Seasonal variability of kelp dissolved organic carbon release driven by decay not growth: a key relationship for Indigenous stewards to monitor

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1   Seasonal variability of kelp dissolved organic carbon release driven by decay not growth: a key

2   relationship for Indigenous stewards to monitor[1]

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14   Running title: Seasonal kelp DOC release and decay

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17   *Abstract*

18   Macroalgae are foundational to the health of many Indigenous social-ecological systems,

19   and their production of dissolved organic carbon (DOC) serves various biogeochemical roles.

20   Improved understanding of seasonal variations in DOC release as an ecophysiological response

21   could therefore help Indigenous stewards balance these implications. However, multi-year

22   seasonal studies of macroalgal DOC release are few and the underlying roles of passive and

23   active DOC diffusion need clarifying. This study focuses on the kelp *Saccharina japonica* var.

24   *religiosa* (class Phaeophyceae) from Oshoro Bay, Ainu Mosir (Hokkaido). The conclusions are

25   supported by three years (2020–2022) of data, including 1091 DOC samples from 16 incubation

26   experiments (t = 4–9 days) comparing individual kelp (n = 88) to in situ seawater control tanks

27   (n = 31) under different photosynthetically active radiation (PAR) treatments (200, 400, 1200, or

28   1500 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}). Differences in PAR, dry weight biomass, sea surface

29   temperature, or salinity could not explain DOC release rate variability, which was high between

30   individual kelp. Instead, there were significant intra-annual differences, with mean DOC release

31   rates (mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}) ($\pm$ standard error between n kelp) higher (p < 0.05) during the

32   autumn "late decay" period (0.82 $\pm$ 0.12, n = 27) compared to the winter "early growth" period

33   (0.20 $\pm$ 0.028, n = 10) and summer "early decay" period (0.34 $\pm$ 0.066, n = 24). Monitoring this

34   relationship between seasonal decay and macroalgal DOC release may therefore help inform

35   Indigenous stewardship strategies.

36   **Key index words**: Blue Carbon; dissolved organic carbon; Indigenous methodologies; kelp;

37   light; macroalgae; seasonal variability

38   **Abbreviations:** DOC, dissolved organic carbon; PAR, photosynthetically active radiation

Introduction

40   The primary objective of this study is to provide insights into the mechanisms controlling

41   seasonal macroalgal dissolved organic carbon (DOC) release variability to help Indigenous

42   coastal stewards anticipate variable local DOC accumulation and plan for ecological

43   implications. Specifically, macroalgal DOC release is an ecophysiological response (Hurd et al.,

44   2014) and serves many biogeochemical roles that can impact microbial activity, oxygen

45   concentrations, pH values, or Blue Carbon sequestration (Carlson and Carlson, 1984; Wada and

46   Hama, 2013; Carlson and Hansell, 2015; Edworthy et al., 2023). Understanding trends in

47   macroalgal DOC release may therefore be useful to Indigenous stewards when considering

48   selective harvesting strategies or adjusting engineering controls. For example, Indigenous

49   integrated multi-trophic aquaculture such as loko iʻa (fishponds that integrate seaweed

50   cultivation) in Hawaiʻi are engineered to adjust water exchange (Keala et al., 2007) within the

51   context of broader systems of social-ecological resource governance (Winter et al., 2018).

52   Therefore, monitoring the relationship between macroalgal DOC release and factors such as

53   environmental parameters or seasonal growth stage may be one relevant metric for decision

54   making.

55   The orientation of this macroalgal ecophysiology and biogeochemistry experiment

56   toward empowering sovereign Indigenous seaweed cultivation is based on the lead author's

57   research methodology (Carlson, 2024) as a diasporic Kanaka ʻŌiwi (Native Hawaiian) in Ainu

58   Mosir (Hokkaido) and is therefore an intrinsic part of this research. This application is consistent

59   with the broader obligations of geoscience to advance decolonization (i.e., Black and Indigenous

60   sovereign liberation) (Yusoff, 2018; Liboiron, 2021; Sultana, 2022; Carlson, 2024). This

61   discussion is also critically relevant to this field of research because Indigenous coastal

62   stewardship and biocultural restoration are essential for social-ecological health (Morishige et

63   al., 2018; Bennet et al., 2021; Jacobs et al., 2022). To be clear, this also applies to Ainu People

64   throughout Ainu Mosir (Grunow et al., 2019; Ishihara, 2020; Uzawa, 2020), inclusive of this

65   study's sampling location of Oshoro Bay. However, Hokkaido University's Oshoro Marine

66   Biological Station currently manages access to the sampling location and there are no established

67   mechanisms for Indigenous community peer-review, consent, or community-researcher

68   partnerships as exist elsewhere for geoscience research (Liboiron et al., 2018; Alegado et al.,

69   2023).

70   Since this study is focused on macroalgal DOC release as an ecophysiological

71   mechanism (and how these insights might be relevant to Indigenous monitoring and

72   stewardship), Indigenous Knowledge of kelp is not the subject of investigation and is not

73   discussed here in detail. However, it is important to briefly comment on the cultural relevance of

74   kelp to Ainu People. First, the historical cultivation of kelp by Ainu People is not disputed

75   (Kawai et al., 2012). Moreover, the Japanese word konbu derives from the (southern regional)

76   Ainu word kompu, giving some indication of its prominent societal role. Currently, kelp

77   continues to be culturally relevant, for example, in cuisine such as kompusito (Kaminaga, 2018).

78   While settler-colonialism continues to disrupt modern Ainu kelp cultivation from being practiced

79   at larger scales, Ainu People and culture persist. Therefore, Ainu People interested in kelp

80   cultivation may find these results on the seasonal variations in macroalgal DOC release relevant

81   to current or future stewardship and harvesting practices.

82   In terms of biogeochemical knowledge gaps, the scope of this study addresses the

83   scarcity of multi-year seasonal data on macroalgal DOC release (e.g., Abdullah and Fredriksen,

84   2004; Wada et al., 2007; Paine et al., 2023a) as well as conflicting experimental evidence

85   regarding the links between macroalgal DOC release and active photosynthetic processes

86   compared to passive leakage processes related to biological stress (e.g., Weigel and Pfister,

87   2021; Paine et al., 2021). Abdullah and Fredriksen (2004) commented that exudation was high

88   during high production (March and June) although the difference was not significant. The

89   seasonal trend in Paine et al. (2023a) was that DOC release was highest in spring with

90   consecutively decreasing values in summer, fall, and winter. However, this trend was not

91   attributable to biomass and instead was driven by nitrogen limitation (i.e., the ratio of carbon to

92   nitrogen in the tissue as well as NO_3^- availability in the seawater). The seasonal trend in Wada et

93   al. (2007) was that DOC release was highest during growth (April and May), lower in fall

94   (October) and winter (December), but lowest in late summer (August). The assumption given

95   was that DOC release was associated with primary production, not biomass, although the

96   significantly lower August values were not explained. Based on these limited data, contrasting

97   trends, and differing drivers, there is a need for more long-term seasonal DOC release studies

98   with sufficient sample sizes to gain insights into the underlying mechanisms driving variations.

99   While there is clear evidence that a primary driver of seasonal DOC release variability is

100 nitrogen limitations (Paine et al., 2023a), previous and concurrent data analyzed by our

101 laboratory indicates that *S. japonica* var. *religiosa* C:N ratios are typically between 8–11

102 (maximum of 13) at Oshoro Bay, without significant seasonal differences (Okazaki,

103 unpublished; Nakanishi, unpublished; Togawa, unpublished). For context, a C:N ratio less than

104 10 generally indicates nitrogen sufficiency and above 20 indicates nitrogen limitation (Hurd et

105 al., 2014). The global mean molar ratio of seaweed C:N is 20 based on 495 species (Sheppard et

106 al., 2023). Given this, we instead test the hypothesis that, without nitrogen limitations, seasonal

107 DOC release varies according to in situ growth and decay conditions. To do so, this study

108   assesses the impact of variable photosynthetically active radiation (PAR), correlations between

109   DOC release and biomass, and tests for significant differences intra-annually between winter

110   "early growth", spring "late growth", summer "early decay", and autumn "late decay" life cycle-

111   based seasonal stages.

112   Therefore, 16 sampling events and incubation experiments were conducted seasonally (4

113   to 6 times per year) over three years (2020–2022) to characterize DOC release from the kelp

114   *Saccharina japonica* var. *religiosa* (class Phaeophyceae), collected from Oshoro Bay. Clarifying

115   these mechanistic relationships may be particularly useful to Indigenous coastal stewards. For

116   example, if macroalgal DOC release were strongly controlled by photosynthetic processes and

117   primary production, Indigenous stewards could use biomass growth as an appropriate proxy. On

118   the other hand, if DOC release were strongly influenced by passive leakage, signs of macroalgal

119   biological stress or environmental change may be more relevant proxies.

120   While the precise cellular mechanisms controlling DOC release are outside the scope of

121   this study, previous research has highlighted the importance of the "overflow hypothesis" where

122   photosynthesis outpaces growth requirements (Nagata, 2000), as well as DOC release being

123   enhanced by both nitrogen limitations (Mizuta et al., 1994; Weigel and Pfister, 2021; Paine et al.,

124   2023a) and iron limitations (Paine et al., 2023b). Moreover, while the seasonality of macroalgal

125   DOC release has been established for decades (Mann, 1973; Hatcher et al., 1977; Johnston et al.,

126   1977), the lack of recent empirical data has resulted in synthesis papers making annualized

127   generalizations based on few or no seasonal data (e.g., Barrón et al., 2014). Such generalizations

128   are typically based on the disputed assumption that DOC release is proportional to primary

129   production or biomass (Khailov and Burlakova, 1969; Sieburth, 1969). Estimates based on

130   limited data therefore critically overlook essential seasonal, environmental, or biological

131   variations related to passive exudation.

132   With this in mind, this study aims to improve understanding of the variability of kelp

133   DOC release, with a particular focus on the effects of PAR and other environmental parameters,

134   in addition to seasonal variability related to growth stage. While the results of this study on

135   macroalgal DOC release mechanisms will have the greatest place-based relevance to Oshoro Bay

136   and Ainu Mosir, they may also provide useful insights to Indigenous Peoples globally. However,

137   it must be emphasized that any insights discussed here cannot take precedence over place-based

138   Indigenous Knowledge of seaweed cultivation, which has persisted for millennia and continues

139   to evolve (Abbott and Williamson, 1974; Kobluk et al., 2021; Reid et al., 2022). Nevertheless,

140   settler-colonialism has disrupted Indigenous Knowledge and systems of governance in many

141   places (Whyte, 2018). Therefore, general insights from this study may be relevant to the

142   processes of rebuilding more nuanced place-based stewardship practices globally.

143   *Methods*

144   **Field site**

145   Hokkaido University's Oshoro Marine Biological Station was originally founded in 1908

146   as an affiliated facility of Tohoku Imperial University. Oshoro Bay is on the west coast of the

147   Shakotan Peninsula, largely protected from wind and waves due to rocky cliffs, with an inlet

148   facing northwest. Tidal level differences on the Sea of Japan coast are relatively small, creating

149   good habitat for marine flora and fauna as well as facilitating collection and measurement

150   activities. Reported flora and fauna on the shore include 208 species of marine algae, 389 species

151   of invertebrates, 85 species of fishes, and 291 species of plankton (Motoda, 1971; Motoda et al.,

152   1987; Yotsukura, 2021).

153   *S. japonica* var. *religiosa* is one of the dominant autotrophs within a shallow, sub-tidal

154   ecosystem along the southwestern portion of Oshoro Bay. The surveyed area is delimited by the

155   temperature and salinity sampling points shown in Figure 1. *S. japonica* var. *religiosa* is an

156   annual prostrate kelp with cyclical biomass at a minimum in winter, growth up to two meters in

157   length from spring to summer, and declining biomass due to grazing, erosion, and natural

158   senescence in autumn (Abe et al., 1985). This kelp forms dense beds in Oshoro Bay that are

159   mainly monospecific, with some *Costaria costata* and *Undaria pinnatifida* interspersed, and

160   cover approximately 500 m^2 along the northeastern shelf edge as well as 1000 m^2 in the

161   southeastern portion of the surveyed area. Within this coastal shelf area, an additional 3000 m^2

162   features mixed macroalgal beds and other marine flora and fauna (Figure 1). Other smaller

163   macroalgae commonly observed during this study include green (e.g., *Ulva sp.*), red (e.g.,

164   *Mazaella japonica* and *Neodilsea yendoana*), and brown (e.g., *Sargassum sp.*) macroalgae.

165   Several other species of macroalgae have been reported at Oshoro Bay in recent (Hoshikawa et

166   al., 2018) and older literature (Matsuyama, 1983; Kawai, 1997).

167   **Field sampling**

168   Field surveys to collect whole kelp individuals for ex situ incubation were completed 16

169   times (January, early March, late March, June, August, and October 2020; January, March,

170   April, July, October, and November 2021; and May, July, October, and November 2022). In situ

171   sea surface temperature and salinity field probe measurements were taken at eight locations

172   within the macroalgal bed area and one reference location within the bay (Figure 1). Sampling

173   was seasonal to account for various growth stages and biological conditions. The kelp samples

174   were detached from the underlying rocky substrate (typical depth of 30–50 cm) along the

175   northeastern shelf edge (Figure 1) where tidal motion was active but moderate. Care was taken to

176   minimize damage to the holdfast and kelp samples were transported in a polyethylene bag with

177   in situ seawater to our laboratory on the Hokkaido University campus in Sapporo within a few

178   hours of collection (42 km drive). Up to six individual kelp were incubated in separate

179   incubation tanks per sampling event.

180   Acid-washed 18-L polyethylene tanks were filled with pre-screened (100 μm mesh)

181   reference seawater for the incubation tanks. This seawater was collected from a pier on the

182   northeast side of the bay about 100 m from the kelp bed sampling location (Figure 1) for all

183   sampling events except August 2020, October 2020, and July 2022, when seawater was collected

184   in the bay by a small fishing boat (Figure 1).

185   **Incubation experiment**

186   After returning to our laboratory in Sapporo, kelp samples were gently rinsed with

187   seawater from the reference point outside the macroalgal bed area. Rinsing was done to reduce

188   the effect of DOC released during transportation and to reduce epibiota such as attached

189   microalgae or grazers, while minimizing disruptions to the kelp microbiome. The kelp samples

190   were then placed in clear polystyrene tanks filled with approximately three liters of the same

191   reference seawater, fully submerging the kelp while leaving approximately two liters of

192   headspace. The top of each tank was covered in a plastic wrap. Tank seawater volumes were

193   confirmed by weight. Kelp and control tanks of reference seawater were incubated at the in situ

194   sea surface temperature for 4–9 days ($t = 9$ days in January 2020, $t = 7$ days from early March

195   2020 through January 2021, $t = 5$ days from March 2021 through July 2021, and $t = 4$ days from

196   October 2021 through November 2022).

197   The multi-day incubation period was chosen to assess the linearity of kelp DOC release

198   rates. Non-linear kelp DOC release may be an indication of an adverse incubation environment,

199   such as the development of anoxia or insufficient nutrients. Concerns regarding decreasing

200   nitrogen concentrations are particularly relevant given that previous studies indicate DOC release

201   should increase with nitrogen limitations (Weigel and Pfister, 2021; Paine et al., 2023a).

202   Likewise, live photosynthesizing tissue and dead tissue are expected to release DOC at

203   significantly different rates (Paine et al., 2021), and a sufficiently long incubation may be able to

204   clearly differentiate between the two phases.

205   The potential effect of irradiance on DOC release rates was tested in each of the sampling

206   events ($n = 16$ events) by treating half of the incubated kelp to a lower irradiance treatment and

207   half to a higher irradiance treatment. The lower irradiance exposure was 200 µmol photons $\cdot$ m^{-2}

208    $\cdot$ s^{-1} from artificial LED sources for all sampling events. The higher irradiance exposures varied

209   and were 400 (incubation experiments from January 2020 to July 2021) or 1200 (incubation

210   experiments from May 2022 through November 2022) µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} from artificial

211   LED. The artificial cool white LED light sources were controlled by a light/dark timer set

212   according to the actual daylight hours (photoperiod). When testing the effect of natural

213   irradiance, the higher (natural) irradiance treatment levels were 2500 (October 2021) and 1500

214   (November 2021) µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}.

215   Because the *S. japonica* var. *religiosa* bed was shallow (less than 50 cm depth), dense,

216   and subject to tidal motion, in situ sub-surface irradiance was variable and certain in situ kelp

217   would be periodically exposed to direct irradiance. Therefore, the 200 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}

218   irradiance was representative of kelp subject to dense community shading, 400 µmol photons $\cdot$

219   m^{-2} $\cdot$ s^{-1} was representative of submerged kelp not subject to community shading, and 1200

220   µmol photons m^{-2} s^{-1} was an upper limit representative of kelp periodically exposed by tidal

221   motions to direct irradiance on a sunny day. Maximum above water irradiance on sunny summer

222   days was approximately 2500 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}.

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

224   tier. These control samples assessed the potential for DOC contamination from the incubator

225   environment or during the sampling process, as well as any detectable DOC trends due to

226   plankton activity. The incubation experiments lasted between 4–9 days to assess potential

227   impacts from artificial stress responses. Incubated control seawater DOC concentrations showed

228   no evidence of accumulation, despite some fluctuations within the incubation periods (Figure 2e,

229   Figure S1). The mean coefficients of variation (± SE) over the course of the incubation

230   experiments were 5.2% ± 0.96% ($n = 16$) for DOC concentrations in control tanks treated to

231   lower irradiance, 4.3% ± 0.53% ($n = 15$) for higher irradiance treatments, and 4.8% ± 0.56% ($n =$

232   31) overall. These fluctuations were likely due to a combination of minor spatial heterogeneities

233   within the incubated control seawater and phytoplankton and bacterial DOC dynamics. Mean

234   control DOC concentrations were used as the baseline to determine kelp-derived DOC inventory

235   accumulation.

236   Seawater samples from the incubation tanks were taken with a 25-mL syringe and

237   immediately filtered through a pre-combusted (450 °C for 5 hours) 0.7 µm Whatman glass-fiber

238   filter (GF/F). The syringes were rinsed with 4-mL seawater samples three times before taking a

239   50-mL sample. The decreasing volume in the tank was accounted for to normalize the increasing

240   DOC concentrations throughout the incubation period, and the final seawater volume was

241   confirmed by weight at the end of the incubation. The seawater samples were frozen at −30 °C in

242   60-mL amber borosilicate glass sample bottles until analysis. The bottles were cleaned before

243   use, first in a detergent bath, followed by a 1.2 M HCl bath, then pre-combusted at 550 °C for 5

244   hours.

245   At the end of the incubation, kelp wet weight was measured by weighing the incubation

246   tank before and after removing the kelp sample, in addition to confirming the wet weight on

247   aluminum foil before drying. The removed kelp samples were then dried at 60 °C on aluminum

248   foil until a constant dry weight was achieved, typically after 4 to 5 days. DOC release results for

249   each kelp were normalized by their respective dry weight.

250   **DOC analyses**

251   All seawater samples were analyzed for DOC by a total organic carbon analyzer

252   (Shimadzu TOC-5000A or TOC-V) according to the high-temperature combustion method. DOC

253   samples were acidified by adding 100 µL of 2 M HCl to ensure the pH was lower than 3 and that

254   dissolved inorganic carbon (DIC) would be removed after sparging for 10 minutes. Each sample

255   was injected into the combustion column at least 3 times with a coefficient of variation within

256   2%.

257   Potassium hydrogen phthalate was used to make a standard stock solution of 8.3×10^4

258    $\mu mol \cdot L^{-1}$ (1000 ppm) DOC. The standard stock solution was typically diluted to concentrations

259   between 42 and 2.7×10^3 $\mu mol \cdot L^{-1}$ DOC (0.5–32 ppm) to calibrate the analyzer with a five or

260   six point linear regression model (100 µL analytical injections). For higher concentrations,

261   standard stocks up to 3.3×10^4 $\mu mol \cdot L^{-1}$ DOC (400 ppm) were used to calibrate separate five

262   point linear regression models (13 µL analytical injections). In general, the analyzer was initially

263   conditioned with Milli-Q, standard potassium hydrogen phthalate samples, and seawater

264   standards. Subsequently, Milli-Q and standard samples were checked after analyzing five

265   seawater samples. Other methods of ensuring replicability included re-analyzing samples within

266   or between analysis runs. Coefficients of variation greater than 2% or significant deviations

267   between standard sub-samples triggered re-conditioning or maintenance before proceeding. To

268   assess spatial heterogeneity of DOC within the incubation tanks, duplicate ($n = 12$) DOC

269   samples were collected at the end of the November 2021 incubation experiments and triplicate (*n*

270   = 18) DOC samples were collected at the end of the May 2022, July 2022, October 2022, and

271   November 2022 incubation experiments (Figure S2).

272   *Results*

273   **Biomass and environmental parameters**

274   Mean biomass (grams dry weight per individual) of the incubated kelp varied consistent

275   with its annual life cycle (± SE between *n* kelp replicates) (Figure 2a). Inter-annually, while the

276   highest average biomass was recorded in July 2021 (10.8 ± 2.0, *n* = 6), followed by June 2020

277   (7.93 ± 0.48, *n* = 6), then July 2022 (5.95 ± 1.2, *n* = 6), the differences were not significant (one-

278   way ANOVA, *p* > 0.05) despite a four-fold range in individual magnitudes (3.97–17.9) (Figure

279   S1). Average peak biomass can therefore be summarized over the three-year period as 8.2 ± 0.89

280   g DW (*n* = 18). Interannual differences in biomass were also not significant for other periods.

281   In situ sea surface temperature and salinity means represented eight sampling locations

282   within the macroalgal bed area and one reference point within Oshoro Bay for each sampling

283   event (± SE between sampling locations). Sea surface temperature varied from 5.1 ± 0.17 in

284   January 2020 to 23.5 ± 0.17 °C in August 2020 (Figure 2c). Salinity varied from 28.9 ± 0.3 in

285   late March 2020 to 33.71 ± 0.09 in July 2021 (Figure 2d).

286   Mean incubated in situ seawater DOC concentrations (± SE of *n* samples during the given

287   incubation) varied from a low of 66 ± 3.8 µmol · L^{-1} (*n* = 8) in January 2020 to a high of 88 ±

288   0.78 µmol · L^{-1} (*n* = 12) in July 2022. There were no significant paired differences in DOC

289   concentrations between control seawater incubated at lower or higher irradiances (Figure 2e).

290   **Individual kelp DOC release rate variability**

291   Mean kelp DOC release rates (mg C · gram dry weight^{-1} d^{-1}) (± SE between kelp

292   replicates) were calculated as least squares means from linear regressions of elapsed incubation

293   time and the corresponding kelp-derived DOC inventory (mg C $\cdot$ g DW^{-1}). These results and

294   supporting statistical parameters are summarized in Table S1. Kelp DOC release was

295   significantly ($p < 0.05$) linear for all kelp incubations except one kelp in January 2021 and the

296   three dead kelp in October 2021. All kelp samples enhanced the DOC inventory relative to the

297   initial inventory and to the concurrent control inventories (Figure 3, Figure 4, and Figure S1).

298   Mean DOC release rates varied from a low of 0.18 ± 0.035 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1} ($n = 6$) in

299   August 2020 to a high of 1.3 ± 0.26 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1} ($n = 6$) in November 2022 (Figure 3),

300   while the absolute minimum rate was 0.066 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1} for a kelp incubated in August

301   2020 and the absolute maximum rate was 2.4 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1} for a kelp incubated in

302   October 2020 (Table S1). Replicate DOC samples had coefficients of variation (representing

303   spatial heterogeneity of DOC within the incubation tanks) of $2.7\% \pm 1.0\%$ (November 2021, $n =$

304   6), $3.8\% \pm 1.1\%$ (May 2022, $n = 6$), $7.8\% \pm 3.1\%$ (July 2022, $n = 6$), $2.0\% \pm 0.5\%$ (October

305   2022, $n = 6$), and $3.4\% \pm 0.8\%$ (November 2022, $n = 6$) (Figure S2).

306   **Relationship of biomass and environmental parameters with DOC release**

307   A linear regression of biomass (g DW $\cdot$ ind^{-1}) and DOC release rates per individual kelp

308   (mg C $\cdot$ ind^{-1} $\cdot$ d^{-1}) (Figure 5a) was significant ($p = 1.2$ x 10^{-5}) and indicates that biomass

309   explains 21% of the variation in the DOC release rates. However, individual linear regressions

310   between DOC release rates and biomass within each sampling event indicated that only five (late

311   March 2020, March 2021, July 2021, November 2021, and May 2022) of the 16 experiments

312   were significantly linear (Table S2).

313   A linear regression of photoperiod (hours) and biomass-normalized DOC release rates

314   (mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}) was significant ($p = 0.011$), explaining 7.5% of the variation in DOC

315   release rates. The linear relationship was negative, indicating a tendency for kelp treated to

316   longer photoperiods to have lower DOC release rates. There were no statistically significant

317   linear relationships between salinity or sea surface temperature and DOC release rates (Figure 4c

318   and 4d).

319   **Relationship of irradiance with DOC release**

320   Mean (± SE) DOC release rates (mg C · g DW^{-1} · d^{-1}) for each of the four irradiance

321   levels were 0.53 ± 0.084 (200 µmol photons · m^{-2} · s^{-1}, $n = 44$), 0.43 ± 0.10 (400 µmol photons ·

322   m^{-2} · s^{-1}, $n = 26$), 0.65 ± 0.12 (1200 µmol photons · m^{-2} · s^{-1}, $n = 12$), and 0.62 ± 0.095 (1500

323   µmol photons · m^{-2} · s^{-1}, $n = 3$) (Figure 6a). Therefore, there was a slight tendency for higher

324   DOC release rates at higher irradiance exposures, but the differences between groups were not

325   significant and there was no significant ($p = 0.36$) linear relationship between DOC release rate

326   and PAR exposure (Figure 6a). In addition, the mean daily PAR exposure (mol photons m^{-2} s^{-1}),

327   which factors in the seasonally variable photoperiod, did not have a significant ($p = 0.73$) linear

328   relationship with DOC release rate (Figure 6b).

329   Paired comparisons of the experimental effect of irradiance from artificial LED sources

330   between qualitatively lower or higher irradiances (i.e., excluding the October and November

331   2021 results) were also made. Overall, the low irradiance treatment incubations were associated

332   with slightly higher DOC release rates (0.52 ± 0.096, $n = 38$) compared to the DOC release rates

333   (0.50 ± 0.080, $n = 38$) from the higher irradiance treatments. There were also no significant

334   differences ($p < 0.05$, two-tail t-tests) within any of the sampling events comparing mean DOC

335   release rates treated to low or high irradiance levels (Figure 6c).

336   The October 2021 experiment attempted to compare the effect of artificial and natural

337   irradiance exposure (200 and 2000 µmol photons · m^{-2} · s^{-1}), but the kelp ($n = 3$) treated to

338   natural irradiance died and DOC release was non-linear. Specifically, DOC release rates were 1.9

339     $\pm$ 0.43 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1} (n = 3) during the initial incubation period (t = 0–1 d), 88 $\pm$ 25 mg C

340     $\cdot$ g DW^{-1} $\cdot$ d^{-1} (n = 3) in the following period (t = 1–2 d), and −4.7 $\pm$ 3.8 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}

341   (n = 3) in the final period (t = 2–4 d) (Figure 7, Table S1).

342   The effect of natural irradiance (1500 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) was again investigated in

343   the November 2021 experiment, with tissue death avoided (further details provided in the

344   Discussion). There was no significant difference (p = 0.16, two-tail t-test) in DOC release rates

345   between the artificial and natural treatments in that experiment (0.52 $\pm$ 0.060 [n = 3] and 0.62 $\pm$

346   0.096 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1} [n = 3], respectively) (Figure 6c, Figure 7).

347   **Seasonal growth stage and DOC release**

348   To quantitatively test significant intra-annual differences, the aggregated data was

349   separated according to the four boreal seasons (based on equinox dates). In terms of overall

350   biomass trends and peak biomass being reached between June and July (Figure 2a), the four

351   seasonal categories can also be ascribed qualitative "growth stage" labels, as follows: winter

352   (early growth), spring (late growth), summer (early decay), and autumn (late decay). The data

353   was also categorized into eight bi-seasonal periods for additional insights, as follows: early

354   winter (n = 6), late winter (n = 4), early spring (n = 12), late spring (n = 12), early summer (n =

355   18), late summer (n = 6), early autumn (n = 15), and late autumn (n = 12) (Figure 8).

356   A two-way fixed factor analysis of variance (ANOVA) tested the effect of seasonal

357   period and irradiance level (200, 400, 1200, or 1500 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}) on DOC release

358   rates using Type-II sums of squares for an unbalanced design. The statistical results indicated

359   that irradiance was not a significant factor (p = 0.83) while seasonal period was a significant

360   factor (p = 0.0013). Tukey Honest Significant Differences pairwise tests then confirmed the

361   significant differences ($p < 0.05$) were between the autumn "late decay" (0.82 ± 0.12) seasonal

362   period and the winter "early growth" (0.20 ± 0.028, $p = 0.0051$) and summer "early decay" (0.34

363   ± 0.066, $p = 0.0044$) seasonal periods (Figure 8, Figure S1, Appendix S1, Appendix S2).

364   *Discussion*

365   **Linearity of kelp DOC release rates**

366   Regressions of DOC accumulation over the corresponding incubation period for each

367   individual kelp ($n = 85$) were significantly ($p < 0.05$) linear except for one individual experiment

368   ("low light kelp 1") in January 2021. This non-linearity was because the DOC concentrations of

369   the third and fifth samples (76 and 77 $\mu mol \cdot L^{-1}$) were significantly higher than the other

370   samples in that incubation period (68 ± 0.49 $\mu mol \cdot L^{-1}$, $n = 7$). However, they were not

371   considered true outliers given their concentrations were within two standard deviations of the

372   control tank DOC concentrations for the same period (72 ± 1.3 $\mu mol \cdot L^{-1}$, $n = 5$, standard

373   deviation $= 2.8$). In addition, the absolute low mean biomasses in January 2020 (0.45 g DW, $n =$

374   2) and January 2021 (0.45 g DW, $n = 4$), just 4% of the mean peak biomass in July 2021,

375   resulted in highly sensitive fluctuations in the biomass-normalized kelp-derived DOC inventories

376   (mg C $\cdot$ g DW^{-1}). This also explains why biomass-normalized DOC release rates were lower in

377   August 2020 compared to January 2020 and January 2021, despite the actual enhancement of

378   DOC concentration ($\mu mol \cdot L^{-1}$) being less in the winter months.

379   While linear regressions between elapsed incubation time and kelp-derived DOC

380   inventory were significant for all other incubated kelp, visual inspections of the individual curves

381   indicate potential non-linearity due to saturation (Figure S1). For example, "low light kelp 1" in

382   late March 2020 reached a peak of 3.6 mg C $\cdot$ g DW^{-1} at $t = 1.7$ days, decreasing to 2.6 mg C $\cdot$ g

383   DW^{-1} by $t = 6.7$ days. Therefore, while the least squares mean DOC release rate was 0.63 mg C

384 $\cdot$ g DW^{-1} $\cdot$ d^{-1} ($R^2 = 0.68$, $p = 3$ x 10^{-5}), the initial phase of positive accumulation (at $t = 1.7$

385 days) might be better represented as 2.1 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}, while the final DOC inventory (at

386 $t = 6.7$ days) implies an overall rate of 0.39 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}. Therefore, the use of least

387 squares mean DOC release rates in this study is only for relative comparison and is not intended

388 as a predictive tool or an assumption that actual kelp DOC release is linear.

389 However, it should be noted that concentrations above 600 µmol $\cdot$ L^{-1} were routinely

390 achieved without clear saturating effects, including a peak DOC concentration of 2000 µmol $\cdot$

391 L^{-1} achieved by "high light kelp 3" in October 2020 (Figure S1k). Also, when including results

392 from the dead kelp in October 2021, "high light kelp 2" exceeded 25000 µmol $\cdot$ L^{-1} (Figure

393 S1w). Therefore, it is unlikely that the "potentially non-linear" outliers can solely be explained

394 by a saturating effect of high DOC concentrations. Instead, more nuanced studies of the complex

395 interactions of ecophysiology are needed. While the results in this study are simplified to assume

396 linear DOC release rates (based on the majority of results exhibiting statistically significant

397 linear regressions), it is important to keep in mind the reality of complex and non-linear

398 interactions when making any generalizations.

399 **Active exudation: relationship of biomass with DOC release**

400 To explain the variability in DOC release between biological replicates, the potential for

401 biomass to drive DOC release was considered. Normalizing DOC release rates for biomass is

402 standard practice given the expectation that they are strongly linked. In this study, there was a

403 weak linear relationship indicating that biomass explained 21% of the variation in individual

404 DOC release rates (Figure 5a). However, when assessing kelp biomass and DOC release rate

405 results for each sampling event separately, only five of the 16 sampling event data sets

406 demonstrated a significant linear relationship between biomass and DOC release rate (Table S2).

407   This indicates that biomass cannot generally be considered significantly linearly correlated with

408   DOC release rates. Moreover, DOC release rates per individual kelp (mg C · ind^{-1} · d^{-1}) did not

409   increase seasonally with increasing biomass before decreasing as biomass was lost due to

410   grazing and erosion. Instead a second peak in DOC release rates was reached in the autumn

411   (October–November) (Figure 8a and 8b) despite the lower biomass (Figure 2a). These multiple

412   lines of evidence demonstrate that biomass was a weak factor in kelp DOC release.

413   **Active exudation: relationship of irradiance with DOC release**

414   Irradiance levels are considered an explanatory factor on DOC release rate variability.

415   For example, Reed et al. (2015) indicated that sea surface irradiance was the most significant

416   factor contributing to high temporal variation in *Macrocystis pyrifera* DOC release rates. In that

417   study, irradiance accounted for 13% of the DOC release variation, when blade stage, sampling

418   date, epiphyte load, blade C:N, and temperature were included as the other tested factors (Reed

419   et al., 2015). However, there was no significant effect of irradiance in our results, even after

420   extending the initial experimental design to compare irradiance levels of 200 and 1200 μmol

421   photons · m^{-2} · s^{-1} in the 2022 incubation experiments. In addition, the mean daily PAR

422   exposure (mol photons m^{-2} s^{-1}), which factors in the seasonally variable photoperiod, did not

423   have a significant ($p = 0.73$) linear relationship with DOC release rate (Figure 6b). This indicates

424   that the significant linear relationship between photoperiod and DOC release rate is not related to

425   irradiance exposure but to another seasonal variable.

426   Because artificial irradiance is qualitatively different from natural light (e.g., ultraviolet

427   spectrum), it is possible that natural irradiance would induce different DOC release responses.

428   We tested this complication in the October 2021 and November 2021 experiments by comparing

429   three kelp incubated at artificial LED irradiance levels of 200 μmol photons · m^{-2} · s^{-1} and three

430   kelp incubated at natural irradiance levels varying between 1000–2500 µmol photons · m^{-2} · s^{-1}.

431   However, due to kelp death, the October 2021 results were not representative of the effect of

432   natural irradiance. Therefore, only the November 2021 results are discussed in this section on

433   natural irradiance and the October 2021 results will be discussed in the following section on the

434   roles of death and decay.

435   The November 2021 incubation experiment averaged natural irradiance levels of 1500

436   µmol photons · m^{-2} · s^{-1} with no signs of tissue death induced. The difference between

437   November 2021 kelp DOC release rates treated to artificial and natural irradiance was not

438   significant (0.52 ± 0.060 [$n = 3$] and 0.62 ± 0.096 mg C · g DW^{-1} · d^{-1} [$n = 3$], respectively)

439   (Figure 6c). Based on this, the primary use of artificial LED instead of natural irradiance in this

440   study was determined to have not significantly skewed DOC release rates.

441   **Passive exudation: DOC release from decaying and dead kelp**

442   The October 2021 incubation experiment induced tissue death of the three kelp exposed

443   to direct natural irradiance exceeding 2000 µmol photons · m^{-2} · s^{-1} (in contrast to the decaying

444   but not dead kelp exposed to the lower artificial irradiance). This October 2021 ("late decay"

445   period) result was also an indication that tissue death had not unknowingly occurred in samples

446   from other sampling events. This was concluded based on the nearly two orders of magnitude in

447   difference between DOC release from naturally decaying (but otherwise healthy) kelp and dead

448   kelp in October 2021.

449   Specifically, DOC release rates were comparable to previous high results (1.9 ± 0.43 mg

450   C · g DW^{-1} · d^{-1} , $n = 3$) for the initial incubation period ($t = 0$–1 d), unprecedentedly high (88 ±

451   25 mg C · g DW^{-1} · d^{-1} , $n = 3$) in the following period ($t = 1$–2 d), and negative or stable (−4.7 ±

452   3.8 mg C · g DW^{-1} · d^{-1} , $n = 3$) in the final period ($t = 2$–4 d) (Figure 7, Table S1). The

453   extremely high DOC release upon death was more than an order of magnitude higher than the

454   highest individual DOC release rate recorded from live kelp (2.4 mg C · g DW^{-1} · d^{-1}, October

455   2020) (Table S1). For further context, approximately 10 mg C · g DW^{-1} · d^{-1} could be

456   considered a critical threshold indicating potential tissue death as it corresponds to 1% of the dry

457   weight biomass being shed as DOC on a daily basis. This indicates that the kelp were likely still

458   alive in the initial period and the extreme DOC release during the following period was a short-

459   term response upon death. Post-death, some DOC may have continued to be passively exuded

460   but microbial consumption of DOC appears to have been the dominant dynamic.

461   When also considering the lack of a significant difference in DOC release rates treated to

462   natural irradiance in the November 2021 experiment, the high DOC release in the kelp exposed

463   to natural irradiance in October 2021 was determined to be due to tissue death and not

464   representative of the qualitatively different characteristics of natural light. The DOC release rates

465   from the dead kelp ($n = 3$) in October 2021 are therefore presented separately from the primary

466   dataset.

Passive exudation: relationship of salinity and temperature changes with DOC release

468   A previous study at Oshoro Bay associated the drop in seawater salinity observed from

469   April to May 1999 and concurrent seawater temperature increase with severe lesions and thallus

470   bleaching on *S. japonica* var. *religiosa* (Vairappan et al., 2001) and these seasonal fluctuations

471   may also impact DOC release. Elsewhere, the effect of in situ experimental heatwaves on

472   *Caulerpa prolifera* DOC release indicated no significant difference in DOC release rates

473   between temperature treatments in the summer and a significantly lower (negative) DOC flux in

474   the winter (Egea et al., 2023). At Oshoro Bay, sea surface temperatures have historically varied

475   from 5–22 °C (Motoda, 1971; Motoda et al., 1987; Yotsukura, 2021). Therefore, the August

476   2020 temperature (23.5 °C) represents a historical exceedance, but the impact of historically high

477   temperatures on DOC release is not clear from this study. Overall, however, linear regressions of

478   temperature and salinity with DOC release rates in our study were not significant ($p = 0.53$ and p

479    $= 0.57$, respectively).

Comparability of macroalgal DOC release rates

481   A wide range of DOC release rates have been reported for different macroalgae (Paine et

482   al., 2021). Three recent studies with useful comparisons are highlighted here. From these

483   comparisons, we can conclude that the results of our study show some comparability to other

484   studies, are generally on the lower end of reported DOC release rates, and that overall, there are

485   several environmental and biological factors that complicate generalized reviews of macroalgal

486   DOC release rate data.

487   First, a seasonal study on the kelp *Ecklonia cava* in a subtropical bay on the main island

488   of Japan reported mean (± SE) DOC release rates with the minimum value (0.12 ± 0.093 mg C ·

489   g DW^{-1} · d^{-1}) in August 2003 and the maximum (5.8 ± 1.0 mg C · g DW^{-1} · d^{-1}) in April 2004

490   (Wada et al., 2007). Even though the low August values of Wada et al. (2007) are similar to the

491   August results of this study (0.14 ± 0.038 mg C · g DW^{-1} · d^{-1}, $n = 6$; Figure 3 and Table S1),

492   the maximum value was several times that of the highest mean values reported in this study

493   (November 2022, 1.3 ± 0.26 mg C · g DW^{-1} · d^{-1}, $n = 6$; Figure 3 and Table S1), and also higher

494   than the overall maximum individual DOC release rate (October 2020, 2.4 mg C · g DW^{-1} · d^{-1};

495   Figure 3 and Table S1). Another study in subtropical Japan by Watanabe et al. (2020), on the

496   brown macroalgae *Sargassum horneri*, was limited to February and March 2020 during the

497   period of peak primary productivity, and results were comparable (1.5 ± 0.62 in February and 1.8

498   ± 0.62 mg C · g DW^{-1} · d^{-1} in March) to the highest results of this study from the spring "late

499   growth" and autumn "late decay" periods (Figure 8a). Similar to the highest results from Wada et

500   al. (2007) and several times higher than the results for this study, cultured *S. japonica* in a

501   temperate bay in China was reported to release 6.2 (January) and 7.0 (April) mg C · g DW^{-1} ·

502   d^{-1}, despite being the same species as the kelp in this study and of a similar size (0.74 m in

503   January, 1.3 m in April; Gao et al., 2021). Based on the high individual variability seen in these

504   studies, it is not clear if such variability between and within studies can also be attributed to

505   biological stress or are inherent to other local abiotic- and biotic- factors such as physiology,

506   climate, or in situ natural irradiance.

507   **Implications of passive DOC release for Blue Carbon estimates**

508   Quantifying DOC outwelling (i.e., lateral export) from macroalgal habitats remains an

509   important, yet unresolved component of marine carbon sequestration estimates, despite increased

510   interest (Santos et al., 2021). Based on the importance of the autumn "late decay" period (Figure

511   8) and the decoupling from PAR (Figure 6), these results indicate that passive DOC release is as

512   important or more important than active, photosynthetically driven, DOC release. This means

513   that extrapolating Blue Carbon estimates from data that does not account for seasonal variation

514   will be fundamentally flawed.

515   As a specific example, if only one sampling event had been conducted in this study, the

516   percent difference between that event's mean DOC release rate and the weighted annualized

517   mean (0.45 mg C · g DW^{-1} · d^{-1}) could be up to 186% ± 60% (November 2022, $n = 6$) and the

518   DOC release rate from a single kelp sample could be up to 441% higher (October 2020, "low

519   light kelp 1") (Figure 9). Based on seasonal averages, mean DOC release rates from multiple

520   sampling events only conducted during a single seasonal period would have deviated from the

521   weighted annualized mean by −55% ± 6% in winter "early growth" ($n = 10$), +14% ± 25% in

522   spring "late growth" ($n = 24$), −22% ± 15% in summer "early decay" ($n = 24$), or +85% ± 26%

523   in autumn "late decay" ($n = 27$). Therefore, attempts to annualize kelp DOC release rates based

524   on data from a few kelp individuals, a few sampling events, or a single season should be

525   considered skeptically.

526   The kelp DOC release rate results in this study also add to the existing literature that

527   challenges the assumption that DOC release is proportional to biomass or primary production.

528   Instead, our results show that DOC release may be as significant or more significant during a

529   period of senescence when there is effectively no primary production or biomass growth.

530   Previous studies have acknowledged that estimating DOC release as a fraction of primary

531   production is not ideal, but the decoupling shown here and elsewhere is an indication that this

532   practice is highly misleading even as an approximation.

533   With respect to the growing interest in commercially farmed kelp as a Blue Carbon

534   strategy, the explicit objective of minimizing stressed tissue and harvesting kelp in prime

535   condition, before stress and decay conditions have advanced, could result in disproportionately

536   reducing the actual DOC released in situ and ultimately sequestered. This effect could be further

537   magnified due to the important role of microbially derived or transformed DOC, especially with

538   regard to the microbial carbon pump and the generation of recalcitrant or refractory DOC

539   (Brophy and Carlson, 1989; Ogawa et al., 2001; Jiao et al., 2010; Jiao et al., 2018). Likewise,

540   while detrital export was not quantified in this study, this Blue Carbon pathway is likely also

541   enhanced by stress and decay conditions (Newell et al., 1980; Krumhansl and Scheibling, 2012;

542   Pedersen et al., 2020).

543   Yet, in light of the negative effects of industrial-scale Blue Carbon projects (Boyd et al.,

544   2022; Ricart et al., 2022), it is critical to emphasize that any Blue Carbon credits should benefit

545   Indigenous Peoples and governance of balanced social-ecological systems. Indeed, projects

546   centered on pursuing carbon credits for profit as the primary objective are already resulting in

547   unintended consequences in addition to furthering Indigenous disposession (Asiyanbi, 2016;

548   Morrow et al., 2020).

549   **Implications of passive macroalgal DOC release for Indigenous stewards**

550   While this study was specific to the kelp *S. japonica* var. *religiosa* in Oshoro Bay, there

551   are some qualitative implications that may at least provide insights for other locations and

552   species. Therefore, Indigenous coastal stewards may find the following conclusions from this

553   study relevant in confirming or supplementing existing knowledge from their experiences:

554   1) Kelp DOC release rates vary throughout the year, even when nutrients are sufficient, and

555   should be closely and frequently monitored for their ecological impacts (Figure 3, 4, 6,

556   and 8);

557   2) Kelp DOC release rates were highly variable between individual kelp regardless of

558   biomass (especially in late March and October 2020 and 2021), and likely related to

559   individual biological stress conditions (Table S1, Figure 3, 4, 6, and 7);

560   3) Kelp DOC release did not vary significantly with in situ temperature or salinity, but these

561   are important parameters to monitor for other ecological impacts (Figure 5);

562   4) Kelp DOC release only required low levels of light, with no significant differences in

563   DOC release rates between irradiance levels from 200 (representative of submerged

564   dense self-shading) to 1500 (representative of periodic direct exposure to sunny weather)

565   μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} or as a function of mean daily PAR (mol photons $\cdot$ m^{-2} $\cdot$ d^{-1})

566   (Figure 6);

567   5) The autumn "late decay" period may be commonly overlooked because of lower biomass

568   and no growth, yet even DOC release rates factoring in total biomass (mg C $\cdot$ ind^{-1} $\cdot$ d^{-1})

569   were seasonally higher in autumn compared to summer, and both early autumn and late

570   autumn were comparable to the bi-seasonal peak in early summer (Figure 8b);

571   6) The significantly higher kelp DOC release rates during the autumn "late decay" period

572   and during kelp death may fuel significant microbial activity and potential deoxygenation

573   in more stagnant areas (Figure 7 and 8);

574   7) Monitoring kelp DOC release is primarily relevant for managing its ecological

575   implications—ecosystem services such as Blue Carbon sequestration should be

576   considered co-benefits of holistic Indigenous social-ecological stewardship that is fully-

577   funded without the need for accounting.

578   *Conclusion*

579   This study showed statistically significant ($p < 0.05$) seasonal differences in kelp DOC

580   release rates between the autumn "late decay" (0.82 ± 0.12 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}, $n = 27$) period

581   and the winter "early growth" (0.20 ± 0.028 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}, $n = 10$) and summer "early

582   decay" (0.34 ± 0.066 mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}, $n = 24$) periods. These seasonal variations in kelp

583   DOC release rates were not attributable to seasonal variations in salinity, sea surface

584   temperature, or biomass. There was also no significant relationship between PAR and DOC

585   release rates across three artificial irradiance levels of 200, 400, and 1200 μmol photons $\cdot$ m^{-2} $\cdot$

586   s^{-1} or when compared to natural irradiance levels of 1500 μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}. In total, these

587   three years of year-round data (based on 1091 DOC samples, 88 incubated kelp, and 16 sampling

588   events) provide substantial evidence for the importance of passive exudation over active

589   exudation as the primary driver stimulating seasonal variations in kelp DOC release, even when

590   nitrogen is sufficient year-round. These conclusions indicate that annualizing non-seasonal data

591   (e.g., in recent Blue Carbon estimates) based on the assumed proportionality of DOC release and

592   primary production is a fundamentally flawed approach.

593   Indeed, the complex variability of macroalgal DOC release shown here highlights the

594   need for Indigenous stewardship of these ecosystems. Where this fundamental right is already

595   being exercised, these results may guide monitoring and cultivation practices toward greater

596   attention to seasonal variations linked to stress and decay conditions. By monitoring macroalgal

597   ecosystems year-round, Indigenous stewards may be able to assess and anticipate periods of

598   acute environmental changes as well as natural decay periods that could stimulate enhanced

599   macroalgal DOC release. Indigenous stewardship of macroalgal health, including DOC release

600   as an ecophysiological stress response, remains critical for broader social-ecological health.

601   ***Authors' contributions***

602   A. K. Carlson: Conceptualization (Lead), Formal analysis (Lead), Funding acquisition (Equal),

603   Investigation (Lead), Methodology (Lead), Writing—original draft preparation (Lead),

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605   T. Yoshimura: Funding acquisition (Equal), Resources (Equal), Supervision (Supporting),

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607   I. Kudo: Conceptualization (Supporting), Funding acquisition (Equal), Investigation

608   (Supporting), Methodology (Supporting), Resources (Equal), Supervision (Lead), Writing—

609   review and editing (Equal).

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617   *Conflicts of interests*

618   The authors declare that they have no conflicts of interest.

619   *Supplementary information*

620   Supplementary materials are available in the online version of this article.

621   *Data availability*

622   All data analyzed for this publication are included in this article and its supplementary

623   information files. The database in spreadsheet format is available upon request.

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809   ***Figure captions***

810   Figure 1. July 2021 aerial images showing an overview of Oshoro Bay, the kelp sampling

811   location, temperature and salinity measurement locations, and reference seawater sampling

812   locations. An inset of the relative location of Oshoro Bay on the Shakotan peninsula in western

813   Ainu Mosir (Hokkaido) is also provided (Google Earth 2021).

814   Figure 2. Annual cycles of biomass and environmental parameters. Data are (a) means ($\pm$ SE

815   between kelp, $n = 2$–6) of individual kelp dry weight biomasses (g DW $\cdot$ ind^{-1}), (b) photoperiod

816   hours used for the incubation experiments, (c) means ($\pm$ SE between sampling locations, $n = 9$)

817   of in situ sea surface temperature (°C), (d) means ($\pm$ SE between sampling locations, $n = 9$) of

818   salinity (parts per thousand), and (e) concentrations of DOC in the incubated control seawater

819   tanks ($\pm$ SE between samples within the respective incubation period). In situ sampling locations

820   are shown in Figure 1. Low irradiance designations indicate exposure to 200 μmol photons $\cdot$ m^{-2}

821　　$\cdot$ s^{-1} from artificial LED sources. High irradiance designations vary and indicate exposure to 400

822　　(incubation experiments from January 2020 to July 2021) or 1200 (incubation experiments from

823　　May 2022 through November 2022) μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} from artificial LED or 1500

824　　(November 2021) μmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} from natural irradiance. Some error bars are smaller

825　　than the data symbol.

826　　Figure 3. Mean individual kelp DOC release rates by sampling event. Black data points are

827　　means ($\pm$ SE) of the individual kelp DOC release rates (mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}) within each

828　　sampling event. Some error bars are smaller than the data symbol. White data points represent

829　　the individual kelp DOC release rates calculated as least squares means from linear regressions

830　　of DOC concentrations ($n = 5$–17 samples per incubation) at regular intervals during the

831　　incubation period ($t = 4$–9 days). Each sampling event incubated $n = 6$ kelp except January 2020

832　　($n = 2$), January 2021 ($n = 4$), early March 2020 ($n = 4$), and October 2021 ($n = 3$).

833　　Figure 4. Mean kelp-derived DOC inventory accumulation. Data are mean ($\pm$ SE) kelp-derived

834　　DOC inventory (mg C $\cdot$ g DW^{-1}) of all kelp ($n = 6$, except January 2020 [$n = 2$], January 2021 [n

835　　$= 4$], early March 2020 [$n = 4$], and October 2021 [$n = 3$]) for a given sampling event as a

836　　function of elapsed incubation time ($t = 4$–9 days). Data are categorized seasonally into (a)

837　　winter, (b) spring, (c) summer, and (d) autumn.

838　　Figure 5. DOC release rates and environmental parameters. Relationships between (a) the

839　　individual kelp DOC release rates (mg C $\cdot$ ind^{-1} $\cdot$ d^{-1}) and corresponding individual kelp biomass

840　　(g DW $\cdot$ ind^{-1}), as well as the individual biomass normalized kelp DOC release rates (mg C $\cdot$ g

841　　DW^{-1} $\cdot$ d^{-1}) and (b) photoperiod hours, (c) mean in situ sea surface temperature (°C), and (d)

842　　mean in situ salinity. DOC release rates ($n = 85$) are least squares means for each individual kelp

843　　across the 16 sampling events. Linear regression equations and significance of the slope

844   coefficient shown. Significant linear trendline ($p < 0.05$) only applicable to (a) and (b).

845   Figure 6. Irradiance and DOC release rates. Data are (a) individual kelp DOC release rates (mg C

846      $\cdot$ g DW^{-1} $\cdot$ d^{-1}) as a function of their corresponding irradiance treatment, with mean ($\pm$ SE) DOC

847   release rates in black aggregating values within each of the four irradiance treatment levels (200,

848   400, 1200, and 1500 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}), (b) mean ($\pm$ SE) individual kelp DOC release

849   rates (mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}) as a function of their corresponding mean daily PAR exposure (mol

850   photons $\cdot$ m^{-2} $\cdot$ d^{-1}), and (c) mean DOC release rates ($\pm$ SE) for their corresponding qualitative

851   (low or high) irradiance treatment within each sampling event ($n = 16$). Low irradiance

852   designations indicate exposure to 200 µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} from artificial LED sources. High

853   irradiance designations vary and indicate exposure to 400 (incubation experiments from January

854   2020 to July 2021) or 1200 (incubation experiments from May 2022 through November 2022)

855   µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1} from artificial LED or 1500 (November 2021) µmol photons $\cdot$ m^{-2} $\cdot$ s^{-1}

856   from natural irradiance. There were no significant differences ($p < 0.05$, two-tail t-tests) within

857   any of the sampling events comparing mean DOC release rates treated to low or high irradiance

858   levels.

859   Figure 7. Mean DOC release rates from live senescent kelp and three stages of kelp death (pre-

860   death, death phase 1, and death phase 2) in October 2021. November 2021 results comparing live

861   kelp under artificial and natural irradiance are included to demonstrate extreme DOC release in

862   October 2021 was related to kelp death and not the effect of natural irradiance.

863   Figure 8. Mean DOC release rates by season. Data are means ($\pm$ SE) of kelp DOC release rates

864   represented as a) biomass normalized rates (mg C $\cdot$ g DW^{-1} $\cdot$ d^{-1}) and (b) raw rates per

865   individual kelp (mg C $\cdot$ ind^{-1} $\cdot$ d^{-1}), with results aggregated according to eight bi-seasonal

866   categories. Shading and border effects visually differentiate results by the four seasons.

867   Figure 9. Percent difference (%) of experimental DOC release rates from weighted annualized

868   mean DOC release rate. Data are (a) means (± SE) of the percent differences (%) for each

869   sampling event in black, with individual kelp results in white or (b) means (± SE) of the %

870   differences for each sampling event aggregated according to bi-seasonal period. The annualized

871   mean DOC release rate of 0.45 mg C · g DW^{-1} · d^{-1} was calculated from bi-seasonal weighted

872   averages.

873   ***Supplementary material captions***

874   Figure S1. Incubation time-series of volume-corrected DOC concentrations (µmol · L^{-1}) and

875   biomass-normalized kelp-derived DOC inventories (mg C · g DW^{-1} · d^{-1}) for all incubated kelp

876   (n = 88) and control seawater (n = 31). Low light designations indicate exposure to

877   photosynthetically active radiation (PAR) of 200 µmol photons · m^{-2} · s^{-1} from artificial LED

878   sources. High light designations vary and indicate exposure to 400 (incubation experiments from

879   January 2020 to July 2021) or 1200 (incubation experiments from May 2022 through November

880   2022) µmol photons · m^{-2} · s^{-1} from artificial LED sources, or 1500 (November 2021) or 2000

881   (October 2021) µmol photons · m^{-2} · s^{-1} from natural irradiance. Each pair of graphs correspond

882   to the 16 incubation experiments conducted in (a)–(b) January 2020, (c)–(d) early March 2020,

883   (e)–(f) late March 2020, (g)–(h) June 2020, (i)–(j) August 2020, (k)–(l) October 2020, (m)–(n)

884   January 2021, (o)–(p) March 2021, (q)–(r) April 2021, (s)–(t) July 2021, (u)–(v) October 2021

885   (live kelp), (w)–(x) October 2021 (dead kelp), (y)–(z) November 2021, (aa)–(ab) May 2022, (ac)–

886   (ad) July 2022, (ae)–(af) October 2022, and (ag)–(ah) November 2022.
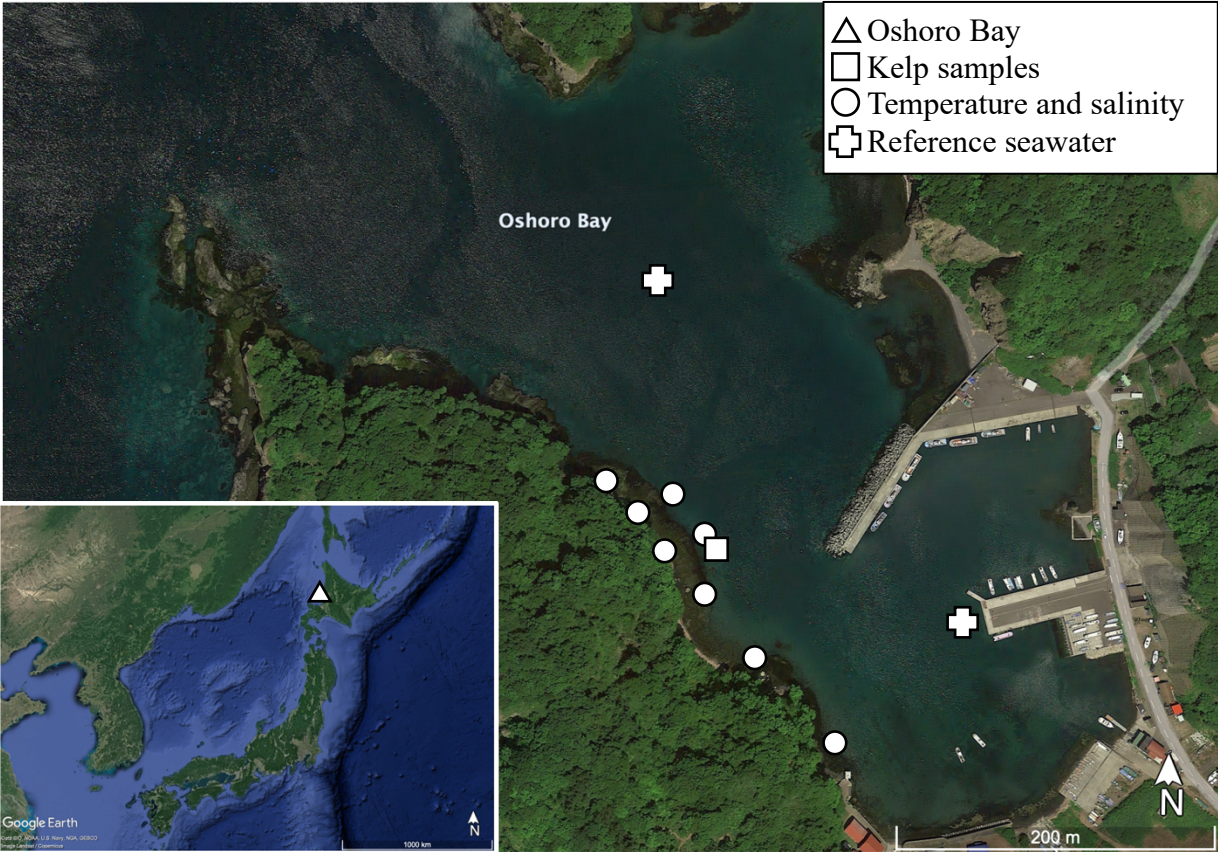
887   Figure S2. Coefficients of variation (%) for replicated DOC samples at the end of incubation

888   experiments in November 2021, May 2022, July 2022, October 2022, and November 2022. Results

889   represent the spatial heterogeneity of DOC within the incubation tanks.

890   Table S1. Linearity of kelp DOC release rates. DOC release rates (mg C · g DW^{-1} · d^{-1}) are least

891   squares means from linear regressions of elapsed incubation time and the corresponding kelp-

892   derived DOC inventory (mg C · g DW^{-1}). Sample sizes ($n = 5$–17) represent the number of

893   incubation seawater samples taken at regular intervals throughout each incubation period ($t = 4$–

894   9 days) and analyzed for DOC. Kelp DOC release was significantly ($p < 0.05$) linear for all kelp

895   incubations except one kelp in January 2021 and the three dead kelp in October 2021. Shading

896   and borders correspond to seasonal categories (Figure 8).

897   Table S2. Linear regression of kelp biomass and DOC release rate by sampling event. Kelp

898   biomass (g DW · ind^{-1}) is individual dry weight and DOC release rates are least squares means

899   (mg C · ind^{-1} · d^{-1}) calculated from linear regressions of volume-corrected DOC concentrations

900   ($n = 5$–17 samples per incubation) throughout the incubation period ($t = 4$–9 days). Sample size

901   corresponds to the number of kelp incubated for a given sampling event ($n = 6$, except for

902   January 2020 [$n = 2$], early March 2020 [$n = 4$], January 2021 [$n = 4$], and October 2021 [$n = 3$]).

903   Appendix S1. Effect of bi-seasonal period and PAR on DOC release: two-way ANOVA (Type

904   II) and Tukey HSD test results with R code

905   Appendix S2. Effect of seasonal period and PAR on DOC release: two-way ANOVA (Type II)

906   and Tukey HSD test results with R code

(a) Mean kelp biomass (g DW · ind⁻¹) vs Sampling date, with series for 2020, 2021, 2022.

(b) Photoperiod (hours) vs Sampling date, with series for 2020, 2021, 2022.

(c) Sea surface temperature (°C) vs Sampling date, with series for 2020, 2021, 2022.

(d) Salinity vs Sampling date, with series for 2020, 2021, 2022.

(e) Seawater control DOC concentration (µmol · L⁻¹) vs Sampling date, with series for 2020 Low irradiance, 2021 Low irradiance, 2022 Low irradiance, 2020 High irradiance, 2021 High irradiance, 2022 High irradiance.

(a) Winter 2020–2022 experiments

Legend:
- ⊙ January 2020
- ◻ January 2021
- ● early March 2020
- ⊙ late March 2020
- ◻ March 2021
- ◻ April 2021
- ▲ May 2022

(b) Spring 2020–2022 experiments

(c) Summer 2020–2022 experiments

Legend:
- ⊙ June 2020
- ◻ July 2021
- △ July 2022
- ● August 2020

(d) Autumn 2020–2022 experiments

Legend:
- ⊙ October 2020
- ◻ October 2021
- △ October 2022
- ■ November 2021
- ▲ November 2022

Axis labels: Kelp-derived DOC inventory (mg C · g DW⁻¹); Incubation time (days)

(a)

(b)

(c)

(d)

(a)

$y = 0.0001x + 0.4778$
$R^2 = 0.0101, p = 0.36$

Kelp DOC release rate $(mg\ C \cdot g\ DW^{-1} \cdot d^{-1})$

PAR
$(\mu mol\ photons \cdot m^{-2} \cdot s^{-1})$

(b)

$y = 0.0012x + 0.5165$
$R^2 = 0.0014, p = 0.73$

Kelp DOC release rate $(mg\ C \cdot g\ DW^{-1} \cdot d^{-1})$

Mean daily PAR
$(mol\ photons \cdot m^{-2} \cdot d^{-1})$

(c)

Kelp DOC release rate $(mg\ C \cdot g\ DW^{-1} \cdot d^{-1})$

○ 2020 High irradiance	□ 2021 High irradiance	△ 2022 High irradiance
● 2020 Low irradiance	■ 2021 Low irradiance	▲ 2022 Low irradiance

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec

Sampling date

PAR (μmol photons · m^{-2} · s^{-1})

(a)

(b)

(a)

(b)

(g)

(h)

Incubation time (days)
23–30 June 2020

(i)

(j)

Incubation time (days)
18–25 August 2020

(k)

(l)

Incubation time (days)
28 October–4 November 2020

(m)

Incubation time (days)
26 January–2 February 2021

(n)

Incubation time (days)
26 January–2 February 2021

(o)

Incubation time (days)
24–29 March 2021

(p)

Incubation time (days)
24–29 March 2021

(q)

Incubation time (days)
22–27 April 2021

(r)

Incubation time (days)
22–27 April 2021

(s)

(t)
6–11 July 2021

(u)
6–11 July 2021

(v)
7–11 October 2021

(w)
7–11 October 2021

(x)
7–11 October 2021 (dead kelp)

7–11 October 2021 (dead kelp)

(y)

(z)

Incubation time (days)
30 November–4 December 2021

(aa)

(ab)

Incubation time (days)
24–28 May 2022

(ac)

(ad)

Incubation time (days)
19–23 July 2022

(ae)

19–23 October 2022

(af)

19–23 October 2022

(ag)

29 November–4 December 2022

(ah)

29 November–4 December 2022

	Least squares mean kelp DOC release rate (mg C · g DW^{-1} · d^{-1}) 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	0.13	NA	NA	0.34	NA	NA
	R^2	0.70			0.84		
	Significance F	7×10^{-3}			7×10^{-3}		
	p	5×10^{-3}			4×10^{-3}		
	n	8			6		
	t	0–9			0–9		
Early March 2020	Mean	0.24	0.32	NA	0.12	0.10	NA
	R^2	0.98	0.97		0.86	0.98	
	Significance F	4×10^{-13}	4×10^{-11}		5×10^{-7}	7×10^{-13}	
	p	9×10^{-14}	1×10^{-11}		3×10^{-7}	2×10^{-13}	
	n	15	15		15	15	
	t	0–7	0–7		0–7	0–7	
Late March 2020	Mean	0.63	0.11	1.0	0.66	0.75	0.10
	R^2	0.68	0.92	0.97	0.99	0.97	0.93
	Significance F	4×10^{-5}	9×10^{-9}	3×10^{-13}	2×10^{-15}	6×10^{-13}	3×10^{-10}
	p	3×10^{-5}	4×10^{-10}	8×10^{-14}	4×10^{-16}	2×10^{-13}	1×10^{-10}
	n	17	17	17	17	17	17
	t	0–7	0–7	0–7	0–7	0–7	0–7
June 2020	Mean	1.4	0.12	0.43	0.64	0.082	0.19
	R^2	0.84	0.82	0.92	0.74	0.92	0.78
	Significance F	2×10^{-6}	1×10^{-5}	4×10^{-8}	6×10^{-5}	2×10^{-7}	2×10^{-5}
	p	1×10^{-6}	8×10^{-6}	2×10^{-8}	4×10^{-5}	9×10^{-8}	1×10^{-5}
	n	14	13	14	14	13	14
	t	0–7	0–7	0–7	0–7	0–7	0–7
August 2020	Mean	0.10	0.11	0.066	0.34	0.088	0.11
	R^2	0.91	0.81	0.75	0.81	0.88	0.95
	Significance F	2×10^{-8}	1×10^{-6}	9×10^{-6}	1×10^{-6}	5×10^{-8}	8×10^{-11}
	p	1×10^{-8}	8×10^{-7}	6×10^{-6}	7×10^{-7}	2×10^{-8}	3×10^{-11}
	n	15	16	16	16	16	16
	t	0–7	0–7	0–7	0–7	0–7	0–7
October 2020	Mean	2.4	0.25	0.24	0.54	0.094	1.7
	R^2	0.91	0.89	0.80	0.93	0.95	0.93
	Significance F	3×10^{-8}	1×10^{-7}	5×10^{-6}	7×10^{-3}	4×10^{-10}	4×10^{-9}
	p	2×10^{-8}	5×10^{-8}	3×10^{-6}	3×10^{-3}	1×10^{-10}	2×10^{-9}
	n	15	15	15	15	15	15
	t	0–7	0–7	0–7	0–7	0–7	0–7

January 2021	Mean	0.16	0.11	NA	0.17	0.27	NA
	R^2	0.29	0.91		0.46	0.81	
	Significance F	0.11	1×10^{-4}		0.034	7×10^{-4}	
	p	0.10	6×10^{-5}		0.030	4×10^{-4}	
	n	9	8		9	9	
	t	0–7	0–7		0–7	0–7	
March 2021	Mean	0.21	0.13	1.6	2.4	0.13	0.58
	R^2	0.91	0.60	0.69	0.90	0.83	0.95
	Significance F	1×10^{-6}	2×10^{-3}	5×10^{-4}	2×10^{-6}	7×10^{-5}	3×10^{-9}
	p	6×10^{-7}	2×10^{-3}	4×10^{-4}	9×10^{-7}	4×10^{-5}	7×10^{-10}
	n	12	12	12	12	11	12
	t	0–5	0–5	0–5	0–5	0–5	0–5
April 2021	Mean	0.11	0.091	0.24	0.28	0.59	0.11
	R^2	0.98	0.98	0.89	0.87	0.97	0.94
	Significance F	1×10^{-9}	5×10^{-10}	2×10^{-6}	8×10^{-6}	5×10^{-9}	9×10^{-8}
	p	3×10^{-10}	1×10^{-10}	1×10^{-6}	4×10^{-6}	1×10^{-9}	3×10^{-8}
	n	12	12	12	12	12	12
	t	0–5	0–5	0–5	0–5	0–5	0–5
July 2021	Mean	0.14	0.22	0.11	0.62	0.20	0.13
	R^2	0.85	0.85	0.94	0.91	0.80	0.85
	Significance F	9×10^{-5}	9×10^{-5}	2×10^{-6}	1×10^{-5}	3×10^{-4}	1×10^{-4}
	p	5×10^{-5}	5×10^{-5}	7×10^{-7}	4×10^{-6}	2×10^{-4}	5×10^{-5}
	n	10	10	10	10	10	10
	t	0–5	0–5	0–5	0–5	0–5	0–5
October 2021	Mean	1.2	0.20	0.59	1.5	1.6	2.8
	R^2	0.90	0.97	0.97	1.0	1.0	0.96
	Significance F	9×10^{-3}	2×10^{-3}	1×10^{-3}	NA	NA	NA
	p	4×10^{-3}	4×10^{-4}	3×10^{-4}	3×10^{-5}	4×10^{-3}	0.14
	n	5	5	5	2	2	2
	t	0–4	0–4	0–4	0–1	0–1	0–1
October 2021 (dead kelp: phase 1)	Mean	NA	NA	NA	68	137	60
	R^2				1.0	1.0	1.0
	Significance F				NA	NA	NA
	p				NA	NA	NA
	n				2	2	2
	t				1–2	1–2	1–2
October 2021 (dead kelp: phase 2)	Mean	NA	NA	NA	−6.9	−9.9	2.8
	R^2				0.79	0.98	0.21
	Significance F				0.30	0.085	0.70
	p				0.30	0.085	0.70
	n				3	3	3
	t				2–4	2–4	2–4

November 2021	Mean	0.49	0.48	0.66	0.65	0.48	0.84
	R^2	0.96	0.88	0.97	0.90	0.97	0.91
	Significance F	2×10^{-3}	0.013	2×10^{-3}	9×10^{-3}	2×10^{-3}	7×10^{-3}
	p	5×10^{-4}	6×10^{-3}	4×10^{-4}	4×10^{-3}	5×10^{-4}	3×10^{-3}
	n	5	5	5	5	5	5
	t	0–4	0–4	0–4	0–4	0–4	0–4
May 2022	Mean	0.31	0.86	0.18	0.27	0.24	0.52
	R^2	0.998	0.99	0.99	0.97	0.996	0.998
	Significance F	3×10^{-5}	5×10^{-4}	2×10^{-4}	2×10^{-3}	6×10^{-5}	3×10^{-5}
	p	2×10^{-6}	7×10^{-5}	2×10^{-5}	4×10^{-4}	5×10^{-6}	2×10^{-6}
	n	5	5	5	5	5	5
	t	0–4	0–4	0–4	0–4	0–4	0–4
July 2022	Mean	0.36	0.48	0.77	0.46	0.89	0.42
	R^2	0.94	0.98	0.98	0.90	0.95	0.97
	Significance F	5×10^{-3}	7×10^{-4}	7×10^{-4}	9×10^{-3}	3×10^{-3}	1×10^{-3}
	p	2×10^{-3}	1×10^{-4}	1×10^{-4}	4×10^{-3}	1×10^{-3}	3×10^{-4}
	n	5	5	5	5	5	5
	t	0–4	0–4	0–4	0–4	0–4	0–4
October 2022	Mean	0.75	0.38	0.36	1.1	1.1	0.60
	R^2	0.90	0.96	0.95	0.91	0.94	0.93
	Significance F	9×10^{-3}	2×10^{-3}	3×10^{-4}	3×10^{-4}	4×10^{-3}	5×10^{-3}
	p	4×10^{-3}	5×10^{-4}	1×10^{-3}	3×10^{-3}	1×10^{-3}	2×10^{-3}
	n	5	5	5	5	5	5
	t	0–4	0–4	0–4	0–4	0–4	0–4
November 2022	Mean	1.3	1.8	2.3	0.36	0.76	1.8
	R^2	0.90	0.96	0.79	0.87	0.97	0.88
	Significance F	0.0097	2×10^{-3}	0.030	0.014	1×10^{-3}	0.012
	p	4×10^{-3}	6×10^{-4}	0.018	7×10^{-3}	3×10^{-4}	5×10^{-3}
	n	5	5	5	5	5	5
	t	0–4	0–4	0–4	0–4	0–4	0–4

Date(s)	Linear coefficient	R^2	p value	n	Significant
January 2020–November 2022	0.35	0.22	7×10^{-6}	85	Yes
January 2020	NA	NA	NA	2	NA
early March 2020	0.10	0.066	0.74	4	No
late March 2020	1.2	0.84	0.010	6	Yes
June 2020	−0.92	0.12	0.50	6	No
August 2020	0.31	0.29	0.27	6	No
October 2020	1.1	0.13	0.48	6	No
January 2021	0.14	0.49	0.30	4	No
March 2021	2.5	0.71	0.035	6	Yes
April 2021	0.23	0.14	0.46	6	No
July 2021	0.67	0.68	0.043	6	Yes
October 2021	−0.64	0.51	0.50	3	No
November 2021	0.48	0.32	0.24	6	No
May 2022	0.99	0.70	0.037	6	Yes
July 2022	0.18	0.42	0.16	6	No
October 2022	0.91	0.44	0.15	6	No
November 2022	0.27	0.038	0.71	6	No

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```
> 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  4.7036  7 2.8776 0.01014 *
PAR        0.0415  1 0.1778 0.67445
Residuals 17.7465 76
---
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_autumn == 0 -0.2027678  0.1702270  -1.191   0.9273
early_summer - early_autumn == 0 -0.3224207  0.1689397  -1.908   0.5343
early_winter - early_autumn == 0 -0.5456850  0.2343551  -2.328   0.2795
late_autumn - early_autumn == 0   0.2019817  0.1937306   1.043   0.9636
late_spring - early_autumn == 0  -0.3330988  0.2366305  -1.408   0.8423
late_summer - early_autumn == 0  -0.6099900  0.2343551  -2.603   0.1629
late_winter - early_autumn == 0  -0.5455741  0.2727291  -2.000   0.4735
early_summer - early_spring == 0 -0.1196530  0.1623023  -0.737   0.9951
early_winter - early_spring == 0 -0.3429172  0.2277942  -1.505   0.7915
late_autumn - early_spring == 0   0.4047494  0.1935688   2.091   0.4153
late_spring - early_spring == 0  -0.1303311  0.2355048  -0.553   0.9992
late_summer - early_spring == 0  -0.4072222  0.2277942  -1.788   0.6158
late_winter - early_spring == 0  -0.3428064  0.2671124  -1.283   0.8959
early_winter - early_summer == 0 -0.2232643  0.2286638  -0.976   0.9746
late_autumn - early_summer == 0   0.5244024  0.1871837   2.802   0.1038
late_spring - early_summer == 0  -0.0106781  0.2312529  -0.046   1.0000
late_summer - early_summer == 0  -0.2875693  0.2286638  -1.258   0.9054
late_winter - early_summer == 0  -0.2231534  0.2678544  -0.833   0.9898
late_autumn - early_winter == 0   0.7476667  0.2518213   2.969   0.0690 .
late_spring - early_winter == 0   0.2125861  0.2853202   0.745   0.9948
late_summer - early_winter == 0  -0.0643050  0.2789898  -0.230   1.0000
late_winter - early_winter == 0   0.0001108  0.3119201   0.000   1.0000
```

late_spring - late_autumn == 0   -0.5350805 0.2418720 -2.212   0.3425
late_summer - late_autumn == 0   -0.8119717 0.2518213 -3.224   0.0348 *
late_winter - late_autumn == 0   -0.7475558 0.2878764 -2.597   0.1646
late_summer - late_spring == 0   -0.2768911 0.2853202 -0.970   0.9754
late_winter - late_spring == 0   -0.2124753 0.3175948 -0.669   0.9973
late_winter - late_summer == 0   0.0644158 0.3119201   0.207   1.0000

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Adjusted p values reported -- single-step method)

```
> 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    3.9956  3  5.7737 0.001261 **
PAR       0.0112  1  0.0488 0.825810
Residuals 18.4544 80
---
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 - Autumn == 0  -0.3190    0.1373  -2.324  0.09923 .
Summer - Autumn == 0  -0.4780    0.1373  -3.482  0.00442 **
Winter - Autumn == 0  -0.6260    0.1823  -3.435  0.00506 **
Summer - Spring == 0  -0.1590    0.1386  -1.147  0.65817
Winter - Spring == 0  -0.3070    0.1813  -1.694  0.32967
Winter - Summer == 0  -0.1481    0.1813  -0.817  0.84418
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Adjusted p values reported -- single-step method)
```