = 0 d)	0.0021	0.0050	0.0014	0.0024
	Recalcitrant	0.0040 ±	0.0092 ±	0.0051 ±	0.0069 ±
	(t = 150 d)	0.0023	0.0025	0.00088	0.00063
humic-like	Initial	0.012 ±	0.024 ±	0.012 ±	0.015 ±
"peak A"	(t = 0 d)	0.00083	0.0027	0.0021	0.0012
	Recalcitrant	0.0082 ±	0.015 ±	0.011 ±	0.017 ±
	(t = 150 d)	0.0025	0.0030	0.0012	0.0015
humic-like	Initial	0.0061 ±	0.012 ±	0.0089 ±	0.010 ±
"peak C"	(t = 0 d)	0.00047	0.0013	0.0012	0.00073
	Recalcitrant	0.0074 ±	0.015 ±	0.010 ±	0.015 ±
	(t = 150 d)	0.0024	0.0027	0.0011	0.0013
humic-like	Initial	0.011 ±	0.018 ±	0.0082 ±	0.013 ±
"peak M"	(t = 0 d)	0.0013	0.0027	0.0010	0.0012
	Recalcitrant	0.0070 ±	0.015 ±	0.010 ±	0.013 ±
	(t = 150 d)	0.0026	0.0027	0.0011	0.0011

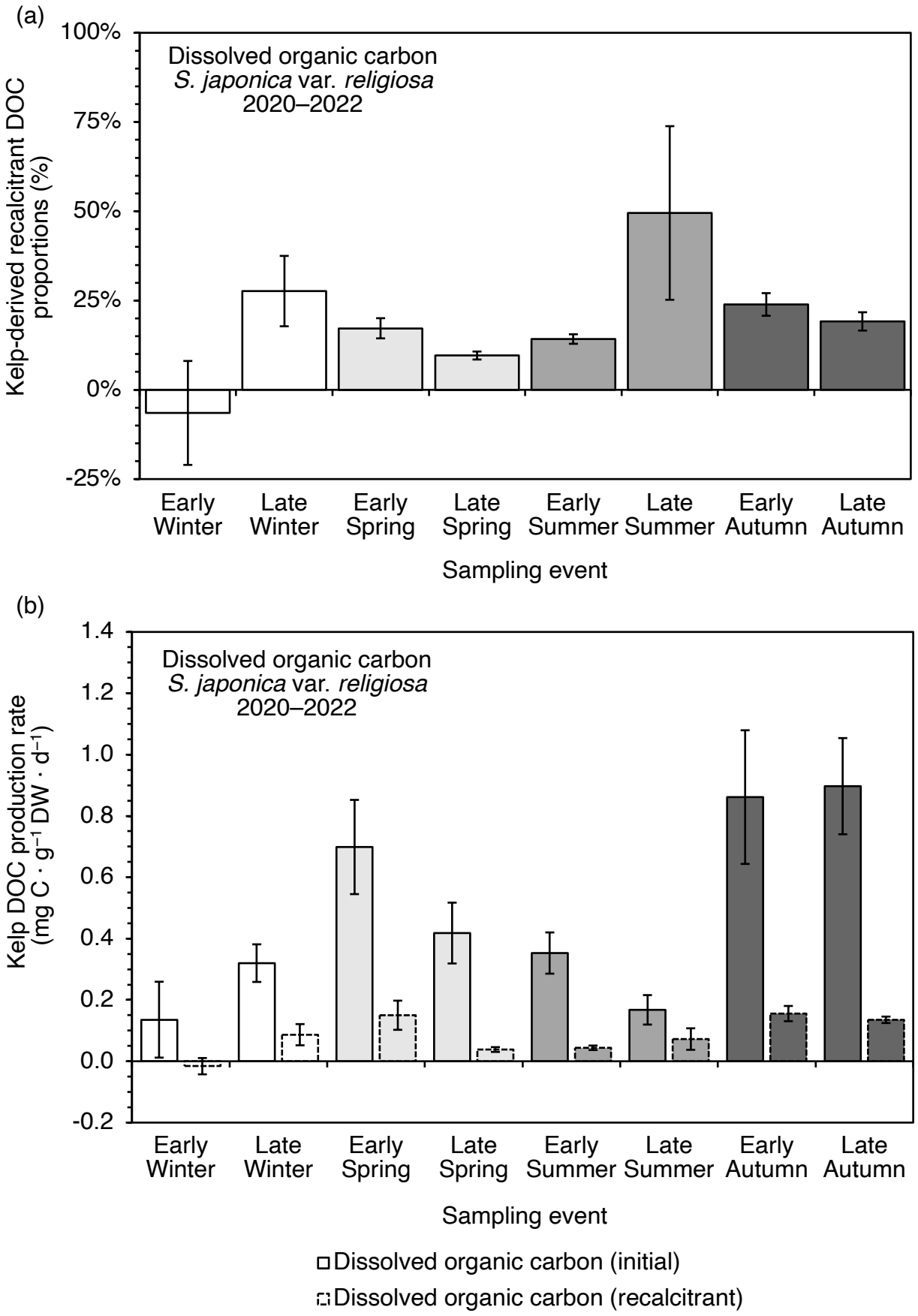

(a)
Dissolved organic carbon
S. japonica var. religiosa
2020–2022
Kelp-derived recalcitrant DOC proportions (%)
100%
75%
50%
25%
0%
-25%
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
(b)
Dissolved organic carbon
S. japonica var. religiosa
2020–2022
Kelp DOC production rate (mg C · g⁻¹ DW · d⁻¹)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
Dissolved organic carbon (initial)
Dissolved organic carbon (recalcitrant)

Figure 3.1. Mean kelp DOC dynamics by season. Data are means (± *SE*) of (a) the relative proportion of recalcitrant DOC remaining after the t = 150 d bioavailability experiments and (b) the kelp-derived DOC production rates (initial: solid border; recalcitrant: dashed border) represented as biomass normalized rates (mg C · g^{-1} DW · d^{-1}), with results aggregated according to eight bi-seasonal categories. Shading effects visually differentiate results by the four seasons.

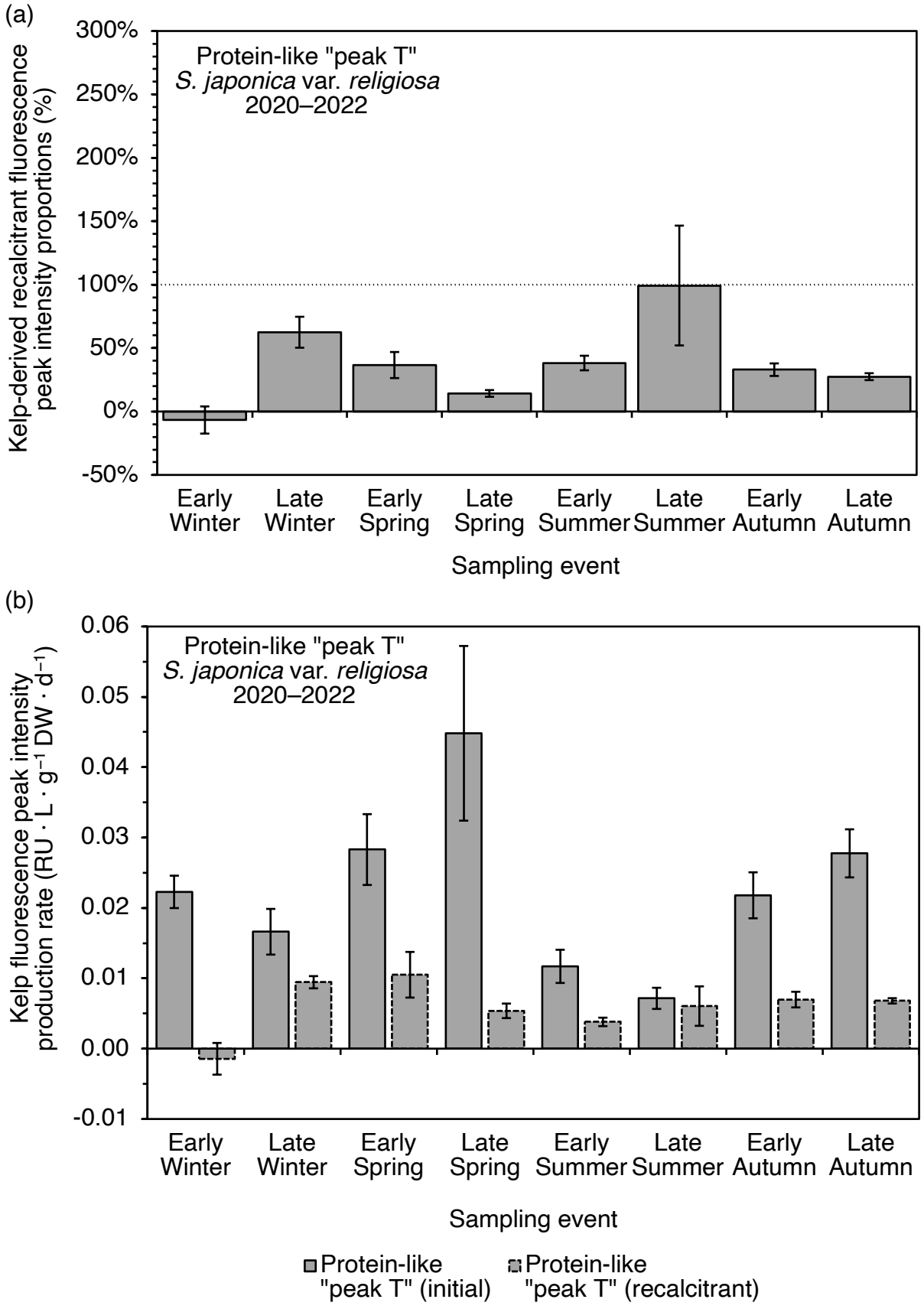

(a)
Protein-like "peak T"
S. japonica var. religiosa
2020–2022
Kelp-derived recalcitrant fluorescence peak intensity proportions (%)
300%
250%
200%
150%
100%
50%
0%
-50%
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
(b)
Protein-like "peak T"
S. japonica var. religiosa
2020–2022
Kelp fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
Protein-like "peak T" (initial)
Protein-like "peak T" (recalcitrant)

Figure 3.2. Mean kelp-derived protein-like "peak T" fluorescence dynamics by season. Data are means (± *SE*) of (a) the relative proportion of recalcitrant fluorescence peak intensity remaining after the t = 150 d bioavailability experiments and (b) the kelp-derived fluorescence production rates (initial: solid border; recalcitrant: dashed border) represented as biomass normalized rates (RU · L · g^{-1} DW · d^{-1}), with results aggregated according to eight bi-seasonal categories.

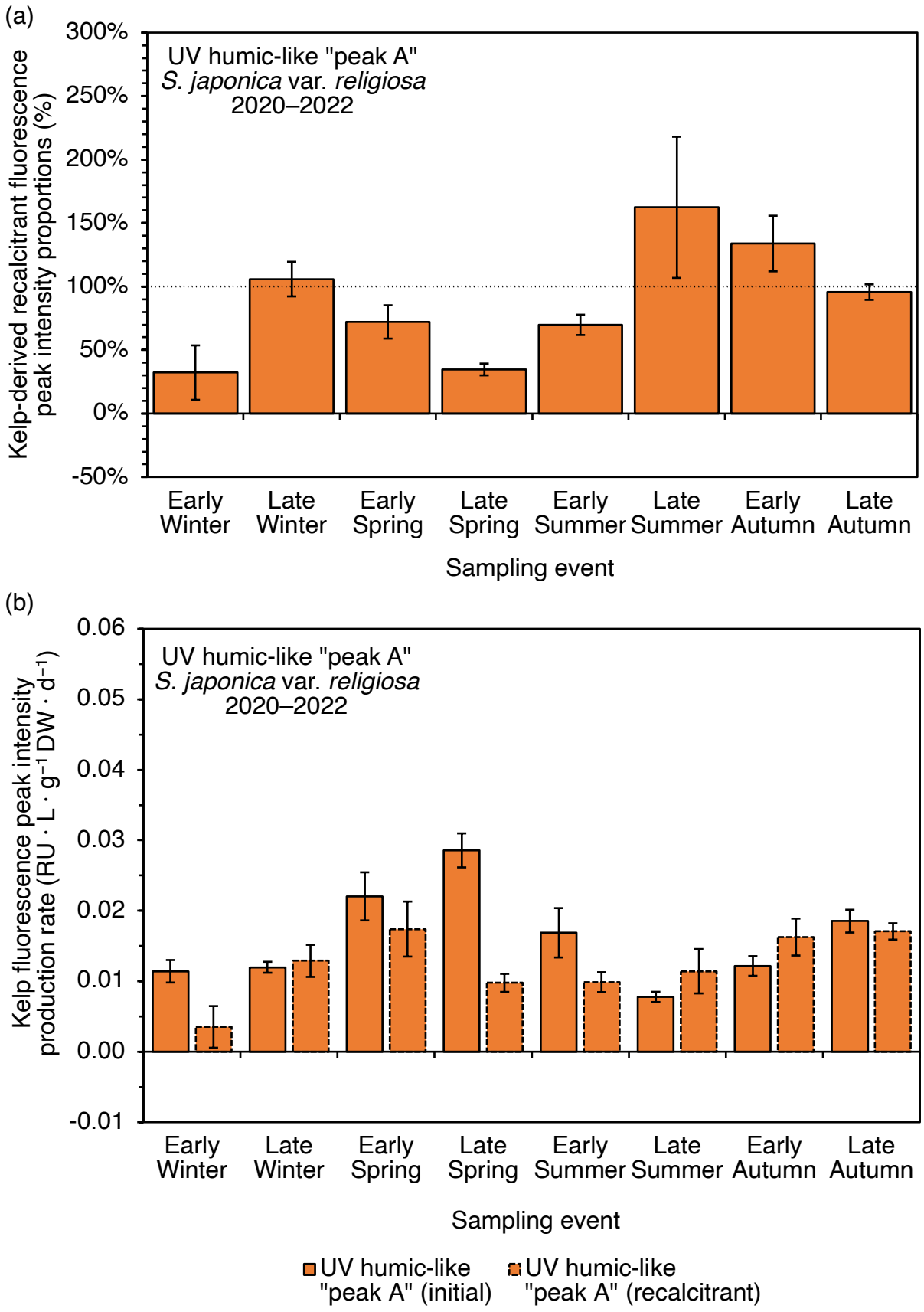

(a)
UV humic-like "peak A"
S. japonica var. religiosa
2020–2022
Kelp-derived recalcitrant fluorescence peak intensity proportions (%)
300%
250%
200%
150%
100%
50%
0%
-50%
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
(b)
UV humic-like "peak A"
S. japonica var. religiosa
2020–2022
Kelp fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
UV humic-like "peak A" (initial)
UV humic-like "peak A" (recalcitrant)

Figure 3.3. Mean kelp-derived UV humic-like "peak A" fluorescence dynamics by season. Data are means (± *SE*) of (a) the relative proportion of recalcitrant fluorescence peak intensity remaining after the t = 150 d bioavailability experiments and (b) the kelp-derived fluorescence production rates (initial: solid border; recalcitrant: dashed border) represented as biomass normalized rates ($RU \cdot L \cdot g^{-1}\ DW \cdot d^{-1}$), with results aggregated according to eight bi-seasonal categories.

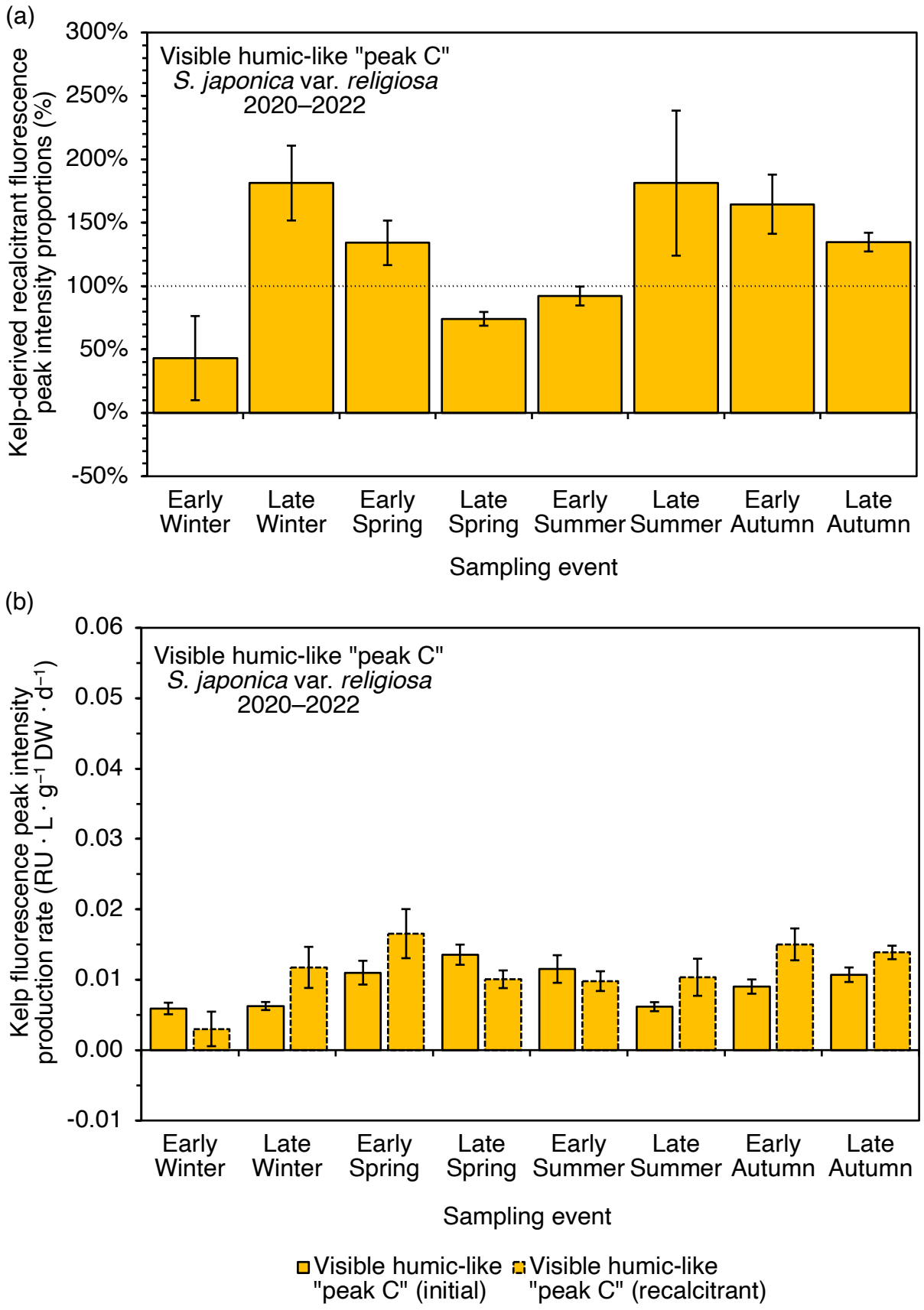

(a)
Visible humic-like "peak C"
S. japonica var. religiosa
2020–2022
Kelp-derived recalcitrant fluorescence peak intensity proportions (%)
300%
250%
200%
150%
100%
50%
0%
-50%
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
(b)
Visible humic-like "peak C"
S. japonica var. religiosa
2020–2022
Kelp fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
Visible humic-like "peak C" (initial)
Visible humic-like "peak C" (recalcitrant)

Figure 3.4. Mean kelp-derived visible humic-like "peak C" fluorescence dynamics by season. Data are means (± *SE*) of (a) the relative proportion of recalcitrant fluorescence peak intensity remaining after the t = 150 d bioavailability experiments and (b) the kelp-derived fluorescence production rates (initial: solid border; recalcitrant: dashed border) represented as biomass normalized rates (RU · L · g^{-1} DW · d^{-1}), with results aggregated according to eight bi-seasonal categories.

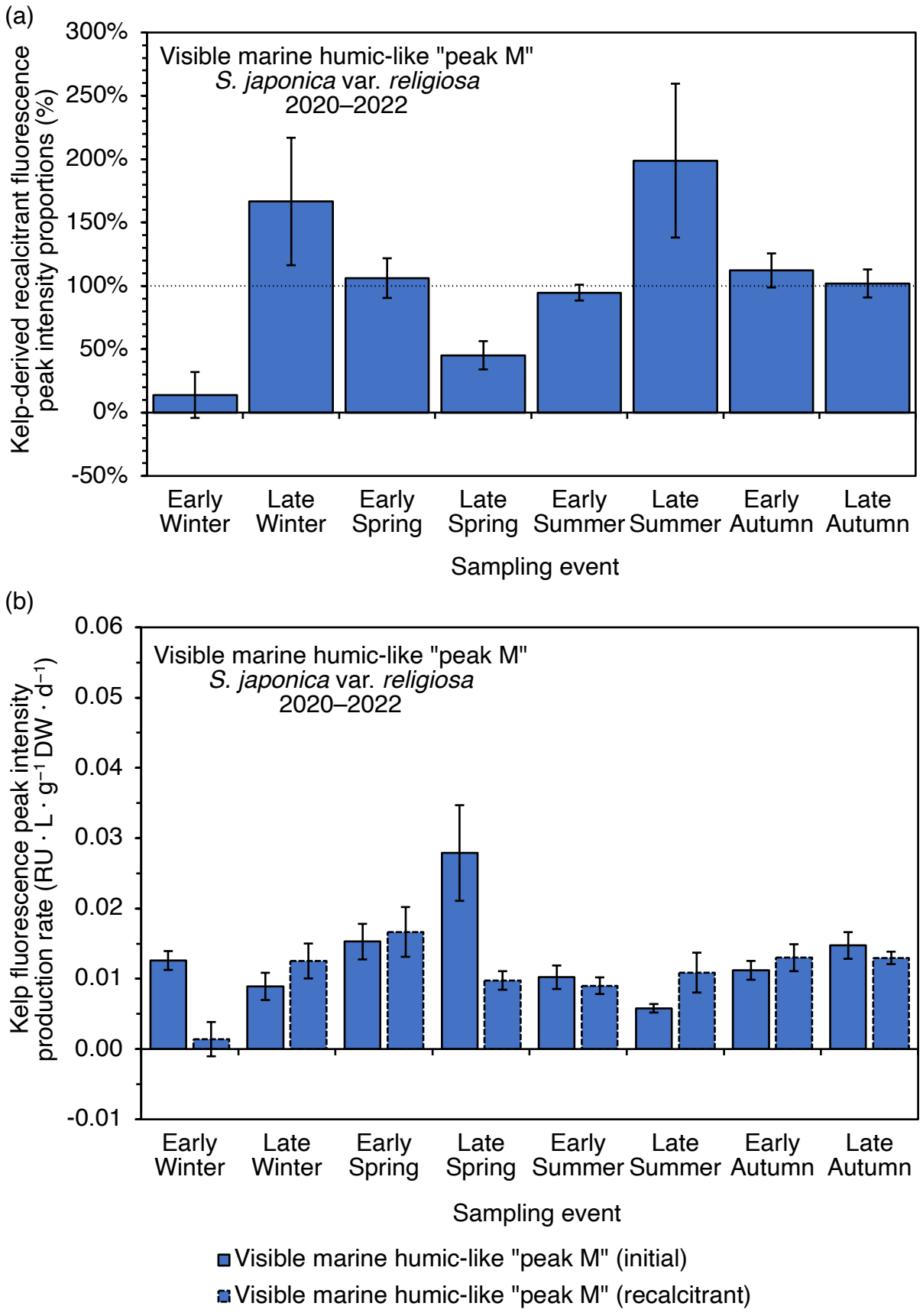

(a)
Visible marine humic-like "peak M"
S. japonica var. religiosa
2020–2022
Kelp-derived recalcitrant fluorescence peak intensity proportions (%)
300%
250%
200%
150%
100%
50%
0%
-50%
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
(b)
Visible marine humic-like "peak M"
S. japonica var. religiosa
2020–2022
Kelp fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
Early Winter
Late Winter
Early Spring
Late Spring
Early Summer
Late Summer
Early Autumn
Late Autumn
Sampling event
Visible marine humic-like "peak M" (initial)
Visible marine humic-like "peak M" (recalcitrant)

Figure 3.5. Mean kelp-derived visible marine humic-like "peak M" fluorescence dynamics by season. Data are means (± *SE*) of (a) the relative proportion of recalcitrant fluorescence peak intensity remaining after the t = 150 d bioavailability experiments and (b) the kelp-derived fluorescence production rates (initial: solid border; recalcitrant: dashed border) represented as biomass normalized rates ($RU \cdot L \cdot g^{-1}\ DW \cdot d^{-1}$), with results aggregated according to eight bi-seasonal categories.

CHAPTER FOUR

Species-specific recalcitrant macroalgal dissolved organic carbon and fluorescence dynamics typically outweighed by in situ heatwave and bleaching stress responses

Abstract

Understanding species-specific variability in macroalgal contributions of total and recalcitrant dissolved organic carbon (DOC) and fluorescence is important to biogeochemical cycles, yet this is the first such study. It is uncertain whether reported differences in species are attributable to phylogenetic differences or to environmental or experimental differences. This study addresses these uncertainties by analyzing seasonal data from nine species across five orders—Fucales (*Sargassum thunbergii*, *Sargassum confusum*), Gelidiales (*Gelidium elegans*), Gigartinales (*Mazzaella japonica*, *Neodilsea yendoana*), Laminariales (*Saccharina japonica* var. *religiosa*, *Costaria costata*), and Ulvales (*Ulva australis*, *Ulva linza*) from Oshoro Bay, Hokkaido, Japan. Macroalgal-derived DOC and fluorescence initial production rates are derived from 4-d ex situ incubation experiments and effective recalcitrant DOC and fluorescence production rates are derived from subsequent 150-d bioavailability experiments (macroalgae removed). This study disentangles the effect of bleached tissue in paired experiments and of the 2023 summer heatwave (30 °C, +5 °C above 2020–2022 baseline) on these dynamics. Results indicate substantial and distinct species-specific differences in recalcitrant proportions (%), initial production rates, and recalcitrant rates, as well as species-specific seasonal trends. Excluding results from bleaching and heatwave stress, the highest recalcitrant DOC proportions were from *S. confusum* (36% ± 0.57%, $n = 3$) and *S. thunbergii* (49%, composite $n = 3$) in autumn, while the highest recalcitrant DOC production rates were from *U. australis* (0.20 mg C · g^{-1} DW · d^{-1}, composite $n = 2$) in spring. However, these differences are significantly outweighed by the typically order of magnitude enhancement effect of bleached tissue (for *U. australis* and *M. japonica*) and heatwave stress (for *S. japonica* var. *religiosa* and *N. yendoana*) on DOC and fluorescence recalcitrance. In contrast, results from *U. australis* during the summer

heatwave were several times lower than in spring. This indicates that studies addressing ecophysiological stress are essential to constraining macroalgal DOC and fluorescence contributions, yet certain species may be significantly more resilient or have contrasting responses to these stresses and must also be studied.

Introduction

Understanding how different macroalgal species variably contribute dissolved organic carbon (DOC) and fluorescent dissolved organic matter (FDOM) to local and global biogeochemical cycles is an important, yet poorly understood subject. As described in previous reports (Paine et al., 2021), empirical studies on macroalgal DOC overall are relatively few. Studies specifically considering recalcitrance and fluorescence are even fewer, and multi-species experiments are non-existent. Single species empirical studies on macroalgal DOC recalcitrance and fluorescence include *Ecklonia cava* (Wada et al., 2008), *Sargassum natans* (Powers et al., 2020), and *Saccharina japonica* (Li et al., 2022; Zhang et al., 2022; Zhang et al., 2023). Kubo and Tanaka (2023) compare recalcitrant DOC and fluorescence between the kelp *E. cava* and the seagrass *Zostera japonica*. Hulatt et al. (2009) studied chromophoric dissolved organic matter (CDOM) production and degradation from 11 macroalgal species, but did not quantitatively measure the corresponding amount of DOC. Paine et al. (2021) reviews macroalgal DOC production for several species and Watanabe et al. (2024) reviews macroalgal DOC recalcitrance across species. It is therefore highly uncertain whether reported differences in species are attributable to phylogenetic differences or to environmental or experimental differences.

Disentangling active exudation and passive leakage mechanisms remains difficult (Weigel & Pfister, 2021; Paine et al., 2021; Paine et al., 2023a; Carlson et al., 2024) and it is not clear how the recalcitrance of DOC may vary across species depending on the release mechanism. In particular, it is known that factors such as desiccation, heat stress, osmotic stress, and distal decay can enhance DOC production by up to or beyond an order of magnitude. Reports on the recalcitrance and fluorescence characteristics of this enhanced DOC leakage have been made in the context of withered *E. cava* (Kubo & Tanaka, 2023), but it is not clear how

stress (e.g., tissue bleaching or heatwave stress) impacts the recalcitrance of macroalgal DOC and fluorescence across species from a single sampling event and location.

The objective of this study was to assess macroalgal DOC production and bioavailability, as well as associated fluorescence characteristics, from a variety of species in the context of observed in situ stress factors. While environmental variations are reduced when considering species from a single site compared to multiple sites, it is still critical to control for factors such as season and environmental parameters that may differentially affect different species. To guide this objective, the following four hypotheses were assessed:

- Hypothesis 1: There will be substantial species-specific differences in macroalgal DOC and fluorescence dynamics (within a single season);
- Hypothesis 2: There will be species-specific seasonal trends in DOC and fluorescence dynamics (for species with multi-seasonal data);
- Hypothesis 3: Heatwave stress will have a significant effect on macroalgal DOC and fluorescence dynamics (relative to other seasons and non-heatwave summers);
- Hypothesis 4: Bleached tissue will have a significant effect on macroalgal DOC and fluorescence dynamics (relative to paired macroalgae without bleached tissue).

Materials and Methods

Place-based research standpoint and methodology

The place-based research standpoint and methodology underlying this study is developed in Chapter 1 of this dissertation (Carlson, 2025), and previously applied to empirical macroalgal biogeochemistry in Chapters 2 and 3 of this dissertation, as well as discussions of the broader social-ecological impacts of Blue Carbon as a climate change mitigation strategy in Chapter 6 of

this dissertation (Carlson, 2024). The importance and relevance of explicit research methodologies and standpoints is well-established (e.g., Smith, [1999] 2021; Wilson, 2008; Oliveira & Wright, 2016; Walter & Andersen, 2016), including for empirical environmental science (Liboiron et al., 2018; Alegado et al., 2023). In brief, the place-based (e.g., Kawai et al., 2012; Kaminaga, 2018; Grunow et al., 2019; Ishihara, 2020; Uzawa, 2020) standpoint defining this research means the results will be most relevant to Ainu People and Ainu Mosir (Hokkaido) and that globalized insights will be primarily appropriate in the context of Indigenous science and social-ecological stewardship (e.g., Morishige et al., 2018; Winter et al., 2018; Bennett et al., 2021; Jacobs et al., 2022).

Macroalgal collection and incubation

Six sampling events were conducted in winter (February 2022 and March 2023), spring (June 2023), summer (August 2023), and autumn (October 2021 and November 2023). In general, the seasonally dominant species were collected for incubation, with relatively larger species individually incubated in replicate 3 L tanks and smaller species composite (n = 2–13) incubated in single species-specific 3 L tanks (i.e., such that each tank incubated a similar biomass of macroalgae). For example, triplicate incubations of individual *S. japonica* var. *religiosa* were conducted in winter, spring, and summer 2023. No *S. japonica* var. *religiosa* were visibly present in winter 2022 or autumn 2023. Two sets of duplicate incubations of individual *Costaria costata* were conducted in winter 2022 to compare the effect of differing photosynthetically active radiation treatments (200 and 400 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}). Triplicate incubations of individual *Sargassum confusum* were conducted in autumn 2023. All species were collected from single sample locations within the shallow subtidal ecosystem at Oshoro Bay.

Composite sampling is an established method for achieving an average value based on a higher sample count. While this forgoes measurements of error, it is a practical method that provides a value closer to the "true" mean that can be relatively compared to other composite sample results, while reducing the required number of samples by up to an order of magnitude. Composite incubations were conducted on *Ulva linza* (winter 2023), *Ulva australis* (winter 2023, spring 2023, summer 2023, and autumn 2021), *Neodilsea yendoana* (spring 2023 and summer 2023), *Mazzaella japonica* (spring 2023 and autumn 2021), *Sargassum thunbergii* (autumn 2023), and *Gelidium elegans* (autumn 2023). Paired composite experiments on the effect of bleached tissue were conducted on *M. japonica* in winter 2023 (bleached: composite n = 13, 3.59 g DW; not bleached: composite n = 5, 3.92 g DW) and *U. australis* in summer 2023 (bleached: composite n = 5, 3.97 g DW; not bleached: composite n = 3, 4.72 g DW). In these experiments, "bleached macroalgae" indicates that bleaching affected more than 50% of the tissue, while "not bleached macroalgae" indicates that no or negligible (< 1%) tissue had visible bleaching.

Seawater sample collection, storage, and DOC analysis

The basic process of seawater sample collection, filtration, bottle storage, bottle cleaning, DOC analysis, and assessing analytical replicability was previously described in Chapter 2 of this dissertation (Carlson et al., 2024) and consistent with best practices established by Halewood et al. (2022). Chapter 2 (Carlson et al., 2024) also described the process of macroalgal collection and incubation and Chapter 3 described the process of macroalgal removal and the experiments on macroalgal-derived DOC bioavailability.

Fluorescence and absorbance analysis

Seawater samples were thawed overnight at about 4 °C and then allowed to reach room temperature immediately prior to the three-dimensional excitation-emission matrix (EEM) spectra measurements. EEM spectra were measured using a spectrofluorometer (Horiba FluoroMax-4) according to the analytical procedure described by Yamashita et al. (2017). Emissions scans from 290 nm to 600 nm at 2-nm intervals were acquired at excitation wavelengths between 250 nm and 450 nm at 5-nm intervals. The bandpass widths were 5 nm for both excitation and emission monochromators. Fluorescence spectra were scanned with an integration time of 0.25 s and were acquired in S/R mode. Samples were measured in a 1-cm quartz cuvette and Milli-Q was used as the blank. Corrections according to Murphy et al. (2010) were made, including subtracting daily Milli-Q water blank of the EEM spectrum to eliminate the water Raman scatter peaks. The inner filter effect was also corrected for with the corresponding absorbance results. Absorbance analysis of DOM was conducted with a spectrophotometer (Shimadzu UV-1800) with a 1 cm cuvette according to the analytical procedure described by Yamashita et al. (2021b). The absorbance spectrum was determined from 250 to 800 nm at 0.5 nm intervals under a medium scan speed. Fluorescence intensities were finally calibrated for cross-instrument comparisons by dividing by the integral of the Raman peak according to Lawaetz and Stedmon (2009). These corrected intensity values are reported as Raman Units (RU) consistent with other studies on macroalgal FDOM (e.g., Kubo & Tanaka, 2023). They can also be simply converted to Quinine Sulfate (QS)-equivalents by the equation QS = RU/0.0767 (Lawaetz & Stedmon, 2009) for direct comparison to additional studies on macroalgal FDOM using such units (e.g., Wada et al., 2008). The resulting fluorescence intensity peak locations were consistent with known peaks and excitation/emission ranges described by

Coble (1996) for comparison to other macroalgal DOC and fluorescence studies (e.g., Wada et al., 2008). As with Chapter 3 of this dissertation, this study performs an additional calculation (described in the following section) to determine the fluorescence intensity values attributable to the macroalgal holobiont, consistent with standard practice for macroalgal-derived DOC calculations. We recommend future studies on macroalgal FDOM and DOC adopt this practice.

Macroalgal-derived DOC and fluorescence calculations

Modified from Chapters 2 and 3 of this dissertation, as well as Paine et al. (2023a), macroalgal-derived DOC inventory (mg C · g^{-1} DW) refers to the amount of DOC attributable to the macroalgal holobiont (i.e., relative to the corresponding control tank DOC inventory and inclusive of macroalgal microbiome DOC dynamics [Bengtsson et al., 2011]) and normalized by the macroalgal dry-weight biomass (g DW). It is calculated as follows:

$$\text{Macroalgal-derived DOC inventory}_t = \frac{\left(C_{\text{macroalgae, t}} - C_{\text{control, }t}\right) \times V}{\text{Macroalgae biomass}}$$

where $C_{\text{macroalgae, }t}$ is the concentration of DOC (mg · L^{-1}) in the seawater sample collected at an elapsed time t after macroalgal removal from the incubation tank (i.e., the start of the bioavailability experiment), $C_{\text{control, }t}$ is the concentration of DOC (mg · L^{-1}) in the seawater sample collected from the corresponding control seawater incubation tank at an elapsed time t after the start of the bioavailability experiment, and V is the volume of seawater in the macroalgal-derived DOC incubation tank at the start of the bioavailability experiment.

Likewise, the macroalgal-derived fluorescence intensity inventory (RU · L · g^{-1} DW) refers to the volumetric amount of intensity attributable to the macroalgal holobiont and normalized by the macroalgal dry-weight biomass (g DW). It is calculated as follows:

$$\text{Macroalgal-derived fluorescence intensity inventory}_t = \frac{\left(I_{\text{macroalgal},\,t} - I_{\text{control},\,t}\right) \times V}{\text{Macroalgae biomass}}$$

where $I_{\text{macroalgal},\,t}$ is the intensity of fluorescence (RU) in the seawater sample collected at an elapsed time t after the start of the bioavailability experiment and $I_{\text{control},\,t}$ is the intensity of fluorescence (RU) in the seawater sample collected from the corresponding control seawater incubation tank at an elapsed time t after the start of the bioavailability experiment.

Therefore, at t = 0 d, the macroalgal-derived inventories represent the total amounts of DOC (mg C · g^{-1} DW) and fluorescence intensity (RU · L · g^{-1} DW) produced during the initial incubation experiment to be used in the subsequent bioavailability experiment. At t = 150 d, the macroalgal-derived inventories represent the amounts that were recalcitrant to degradation by the end of the bioavailability experiment. Recalcitrant proportions (%) are therefore calculated as the ratio of macroalgal-derived inventories at t = 150 d and t = 0 d.

Results

Macroalgal DOC and fluorescence relative recalcitrance

Consistent with Chapter 3 of this dissertation, fluorescence peaks generated during macroalgal incubation and persisting during the bioavailability experiments were characterized based on Coble (1996) as protein- like “peak T”, UV humic-like “peak A”, visible humic-like “peak C”, and visible marine humic-like “peak M”.

DOC concentrations consistently degraded during the bioavailability experiment across seasons. Mean seasonal results across species (± *SE* between each species-specific mean), indicated similarly low recalcitrant DOC proportions in winter (14% ± 3.3%), spring (12% ± 3.3%), and summer (16% ± 7.5%), and about 2 times higher proportions in autumn (30% ± 5.4%) (Figure 4.1). However, there were notable differences between species within each season

(Figure 4.2). In winter 2022 (Figure 4.2a), recalcitrant DOC proportions were 11% ± 0.19% for *C. costata* (*n* = 4). In winter 2023 (Figure 4.2a), recalcitrant DOC proportions were 25% ± 6.9% for *S. japonica* var. *religiosa* (*n* = 3, 0.61 ± 0.20 g DW), 6.9% for *U. australis* (composite *n* = 12, 1.85 g DW), 11% for *U. linza* (composite *n* = 12, 0.59 g DW), 22% for *M. japonica* without bleached tissue (composite *n* = 5, 3.92 g DW), and 6.7% for *M. japonica* with bleached tissue (composite *n* = 13, 3.59 g DW). In spring 2023 (Figure 4.2b), recalcitrant DOC proportions were 12% ± 0.42% for *S. japonica* var. *religiosa* (*n* = 3, 5.6 ± 0.88 g DW), 5.9% for *U. australis* (composite *n* = 2, 4.81 g DW), and 17% for *N. yendoana* (composite *n* = 8, 7.19 g DW). In summer 2023 (Figure 4.2c), recalcitrant DOC proportions were 6.7% ± 1.6% for *S. japonica* var. *religiosa* (*n* = 3, 2.5 ± 0.94 g DW), 10% for *U. australis* without bleached tissue (composite *n* = 3, 4.72 g DW), 9.3% for *U. australis* with bleached tissue (composite *n* = 5, 3.97 g DW), and 38% for *N. yendoana* (composite *n* = 6, 5.8 g DW). In autumn 2021 (Figure 4.2d), recalcitrant DOC proportions were 25% for *U. australis* (composite *n* = 3, 5.6 g DW) and 19% for *M. japonica* (composite *n* = 10, 7.8 g DW). In autumn 2023 (Figure 4.2d), recalcitrant DOC proportions were 36% ± 0.57% for *S. confusum* (*n* = 3, 13 ± 6.7 g DW), 49% for *S. thunbergii* (composite *n* = 3, 6.57 g DW), and 21% for *G. elegans* (composite *n* = 2, 4.0 g DW).

Protein-like "peak T" was the most labile fluorescence signature in winter, spring, and summer (Figures 2a, b, c) across species with one exception in spring 2023 (Figure 4.2b) when protein-like "peak T" from *U. australis* was more recalcitrant (28%) than the humic-like peaks (18–22%). A contrasting pattern was observed in autumn 2021 and 2023 across species (Figure 4.2d). In autumn 2021, "peak T" from *U. australis* was more recalcitrant (40%) than "peak A" (34%) and comparable to "peak C" (43%) and "peak M" (41%). In autumn 2021, "peak T" from *M. japonica* was more recalcitrant (42%) than "peak A" (27%), similar to "peak C" (38%), and

lower than "peak M" (51%). In autumn 2023, protein-like "peak T" was consistently more recalcitrant than UV humic-like "peak A" for all species (*S. confusum*, *S. thunbergii*, and *G. elegans*), and approximately retained 100% of its initial value, similar to humic-like "peak C" and "peak M", for *S. confusum* and *S. thunbergii*. For *G. elegans*, "peak T" was slightly degraded (87%) and "peak C" and "peak M" were enhanced (120% and 137%, respectively).

Fluorescence peaks were enhanced relative to initial values for certain species within each sampling event. In winter 2023, humic-like fluorescence was consistently enhanced for *M. japonica* with bleached tissue ("peak A": 104%, "peak C": 179%, "peak M": 152%) (Figure 4.2a). In summer 2023, humic-like fluorescence was consistently enhanced for *U. australis* with bleached tissue ("peak A": 127%, "peak C": 129%, "peak M": 144%), and selectively enhanced for *N. yendoana* ("peak C": 226%) (Figure 4.2c). In autumn 2023, humic-like "peak C" was consistently enhanced while protein-like "peak T" and humic-like "peak M" were selectively enhanced for *S. confusum* ("peak T": 106% ± 2%, "peak C": 104% ± 3%), *S. thunbergii* ("peak T": 101%, "peak C": 120%, and "peak M": 104%) and *G. elegans* ("peak C": 120%, and "peak M": 137%) (Figure 4.2d).

Seasonal (non-heatwave) macroalgal DOC and fluorescence production rates

Excluding summer 2023 heatwave results, seasonal trends were species-specific, although production rates were generally higher in winter (Figure 4.3a) and spring (Figure 4.3b) compared to autumn (Figure 4.3d). For *S. japonica* var. *religiosa*, spring 2023 DOC production rates (0.43 ± 0.14 mg C · g^{-1} DW · d^{-1}) were slightly higher than in winter 2023 (0.33 ± 0.04 mg C · g^{-1} DW · d^{-1}). For *U. australis*, the spring 2023 rate (3.5 mg C · g^{-1} DW · d^{-1}) was 12 times higher than in autumn 2021 (0.29 mg C · g^{-1} DW · d^{-1}). The season with the overall lowest DOC

production rates was autumn 2023 (Figure 4.3d), for the experiments on *S. thunbergii* (0.085 mg C · g^{-1} DW · d^{-1}), *S. confusum* (0.35 ± 0.035 mg C · g^{-1} DW · d^{-1}), and *G. elegans* (0.41 mg C · g^{-1} DW · d^{-1}). The absolute lowest DOC production rate was for *M. japonica* in winter (0.059 mg C · g^{-1} DW · d^{-1}) which was almost five times lower than in autumn 2021 (0.29 mg C · g^{-1} DW · d^{-1}). Within each season, the highest production rates of fluorescence were for *U. linza* in winter, *U. australis* in spring, *S. japonica* var. *religiosa* and *N. yendoana* in summer, while all results in autumn were similarly low. Protein-like "peak T" fluorescence had the highest fluorescence production rates for each species across seasons, except when results were similarly low (± ≤ 0.01) across fluorescence types, as was the case for *M. japonica* in winter, and *S. japonica var. religiosa* and *N. yendoana* in spring.

Seasonal (non-heatwave) macroalgal DOC and fluorescence recalcitrant rates

Excluding results from heatwave stress and bleached tissue, recalcitrant DOC rates had similar overall ranges within seasons (winter: 0.01–0.14; spring: 0.03–0.20; autumn: 0.04–0.14 mg C · g^{-1} DW · d^{-1}) (Figure 4.4). However, there were species-specific seasonal trends. *U. australis* recalcitrant DOC rates were more than twice as high in spring 2023 (0.20 mg C · g^{-1} DW · d^{-1}) as winter 2023 (0.094 mg C · g^{-1} DW · d^{-1}) and autumn 2021 (0.073 mg C · g^{-1} DW · d^{-1}). *M. japonica* recalcitrant DOC rates were more than four times as high in autumn 2021 (0.055 mg C · g^{-1} DW · d^{-1}) as winter 2023 (0.013 mg C · g^{-1} DW · d^{-1}). However, *S. japonica* var. *religiosa* recalcitrant DOC rates were not significantly different between winter (0.084 ± 0.029 mg C · g^{-1} DW · d^{-1}) and spring 2023 (0.051 ± 0.016 mg C · g^{-1} DW · d^{-1}). Recalcitrant fluorescence production rates were similarly low (0.00–0.020 RU · L · g^{-1} DW · d^{-1}) across winter, spring, and autumn. The primary exception was *U. australis* in spring with recalcitrant

fluorescence production rates of 0.023 ("peak T"), 0.041 ("peak A"), 0.037 ("peak C"), and 0.040 ("peak M") RU · L · g^{-1} DW · d^{-1}.

Intra-annual ratios for heatwave impact on DOC and fluorescence dynamics

Ratios between summer 2023 results and other seasons for the relevant species (*S. japonica* var. *religiosa*, *N. yendoana*, and *U. australis*) are summarized in Table 4.1. The overall highest initial and recalcitrant production rates were in summer 2023, particularly *S. japonica var. religiosa* (initial: 12 ± 3.1 mg C · g^{-1} DW · d^{-1}; recalcitrant: 0.74 ± 0.17 mg C · g^{-1} DW · d^{-1}) and *N. yendoana* (initial: 9.2 mg C · g^{-1} DW · d^{-1}; recalcitrant: 3.5 mg C · g^{-1} DW · d^{-1}). Yet, there were contrasting species-specific seasonal trends of more than an order of magnitude higher to several times lower (Table 4.1). For *S. japonica* var. *religiosa*, initial DOC production during the summer 2023 heatwave was 36 times higher than winter 2023 and 28 times higher than spring 2023, while recalcitrant DOC production in summer 2023 was 8.8 times higher than winter 2023 and 15 times higher than spring 2023. For *N. yendoana*, initial DOC production in summer 2023 was 31 times higher than in spring 2023. For *U. australis*, the summer 2023 DOC production rate was comparatively low (0.65 mg C · g^{-1} DW · d^{-1}), being more than five times lower than in spring 2023 (3.5 mg C · g^{-1} DW · d^{-1}) and two times lower than in winter 2023 (1.4 mg C · g^{-1} DW · d^{-1}), yet twice as high as in autumn 2021 (0.29 mg C · g^{-1} DW · d^{-1}).

The overall highest fluorescence production rates were for *S. japonica* var. *religiosa* ("peak T": 0.75 ± 0.011 RU · L · g^{-1} DW · d^{-1}) and *N. yendoana* ("peak T": 0.70 RU · L · g^{-1} DW · d^{-1}) in summer and several times higher than the next highest rate (*U. australis*, spring: 0.23 RU · L · g^{-1} DW · d^{-1}). For *S. japonica* var. *religiosa*, all fluorescence peaks had production rates between 6.5 and 48 times higher in summer 2023 compared to winter 2023 and spring

2023. For *N. yendoana*, all fluorescence peaks had production rates between 4.1 and 36 times higher in summer 2023 compared to spring 2023. For *U. australis*, all fluorescence peaks had production rates in summer 2023 that were similar to winter 2023, while compared to spring 2023 fluorescence rates were up to eight times lower, and between 10% higher and 2.6 times higher compared to fluorescence rates in autumn 2023. In general, these patterns in the comparisons between summer 2023 results and other seasons were similar for recalcitrant fluorescence production rates, although magnitudes and relative rankings varied (Table 4.1). The highest macroalgal-derived recalcitrant fluorescence production rates (RU · L · g^{-1} DW · d^{-1}) were in the summer, particularly *S. japonica var. religiosa* and *N. yendoana*, which both had several times higher humic-like production rates (0.10–0.14 RU · L · g^{-1} DW · d^{-1}) compared to protein-like "peak T" rates (0.03–0.04 RU · L · g^{-1} DW · d^{-1}).

Inter-annual comparison of heatwave stress on DOC and fluorescence dynamics

Summer heatwave 2023 results for *S. japonica* var. *religiosa* were compared to previous seasonal data from Chapters 2 and 3 of this dissertation (Figure 4.5). DOC production rate results for late summer 2020 (0.17 ± 0.048 mg C · g^{-1} DW · d^{-1}), early summer 2021 (0.20 ± 0.057 mg C · g^{-1} DW · d^{-1}), and early summer 2022 (0.51 ± 0.084 mg C · g^{-1} DW · d^{-1}) were between one and two orders of magnitude lower than late summer 2023 results (12 ± 3.1 mg C · g^{-1} DW · d^{-1}). Recalcitrant DOC production rate results for late summer 2020 (0.068 ± 0.034 mg C · g^{-1} DW · d^{-1}), early summer 2021 (0.028 ± 0.0039 mg C · g^{-1} DW · d^{-1}), and early summer 2022 (0.060 ± 0.011 mg C · g^{-1} DW · d^{-1}) were 11–26 times lower than late summer 2023 results (0.74 ± 0.17 mg C · g^{-1} DW · d^{-1}).

Paired comparison of bleached tissue on DOC and fluorescence dynamics

In paired experiments, macroalgal-derived total DOC production rates (mg C · g^{-1} DW · d^{-1}) were 5 to 50 times higher for macroalgae with bleached tissue (*U. australis* in summer and *M. japonica* in winter, respectively). In the paired experiments on bleached tissue, *M. japonica* with bleached tissue had several times higher fluorescence production rates in winter, while *U. australis* with bleached tissue had higher fluorescence production rates for humic-like peaks but no difference in protein-like "peak T".

Discussion

Species-specific differences in DOC and fluorescence dynamics

The expectation of Hypothesis 1 was that there would be substantial differences between species, within each respective season. Based on Buck-Wiese et al. (2023), one specific expectation was that fucoid species would produce the most proportionally recalcitrant DOC and this was partially confirmed. *S. thunbergii* produced the most recalcitrant DOC (autumn: 49%), followed by *N. yendoana* (summer: 38%), and *S. confusum* (autumn: 35% ± 0.46%). These results were notably higher compared to their respective intra-seasonal results, for example about 4–5 times higher for summer results (*S. japonica* var. *religiosa*: 7% ± 2%, *Ulva australis* without bleached tissue: 10%, *U. australis* with bleached tissue: 9%) and 1.5–2 times higher for autumn results (*G. elegans*: 21%). In winter, *S. japonica* var. *religiosa* (23% ± 1%) and *M. japonica* without bleached tissue (20%) produced DOC that was 2–3 times as recalcitrant compared to *U. australis* (7%), *U. linza* (11%), and *M. japonica* with bleached tissue (7%). In spring, *N. yendoana* produced the most recalcitrant DOC (18%) which was twice as recalcitrant as DOC from *S. japonica* var. *religiosa* (12% ± 1%) and three times as recalcitrant as DOC from *U.*

australis (6%). Excluding the summer 2023 heatwave results, the highest recalcitrant DOC production rates were for *M. japonica* with bleached tissue in winter (0.21 mg C · g^{-1} DW · d^{-1}) and *U. australis* in spring (0.20 mg C · g^{-1} DW · d^{-1}). These results indicate the relative recalcitrance of *N. yendoana* DOC production in spring and summer, while DOC recalcitrance from *S. japonica* var. *religiosa* and *M. japonica* was notable in winter, and was low from both *Ulva* species across winter, spring, and summer.

Hulatt et al. (2009) indicated that brown macroalgae tend to produce more CDOM than red and green macroalgae, although there were notable exceptions. We therefore expected that *S. confusum*, *S. thunbergii*, *S. japonica* var. *religiosa*, and *C. costata* would produce the most humic-like fluorescence. However, in winter 2023, *U. linza* consistently had the highest fluorescence production rates ("peak T": 0.14, "peak A": 0.10, "peak C": 0.080, "peak M": 0.099 RU · L · g^{-1} DW · d^{-1}), typically several times higher than those for *S. japonica* var. *religiosa* and *C. costata*. In spring 2023, *N. yendoana* and *S. japonica* var. *religiosa* produced similar rates of fluorescence, which were up to an order of magnitude lower than *U. australis*. In summer 2023, the enhanced fluorescence production effect was not observed in *U. australis*, resulting in comparatively lower rates by an order of magnitude. However, when comparing *N. yendoana* rates ("peak T": 0.70, "peak A": 0.18, "peak C": 0.060, "peak M": 0.36 RU · L · g^{-1} DW · d^{-1}) and *S. japonica* var. *religiosa* rates ("peak T": 0.75 ± 0.011, "peak A": 0.23 ± 0.0049, "peak C": 0.11 ± 0.011, "peak M": 0.28 ± 0.034 RU · L · g^{-1} DW · d^{-1}) rates, the results were similar. In autumn 2021 and 2023 combined results, *S. confusum*, *S. thunbergii*, *U. australis*, *M. japonica*, and *G. elegans* all produced similar rates of fluorescence, but *U. australis* and *M. japonica* tended to produce slightly higher rates than the brown macroalgae. For example, visible humic-like "peak C" rates were three times higher from *M. japonica* (0.034 RU · L · g^{-1} DW · d^{-1}) than

S. confusum (0.011 ± 0.0011 RU · L · g^{-1} DW · d^{-1}) and visible marine humic-like "peak M" rates were about two times higher from both *M. japonica* and *U. australis* compared to *S. confusum.* In total, these results indicate that in contrast to Hulatt et al. (2009), brown macroalgae were not the dominant producers of humic-like fluorescence. In our study, *U. australis* was the most consistently high producer in three out of four seasons. These results indicate that heatwave and bleaching stress are confounding factors when comparing species and that there may be additional factors that drive any apparent differences between species.

Species-specific seasonal trends in DOC and fluorescence dynamics

Hypothesis 2 expected that the final (biomass normalized) macroalgal-derived DOC contributions would be highest in spring and autumn, consistent with the results for *S. japonica* var. *religiosa* in Chapter 3 of this dissertation. However, *S. japonica* var. *religiosa* results were not significantly different between winter 2023 and spring 2023 results and none were present at Oshoro Bay for collection in autumn 2023. For *U. australis* without bleached tissue, initial DOC production rates were approximately twice as high in spring as winter and autumn. In contrast to *S. japonica* var. *religiosa* and *N. yendoana*, the summer 2023 heatwave did not appear to affect or otherwise had a dampening effect on *U. australis* DOC production as it was seasonally the lowest reported result (0.062 mg C · g^{-1} DW · d^{-1}). *M. japonica* had initial and recalcitrant DOC production rates that were both about four times higher in autumn compared to winter. While *Sargassum* species were only collected in autumn 2023, their relatively high recalcitrant production, coupled with a seasonally high biomass in the absence of the otherwise dominant *S. japonica* var. *religiosa*, are indications of the overlooked importance of the autumn period for macroalgal DOC contributions.

Effect of summer heatwave on recalcitrance

The results during the summer heatwave generally supported the expectations of hypothesis 3, but were species-specific. For example, when comparing *N. yendoana* results between spring and summer, DOC recalcitrance (spring: 18%, summer: 38%) and humic-like "peak C" recalcitrance (spring: 97%, summer: 226%) were both approximately twice as high in the summer. Consistent with expectations, protein-like "peak T" (spring: 27%, summer: 6%) and humic-like "peak M" (spring: 90%, summer: 28%) recalcitrance were three to four times lower in the summer, while humic-like "peak A" was approximately the same in both seasons (spring: 57%, summer: 63%). Results for *U. australis* were likewise mixed, with seasonally high recalcitrance for DOC, humic-like "peak C", and humic-like "peak M" in the summer compared to winter and spring, while protein-like "peak T" was similar to winter and several times lower than spring, and humic-like "peak A" was slightly lower than winter, but several times higher than spring. Therefore, the primary differences when comparing spring and summer results between *N. yendoana* and *U. australis* were for humic-like "peak A" (similar and higher in summer, respectively) and "peak M" (lower and higher in summer, respectively). These results indicate that *Ulva australis* recalcitrance was more readily enhanced during the summer heatwave. For *S. japonica* var. *religiosa*, summer DOC recalcitrance was at a seasonal low, as was protein-like "peak T", while humic-like "peak A" and "peak M" were lower than spring but higher than winter, and humic-like "peak C" was at a seasonal high. While "peak C" recalcitrance was relatively higher compared to winter and spring 2023 results, its value of 104% ± 21% was consistent with the average summer results from 2020–2022 in Chapter 3 of this dissertation. The DOC recalcitrance in summer 2023 (7% ± 2%), as well as the recalcitrance of the other fluorescence peaks, were lower than the average summer results from 2020–2022,

indicating that the summer 2023 heatwave generally reduced recalcitrance except for humic-like "peak C" which was unaffected.

Effect of macroalgal bleaching on recalcitrance

The results supported the expectation of hypothesis 4 that macroalgae with bleached tissue would exhibit substantially different DOC and fluorescence dynamics compared to paired macroalgae without bleached tissue (Figure 4.6). Most notably, in the winter 2023 paired bleaching experiment, *M. japonica* with bleached tissue had a recalcitrant DOC production rate (0.21 mg C · g^{-1} DW · d^{-1}) about 16 times higher than for *M. japonica* without bleached tissue (0.013 mg C · g^{-1} DW · d^{-1}). This enhancing effect was similar and consistent across fluorescence signatures (i.e., 14–16 times higher for *M. japonica* fluorescence and 3.0–3.8 times higher for *U. australis* fluorescence). *U. australis* recalcitrant DOC production was enhanced by a factor of 4.8 in the paired summer sample where tissue was bleached (0.30 mg C · g^{-1} DW · d^{-1}). The effect of bleached tissue on total fluorescence production rates was less than on recalcitrant rates, yet still several-fold to an order of magnitude for *M. japonica*. The effect of bleaching varied between no impact to a doubling (factor of 1.0–1.9) of total fluorescence rates for *U. australis.* In contrast, the effect on total DOC production rates was greater than that on recalcitrant rates for both species—a factor of 53 for *M. japonica* and a factor of 5.2 for *U. australis*. These results strongly indicate that the effect of bleached tissue is to enhance recalcitrant DOC and fluorescence production rates by several-fold.

Results for relative recalcitrant proportions were more mixed. For example, there was a negligible difference for *U. australis* (bleached: 9%, not bleached: 10%). However, *M. japonica* with bleached tissue had lower recalcitrant DOC proportions (7%) compared to samples with no

bleached tissue (20%). Despite this, as stated previously, the overall recalcitrant production rate for *M. japonica* with bleached tissue was still 16 times higher than for samples with not bleached tissue. Regarding fluorescence, humic-like "peak A" and "peak C" were enhanced for both *M. japonica* and *U. australis* with bleached tissue, but so was humic-like "peak M". In Chapter 3 of this dissertation, humic-like "peak M" was not significantly different from initial values across seasons, but some individual results for "peak M" were enhanced during the bioavailability experiment, indicating that there is a pathway for "peak M" fluorescence to be continued to be produced after the removal of macroalgae. "Peak T" was also several-fold more recalcitrant for *U. australis* with bleached tissue (24% compared to 8%) indicating an atypical decoupling with the corresponding DOC results.

Conclusion

This study clarified several important species-specific differences in macroalgal DOC and fluorescence dynamics that had not been reported to date. Namely, the experimental design allowed direct comparisons between species within a single season as well as for species-specific seasonal trends, whereas previous reviews have been limited by confounding environmental factors between study sites. More dramatically, this study showed the order of magnitude enhancement of DOC and fluorescence initial and recalcitrant production under heatwave stress and for macroalgae with bleached tissue. In other words, while the relative recalcitrant proportions remained similar, recalcitrant production was substantially enhanced under in situ stress factors. The finding that this impact differed in magnitude between species, and that for certain species the impact was reversed, highlights the importance of studying macroalgal DOC and fluorescence dynamics under stress conditions for a wide range of species.

Tables and Figures

Table 4.1. Summer heatwave seasonal impact ratios. Data are ratios of summer macroalgal DOC and fluorescence production rates relative to other seasons DOC. Initial rates were calculated at the end of a t = 4 d macroalgal incubation period and recalcitrant rates were calculated after a subsequent t = 150 d bioavailability experiment (macroalgae removed).

		Initial			Recalcitrant		
Species	**Product**	**Winter**	**Spring**	**Autumn**	**Winter**	**Spring**	**Autumn**
Saccharina	DOC	35	29	NA	8.8	15	NA
japonica var.	"peak T"	19	48		5.9	7.3	
religiosa	"peak A"	7.5	9.1		25	6.3	
	"peak C"	8.2	6.5		17	7.4	
	"peak M"	15	18		18	6.6	
Neodilsea	DOC	NA	31	NA	NA	69	NA
yendoana	"peak T"		36			7.9	
	"peak A"		7.2			7.9	
	"peak C"		4.1			9.5	
	"peak M"		23			7.3	
Ulva australis	DOC	0.48	0.19	2.2	0.67	0.31	0.86
	"peak T"	1.2	0.81	2.6	0.91	0.24	0.54
	"peak A"	0.86	0.16	1.9	0.67	0.38	2.8
	"peak C"	0.86	0.14	1.3	1.6	0.51	2.3
	"peak M"	0.77	0.12	1.1	1.6	0.41	1.7

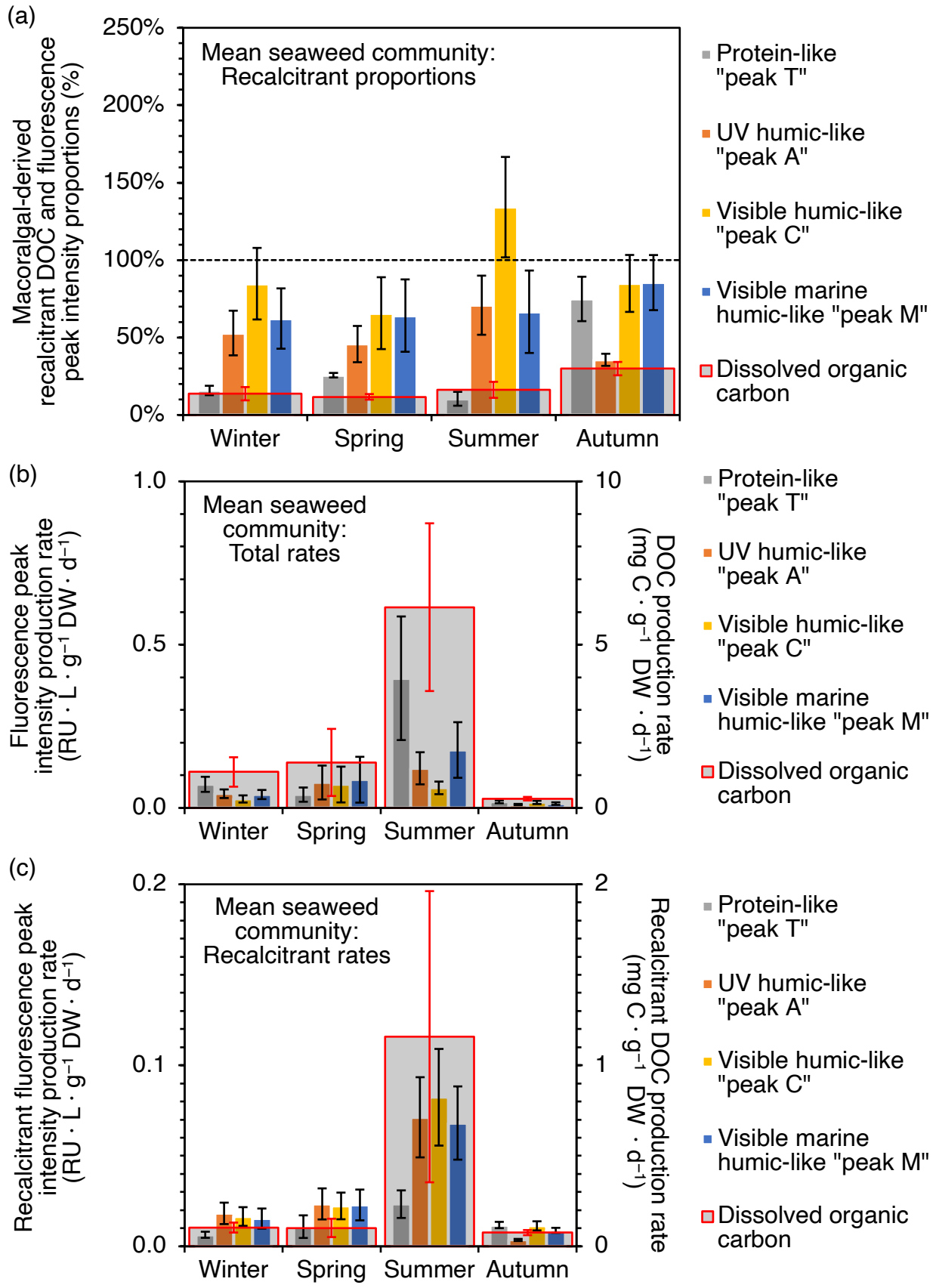
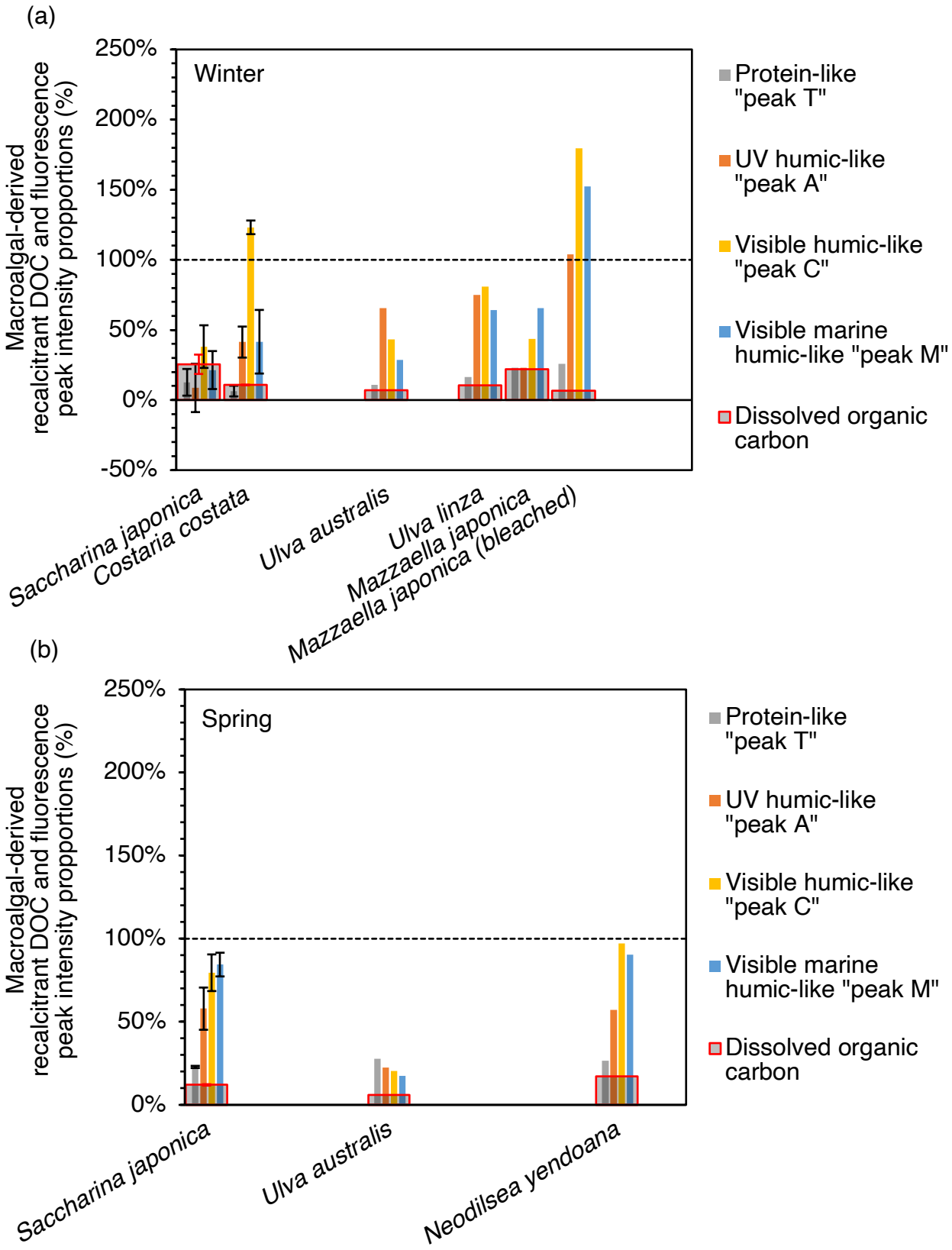
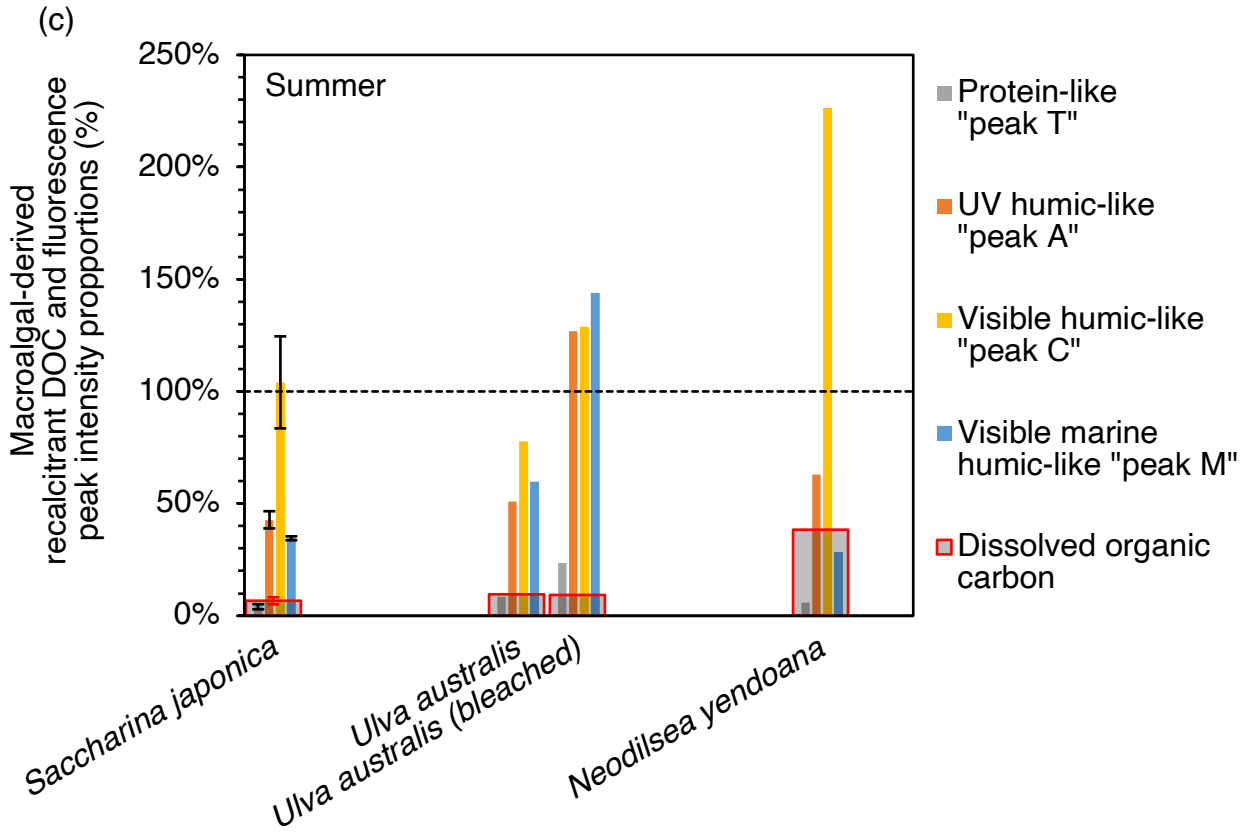

(a)
Mean seaweed community:
Recalcitrant proportions
Macoralgal-derived recalcitrant DOC and fluorescence peak intensity proportions (%)
250%
200%
150%
100%
50%
0%
Winter
Spring
Summer
Autumn
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
(b)
Mean seaweed community:
Total rates
Fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
1.0
0.5
0.0
DOC production rate (mg C · g⁻¹ DW · d⁻¹)
10
5
0
Winter
Spring
Summer
Autumn
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
(c)
Mean seaweed community:
Recalcitrant rates
Recalcitrant fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
0.2
0.1
0.0
Recalcitrant DOC production rate (mg C · g⁻¹ DW · d⁻¹)
2
1
0
Winter
Spring
Summer
Autumn
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon

Figure 4.1. Estimates of mean seasonal seaweed community DOC and fluorescence contributions. Data are mean macroalgal-derived fluorescence peak intensity and DOC contributions in terms of (a) relative percentages of recalcitrant proportions to total contributions, (b) total initial production rates based on macroalgal incubation experiments (t = 4 d), and (c) effective recalcitrant production rates based on subsequent bioavailability experiments (t = 150 d after macroalgal removal). The mean seaweed community is estimated as the mean of the collected macroalgal species and species variability between seasons is intended to approximately reflect in situ variations in species dominance.


(a)
Winter
Macroalgal-derived recalcitrant DOC and fluorescence peak intensity propportions (%)
250%
200%
150%
100%
50%
0%
-50%
Saccharina japonica
Costaria costata
Ulva australis
Ulva linza
Mazzaella japonica
Mazzaella japonica (bleached)
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
(b)
Spring
Macroalgal-derived recalcitrant DOC and fluorescence peak intensity propportions (%)
250%
200%
150%
100%
50%
0%
Saccharina japonica
Ulva australis
Neodilsea yendoana
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon


(c)
Summer
Macroalgal-derived recalcitrant DOC and fluorescence peak intensity proportions (%)
250%
200%
150%
100%
50%
0%
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
Saccharina japonica
Ulva australis
Ulva australis (bleached)
Neodilsea yendoana

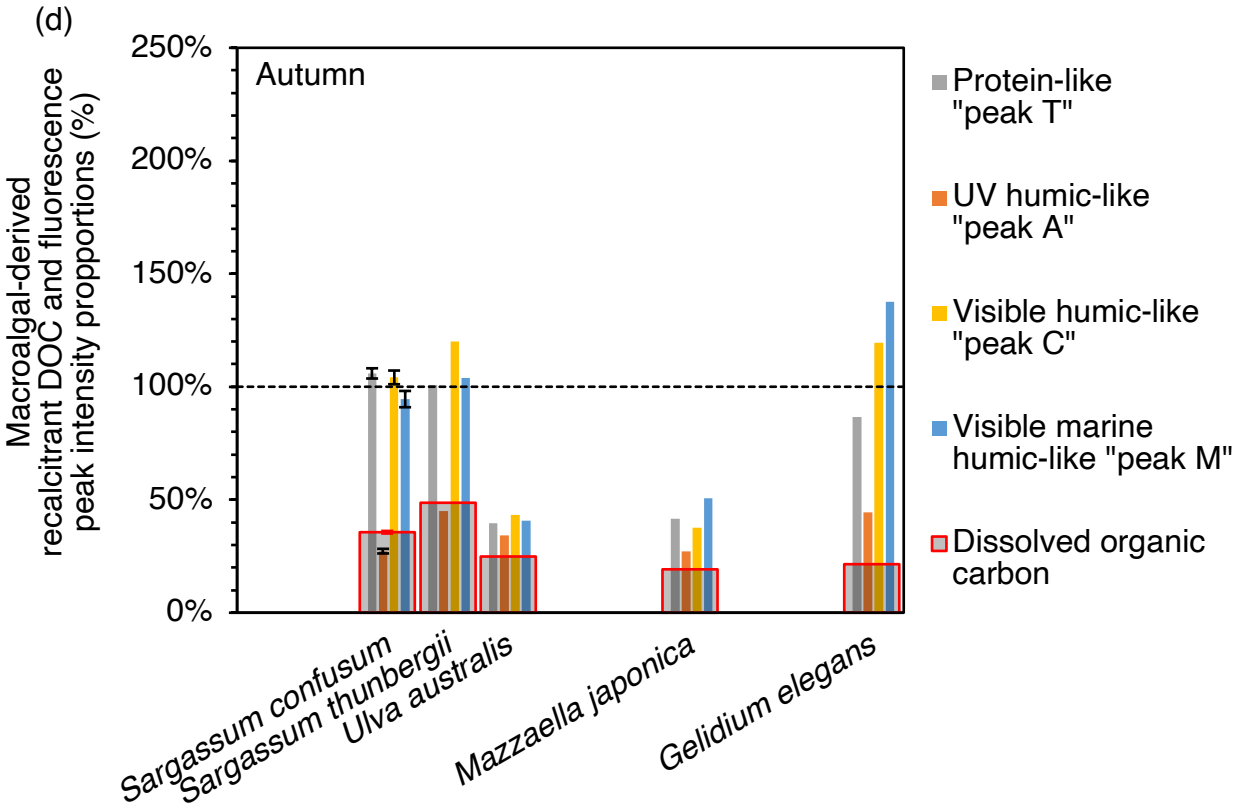
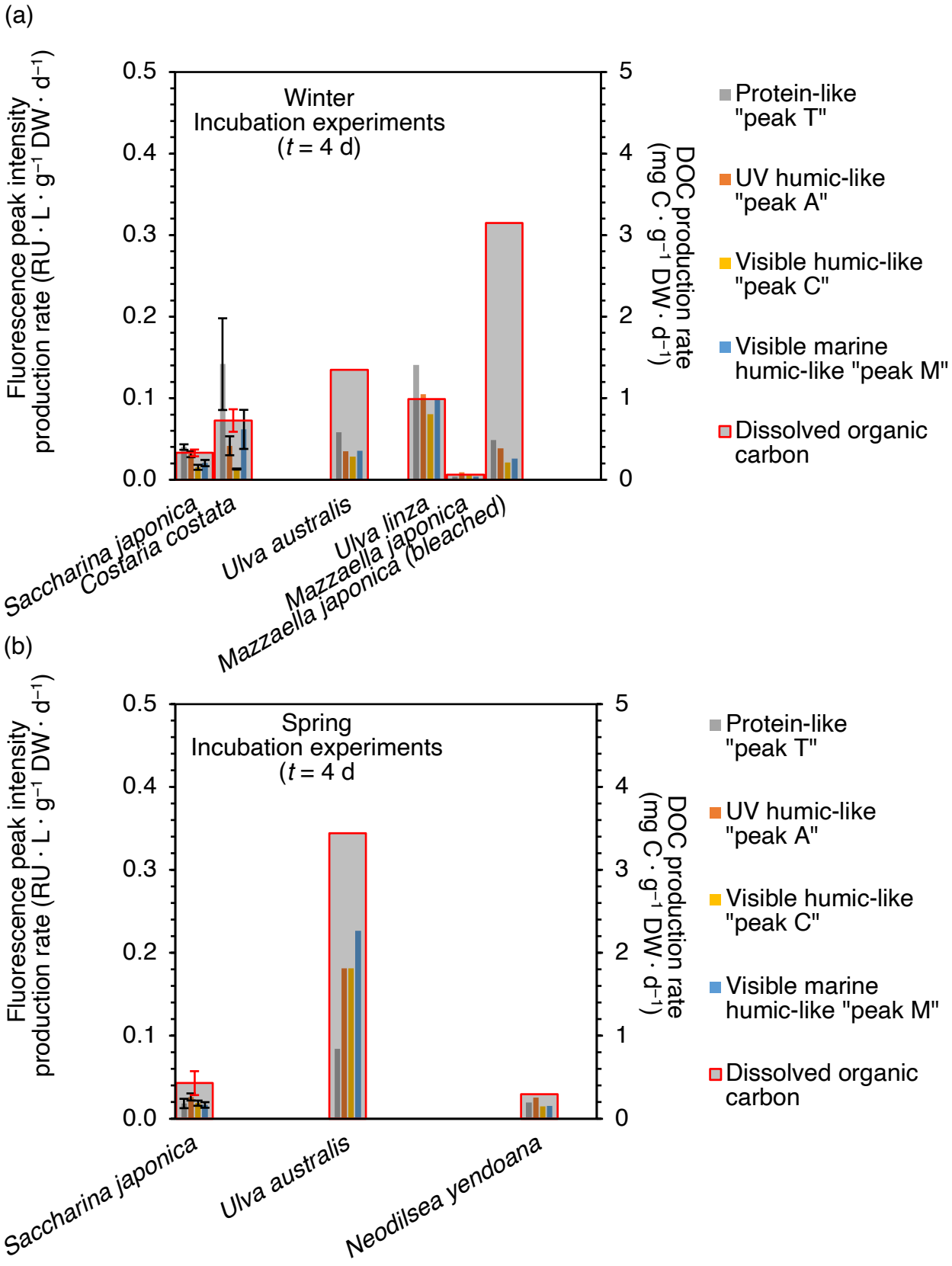

(d)
Autumn
Macroalgal-derived recalcitrant DOC and fluorescence peak intensity proportions (%)
250%
200%
150%
100%
50%
0%
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
Sargassum confusum
Sargassum thunbergii
Ulva australis
Mazzaella japonica
Gelidium elegans

Figure 4.2. Macroalgal recalcitrant DOC and fluorescence proportions by season. Data are means (± *SE* or composite) of the relative proportion of recalcitrant DOC and fluorescence peaks remaining after the t = 150 d bioavailability experiments for (a) winter, (b) spring, (c) summer, and (d) autumn.


(a)
Winter
Incubation experiments
(t = 4 d)
Fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.0
0.1
0.2
0.3
0.4
0.5
0
1
2
3
4
5
Saccharina japonica
Costaria costata
Ulva australis
Ulva linza
Mazzaella japonica
Mazzaella japonica (bleached)
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
(b)
Spring
Incubation experiments
(t = 4 d
Fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.0
0.1
0.2
0.3
0.4
0.5
0
1
2
3
4
5
Saccharina japonica
Ulva australis
Neodilsea yendoana
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon

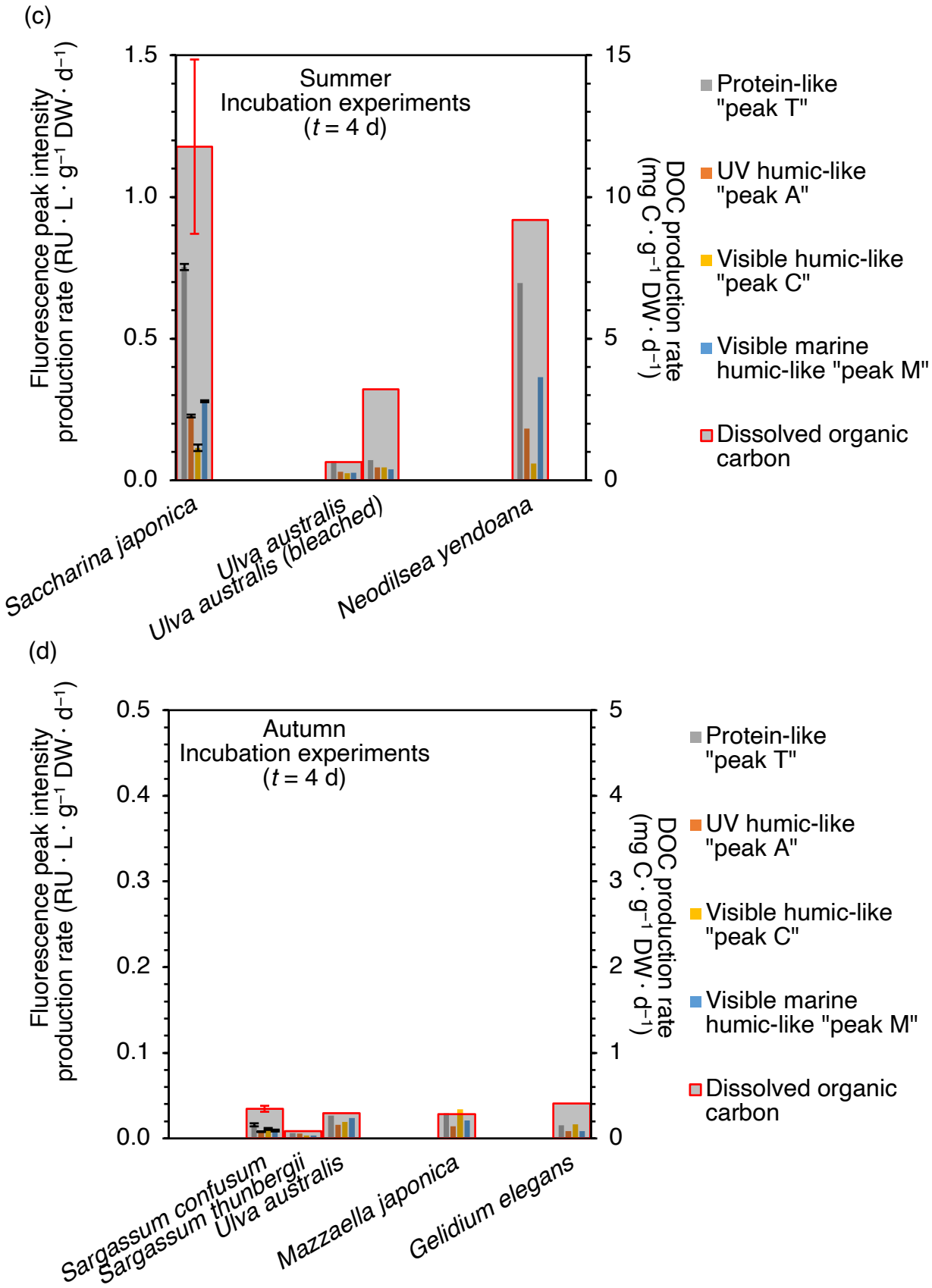
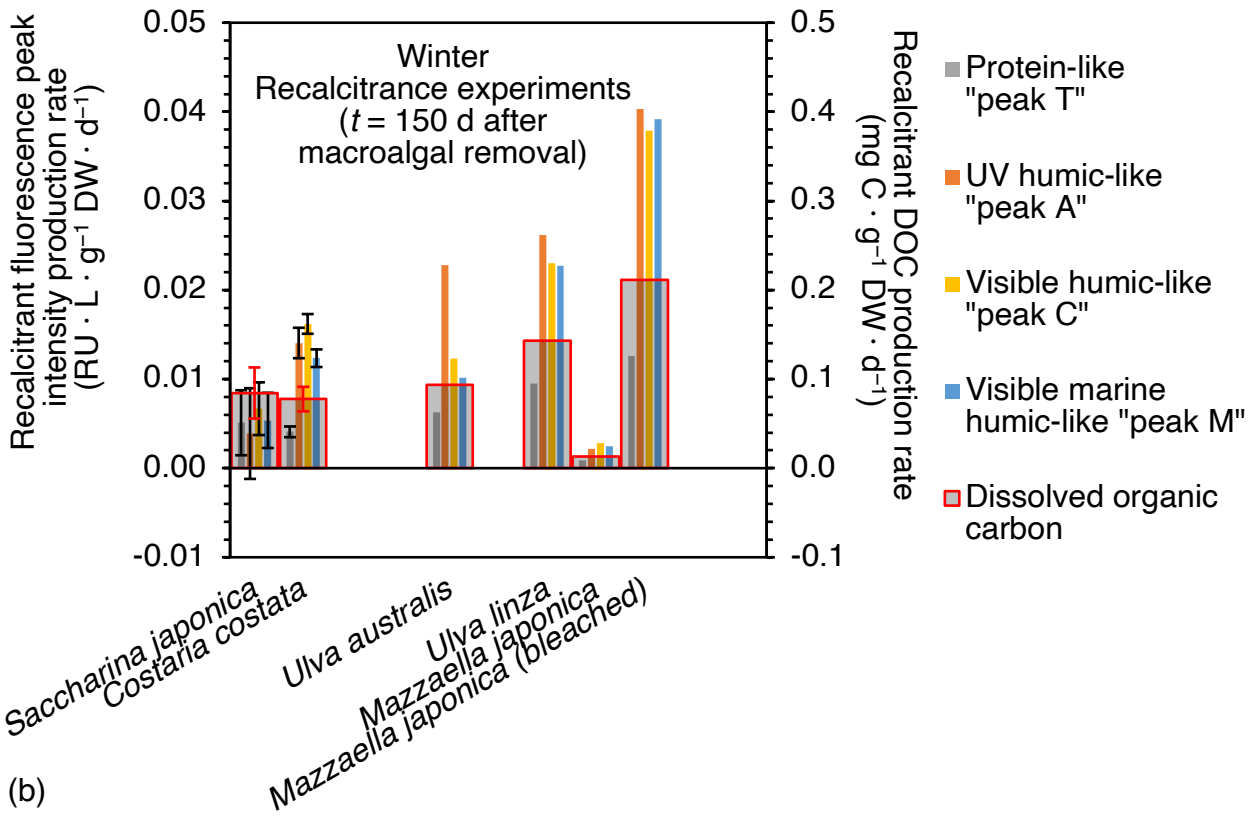
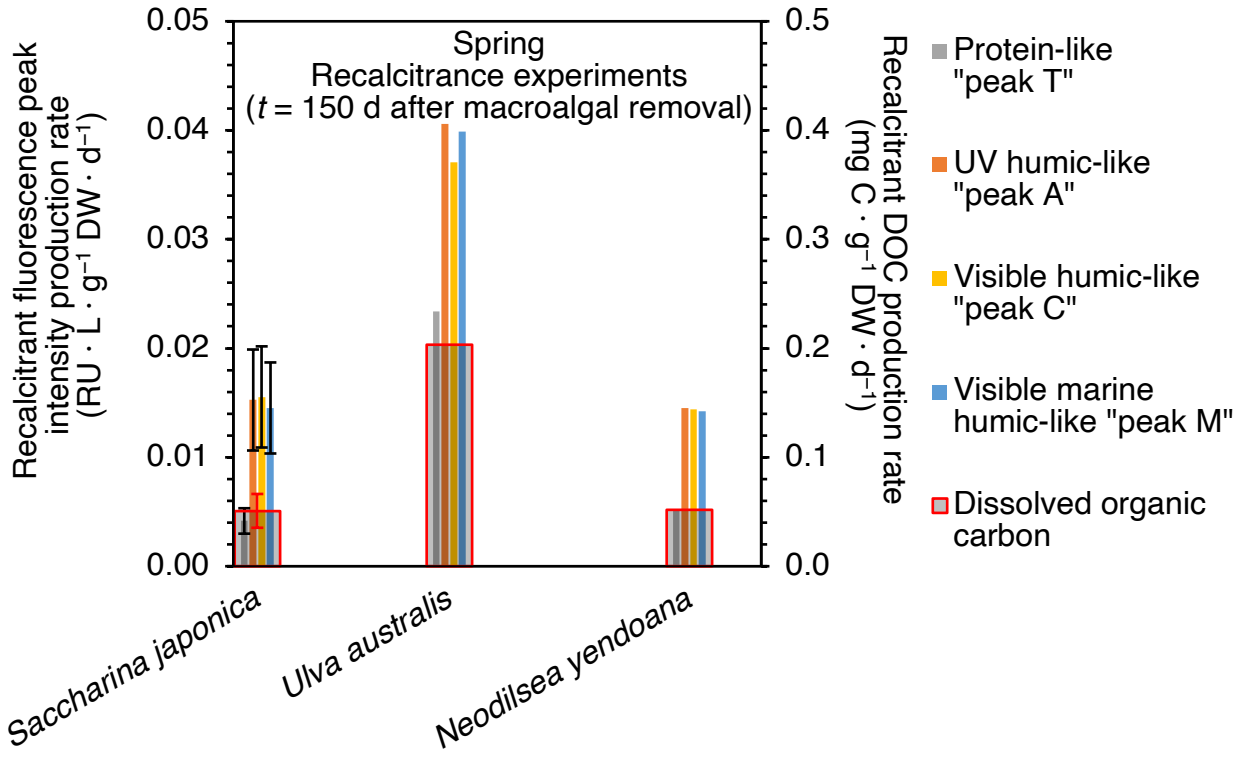

(c)
Summer
Incubation experiments
(t = 4 d)
Fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
DOC production rate (mg C · g⁻¹ DW · d⁻¹)
1.5
1.0
0.5
0.0
15
10
5
0
Saccharina japonica
Ulva australis
Ulva australis (bleached)
Neodilsea yendoana
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
(d)
Autumn
Incubation experiments
(t = 4 d)
Fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.5
0.4
0.3
0.2
0.1
0.0
5
4
3
2
1
0
Sargassum confusum
Sargassum thunbergii
Ulva australis
Mazzaella japonica
Gelidium elegans
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon

Figure 4.3. Macroalgal-derived initial DOC and fluorescence production rates by season. Data are means (± SE or composite) of the macroalgal-derived DOC (mg C · g^{-1} DW · d^{-1}) and fluorescence (RU · L · g^{-1} DW · d^{-1}) production rates at the end of the macroalgal incubation period (t = 4 d) represented as dry-weight biomass normalized rates for (a) winter, (b) spring, (c) summer, and (d) autumn.

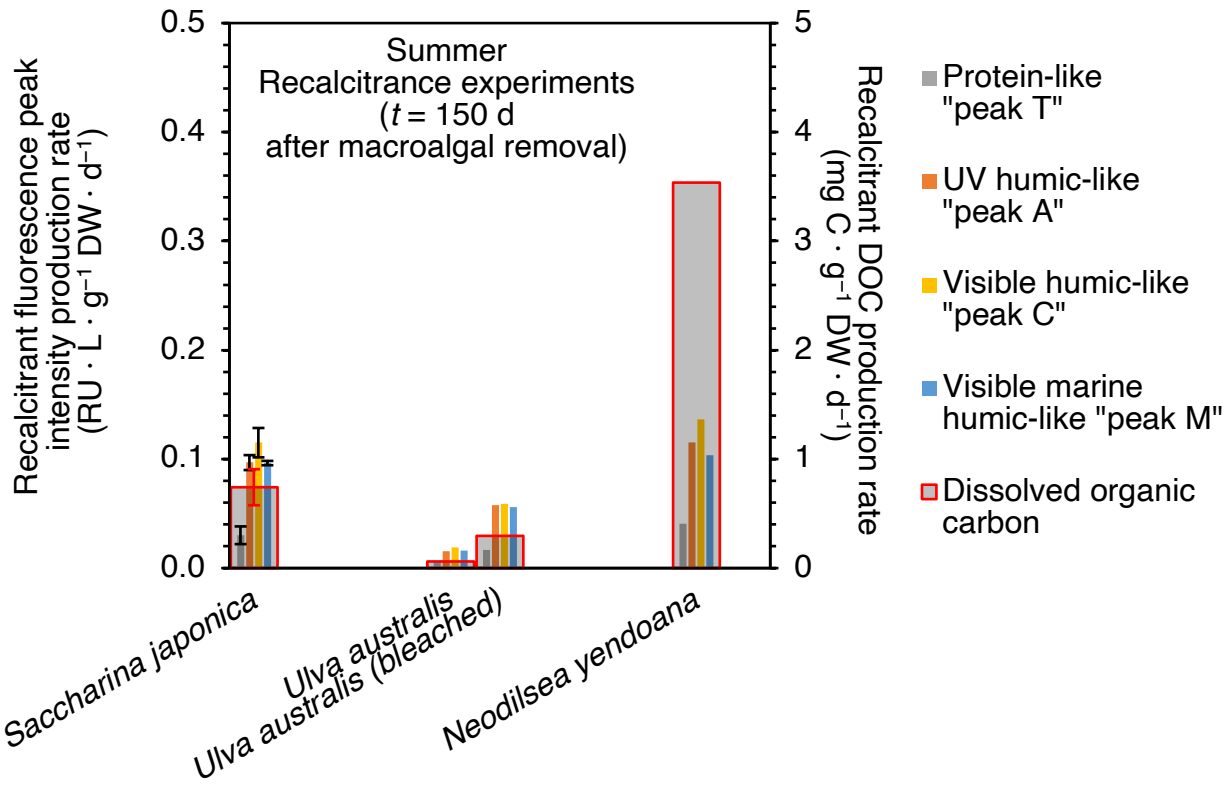
(a)


Winter
Recalcitrance experiments
(t = 150 d after
macroalgal removal)
Recalcitrant fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
Recalcitrant DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
Saccharina japonica
Costaria costata
Ulva australis
Ulva linza
Mazzaella japonica
Mazzaella japonica (bleached)

(b)


Spring
Recalcitrance experiments
(t = 150 d after macroalgal removal)
Recalcitrant fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
Recalcitrant DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.05
0.04
0.03
0.02
0.01
0.00
0.5
0.4
0.3
0.2
0.1
0.0
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
Saccharina japonica
Ulva australis
Neodilsea yendoana

(c)


Summer
Recalcitrance experiments
(t = 150 d
after macroalgal removal)
Recalcitrant fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
Recalcitrant DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.0
0.1
0.2
0.3
0.4
0.5
0
1
2
3
4
5
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
Saccharina japonica
Ulva australis
Ulva australis (bleached)
Neodilsea yendoana

(d)

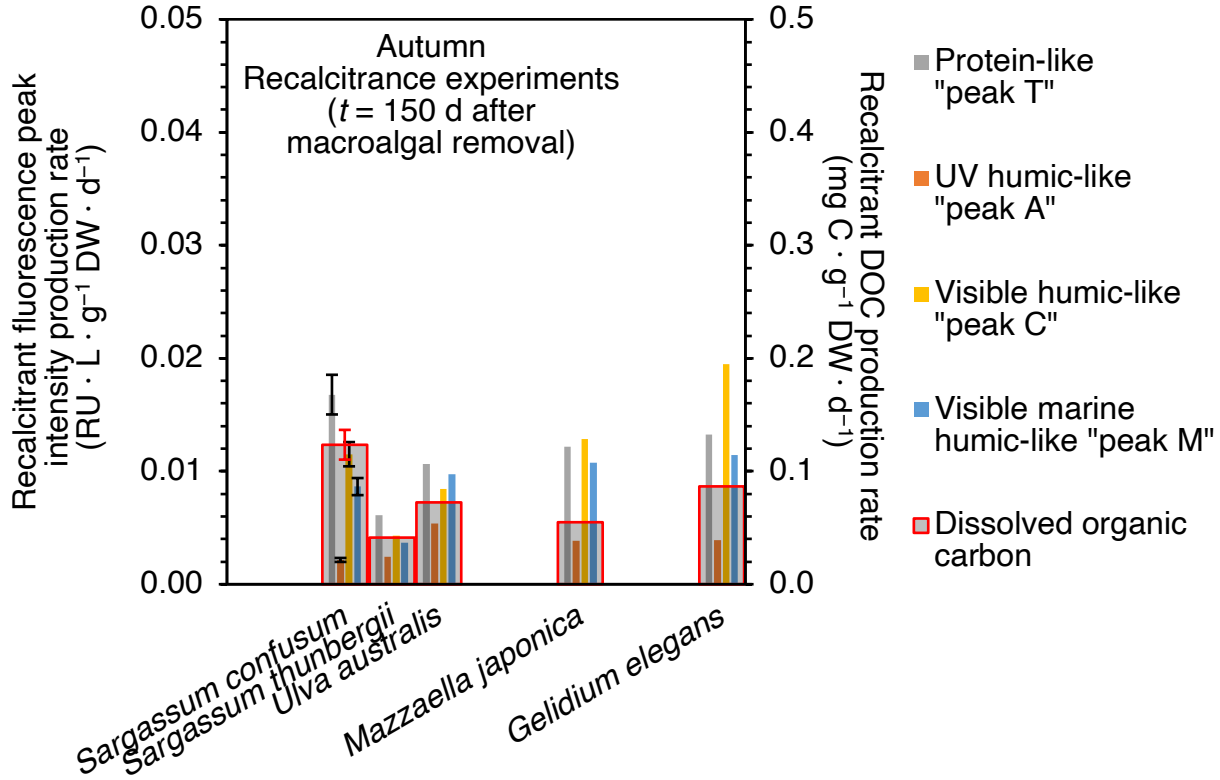

Autumn
Recalcitrance experiments
(t = 150 d after
macroalgal removal)
Recalcitrant fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
Recalcitrant DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.00
0.01
0.02
0.03
0.04
0.05
0.0
0.1
0.2
0.3
0.4
0.5
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
Sargassum confusum
Sargassum thunbergii
Ulva australis
Mazzaella japonica
Gelidium elegans

Figure 4.4. Macroalgal-derived recalcitrant DOC and fluorescence production rates by season. Data are means (± *SE* or composite) of the macroalgal-derived DOC (mg C · g^{-1} DW · d^{-1}) and fluorescence (RU · L · g^{-1} DW · d^{-1}) effective recalcitrant production rates at the end of the bioavailability experiments (t = 150 d after macroalgal removal) represented as dry-weight biomass normalized rates for (a) winter, (b) spring, (c) summer, and (d) autumn.

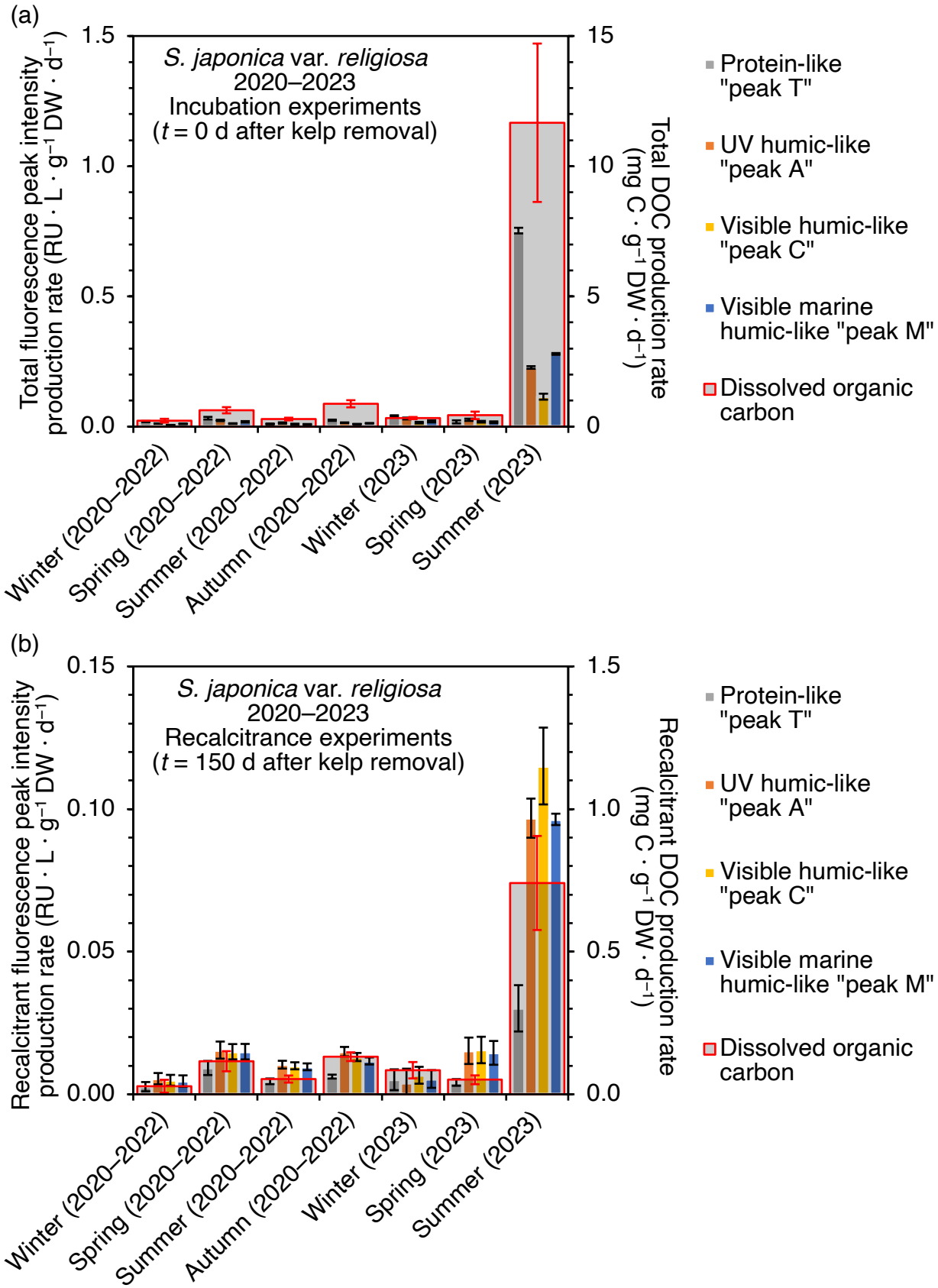

(a)
S. japonica var. religiosa
2020–2023
Incubation experiments
(t = 0 d after kelp removal)
Total fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
Total DOC production rate (mg C · g⁻¹ DW · d⁻¹)
1.5
1.0
0.5
0.0
15
10
5
0
Winter (2020–2022)
Spring (2020–2022)
Summer (2020–2022)
Autumn (2020–2022)
Winter (2023)
Spring (2023)
Summer (2023)
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon
(b)
S. japonica var. religiosa
2020–2023
Recalcitrance experiments
(t = 150 d after kelp removal)
Recalcitrant fluorescence peak intensity production rate (RU · L · g⁻¹ DW · d⁻¹)
Recalcitrant DOC production rate (mg C · g⁻¹ DW · d⁻¹)
0.15
0.10
0.05
0.00
1.5
1.0
0.5
0.0
Winter (2020–2022)
Spring (2020–2022)
Summer (2020–2022)
Autumn (2020–2022)
Winter (2023)
Spring (2023)
Summer (2023)
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon

Figure 4.5. Inter-annual comparison of heatwave stress on kelp DOC and fluorescence production rates. Data are mean (± *SE* between *S. japonica* var. *religiosa* replicates) (a) total rates calculated at the end of the incubation experiments and (b) effective recalcitrant rates based on the recalcitrant portions remaining at the end of the t = 150 d bioavailability experiments. Summer 2023 heatwave results for *S. japonica* var. *religiosa* compared to previous seasonal data from 2020–2022, as reported in Chapter 3 of this dissertation.

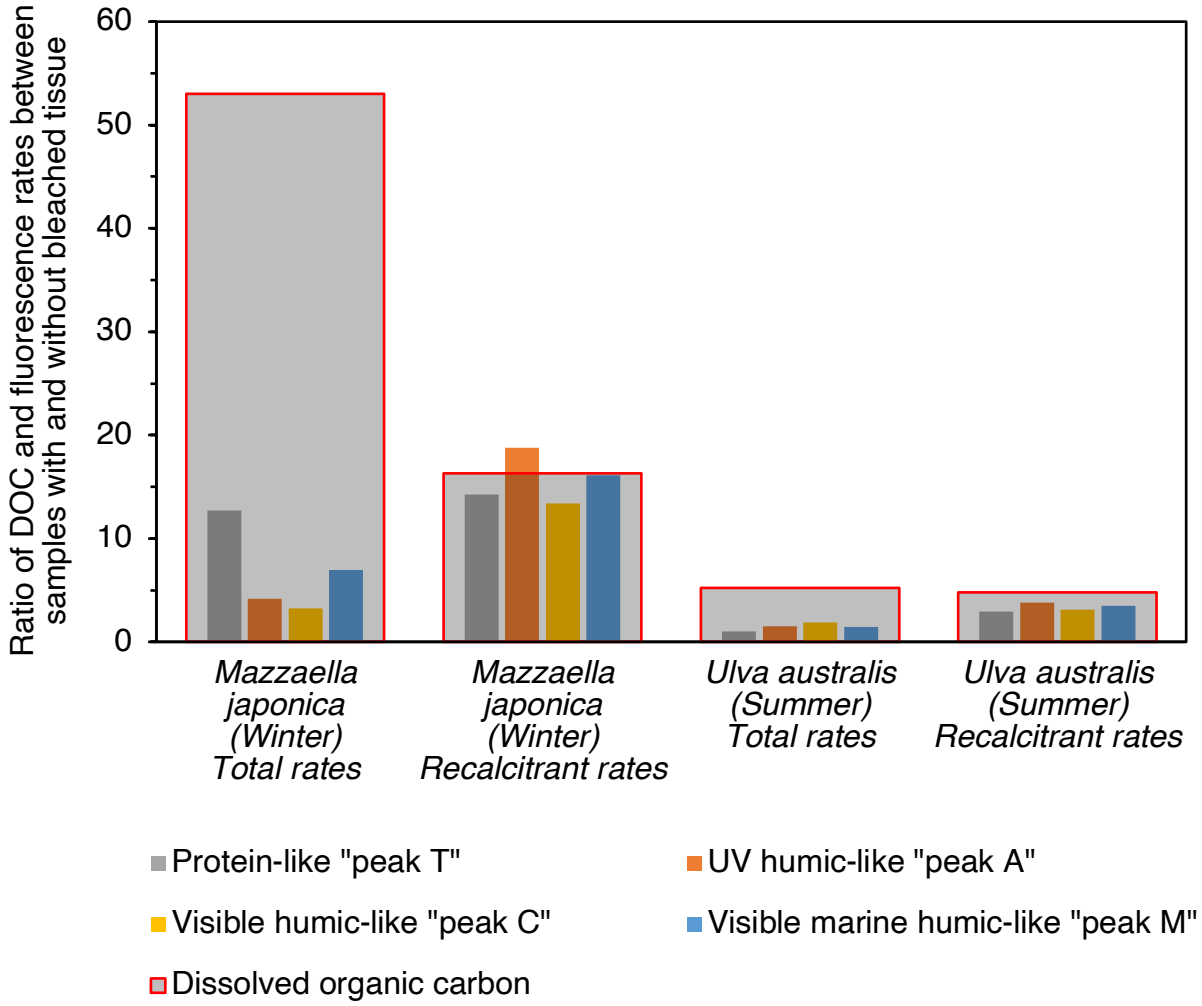


Figure 4.6. Relative effect of bleached tissue on total and recalcitrant DOC and fluorescence production rates. Ratio of production rates from composite samples with and without bleached tissue for *M. japonica* in winter 2023 (bleached: composite n = 13, 3.59 g DW; not bleached: composite n = 5, 3.92 g DW) and *U. australis* in summer 2023 (bleached: composite n = 5, 3.97 g DW; not bleached: composite n = 3, 4.72 g DW). Recalcitrant production rates determined from bioavailability experiments (t = 150 d after macroalgal removal) following the initial macroalgal incubation experiments (t = 4 d).

CHAPTER FIVE

Initial steps toward fluorescence tracing of macroalgal recalcitrant dissolved organic carbon at Oshoro Bay

Abstract

Studies on dissolved organic matter (DOM) concentrations and associated fluorescence peak intensities generally indicate that they are decoupled, despite attempts to establish proportionality for the purpose of using fluorescence as a convenient proxy for DOM with remote sensing potential. More narrowly, there is interest in using macroalgal-derived fluorescence as a tracer to estimate macroalgal-derived dissolved organic carbon (DOC) contributions, especially in the context of Blue Carbon as a climate change mitigation strategy. This study analyzes four years (2020–2023) of seasonal data from in situ seawater samples, macroalgal incubation experiments, and subsequent 150-d bioavailability experiments on nine species of macroalgae from Oshoro Bay, Hokkaido, Japan. Results indicate that overall linear regressions between macroalgal-derived DOC (μM) and fluorescence peak intensity (RU) were significant ($p < 0.05$) for all four fluorescence peak signatures. However, data from initial (post-incubation) samples had lower ($R^2 < 0.70$) correlation values, while data from final samples (post-bioavailability) had higher ($R^2 > 0.70$) correlation values. Correlation values and linear significance also improved when assessing mean data across multiple macroalgal species instead of a single species. Therefore, eight bi-season-specific ratios between protein-like "peak T" intensities and DOC concentrations from mean macroalgal post-bioavailability seawater samples were established ($p < 0.05$, $R^2 > 0.70$). Applying these ratios to known in situ "peak T" intensities acted as a preliminary predictive model. From this, the estimated macroalgal contributions to in situ DOC were 24%–44% (23–37 μM) of the local DOC pool, consistent with other empirical reports. These relationships indicate that variable, yet significant proportionality can be established between fluorescence peak intensities and DOC, especially for recalcitrant characteristics.

Introduction

Macroalgae are known to release fluorescent protein-like and humic-like dissolved organic matter (DOM) which affords various insights into organic composition and biogeochemical fate (Wada et al., 2008; Powers et al., 2020; Zhang et al., 2023). However, monitoring, reporting, and verification (MRV) of recalcitrant macroalgal dissolved organic carbon (DOC) remains challenging despite a recent increase in longer term (year-round or multi-year) empirical studies on macroalgal DOC production (Wada et al., 2007; Weigel & Pfister, 2021; Paine et al., 2023a; Carlson et al., 2024) and bioavailability (Wada et al., 2008; Chapters 3 and 4 of this dissertation). Fluorescence has been proposed as a potentially useful proxy for tracing macroalgal DOC contributions to carbon sequestration, but significant uncertainties remain. Parlanti et al. (2000) previously compared fluorescence correlations between seawater samples collected in situ across multiple years and from macroalgae (*Ulva lactuca*) incubations from a single sampling event. Therefore, there remains significant uncertainty regarding variable proportionality between macroalgal-derived DOC and fluorescence in terms of seasonal, species-specific, and place-based differences. Several short-term studies (i.e., one or two sampling events) on macroalgal DOC and fluorescence have focused on the recalcitrant characteristics, optical properties, photochemical transformations, or other factors related to kinetics (Zhang & Wang, 2017; Powers et al., 2020; Li et al., 2022; Zhang et al., 2022; Kubo & Tanaka, 2023; Zhang et al., 2023), but did not or could not establish meaningful proportionality between DOC and fluorescence for the purpose of in situ tracing. It is therefore not clear whether fluorescence can be used as a signature tracer or if quantifiable proportionality can be established.

In other contexts, attempts to correlate DOC concentrations and fluorescence peak intensities based on in situ samples alone have typically not been successful in establishing

proportionality or significant predictive power. However, this has some advantages as described by Baker et al. (2008) as it can enable correlations between DOM fluorescence and functional properties such as benzo[a]pyrene binding, alumina adsorption, hydrophilicity, and buffering capacity. DOM fluorescence has also been used to instead qualitatively track the origins of production, such as identifying the advection of pore water DOM from surface sediments into a river-dominated estuary (Osburn et al., 2012). Therefore, studying DOM fluorescence can have broad applications not limited to predicting DOC concentrations.

The objective of this study was to assess linear regressions between in situ seawater DOM fluorescence peak intensities and DOC concentrations from Oshoro Bay, Hokkaido, Japan, as well as from seawater samples taken from macroalgal incubation and bioavailability experiments (nine species collected from Oshoro Bay) conducted year-round from 2020–2023. Based on the existing literature, it is conjectured that proportionality between macroalgal-derived fluorescence peak intensities and DOC concentrations may be significantly linear, but has been obscured due to variability at multiple scales such as season, seawater sample time, and species differences. To resolve these uncertainties and build a preliminary predictive model of macroalgal contributions to in situ DOC, the following three hypotheses were tested:

- Hypothesis 1: Proportionality between macroalgal-derived fluorescence peak intensities (RU) and DOC concentrations (μM) will be season-specific;
- Hypothesis 2: Proportionality between macroalgal-derived fluorescence peak intensities (RU) and DOC concentrations (μM) will differ between post-incubation and post-bioavailability experiment samples;
- Hypothesis 3: Proportionality between macroalgal-derived fluorescence peak intensities (RU) and DOC concentrations (μM) will vary according to species assemblage.

Materials and Methods

Place-based research standpoint and methodology

The place-based research standpoint and methodology intrinsic to this study was developed in Chapter 1 of this dissertation, and previously applied to empirical macroalgal biogeochemistry (Chapters 2, 3, and 4). Chapter 6 discusses the broader social-ecological impacts of Blue Carbon as a climate change mitigation strategy. The importance and relevance of explicit research methodologies and standpoints is well-established (e.g., Smith, [1999] 2021; Wilson, 2008; Oliveira & Wright, 2016; Walter & Andersen, 2016), including for empirical environmental science (Liboiron et al., 2018; Alegado et al., 2023). In brief, the place-based (e.g., Kawai et al., 2012; Kaminaga, 2018; Grunow et al., 2019; Ishihara, 2020; Uzawa, 2020) standpoint defining this research means the results will be most relevant to Ainu People and Ainu Mosir (Hokkaido) and that globalized insights will be primarily appropriate in the context of Indigenous science and social-ecological stewardship (e.g., Morishige et al., 2018; Winter et al., 2018; Bennett et al., 2021; Jacobs et al., 2022). Specific to this chapter, establishing place- and context-specific correlations between macroalgal-derived fluorescence and DOC concentrations may facilitate improved monitoring of DOC due to its suitability to future applications of in situ or remote sensing of fluorescence. Explicit implications of this study's findings within the context of Indigenous science and social–ecological stewardship will be discussed in the Summary of this dissertation.

Macroalgal collection and incubation

Macroalgal collection, incubation experiments to quantify initial DOC and fluorescence production, and bioavailability experiments to quantify recalcitrant DOC and fluorescence

production are previously described in Chapters 2, 3, and 4 of this dissertation.

Seawater sample collection, storage, and DOC analysis

The basic process of seawater sample collection, filtration, bottle storage, bottle cleaning, DOC analysis, and assessing analytical replicability was previously described in Chapter 2 of this dissertation (Carlson et al., 2024) and consistent with best practices established by Halewood et al. (2022). Chapter 2 (Carlson et al., 2024) also described the process of macroalgal collection and incubation and Chapter 3 described the process of macroalgal removal and the experiments on macroalgal-derived DOC bioavailability. The same collection and storage process was used for in situ seawater DOC samples, which were collected from the eight stations within the shallow subtidal ecosystem and one reference location at the Oshoro Bay pier described in Chapters 2 and 3.

Fluorescence and absorbance analysis

Seawater samples were thawed overnight at about 4 °C and then allowed to reach room temperature immediately prior to the three-dimensional excitation-emission matrix (EEM) spectra measurements. EEM spectra were measured using a spectrofluorometer (Horiba FluoroMax-4) according to the analytical procedure described by Yamashita et al. (2017). Emissions scans from 290 nm to 600 nm at 2-nm intervals were acquired at excitation wavelengths between 250 nm and 450 nm at 5-nm intervals. The bandpass widths were 5 nm for both excitation and emission monochromators. Fluorescence spectra were scanned with an integration time of 0.25 s and were acquired in S/R mode. Samples were measured in a 1-cm quartz cuvette and Milli-Q was used as the blank. Corrections according to Murphy et al. (2010)

were made, including subtracting daily Milli-Q water blank of the EEM spectrum to eliminate the water Raman scatter peaks. The inner filter effect was also corrected for with the corresponding absorbance results. Absorbance analysis of DOM was conducted with a spectrophotometer (Shimadzu UV-1800) with a 1 cm cuvette according to the analytical procedure described by Yamashita et al. (2021b). The absorbance spectrum was determined from 250 to 800 nm at 0.5 nm intervals under a medium scan speed. Fluorescence intensities were finally calibrated for cross-instrument comparisons by dividing by the integral of the Raman peak according to Lawaetz and Stedmon (2009). These corrected intensity values are reported as Raman Units (RU) consistent with other studies on macroalgal FDOM (e.g., Kubo & Tanaka, 2023). They can also be simply converted to Quinine Sulfate (QS)-equivalents by the equation QS = RU/0.0767 (Lawaetz & Stedmon, 2009) for direct comparison to additional studies on macroalgal FDOM using such units (e.g., Wada et al., 2008). The resulting fluorescence intensity peak locations were consistent with known peaks and excitation/emission ranges described by Coble (1996) for comparison to other macroalgal DOC and fluorescence studies (e.g., Wada et al., 2008).

Results

In situ fluorescence and DOC

Stations 1, 2, 4, and 6, were inland (sub-tidal) locations with moderate macroalgal cover and no kelp. Stations 3 and 5 were dense kelp beds on the shelf-edge and subject to the highest water exchange. Station 7 was a sandy barren area and station 8 was an inland (sub-tidal) dense kelp bed with relatively low water exchange (Figure S5.1). In situ surface seawater DOC (µM) was first averaged across the nine sampling stations and then seasonally averaged (± *SE* between

n sampling events) (Figures 5.1, S5.2). Seasonally-averaged spatial variations indicated that the stations with the lowest and highest DOC concentrations were not consistent between winter (low: station 5, 68 ± 4.5 μM; high: station 4, 84 ± 9.9 μM), spring (low: reference points, 79 ± 3.3 μM; high: station 5, 107 ± 14 μM), summer (low: reference points, 88 ± 4.7 μM; high: station 2, 110 ± 8.3 μM), and autumn (low: station 5, 69 ± 4.6 μM; high: station 8, 75 ± 1.4 μM) results. The reference points (pier or bay interior) had lower DOC concentrations than the macroalgal area average for all seasons, except autumn (reference points: 74 ± 2.1 μM), when spatial variability was the lowest. A seasonally-weighted average of all data indicated that mean DOC (± *SE* between seasons) was lowest at the reference points (78 ± 4.6 μM) and highest at station 4 (90 ± 5.5 μM). Within the macroalgal bed area, stations 3 (83 ± 5.1 μM), 5 (85 ± 11 μM), 7 (80 ± 5.6 μM), and 8 (83 ± 5.5 μM) were generally lower than stations 1 (88 ± 9.2 μM), 2 (89 ± 9.7 μM), 4 (90 ± 5.5 μM), and 6 (87 ± 6.4 μM) (Figure S5.2). The overall seasonal pattern indicated that in situ DOC was higher in the spring (94 ± 3 μM, $n = 5$ events) and summer (96 ± 6 μM, $n = 4$ events) compared to the winter (75 ± 5 μM, $n = 5$ events) and autumn (73 ± 3 μM, $n = 6$ events) (Figure 5.1). For in situ fluorescence signatures, protein-like "peak T" and humic-like "peak A" were higher than humic-like "peak C" and "peak M" for all seasons, including when compared at the scale of each sampling station (Figures 5.1, S5.2).

Linear regressions between in situ fluorescence peak intensities and DOC concentrations were disaggregated by season for 2020–2023 data (20 sampling events). All regressions were seasonally significant (ANOVA, $p < 0.05$), except for humic-like "peak A" in autumn ($p = 0.52$, $R^2 = 0.0076$, $df = 1$, error $df = 55$, $F = 0.42$). R^2 values were low across fluorescence peaks and seasons, with higher values in summer (0.55–0.64) relative to winter 0.14–0.42), spring (0.20–0.61), and autumn (0.0076–0.15). When disaggregating into bi-seasonal periods, linear

regressions that were not significant (ANOVA, $p > 0.05$) included "peak A" ($p = 0.19$) in early winter and "peak T" ($p = 0.64$), "peak C" ($p = 0.83$), and "peak M" ($p = 0.28$) in early autumn. This scale of analysis increased R^2 values, resulting in high values (> 0.70) for "peak T", "peak C", and "peak M" in late winter and for "peak T", "peak A", and "peak M" in late summer.

Macroalgal fluorescence and DOC proportionality: post-incubation

Linear regressions were analyzed between fluorescence peak intensities (RU) and DOC concentrations (μM) for seawater samples collected at the end of the macroalgal incubation experiments. Data from 2020–2022 kelp incubation samples indicated that regressions for all fluorescence peaks were significant (ANOVA, $p < 0.05$) across seasons except "peak A" and "peak M" in winter and "peak T" in summer (Figure 5.3a). R^2 values varied considerably in winter (0.28–0.91), spring (0.35–0.76), summer (0.050–0.81), and autumn (0.51–0.74). R^2 values were above 0.70 for protein-like "peak T" (0.84) and humic-like "peak C" (0.91) in the winter; for humic-like "peak C" (0.76) in the spring; for humic-like "peak A" (0.81) in the summer; and for humic-like "peak A" (0.74) and humic-like "peak C" (0.70) in the autumn.

Incubation experiments ($t = 4$ d duration) on multiple macroalgal species were conducted in 2023, with seasonally aggregated results estimating mean seaweed community dynamics. For macroalgal incubation samples ($t = 0$ d after macroalgal removal), linear regressions analyzed were significant (ANOVA, $p < 0.05$) across seasons, with one exception—humic-like "peak C" in summer 2023 ($p = 0.19$, $R^2 = 0.39$, $df = 1$, error $df = 4$, $F = 2.52$) (Figure 5.4a). Otherwise, correlations in winter were moderate to high ($R^2 = 0.65$–0.87), consistently high in spring ($R^2 = 0.98$–0.996), high ($R^2 = 0.83$–0.93) in summer except for humic-like "peak C" ($R^2 = 0.39$), and consistently high in autumn ($R^2 = 0.98$–0.99).

Macroalgal fluorescence and DOC proportionality: post-bioavailability

For macroalgal-derived bioavailability samples (t = 150 d after macroalgal removal), all linear regressions analyzed were significant (ANOVA, $p < 0.05$), except for summer 2020–2022 kelp results for "peak T" ($p = 0.12$, $R^2 = 0.12$, $df = 1$, error $df = 20$, $F = 2.65$), "peak C" ($p = 0.13$, $R^2 = 0.11$, $df = 1$, error $df = 20$, $F = 2.50$), and "peak M" ($p = 0.15$, $R^2 = 0.10$, $df = 1$, error $df = 20$, $F = 2.29$) (Figure 5.3b). Otherwise, correlations from 2020–2022 kelp data were high in winter ($R^2 = 0.72$–0.85), spring ($R^2 = 0.88$–0.98), and autumn ($R^2 = 0.78$–0.93). For 2023 mean seaweed community estimate results, correlations were high in winter ($R^2 = 0.990$–0.994), high in spring ($R^2 = 0.98$–0.996), high ($R^2 = 0.81$–0.93) in summer except for humic-like "peak C" ($R^2 = 0.67$), and high in autumn ($R^2 = 0.92$–0.999) (Figure 5.4b).

Discussion

Fluorescence and DOC proportionality controlled by context

The three hypotheses of this chapter expected that proportionality between fluorescence peak intensities (RU) and DOC concentrations (µM) would have (1) season-specific differences, (2) sample time-specific differences, and (3) macroalgal assemblage differences. If these differences were substantial, the expectation was that disaggregating by context would result in more significantly linear results with stronger correlations. Integrating the results shows this to be the case and allows for preliminary steps toward building a predictive model.

In general, R^2 values increased from annualized to seasonal data and again from seasonal to bi-seasonal data. For example, R^2 values for the full 2020–2022 kelp post-incubation data set were 0.21–0.52 (0/4 results > 0.70), while six results were above 0.70 when disaggregating by season, and 16 results were above 0.70 when disaggregating by bi-season. However, the

increased seasonal specificity also resulted in proportionally less individual results that were significantly (ANOVA, $p < 0.05$) linear (e.g., full data set: 4/4, seasonal: 13/16, bi-seasonal: 18/32). R^2 values for the full 2020–2022 kelp post-bioavailability data set were 0.41–0.59 (0/4 results > 0.70), whereas 12 of 16 results were above 0.70 when disaggregating by season, and 20 of 32 results were above 0.70 when disaggregating by bi-season. The proportion of significantly linear results decreased between the full data set (4/4) and the seasonal (13/16) and bi-seasonal (22/32) disaggregations. For 2023 mean seaweed community estimate post-incubation data, the number of significantly linear regressions decreased slightly from the full data set (4/4) to the seasonal data set (15/16), while R^2 values > 0.70 proportionally increased slightly from the full data set (3/4) to the seasonal data set (13/16). For 2023 mean seaweed community estimate post-bioavailability data, all linear regressions were significant ($p < 0.05$) for both the full and seasonal data sets, while R^2 values > 0.70 proportionally increased from the full data set (3/4) to the seasonal data set (15/16).

Overall, these trends show that disaggregating by season or bi-season revealed specific periods when linear regressions were not significant or were weakly correlated. Summer was the primary season with a weaker linear relationship between fluorescence peak intensities and DOC concentrations. R^2 values were generally higher for more recalcitrant samples taken at the end of the bioavailability experiments. However, summer "peak C" correlations with DOC were still not significant for 3 of 4 peaks in kelp 2020–2022 data and the remaining peak ("peak A") was still weakly correlated ($R^2 = 0.46$). Integrating these trends indicates that using ratios from data that is (1) disaggregated by bi-season, (2) sourced post-bioavailability experiments, and (3) representative of mean macroalgal community and not a single species, results in increasingly significant and well correlated ratios that may be appropriate for a preliminary predictive model.

Predicting in situ DOC from known fluorescence peak intensities

R^2 values from in situ samples were substantially lower than for macroalgal-derived samples. However, they were significant across fluorescence types with relatively higher R^2 values in spring and summer, likely due to the wider range of DOC concentrations and fluorescence peak intensities during those seasons. This in turn may be due to the relatively higher in situ contributions of macroalgal-derived DOC and fluorescence in the spring and summer. Overall, protein-like "peak T" and humic-like "peak A" were higher than humic-like "peak C" and "peak M". Because the former two peaks are more strongly associated with being directly derived from live macroalgae, this is an indication that the in situ seasonality may be largely attributable to macroalgae. Spatial variability in DOC and in situ fluorescence indicated that there were no significant differences between sampling stations. This may indicate that the relatively small area in the inner bay is well mixed.

Because protein-like "peak T" is primarily associated with labile macroalgal DOM production, it is considered the best potential proxy for predicting DOC concentrations in situ. As discussed in Chapters 3 and 4, "peak C" and "peak M" are likely related to microbiological processes as their peak intensities continued to enhance in the absence of macroalgae during those bioavailability experiments, while "peak A" was typically conserved. They are therefore not expected to be strong predictors of macroalgal contributions of DOC and fluorescence in situ. Therefore, the ratios established for "peak T" in the predictive model described previously were applied to the known "peak T" fluorescence intensities in situ to calculate predicted in situ contributions (Figure 5.5). This predictive calculation estimated macroalgal contributions with little seasonal variation between winter (35 ± 2 μM; 44% ± 3%), spring (23 ± 1 μM; 24% ± 3%), summer (37 ± 10 μM; 38% ± 11%), and autumn (34 ± 2 μM; 44% ± 3%). Because the model

was based on “peak T” fluorescence 150 d after macroalgal removal from incubation, the predictive ratio may represent semi-labile or semi-recalcitrant contributions, which would not be expected to vary significantly. Contributions of this order are not without precedent as Pfister et al. (2019) reported kelp elevating local DOC concentrations by 50%.

Conclusion

This chapter identified significant linear relationships between fluorescence peak intensities and DOC concentrations that were particularly well correlated for post-bioavailability experiment samples from a mean macroalgal community assemblage that were disaggregated by bi-seasonal period. This informed a preliminary predictive model that while limited and highly context-specific, indicted substantial yet not unprecedented macroalgal contributions to the local semi-recalcitrant DOC pool. While direct quantitative attribution and traceability of macroalgal-derived DOC and fluorescence to in situ biogeochemistry remains highly challenging, these results show the promise of fluorescence characteristics to serve as proxies for variable DOC pathways, provided that site-specific spatial and temporal variabilities are well-studied first.

Figures

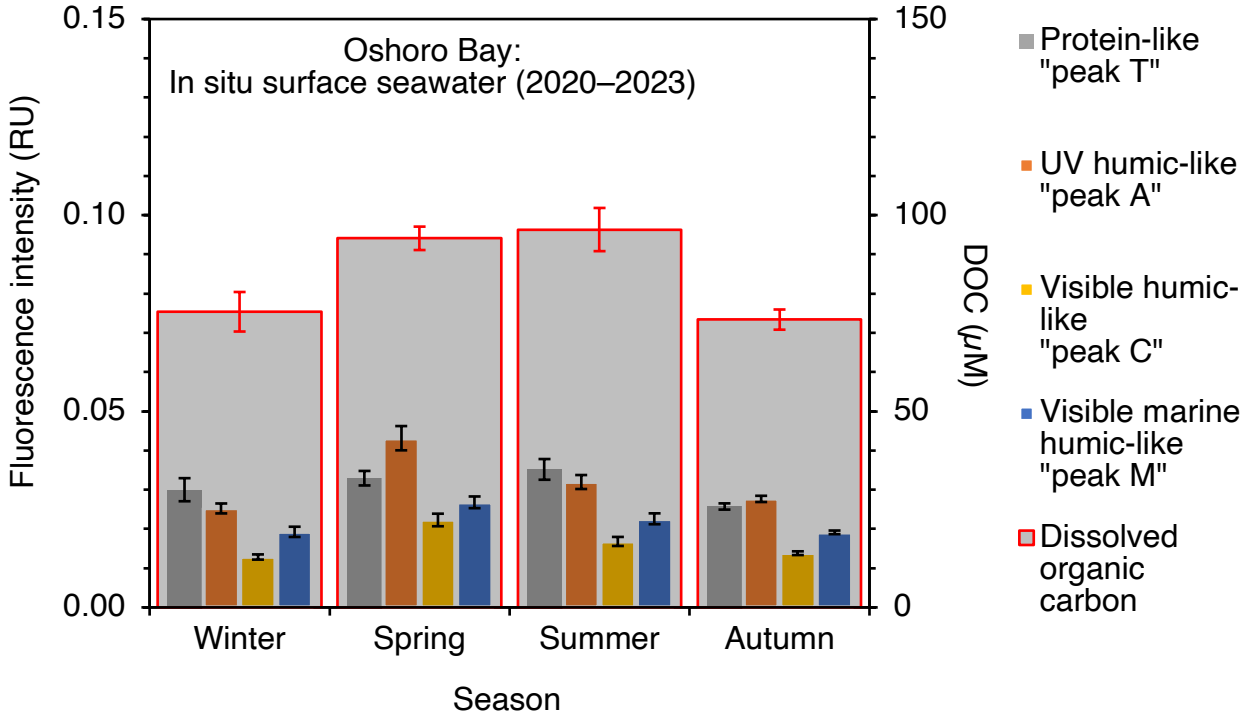


Figure 5.1. Seasonal in situ fluorescence and DOC. Mean seasonal (± *SE* between sampling events) fluorescence peak intensities (RU) and DOC concentrations (μM) for in situ surface seawater samples collected at Oshoro Bay from 2020–2023. Each sampling event collected samples from up to nine stations and represents a spatial average (Figure S5.1).

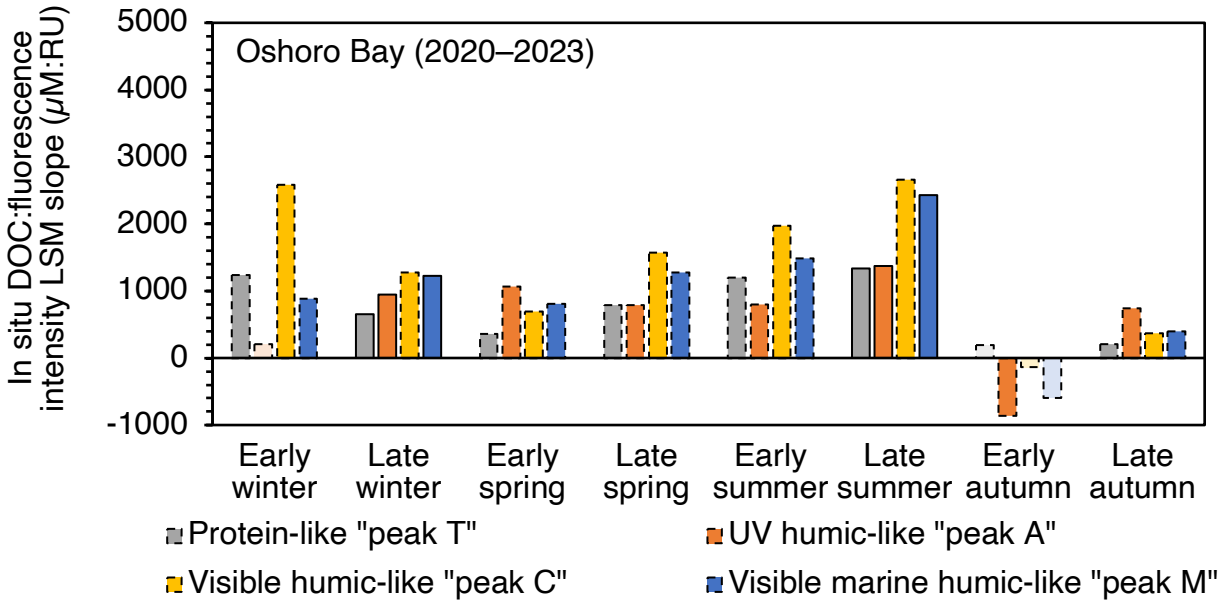


Figure 5.2. Ratios of in situ DOC to fluorescence peak intensity for seawater samples from Oshoro Bay. Ratios are calculated as least squares mean slopes from a linear regression analysis of the corresponding data set. Results that did not demonstrate a significant ($p < 0.05$) linear relationship between DOC concentrations (μM) and fluorescence peak intensities (RU) are marked with 80% transparency shading. Linear regression results with an $R^2 < 0.70$ are marked with dashed borders. Data are categorized into eight bi-seasonal periods, with ratios calculated for the four fluorescence intensity peaks generated during the macroalgal incubation and bioavailability experiments.

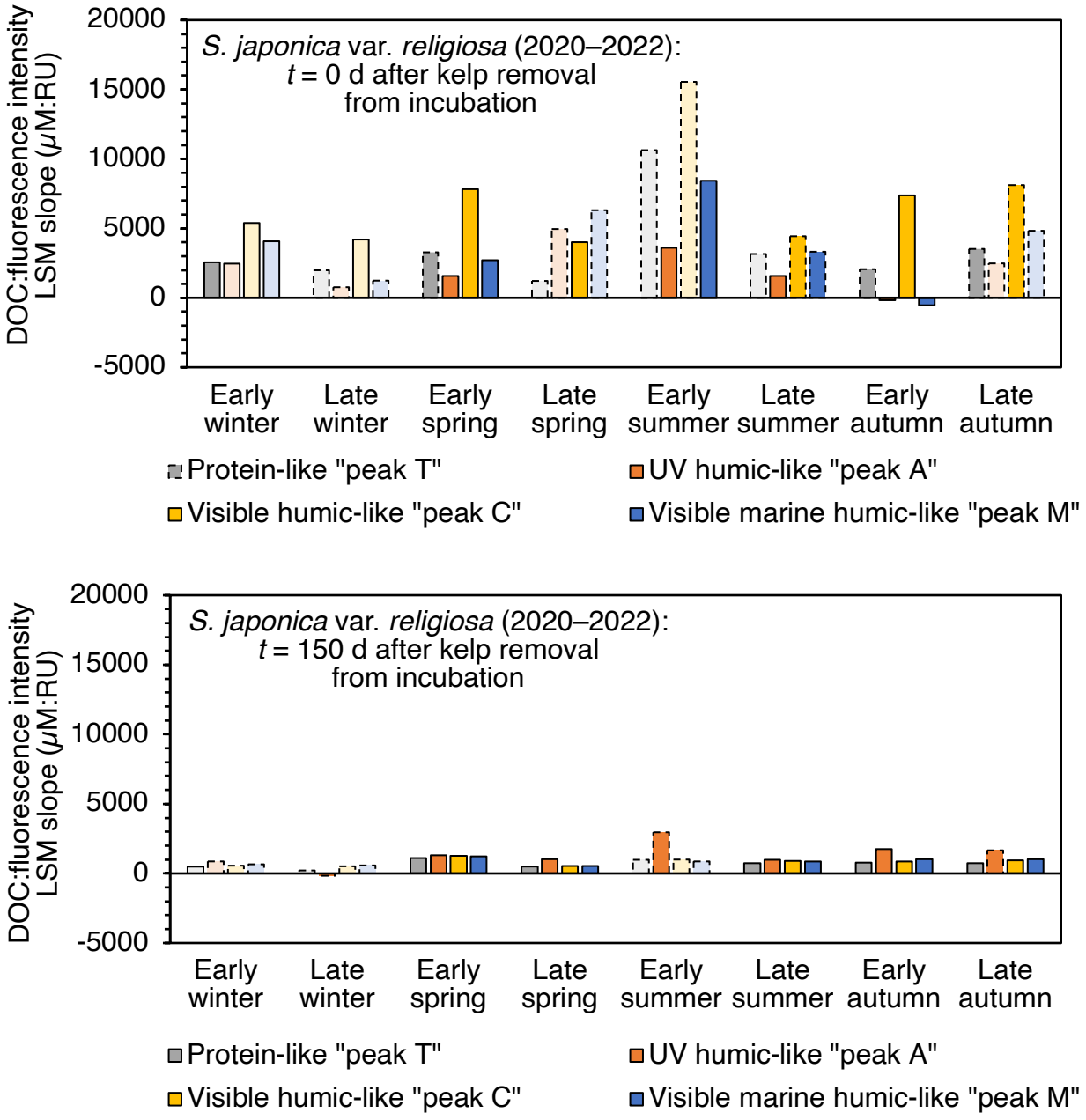


Figure 5.3. Ratios of DOC concentrations to fluorescence peak intensity for seawater samples from the *S. japonica* var. *religiosa* experiments. Results are from (a) kelp incubation experiment samples and (b) corresponding bioavailability experiment samples. Ratios are calculated as least squares mean slopes from a linear regression analysis of the corresponding data set. Results that did not demonstrate a significant ($p < 0.05$) linear relationship between DOC concentrations (µM) and fluorescence peak intensities (RU) are marked with 80% transparency shading. Linear

regression results with an $R^2 < 0.70$ are marked with dashed borders. Data are categorized into eight bi-seasonal periods, with ratios calculated for the four fluorescence intensity peaks generated during the macroalgal incubation and bioavailability experiments.

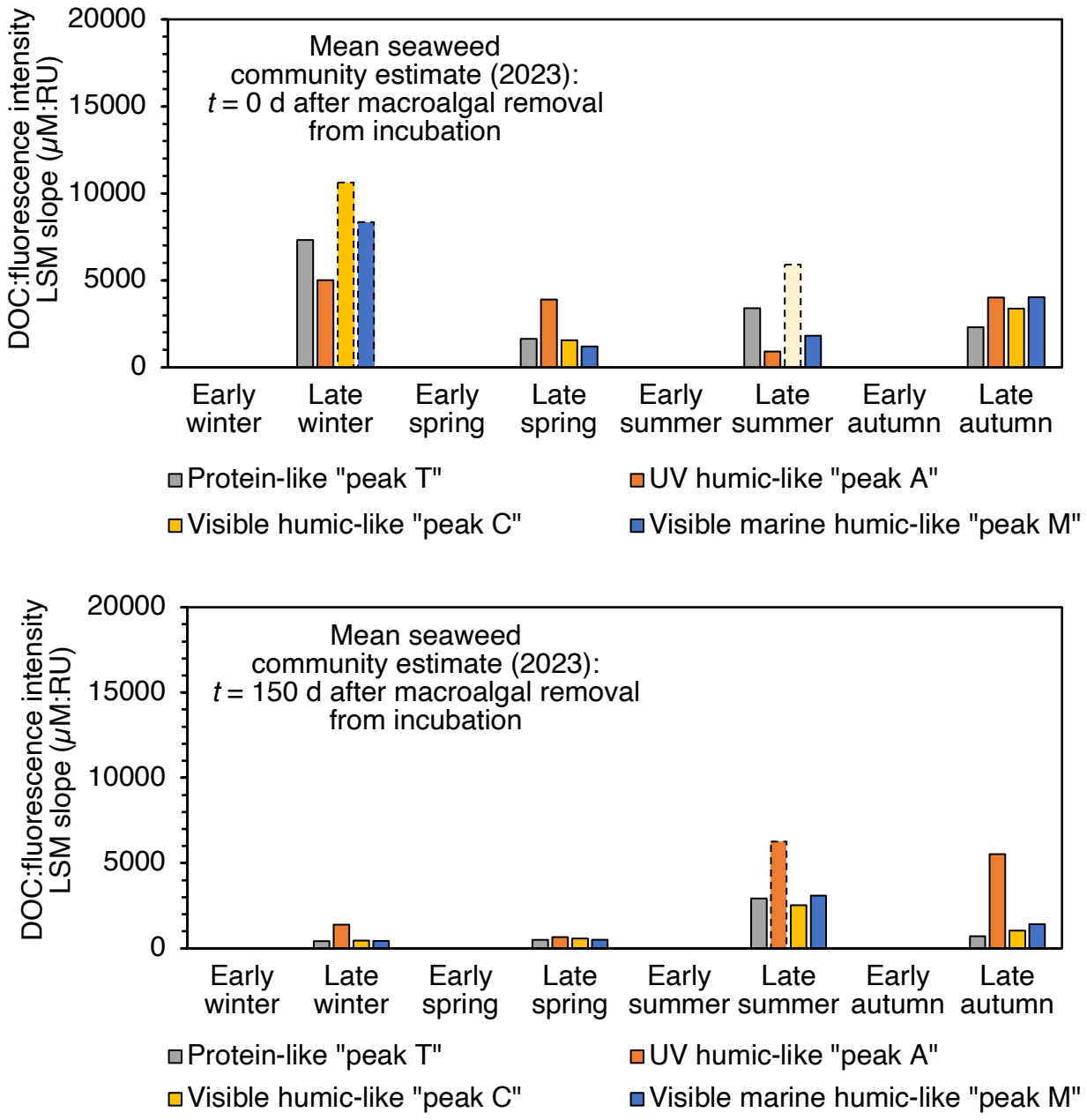


Figure 5.4. Ratios of DOC concentrations to fluorescence peak intensity for seawater samples from the 2023 experiments on multiple macroalgal species. Results are from (a) macroalgal incubation experiment samples and (b) corresponding bioavailability experiment samples. Ratios are calculated as least squares mean slopes from a linear regression analysis of the corresponding data set. Results that did not demonstrate a significant ($p < 0.05$) linear relationship between

DOC concentrations (μM) and fluorescence peak intensities (RU) are marked with 80% transparency shading. Linear regression results with an $R^2 < 0.70$ are marked with dashed borders. Data are categorized into eight bi-seasonal periods, with ratios calculated for the four fluorescence intensity peaks generated during the macroalgal incubation and bioavailability experiments.

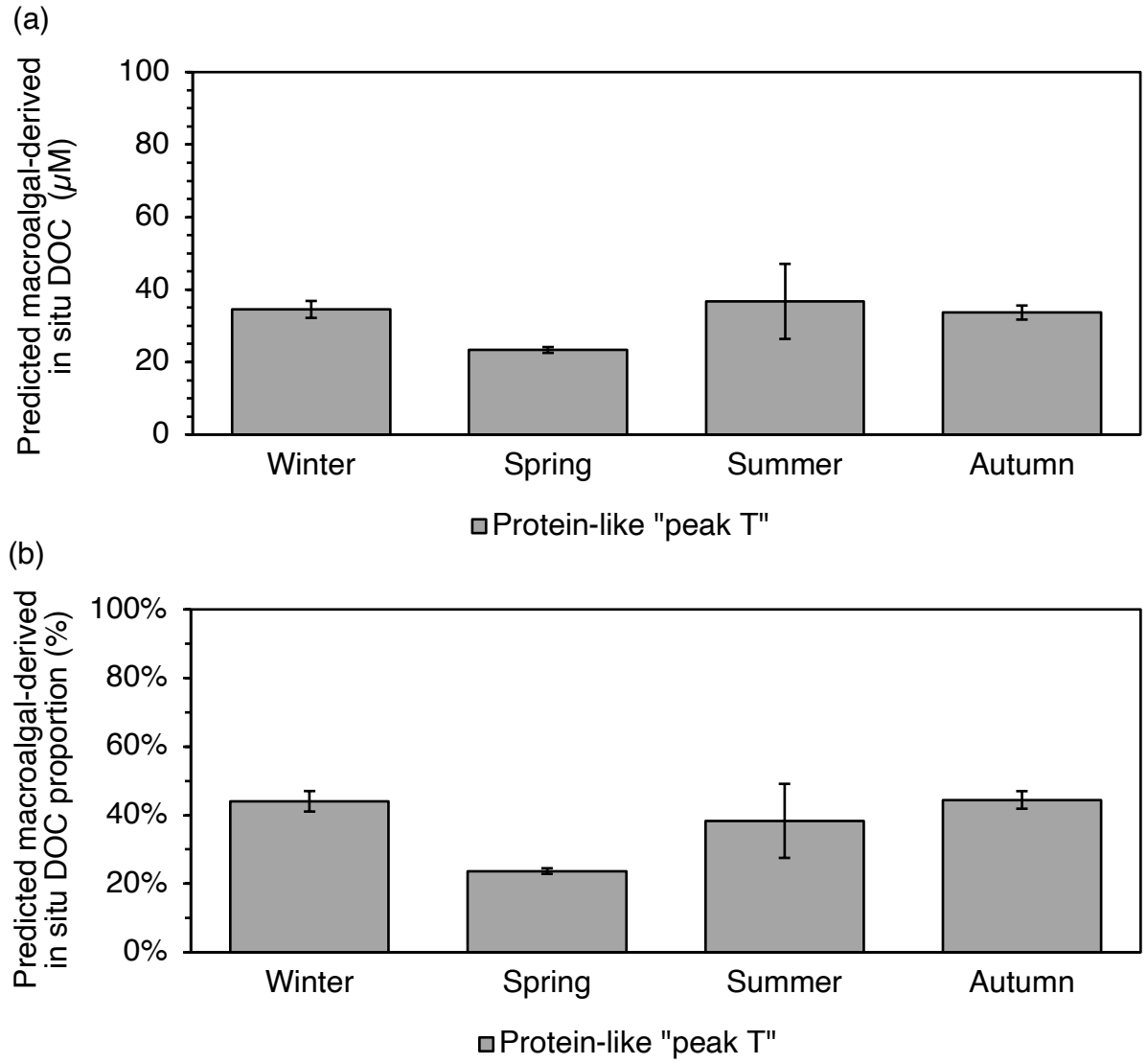


Figure 5.5. Macroalgal-derived DOC in situ contribution predictions. Data are means (± *SE*) for (a) predicted DOC concentration (μM) contribution and (b) predicted DOC proportion (%) contribution, for the four seasons. The prediction model is based on the significant ($p < 0.05$) and well-correlated ($R^2 > 0.70$) proportionality between DOC concentrations and protein-like "peak T" fluorescence intensities in the bioavailability experiment seawater samples from the 2023 mixed macroalgal species data set. The prediction model ratios were then applied to the actual measured in situ "peak T" intensities for seawater samples from Oshoro Bay from 2020–2023. The results therefore represent the average contributions over this four year period.

Supplementary Figures

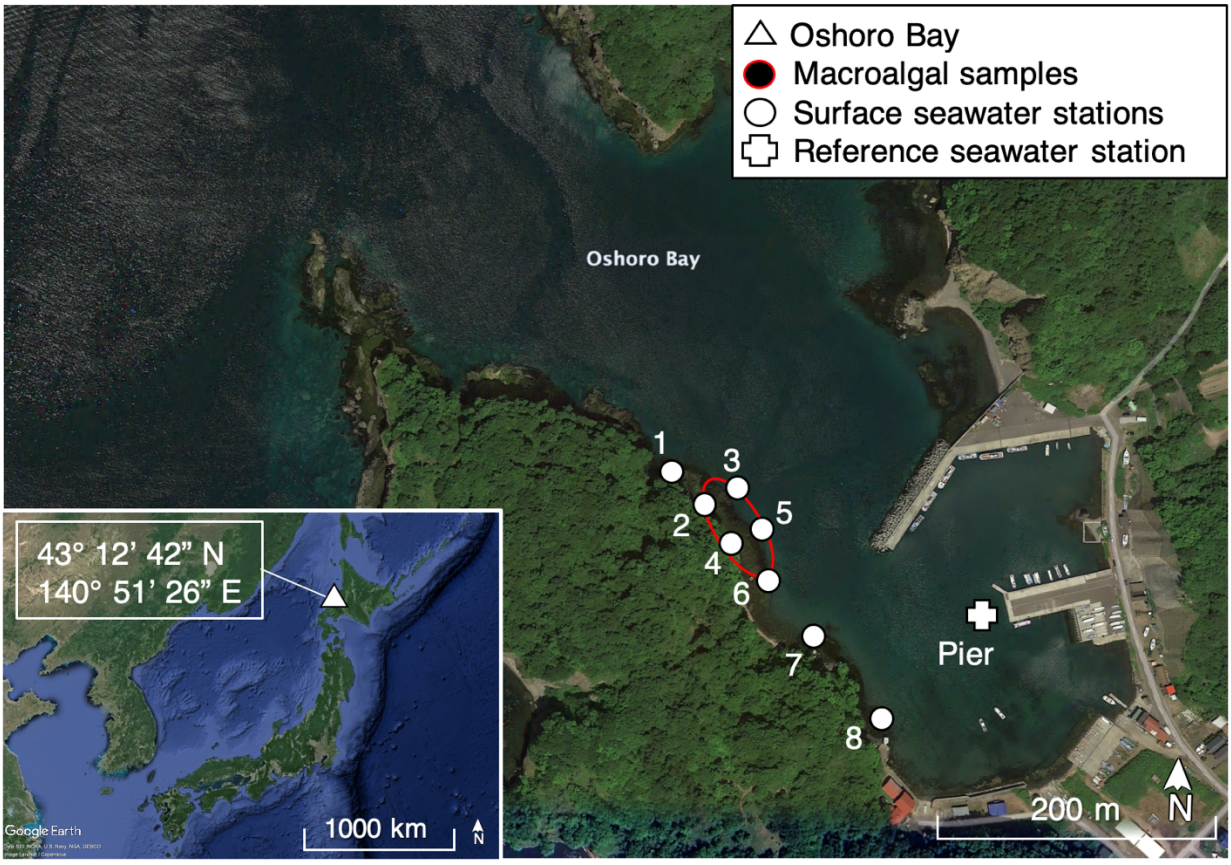
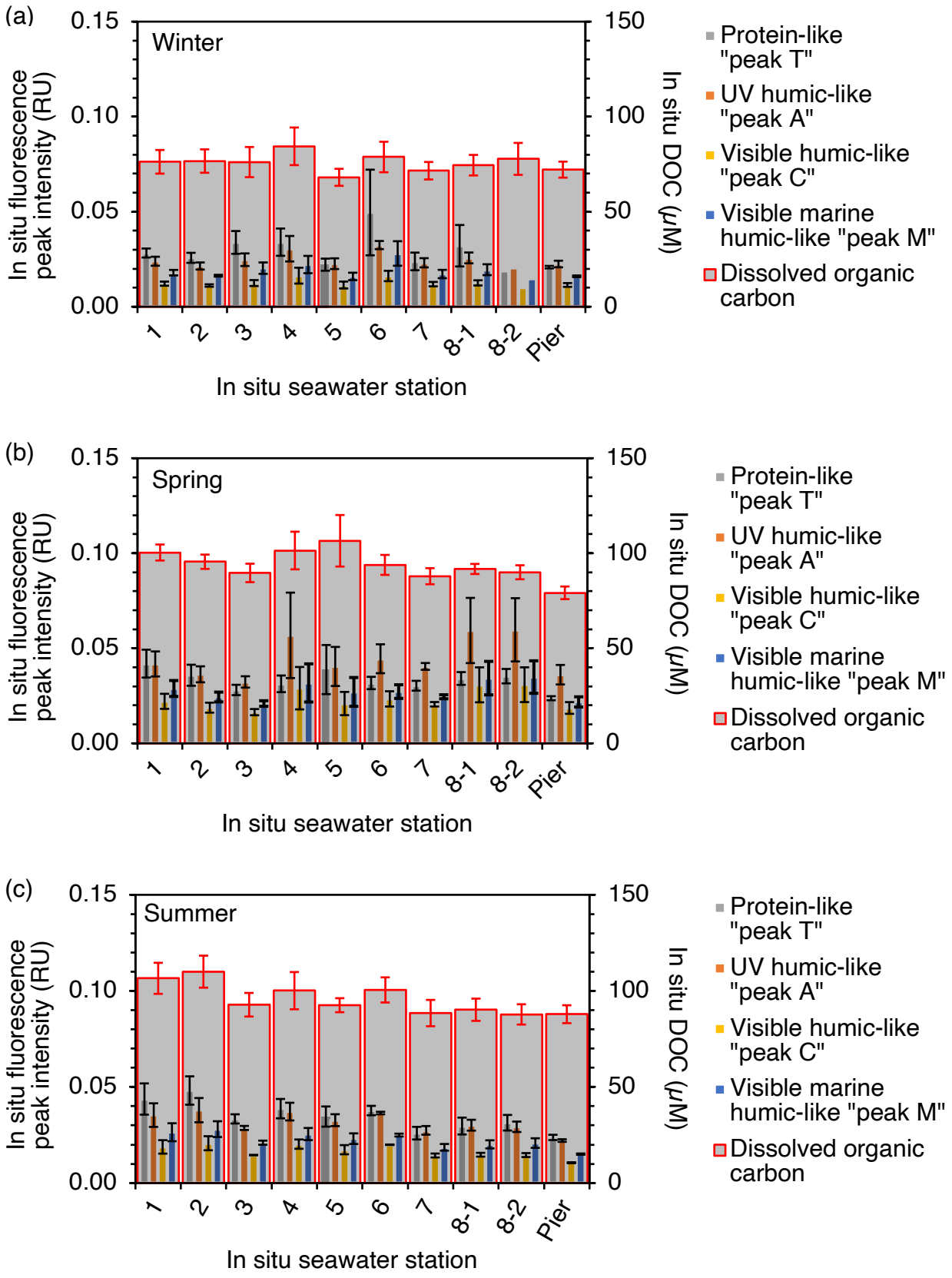


Figure S5.1. July 2021 aerial images showing an overview of Oshoro Bay, the numbered sampling locations (1–8) within the macroalgal bed area, and the reference seawater sampling location at the pier. An inset of the relative location of Oshoro Bay on the Shakotan peninsula in Hokkaido is also provided (Google Earth 2021).


(a)
Winter
(b)
Spring
(c)
Summer
In situ fluorescence peak intensity (RU)
In situ DOC (μM)
0.15
0.10
0.05
0.00
150
100
50
0
1
2
3
4
5
6
7
8-1
8-2
Pier
In situ seawater station
Protein-like "peak T"
UV humic-like "peak A"
Visible humic-like "peak C"
Visible marine humic-like "peak M"
Dissolved organic carbon

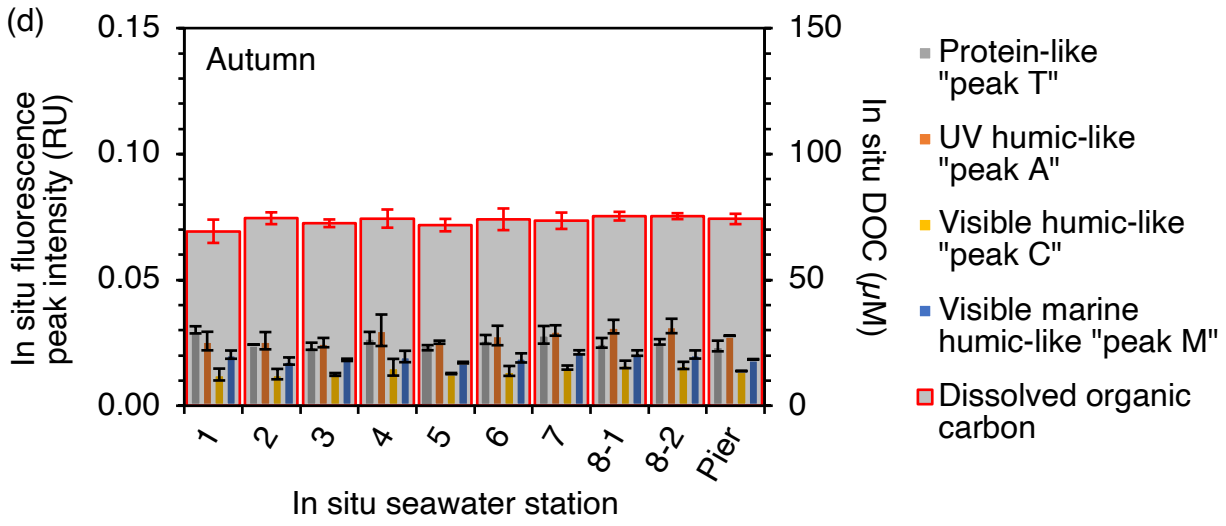


Figure S5.2. In situ DOC and fluorescence. Sea surface in situ DOC (μM) and fluorescence peak intensity (RU) results from eight unique sample stations within the macroalgal bed area (duplicate samples at station 8) and one sample station at the pier within Oshoro Bay (100 m from the macroalgal bed area). Data are means (± *SE* between events) of 20 sampling events from 2020–2023 and are categorized by season: (a) winter, (b) spring, (c) summer, and (d) autumn.

CHAPTER SIX

AlterNatives to Blue Carbon Coloniality: An ʻŌiwi Perspective on Redirecting Funding to Indigenous Stewardship

A version of this chapter is accepted for publication (In Press) as Chapter 8 of a Routledge peer-reviewed book, forthcoming 8 October 2024 (https://www.routledge.com/Confronting-Climate-Coloniality-Decolonizing-Pathways-for-Climate-Justice/Sultana/p/book/9781032737850):

Carlson, A. K. (2024). AlterNatives to Blue Carbon Coloniality: An ʻŌiwi Perspective on Redirecting Funding to Indigenous Stewardship. In F. Sultana (Ed.), *Confronting Climate Coloniality: Decolonizing Pathways for Climate Justice* (pp. 121–136). London and New York: Routledge. https://doi.org/10.4324/9781003465973-10

Abstract

The Blue Carbon sequestration potential of marine photosynthesizers is being pursued as a nature-based climate change mitigation strategy, yet the commercial, industrial, and colonial aspects of these projects are instead resulting in a perpetuation of climate colonialism. Specifically, narrow ecosystem services accounting leads to perverse prioritization of carbon dioxide removal (CDR) over holistic social-ecological health, carbon offsets provide cover for the continuation of extractive corporate and colonial operations, industrial-scale interventions result in negative social-ecological disruptions, and even small-scale non-Indigenous projects exacerbate the loss of Indigenous coastal sovereignty. Therefore, funding and labor toward colonial Blue Carbon projects is ultimately counterproductive to holistic social-ecological vitality and should be re-directed toward the full-scale restoration of Indigenous aquaculture and coastal cultivation practices (within sovereign social-ecological systems). Moreover, since Blue Carbon and other ecosystem services should be considered a co-benefit of Indigenous stewardship and restoration, their funding should not be dictated by colonial monitoring, reporting, and verification (MRV) requirements. These conclusions are discussed within the global context, while also grounded in Hawai‘i through Kanaka ‘Ōiwi (Native Hawaiian) worldviews. Ultimately, these ongoing and practical Indigenous alternatives to Blue Carbon and climate coloniality must be urgently prioritized to achieve a decarbonized and decolonized world.

Introduction

The climate crisis is rooted in the ongoing effects of systemic colonialism (Whyte, 2018; Liboiron, 2021a, 2021b; Sultana, 2022a, 2022b). Therefore, when climate change mitigation strategies replicate and perpetuate coloniality, they are ultimately counterproductive and ineffective (Townsend et al., 2020). Climate change mitigation is defined as reducing greenhouse gas emissions or removing those gases from the atmosphere (IPCC, 2022), and the carbon offset or credit market is meant to mediate projects related to these goals. However, the coloniality of many mitigation strategies is well established at multiple scales, including the capitalistic incentives of the carbon market (Bachram, 2004; Bumpus & Liverman, 2011), the geoengineering scale of carbon dioxide removal (CDR) projects (Carton et al., 2020; Honegger et al., 2021), the colonial violence of extractivism and exacerbated inequality (Dunlap & Jakobsen, 2020), and the land grabs involved in forest carbon management projects and "fortress" style conservation (Chomba et al., 2016; Asiyanbi et al., 2019; Sène, 2023). Despite the documented harms and barriers, some Indigenous nations or communities continue to engage with carbon credit markets as the best available option under colonial capitalism (Wylie et al., 2016; Townsend et al., 2020; Jones, 2022). Based on these critiques and compromised realities, decolonial funding priorities are required to enable the prioritization of sovereign Indigenous social-ecological health. I approach these issues from my research standpoint and methodology as a Kanaka ʻŌiwi (Native Hawaiian) environmental scientist and marine biogeochemist to ground the discussion while maintaining a global context. At the broadest level, I argue that full-scale decolonization and Indigenization is necessary to address the climate and other planetary crises.

What is my kuleana as a diasporic Kanaka ʻŌiwi to speak on this issue? In ʻōlelo Hawaiʻi (Hawaiian language, translations from Pukui & Elbert, 1986), kuleana refers to the ancestral rights, responsibilities, authorities, and obligations Kānaka (People) have to each other and to ʻāina (all that sustains, land, environment) (Aikau et al., 2016). Kuleana in research is intimately tied to kūlana (position, standpoint, positionality) and moʻokūʻauhau (genealogies) (Wilson-Hokowhitu, 2019, Alegado et al., 2023). They are rooted in my pilina (relationships) to and lineal descent from the ahupuaʻa (traditional community divisions) of Waiākea, Honuʻapo, and Niuliʻi on Hawaiʻi Island and Waiheʻe and Wailuku on Maui. My research methodology at Hokkaido University (Chapter 1 of this dissertation; Carlson, 2025) confronts the kuleana of my seaweed biogeochemistry research to lands and Peoples at multiple scales—local (Ainu Mosir, the Indigenous homelands of Ainu People), personal (Hawaiʻi and Kānaka ʻŌiwi), and global (Indigenous Peoples and stewardship methodologies broadly). Through that framework, I also discuss the specific implications of my laboratory-based results on macroalgal dissolved organic carbon dynamics for Blue Carbon and sovereign Indigenous stewardship in the Summary of this dissertation and in Carlson et al. (2023). My kūlana and moʻokūʻauhau give me the kuleana to argue here that the coloniality of typical Blue Carbon projects renders them ineffective as climate solutions and perpetuate harm toward Indigenous Peoples.

By definition (Nellemann et al., 2009), Blue Carbon projects seek to place the burden of climate change mitigation and adaptation on vegetated coastal ecosystems (e.g., kelp forests or farms, mangrove forests, seagrass meadows, or salt marshes). To be clear on terminology, Blue Carbon ecosystem restoration or afforestation are (potential) forms of marine CDR while Blue Carbon ecosystem conservation is a form of greenhouse gas emission avoidance. Marine CDR is therefore not always equivalent to Blue Carbon and also encompasses non-vegetation strategies

such as olivine enhanced weathering in coastal seabeds (The Royal Society, 2018; Morrow et al., 2020). This broader literature on marine CDR is considered here in terms of its relevance to Blue Carbon. For example, assessments of Blue Carbon projects as a marine CDR strategy have considered factors such as how effective they actually are at sequestering carbon (Williamson & Gattuso, 2022), the ecological impacts (Boyd et al., 2022), and governance and ethical issues (Ricart et al., 2022). However, these are generally posed as solvable issues without confronting their inherent coloniality. It bears emphasizing that an apparent lack of overtly negative ecological consequences does not address the intrinsic social-ecological harms tied to coloniality. In contrast, direct critiques of Blue Carbon conservation projects have been more limited, while acknowledging issues of injustice in the broader field of conservation (Huxham et al., 2023). Overall, targeted discussions of the inherent coloniality of engaging in Blue Carbon accounting are lacking, thereby sidelining more effective decolonial alternatives.

Based on my research background, the focus here will be on extending the critiques of climate coloniality to include nature-based Blue Carbon projects—the key thesis is that their fundamental coloniality cannot be reformed and that they center the wrong objectives. To do so, this chapter will focus on five key aspects of Blue Carbon coloniality. The first issue, "Extractive Benefits of Blue Carbon Verification", discusses how the carbon offset market sets an inherently extractive and colonial relationship between Blue Carbon project managers and verifiers. The second issue, "Inflated and Uncertain Value of Blue Carbon Credits", discusses how carbon offsets do not materially mitigate climate change and instead provide cover for the continuation of extractive corporate and colonial operations (Bumpus & Liverman, 2011). The third issue, "Invasive Ecology of Blue Carbon Interventions", discusses how a fixation on carbon credits (or any other so-called ecosystem service) incentivizes extractive capitalistic processes and

prioritizes carbon accounting (Shapiro-Garza et al., 2020) at the expense of the holistic biocultural system (Pascua et al., 2017). The fourth issue, "Indigenous Displacement by Blue Carbon Funding Priorities", discusses non-Indigenous organizations that are disproportionately profiting from Blue Carbon schemes and displacing Indigenous coastal sovereignty. The fifth issue, "Indigenous Erasure by Blue Carbon Scientists" highlights current examples and potential risks of Indigenous Knowledges and Values being appropriated by scientists at the expense of Indigenous Peoples. These five key issues perpetuate and entrench the systems of extractive capitalism, corporate status-quo reproduction, ecological degradation, and settler-colonial usurpation of Indigenous sovereignty that are at the root of the climate crisis.

As an ʻŌiwi environmental scientist, I understand that science and scientists have obligations to advance decolonization in and beyond our research (Smith, [1999] 2021; Oliveira & Wright, 2016; Liboiron, 2021a; Jacobs et al., 2022; Carlson, 2025) and that this is not a metaphorical or theoretical struggle (Fanon, [1961] 2004; Tuck & Yang, 2012; Goodyear-Kaʻōpua et al., 2014) but one for ʻāina momona (thriving social-ecological communities) (Andrade et al., 2022). The restoration of sovereign Indigenous social-ecological systems globally should be the guiding objective in confronting the climate crisis (Winter et al., 2018; Townsend et al., 2020; Dawson et al., 2021; Fisk et al., 2021), instead of simply centering carbon accounting at the expense of social-ecological justice. I will therefore follow my critique of Blue Carbon coloniality with a discussion of loko iʻa restoration projects in Hawaiʻi as a tangible "AlterNative" example of what is possible. As a brief preview, loko iʻa are Native Hawaiian multi-trophic fishponds that were prevalent for nearly a millennia prior to European invasion (Keala et al., 2007) and are prominent sites of resurgent sovereignty.

From these critiques and alternatives, the key praxis-based thesis of this chapter is that scientists, researchers, activists, and other policy-influencers must support the full restoration of Indigenous governance and stewardship systems by dismantling the coloniality of funding priorities and requirements that currently hamper further progress. In other words, the time, labor, and funding spent on monitoring, verification, and reporting (MRV) of carbon credits would be better spent directly empowering Indigenous Peoples. This chapter's primary contributions are therefore to serve as an intervention by (1) extending previously made arguments to the context of Blue Carbon, (2) challenging the coloniality of specific Blue Carbon operations, and (3) offering coastal-specific Indigenous alternatives using Hawai‘i and Kanaka ‘Ōiwi stewardship models as a case example. In confronting climate coloniality, a seemingly monumental task, I turn to an ‘ōlelo no‘eau (Hawaiian proverb): "Hiolo ka pali kū, nahā ka pali pa‘a" ("The standing precipice falls, the solid cliff breaks" or "The resistance is broken down at last") (Pukui, 1983, ‘Ōlelo No‘eau 1011). So too, will colonialism be broken down and fall.

Extractive Benefits of Blue Carbon Verification

In assessing the extractively colonial relationship between Blue Carbon verifiers and community-led Blue Carbon projects, I will at first uncritically assume all aspects of the project and the verifier are ideal (leaving the critiques to later sections) to show that the fundamental coloniality of the market incentives cannot be reformed even in a best-case scenario. The largest overall carbon credit certifier (over 855 million credits) is the Washington, D.C.-based non-profit Verra (Jones, 2022). Recently, Verra has started developing methodologies for Blue Carbon projects, including a seagrass project coordinated by the Virginia Institute of Marine Science and The Nature Conservancy, as well as a mangrove project in Senegal by the non-profit Livelihoods

(Jones, 2021). Another verifier is Plan Vivo, which certified the first Blue Carbon project (Mikoko Pamoja in Kenya) in 2014, and has since certified others in Madagascar, Mexico, Honduras, Tanzania, and Indonesia (Wylie et al., 2016; Plan Vivo, 2023). To varying degrees, several of these projects have been lauded as community-led Blue Carbon projects where the certifier has developed long-term relationships with local communities (Wylie et al., 2016; Herr et al., 2019). That said, there are certainly complications to this narrative that are discussed later or elsewhere (Blake, 2023). At a minimum, community-led projects can be assumed to be an improvement over overtly outsider-led projects (Asase et al., 2021) and they can provide some benefits to Indigenous communities (Wylie et al., 2016; Herr et al., 2019). These community benefits are therefore presented as evidence that engagement with the Blue Carbon market can improve social equity.

However, dependence on carbon markets will always be unhealthy in the long-term due to the skewed prioritization of carbon drawdown (Bachram, 2004; Pascua et al., 2017) and the small percentage of profits directly returned to the community after accounting and certification costs. For example, 2013–2014 prices for Mikoko Pamoja carbon credits were U.S. $6.50–10.00, and annual proceeds for community implementation of the project has been approximately U.S. $12,500—just enough for one full time staff member (Wylie et al., 2016). For added context, the highest Blue Carbon credit prices have been about U.S. $15 per credit, while forest carbon credits can often be less than U.S. $1. Therefore, the Mikoko Pamoja example highlighted here is typical of a best case scenario across the carbon market that is still completely insufficient. To advocate for truly sovereign Indigenous stewardship of these Blue Carbon ecosystems means a full emancipation from the colonial structures that force communities into dependent and extractive relationships.

Inflated and Uncertain Value of Blue Carbon Credits

Decades of research have highlighted concerns with forest carbon credit quality and verification methodologies (Guizar-Coutiño et al., 2022; Blake, 2023), yet Blue Carbon projects are often touted as superior in terms of durability. For example, biogeochemical research has indicated that mangroves, salt marshes, and seagrasses sequester more carbon per unit area than terrestrial forests (Duarte, 2017), and marine vegetation are ostensibly at less risk compared to the increasing reality of forest fires quickly burning through a project's carbon. Even if these claims were technically sound without exception, this narrow focus ignores more fundamental flaws regarding the quality of Blue Carbon credits. Namely, Blue Carbon projects operate in the same carbon market subject to the same buyers and verifiers (e.g., Verra) that have already been widely critiqued for overstating actual climate change mitigation and deforestation prevention (Blake, 2023). Despite this, too many marine scientists are narrowly focused on establishing the science of carbon sequestration potential while overlooking the parallels and overlaps with fraud and mismanagement in forest carbon projects (Bachram, 2004; Carton et al., 2020). By uncritically claiming Blue Carbon accounting research as essential for climate change mitigation, scientists are inflating and misconstruing the holistic impact of these projects.

Moreover, the perceived "high-quality" of Blue Carbon is also debatable as rising seawater temperatures and increased acidification also threaten these ecosystems (Williamson & Gattuso, 2022), and even carbon exported to deeper layers of the ocean may be subject to bacterial remineralization or returned to the atmosphere on timescales shorter than previously assumed (Ricart et al., 2022). The ability to restore ecosystems is complicated and prone to failure, with difficulties increasing as the climate changes. This has necessitated artificial strategies such as the creation of artificial reefs or the use of concrete blocks that leach nutrients

and other chemicals as an anchor for macroalgae to grow on. Likewise, research and restoration efforts are increasingly looking to gene modification to seed heat tolerant variants (Eger et al., 2022). As the complexity of these restoration efforts increase, so do the costs and the potential negative consequences (Williamson & Gattuso, 2022). Therefore, the narrative that Blue Carbon projects are win-win and higher-quality than land-based projects is misleading. Instead, the uncertainty regarding how much carbon is actually sequestered means that companies purchasing Blue Carbon credits may be able to continue polluting at a discount.

In contrast to Indigenous engineering practices that refined eco-mimicry (Winter et al., 2020) over hundreds of years (e.g., multi-trophic fishpond aquaculture that feed local communities), the goals of Blue Carbon geoengineering at the scales required for globally significant carbon drawdown represent a massive and untested intervention. In fact, they often require massive preparatory interventions simply to create and maintain the appropriate conditions for the primary intervention. For example, proposals for open ocean afforestation of kelp would first require controversial and scientifically-fraught attempts at iron fertilization. This is because kelp require concentrations of iron above 20 nanomoles per liter, which is 1000 times greater than typical open ocean concentrations (Paine et al., 2023b). The myriad difficulties in implementing the geoengineering feat itself and tracing the fate of sequestered carbon (Hurd et al., 2022) remain significant. Moreover, the resources spent on preparatory interventions, as well as monitoring, verification, and reporting (MRV), ultimately distract from and do not advance actual climate change mitigation or social-ecological restoration.

Invasive Ecology of Blue Carbon Interventions

Beyond the complexities of implementing and accounting Blue Carbon projects, the ecological consequences of the supposedly "desired" intervention are also concerning. First, the incentive to focus on fast growing monocultures shifts complex ecosystems into simple and vulnerable cash crops (Campbell et al., 2019)—a phenomenon with extensive terrestrial parallels. On top of this, nearshore macroalgae grown for the explicit purpose of export and deep sea burial may result in additional negative ecosystem effects (Boyd et al., 2022). In such scenarios, several concerns are related to the invasive characteristics of the nearshore macroalgae themselves, their microbiome, and the attached epifauna, relative to the offshore ecosystems (Bonthond et al., 2021). Relatedly, the invasive macroalgae would also act parasitically in terms of nutrient (nitrogen and phosphorus) uptake. Open ocean waters will typically have lower nutrient concentrations, primarily sustaining phytoplankton with lower nutrient demands than macroalgae (Berger et al., 2023). Therefore, if the invasive macroalgae are able to survive on the open ocean nutrients, they will not only do so at the expense of the native phytoplankton communities, but also impact mesozooplankton through vertical column shading (Wu et al., 2023). These represent fundamental issues with the basic theory of transferring nearshore macroalgae to the open ocean for the purpose of carbon drawdown.

This section also considers a Hawai‘i specific example of how one lauded Blue Carbon ecosystem, the mangrove, has destroyed coastal ecosystems through its invasive growth. This highlights how discussions focusing on the Blue Carbon potential of a given species cannot be generally applied. This is because any actual beneficial ecosystem roles that species may fill in their natural habitat can quickly turn destructive when it is out of balance. Mangroves were introduced to Hawai‘i and currently are the source of issues ranging from excessive

sedimentation, stagnant water flows, and displacement of native species (Möhlenkamp et al., 2018). Hawai‘i is perhaps the only location where concentrated efforts are made to remove mangroves. However, to be clear, Indigenous reciprocal relationships with place (Morishige et al., 2018) can facilitate the balanced integration of so-called invasive species into a thriving social-ecological system (Wehi et al., 2023). Therefore, the critique of these invasive characteristics is more accurately concerned with acts of anthropogenic manipulation (geoengineering) that lack any pilina (intimate reciprocal relationships; Osorio, 2021) thereby leading to social-ecological disruption.

In addition to the invasive ecological aspects of Blue Carbon species, whether through intentional geoengineering or “unintentional” colonial introduction, “native” species can also have negative impacts when opportunistic growth is possible. For this reason, these critiques can also apply to industrial nearshore aquaculture where certain species are allowed or encouraged to outcompete others at large-scales. The complications that this poses are readily apparent based on the consequences of massive kelp farming in China (Hu et al., 2021). While the use of integrated multi-trophic aquaculture to create a better balance in biogeochemical cycles mitigates several consequences, others remain and deserve close inspection. This theme is closely tied to Kanaka ‘Ōiwi ideas of lōkahi or social-ecological balance (McGregor, 2007) and ensuring all species are fulfilling positive roles that allow ecosystems to thrive instead of extracting benefits at the expense of others. Two summarizing points are central here: (1) that uncritically lauded Blue Carbon species can in fact be destructively invasive, and (2) that even a so-called native species can be destructive if it is grown and manipulated at the expense of others.

Indigenous Displacement by Blue Carbon Funding Priorities

The previous sections discussed the inherently colonial system (verification, credits, and unbalanced interventions) characteristic of engagement with the Blue Carbon market, even by ostensibly community or Indigenous-led projects, but it is important to specifically call out the ways non-Indigenous companies are using Blue Carbon and marine CDR strategies to secure disproportionate funding and control Indigenous coastal ecosystems. While Indigenous-led Blue Carbon projects can have significant community value (Herr et al., 2019), especially if they are fully funded and independent of carbon markets and verifiers, they are at risk of being overshadowed and displaced by settler-led operations. One significant driver of this power imbalance is the funding priorities and metrics of settler-colonial governments, including perceptions regarding the "capacity" to manage larger (e.g., greater than U.S. $1 million) projects. As an illustrative example, Running Tide (a Maine, USA-based company) recently raised a record US $54 million for marine CDR (Breighner, 2023), before abruptly shutting down operations in June 2024 (Velev, 2024). Likewise, one operation in Hawai‘i earned U.S. $4.2 million from a single U.S. Department of Energy grant to "develop technologies to deliver deep seawater nutrients to a novel macroalgae production farm concept suitable for deployment in tropical and subtropical deep ocean environments" (ARPA-E, 2017). In contrast, a typical loko i‘a restoration non-profit has to piece together grants up to a thousand times smaller to keep a small operation afloat. For example, the maximum grant request from one popular and long-running Hawai‘i grassroots fund is U.S. $5,000 (Hawai‘i People's Fund, 2023). This disproportionate scale of funding available to non-Indigenous (especially techno-fix and geoengineering oriented) operations is not aligned with decarbonized and decolonized futures.

Indigenous Erasure by Blue Carbon Scientists

It must be emphasized that the Indigenous worldviews and knowledge systems enabling social-ecological stewardship are deeply rooted and cannot be replicated by non-Indigenous people or organizations posing as equity-minded allies. This is not merely a hypothetical concern as settlers continue to position themselves as the experts on Indigenous topics, including Traditional Ecological Knowledges (Jacobs et al., 2025). In Hawai‘i, this has manifested itself as an extension of Asian settler-colonialism where certain biocultural scientists continue to position themselves as experts of Native Hawaiian knowledge and culture, or even obscure their own positionality to deceptively imply that they are Kanaka ‘Ōiwi themselves (Ikehara, 2017). In Blue Carbon spaces, there have been calls for the integration (i.e., assimilation) of Indigenous Knowledges and Values into Blue Carbon projects led by settlers (e.g., in Australia) with little (i.e., ornamental) regard for actual Indigenous Peoples, lands, or sovereignty. Yet, at its core, there is a fundamental problem with the displacement and loss of political rights that Indigenous People constantly face due to settler-colonialism, regardless of whether the settler has "acknowledged the land". Indigenous sovereignty remains a political issue and it does Indigenous Peoples no good for settlers to appropriate as much Indigenous Knowledge and worldviews as possible, claim that they have achieved a deep understanding of biocultural stewardship, and relegate actual Indigenous Peoples as unnecessary or as perpetual informants with no path to restored sovereignty.

These issues are not new or unique and are related to the broader phenomenon of colonial epistemological domination and authority over the inferior Other (Said, [1978] 2003). Yet the historical parallels continue to be ignored, so it must be reiterated that arguments for Indigenous praxis are not to inspire settlers to mold them to their (still) colonial visions. Instead, these

arguments aim to show the fundamental flaws with climate "solutions" that are wedded to existing and ongoing colonial systems. Unless a settler is advocating for a whole hearted refusal of the colonial system and is committed to work with and for Indigenous systems of governance, no amount of appropriating Indigenous epistemologies will erase the colonial core.

AlterNative Futures

While the coloniality of Blue Carbon projects is ultimately counterproductive to holistic social-ecological vitality, these Blue Carbon ecosystems (seagrasses, salt marshes, mangroves, and macroalgae) are still vital to Indigenous social-ecological health (McGregor et al., 2003; Jacobs et al., 2022; Quevedo & Kohsaka, 2024) and do have relevant climate change mitigation roles (Nellemann et al., 2009; Duarte, 2017). Indigenous Peoples (from the community to national and international scales) must have the resources and sovereignty to steward these important ecosystems beyond a narrow focus on Blue Carbon accounting (Townsend et al., 2020; Dawson et al., 2021). Loko iʻa (Native Hawaiian fishpond systems) are discussed here as a model example of how Indigenous aquaculture was, is, and can be a superior alternative to both industrialized aquaculture (in terms of sustainable and multi-trophic productivity) and Blue Carbon projects (in terms of climate change mitigation impact).

However, to understand the value of loko iʻa requires a shift in worldview—their value is not in the profitability of their seafood or any potential Blue Carbon credits. Their value lies in their historical ability to sustainably feed local populations within an integrated system that connected loʻi kalo (taro patches), loko iʻa, and community-managed fisheries (Winter et al., 2018). The development and evolution of these Indigenous resource management systems over hundreds if not thousands of years sustained populations rivaling modern numbers. Yet under

U.S. occupation, Hawai‘i relies on 90% of imports, and even 63% of locally consumed seafood is imported (Geslani et al., 2012). Likewise, while the fish consumed from a loko i‘a certainly do not contribute to carbon sequestration (Mariani et al., 2020) and the limu (macroalgae) grown or harvested will (at most) minimally contribute to Blue Carbon inventories, loko i‘a can still meaningfully contribute to climate change mitigation. Holistically, the restoration of local Indigenous aquaculture can avoid the significant greenhouse gas emissions that would be required during importation. When evaluated on the metrics that truly matter (sustainable social-ecological abundance), loko i‘a are clearly superior to narrow profit-oriented schemes.

Currently, over 100 kia‘i loko (fishpond stewards, guardians) are restoring and caring for at least 60 sites through the Hui Mālama Loko I‘a network (Kua‘āina Ulu ‘Auamo, 2021). Through decades of annual gatherings and collective work, kia‘i loko are centering, sharing, and evolving Indigenous science, monitoring, and aquaculture methodologies for the benefit of local Indigenous communities. Kilo ‘āina (rigorous environmental observation) is used to develop pilina (intimate relationships) and ‘ike (knowledge, understanding, insights) of the fishpond and surroundings. Many loko i‘a host educational activities with ‘ōlelo Hawai‘i immersion schools, thereby contributing to the next generation of kia‘i loko who are deeply rooted in the language of the ‘āina. Loko i‘a become community hubs through these relationships with local schools, as well as volunteer work days and an improvement of local seawater quality and aquaculture productivity (Kua‘āina Ulu ‘Auamo, 2021). Through this communal and relational work, loko i‘a are a distinctly Indigenous form of aquaculture that in reality is far broader in scope and impact.

It is also worth noting that not all kia‘i loko or others helping in the restoration process are Kanaka ‘Ōiwi. However, when these non-Indigenous people are clear about their positionality and participate in rebuilding Indigenous systems that are led by and for Indigenous

communities, they are welcome allies. Therefore, even non-ʻŌiwi kamaʻāina (local, familiar, child of the land) children are being raised in an Indigenous education system that is firmly led by ʻŌiwi people and epistemologies but makes room for local allies. It should be clear that these supportive and integrated roles are critically distinct from cases of non-ʻŌiwi asserting themselves as experts and decision-makers over Kānaka ʻŌiwi and ʻāina Hawaiʻi. In this way, the broader sovereignty and cultural renaissance movements that loko iʻa restoration is a part of are also a strong model for what Indigenous resurgence can achieve, even while operating within a settler-state.

The value systems underlying loko iʻa will have corollaries with Indigenous stewardship practices elsewhere, and can be a model for those seeking to strengthen Indigenous aquaculture while remaining rooted in their own place-based context. Loko iʻa show how deep knowledge of and relationships to the land and waters must be central to make striving for social-ecological balance possible. While this is not a straightforward task, a focus on feeding local and Indigenous communities (Andrade et al., 2022), community-wide engagement (Kamelamela et al., 2022), ritual (Kealiikanakaoleohaililani et al., 2018), a deep history of generational care (Liliʻuokalani, 1897), and a long view of generational perpetuation based in Indigenous ecological law (Kanahele-Mossman & Karides, 2021) offers critically different worldviews (Nuʻuhiwa, 2019). They also ultimately offer critically different outcomes of holistic well-being (McGregor et al., 2003) when compared to the industrial model, no matter how many precautions or corrections are made in pursuit of equity. By definition, and as demonstrated by the preceding critiques, industrial or settler-colonial operations perpetuate extractive relationships at the expense of Indigenous Peoples and lands and must be abandoned—they cannot be reformed—in favor of Indigenous-led governance.

Instead, funding for colonial Blue Carbon projects should be diverted to Indigenous aquaculture as a practical alternative to climate coloniality. Indigenous aquaculture and coastal cultivation practices have persisted and are being revitalized, yet the coloniality of funding priorities and requirements continues to be a major limitation to further restoration of sovereign social-ecological systems. Since Blue Carbon and other ecosystem services should be considered a co-benefit of Indigenous stewardship and restoration, ecosystem services monitoring, reporting, and verification (MRV) should not be a requirement to receive funding.

Conclusion

This chapter highlighted five key aspects of Blue Carbon coloniality: (1) "Extractive Benefits of Blue Carbon Verification", (2) "Inflated and Uncertain Value of Blue Carbon Credits", (3) "Invasive Ecology of Blue Carbon Interventions", (4) "Indigenous Displacement by Blue Carbon Funding Priorities", and (5) "Indigenous Erasure by Blue Carbon Scientists". From this, it is clear that the fundamental coloniality of Blue Carbon credits and the larger carbon market makes them false climate solutions. They instead counterproductively re-entrench the systems of extractive capitalism, corporate status-quo reproduction, ecological degradation, and settler-colonial usurpation of Indigenous sovereignty that are at the root of the climate crisis. Thankfully, an alternative, practical, and already in progress pathway is readily available. Ultimately, the restoration of coastal Indigenous sovereignty should be considered a more truly effective climate change mitigation strategy, and therefore, all funding allocated for Blue Carbon and marine CDR projects should be diverted to Indigenous coastal stewardship. This recommendation is realizable in the short-term and is not contingent on a full revolutionary upheaval of colonial capitalism. However, the global restoration of Indigenous sovereignty and

social-ecological systems does remain a necessary long-term vision to fully confront climate coloniality.

My final note is to recall the previously cited ʻōlelo noʻeau on breaking down resistance, in combination with one more traditional proverb: "Nahā ka mākāhā, lele ka ʻupena" (When the [fishpond] sluice gate breaks, the fishnets are lowered) (Pukui, 1983, ʻŌlelo Noʻeau 2088). From this reflection, I offer a newly derived ʻōlelo noʻeau that encapsulates the essence of this chapter:

"Nahā ka pali paʻa, lele ka ʻāina"

(When the solid cliff [of climate coloniality] breaks, life-sustaining lands and waters spring forth)

"Pīpī holo kaʻao" (It is sprinkled, the tale has fled) (Pukui, 1983, ʻŌlelo Noʻeau 2658)

Summary: Insights for Social-Ecology Beyond Blue Carbon

The primary outcomes of this dissertation provide insights into the mechanisms controlling the variability of macroalgal dissolved organic carbon (DOC) and fluorescence dynamics and their value to improved understanding and stewardship of social-ecology beyond a narrow-fixation on Blue Carbon credit accounting. Chapter 1 outlines the basis for this framework—namely the need for all scientists (with a focus here on geo- and environmental scientists) to rigorously consider how their research perpetuates or confronts coloniality, especially climate coloniality. Without understanding our research standpoints and research methodologies, scientists cannot clearly see how their research—however well intentioned—may be contributing to the environmental, climate, and planetary crises that their research ostensibly aims to address. A so-called neutral stance abdicates scientific and ethical responsibilities in the profession. This dissertation itself is a testament to the critical differences this (re-)framing allows as a so-called neutral stance would uncritically assume the validity of Blue Carbon as a climate change mitigation strategy with only technical challenges surrounding monitoring, reporting, and verification. By critically assessing the climate coloniality of this framework, it is clear that the value in studying macroalgal DOC is not in determining Blue Carbon credits but in greater understanding of the complexities of biogeochemistry and social-ecology.

The complex variability of macroalgal DOC dynamics shown in Chapters 2–5 highlights the need for year-round monitoring of macroalgal ecosystems by Indigenous stewards. Where this fundamental right is already being exercised, these results may guide monitoring and cultivation practices toward greater attention to seasonal variations linked to stress and decay conditions. By monitoring macroalgal ecosystems year-round, Indigenous stewards may be able to assess and anticipate periods of acute environmental changes as well as natural decay periods,

bleaching, or heatwaves that could stimulate enhanced macroalgal initial and recalcitrant DOC production. Indigenous stewardship of macroalgal health, including DOC production as an ecophysiological stress response, remains critical for broader social-ecological health. Toward that end, the following integrated conclusions may provide insights (to be adapted based on their respective geographical and cultural contexts) for Indigenous stewards monitoring macroalgal beds on the following relevant topics:

Intra-annual variability

1) Chapter 2 showed that *Saccharina japonica* var. *religiosa* DOC release rates vary throughout the year, even when nutrients are sufficient, and should be closely and frequently monitored for their ecological impacts;
2) Chapter 2 showed that the autumn "late decay" period may be overlooked because of lower kelp biomass and no growth, yet even DOC release rates factoring in biomass (mg C $\cdot$ ind^{-1} $\cdot$ d^{-1}) were seasonally higher in autumn compared to summer, and both early autumn and late autumn were comparable to the bi-seasonal peak in early summer;
3) Chapter 4 showed substantial seasonal differences in DOC and fluorescence production for other macroalgae (e.g., *Mazzaella japonica*: higher in winter than autumn; *Ulva australis*: higher in spring than winter and autumn), yet these differences were minor compared to the impact of bleaching and heatwave stress;

Species variability

4) Chapter 4 showed substantial differences in recalcitrant DOC proportions between species (e.g., within autumn results *Sargassum confusum* [36%] and *Sargassum*

thunbergii [49%] were approximately twice as recalcitrant as to for *U. australis*, *Gelidium elegans*, and *M. japonica* [19%–25%])

5) Chapter 4 showed substantial differences in DOC and fluorescence production between species (e.g., *U. australis* was about four times higher than *S. japonica* var. *religiosa* in winter), yet these differences were less than the typically order of magnitude impact of bleaching and heatwave stress;
6) Chapter 4 showed species specific responses to stress, notably that heatwave stress enhanced initial and recalcitrant DOC production rates by an order of magnitude or more in *Neodilesea yendoana* and *S. japonica* var. *religiosa* but had no effect or a dampening effect (relative to spring results) in *U. australis*;

Individual variability, decoupling from biomass, and impact of stress

7) Chapter 2 showed that *S. japonica* var. *religiosa* DOC release rates were highly variable between individual kelp regardless of biomass, and likely related to individual biological stress conditions;
8) Chapter 2 showed that dead *S. japonica* var. *religiosa* had an order of magnitude higher DOC release rates in the short-term followed by no release or net-consumption of DOC;
9) Chapter 4 showed that bleached tissue in *U. australis* and *M. japonica* enhanced initial and recalcitrant DOC production rates by several times;
10) Chapter 4 showed that summer 2023 heatwave stress enhanced initial and recalcitrant DOC production rates by an order of magnitude or more in *N. yendoana* and *S. japonica* var. *religiosa* but had no effect or a dampening effect (relative to spring results) in *U. australis*;

Role of in situ temperature and salinity

11) Chapter 2 showed that *S. japonica* var. *religiosa* DOC release did not vary significantly within normal ranges of in situ temperature or salinity;
12) Chapter 4 showed that *S. japonica* var. *religiosa* DOC release was enhanced by an order of magnitude during the 2023 summer heatwave (30 °C, +5 °C above 2020–2022 baseline) relative to other seasons in 2023 as well as to 2020–2022 data;

Role of irradiance

13) Chapter 2 showed that *S. japonica* var. *religiosa* DOC release only required low levels of light, with no significant differences in DOC release rates between irradiance levels from 200 (representative of submerged dense self-shading) to 1500 (representative of periodic direct exposure to sunny weather) μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1};

Microbial provisioning

14) Chapter 2 showed significantly higher *S. japonica* var. *religiosa* DOC release rates during the autumn "late decay" period and during initial kelp death, followed by net consumption of DOC after kelp death indicating the potential for significant microbial activity and deoxygenation in more stagnant areas;
15) Chapter 3 showed that *S. japonica* var. *religiosa* directly produced both protein-like ("peak T") and humic-like fluorescence ("peak A") and that concurrently enhanced humic-like fluorescence ("peak C" and "peak M") was likely microbial in origin;
16) Chapter 3 showed that even after DOC concentrations were degraded, humic-like fluorescence continued to be enhanced;

Blue Carbon contributions

17) Chapter 3 showed that recalcitrant DOC proportions from *S. japonica* var. *religiosa* were relatively low year-round (10–20%) indicating that kelp-derived DOC contributes more to heterotrophic bacteria than it does to global carbon sequestration;
18) Chapter 3 showed that both initial and effective recalcitrant DOC production rates from *S. japonica* var. *religiosa* were highest in early spring, early autumn, and late autumn;
19) Chapter 5 showed significant proportionality between fluorescence peak intensities and DOC concentrations from macroalgal incubations and bioavailability experiments, which could tentatively predict in situ local contributions but would not be appropriate to quantify Blue Carbon credits;
20) Chapter 6 reviewed the negative effects of industrial-scale and colonial Blue Carbon projects and emphasized that Blue Carbon funding should be re-directed to Indigenous Peoples and governance of balanced social-ecological systems;
21) Chapters 2–6 showed that monitoring macroalgal DOC dynamics is primarily relevant for managing its ecological implications—ecosystem services such as Blue Carbon sequestration should be considered co-benefits of holistic Indigenous social-ecological stewardship that is fully-funded without the need for accounting.

Conclusion

The original goal of this dissertation was to assess the fundamental science of macroalgal dissolved organic carbon (DOC) dynamics in the context of Blue Carbon as a proposed climate change mitigation strategy. Articulating the research standpoint and methodology of this dissertation highlighted the need to consider the broader impacts in the contexts of climate coloniality and environmental justice. The empirical results showed multiple interactive scales of macroalgal DOC variability—particularly in terms of seasonality, senescence and death responses, and heatwave and bleached tissue stress responses, combined with interactive effects of species-specific responses. These results highlighted the overlooked importance of passive DOC leakage under stress. More broadly, they indicate the need for long-term and place-based studies and stewardship in order to understand highly variable ecophysiological dynamics. There is potential for fluorescence peak intensities to predict macroalgal-derived DOC concentrations in situ, yet likely requiring resource intensive place-based correlation models (as cumulatively developed in this dissertation across the four empirical studies) and not sufficiently precise to be used for Blue Carbon credits. Nevertheless, the intrinsic coloniality of the carbon market and Blue Carbon credits incentives means that even if technical barriers to quantifying macroalgal Blue Carbon can be overcome, Blue Carbon credit schemes remain fundamentally flawed as a climate change mitigation strategy. Therefore, the primary message of this dissertation is that Blue Carbon science should prioritize fundamental science that increases knowledge useful for sovereign Indigenous social-ecological monitoring and restoration. A narrow focus on quantifying carbon budgets to verify carbon credits perpetuates colonial systems and must be rejected.

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