



Variability in the Net Ecosystem Productivity (NEP) of Seaweed Farms

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The important role of vegetated ecosystems in the sequestration of carbon has gained strong interest across a wide variety of disciplines. With evidence growing of the potential for macroalgae ecosystems to capture carbon, there is burgeoning interest in applying newfound knowledge of carbon capture rates to better understand the potential for carbon sequestration. Seaweed farms are expected to play a significant role in carbon capture; advocates for the expansion of seaweed farms are increasing in many countries. In general, seaweed farms are expected to be highly productive, although whether they are autotrophic or heterotrophic ecosystems and hence potential exporters of carbon, is under debate. Therefore, we present our investigation of three seaweed farms, two in northern Japan and one in southern Japan. We examine the frequency of autotrophic days and compare potential rates of carbon capture of the seaweed farms with two natural macroalgae ecosystems and one degraded site. We estimated potential carbon capture rates by calculating the net ecosystem productivity from continuous recordings of dissolved oxygen concentrations under natural environmental conditions. The net ecosystem production rates for the natural ecosystems in Arikawa Bay and Omura Bay were equivalent to 0.043 and 0.054 [g C m⁻² d⁻¹] m⁻¹, respectively. Whereas, for the degraded ecosystem in Tainoura Bay, it was -0.01 [g C m⁻² d⁻¹] m⁻¹. We reveal that the *Undaria pinnatifida* farm in Matsushima Bay experience autotrophy more often than natural ecosystems, although for seaweed farms producing *U. pinnatifida* in Hirota Bay and *Cladospirion okamuranus* at Bise Point, autotrophy was less frequently observed. Nevertheless, up to 14.1 g C m⁻² (0.110 g C m⁻² d⁻¹) was captured by the production of *U. pinnatifida* and 3.6 g C m⁻² (0.034 g C m⁻² d⁻¹) was captured by *C. okamuranus*, and the total yield of carbon captured during 2021 production season for these farms was 43,385 kg C.

Keywords: climate change, aquaculture, blue carbon, dissolved oxygen, seaweed, macroalgae

INTRODUCTION

Vegetated ecosystems are expected to play an important role in sequestering carbon. Interest and research in carbon sequestration by vegetated coastal ecosystems are driving the development of blue carbon strategies to mitigate the effects of climate change (McLeod et al., 2011; Siegel et al., 2021). Some evidence suggests that macroalgae ecosystems can capture carbon dioxide from the environment just as effectively as seagrass, mangrove, and salt marsh ecosystems (Hill et al., 2015; Trevathan-Tackett et al., 2015; Ortega et al., 2019; Gouvêa et al., 2020). Hence, it is expected that macroalgae ecosystems, which cover approximately 3.4 million km² of coastal ocean area, can capture approximately 1.5 Gt C yr⁻¹ (Krause-Jensen and Duarte, 2016). Estimates suggest that approximately 165 Mt C yr⁻¹ may be sequestered for time-scales relevant to the mitigation of climate change (Frontier et al., 2021). Hence, interest in developing seaweed aquaculture as a carbon mitigation tool can be attributed to their global coverage, high rates of productivity, and the perception that there is a high social and economic cost of carbon removal in terrestrial ecosystems (Chung et al., 2011; Boysen et al., 2017).

Approximately 48 million km² of ocean area is believed to be suitable for seaweed aquaculture and has the potential to create a carbon neutral industry by combining traditional fin-fish aquaculture with seaweed aquaculture (Froehlich et al., 2019). Based on annual landings of seaweed harvests from aquaculture farms, an estimated 0.7 Mt C yr⁻¹ was captured in the Asian-Pacific region (Sondak et al., 2017). The global seaweed aquaculture harvest is expected to capture 680 Mt C yr⁻¹ from the environment (Duarte, 2017).

In contrast to seagrass dominated ecosystems, which are expected to sequester some of the captured carbon locally within the sediment of their habitat, macroalgae dominated ecosystems are less able to sequester carbon locally because most macroalgae occur on rocky substrate. Macroalgae ecosystems are expected to export a large fraction of the carbon that is captured through photosynthesis and serve as a carbon source — captured carbon (i.e., about 11% of macroalgal net C production) is exported to adjacent environments and deposited in sediments for relevant time-scales (Krause-Jensen et al., 2018). Recent studies indicate that the biomass produced by macroalgae may continue to capture carbon through photosynthesis after becoming detached from the substrate or thallus as they are exported out of the local habitat and enhance the deposition of detritus away from rocky habitat and into sediments, which can facilitate carbon sequestration (Krumhansl and Scheibling, 2012; Pedersen et al., 2020; Frontier et al., 2021; Smale et al., 2021). The potential for mitigating greenhouse gases, especially carbon dioxide, with macroalgae ecosystems or macroalgae aquaculture is debatable (Muraoka, 2004; Hill et al., 2015; Fillbee-Dexter and Wernberg, 2020; Gallagher et al., 2021; Gallagher et al., 2022) and their status as climate mitigating carbon sinks requires careful inquiry (Howard et al., 2017). Nevertheless, macroalgae ecosystems and seaweed aquaculture are increasingly touted as a key blue carbon strategy (Krause-Jensen and Duarte, 2016; Duarte and Krause-

Jensen, 2017; Duarte et al., 2017; Krause-Jensen et al., 2018; Froehlich et al., 2019; Ortega et al., 2019; Fillbee-Dexter and Wernberg, 2020).

There is little field evidence regarding the amount of carbon removed by seaweed aquaculture farms. Nevertheless, *Saccharina japonica* farms in the Yellow Sea increased dissolved oxygen concentrations and exhibited a deficit in pCO₂ (Xiao et al., 2021). However, a recent study suggests that macroalgae ecosystems are generally heterotrophic and rather than exporting carbon to the deep ocean, these ecosystems are local producers of carbon dioxide due to the influence of allochthonous organic matter sources (Gallagher et al., 2022). Therefore, we explore the potential of seaweed farms in Japan to capture carbon and compare them to natural ecosystems dominated by macroalgae. We infer the potential of seaweed farms and natural ecosystems to capture carbon by estimating their net ecosystem production using continuous recordings of dissolved oxygen, evaluating the proportion of autotrophic days in these ecosystems, and by estimating carbon captured from the total yields of the farms. We expected that the seaweed farms were autotrophic more often than natural ecosystems, since natural ecosystems are expected to be primarily heterotrophic (Gallagher et al., 2022).

MATERIALS AND METHODS

Study Sites, Period, and Macroalgae Taxa

Our data was collected from two natural seaweed ecosystems, one degraded seaweed ecosystem, and three seaweed farms from six geographic location across Japan (**Figure 1**). The natural ecosystems that were examined were seaweed beds dominated by a variety of *Sargassum* taxa. The degraded ecosystem is one that was previously a seaweed abundant ecosystem that has degraded into a state of isoyake (i.e., a state where a seaweed ecosystem degraded into an ecosystem devoid of habitat forming seaweed; Fujita, 2010; Vergés et al., 2014; Eger et al., 2022). Two clusters of seaweed farms were monitored: *Undaria pinnatifida* farms in the north and a *Cladosiphon okamuranus* farm in the south (**Table 1** and **Figure 1**).

Matsushima Bay and Hirota Bay are located in northern Japan and are the sites of the *U. pinnatifida* farms (**Table 1** and **Figure 1**). Both bays have predominantly silty substrates. The seaweed farm at Matsushima Bay is in relatively shallow (ca. 5 m) and enclosed waters, whereas the seaweed farm at Hirota Bay is in deep water with depths ranging from 30 to 40 m. Both bays open to the east, where the mean fetch (number of vectors at the fixed limit) for Hirota Bay was 4832 m (37), whereas the mean fetch for Matsushima Bay was 3254 m (4). Both Matsushima Bay and Hirota Bay experience a similar range in salinity, ranging from 30 to 35 (Ichikawa et al., 2009; Jianxi et al., 2020). Besides *U. pinnatifida*, commercial cultivation of oysters, *Pyropia* spp., and *Saccharina* spp. are present in Matsushima Bay, while scallops are cultivated in Hirota Bay.

Bise Point is located in southern Japan and is the site of the *C. okamuranus* farm. Here, the farm is located within the lagoon of a coral reef in 3 to 6 m of water and faces the ocean to the east

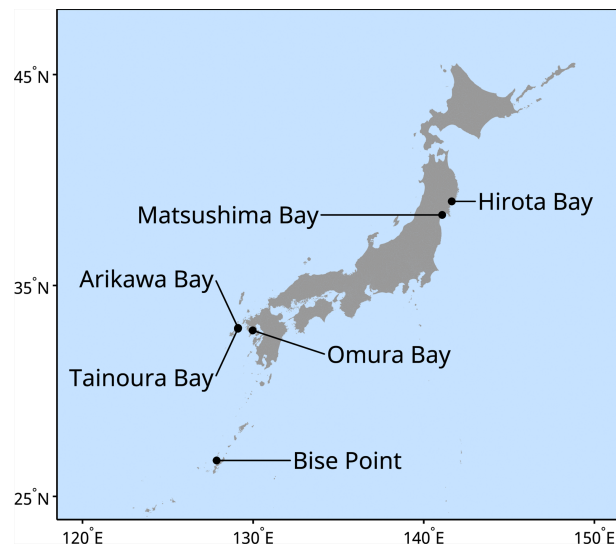


FIGURE 1 | Location of the sites monitored during the study.

with a mean fetch of 7336 m (62). Cultivation of *C. okamuranus* occurs in the lagoon to minimize exposure to strong hydrodynamic forces. Corals and seagrasses such as *Thalassia hemprichii*, *Cymodocea rotundata*, and *Halodule uninervis* can often be observed within the lagoon where salinity ranges from 32 to 35 (Higuchi et al., 2014).

Omura Bay, Arikawa Bay, and Tainoura Bay are located in Nagasaki Prefecture, in western Japan. Omura Bay is a highly enclosed bay, with a narrow and restricted entrance to the northeast. The study site has a mean fetch of 1584 m (3) and is a *Sargassum* spp. dominated ecosystem. The sediment at the site of Omura Bay is a mix of rock and sand. Salinity ranges from 30 to 35 (Nogami and Matsuno, 2001; Tsuchiya et al., 2018). Arikawa Bay and Tainoura Bay are in Nakadori Island, of the Goto Archipelago. Arikawa Bay is a wide north facing bay and is open to the ocean with a mean fetch of 2473 m (14). Tainoura Bay is a long narrow bay facing east with a mean fetch of 1016 (8) and is the site of an ecosystem degraded into an isoyake state, whereas Arikawa Bay is the site of a *Sargassum* spp. dominated ecosystem. Both bays have similar substrates, which is a mix of rock and sand.

All the sites examined in our study are located near large municipalities with armored shores. Although no major rivers drain into study sites, small streams and stormwater drains are present along the shore. Based on the mean fetch, we can rank the relative exposure of the sites from highest to lowest: Bise Point, Hirota Bay, Matsushima Bay, Arikawa Bay, Omura Bay, and Tainoura Bay. Data collection for the natural ecosystems occurred throughout the year; however, there are some gaps in the collection period due equipment malfunction and interruptions caused by tropical storms. Also, data collection for the seaweed farms were restricted to the production season

(**Table 1**). The period of seaweed production is variable and occurs for less than 6 months of the year. Variations in the production period also occurs due to the cultivation of different species and the differences in the environmental conditions. Therefore the comparisons made in this study are made with knowledge of this limitation.

Temperature and Dissolved Oxygen

Water temperature and dissolved oxygen concentrations were recorded with dataloggers (U26-001, Onset Computer Corporation, Bourne, MA, USA) at a rate of one sample every ten minutes. The U26-001 is an optical sensor that uses fluorescence to measure dissolved oxygen concentrations. Loggers were calibrated before and after deployment and referenced against a hand-held optical dissolved oxygen sensor (ProODO, Xylem Inc., Yellow Springs, OH, USA). In the natural and degraded ecosystems, one datalogger was placed directly above the sediment, another 50 cm above the sediment, and third 50 cm below the water surface (i.e., a total of three instruments and mean depth of 3 m for Omura Bay, 5 m for Arikawa Bay, and 8 m for Tainoura Bay). The dataloggers at the seaweed aquaculture farms were placed on the cultivation ropes and 1 m (Bise Point) and 2 m (Hirota Bay and Matsushima Bay) below the cultivation ropes (i.e., a total of two instruments). The instruments were placed so that the majority of the biomass of the seaweed were between the data loggers. Recordings were carried out for four to twenty days before the instruments were retrieved for maintenance and data offloading (e.g., Hinode et al., 2020). Calculations of productivity (as described below) is based on the ensemble mean of the dissolved oxygen time-series recorded by the dataloggers, to account for vertical heterogeneity.

TABLE 1 | Location, state, survey period, the number of recorded days (Survey days), the mean and standard deviation of the temperature during the survey period, and the mean fetch of the study sites.

Location	Latitude (N)	Longitude (E)	State	Start date	End date	Survey days	Temperature mean (°C)	Temperature standard deviation (°C)	Mean wind fetch (m) and the number of vectors at the upper limit in the parenthesis
Hirota Bay, Iwate	39.0240	141.7873	<i>Undaria pinnatifida</i>	2020-12-08	2021-04-15	129	9.7	1.8	4832 (37)
Matsushima Bay, Miyagi	38.3455	141.0808	<i>Undaria pinnatifida</i>	2019-10-17	2020-02-27	133	9.5	4.4	3254 (4)
Matsushima Bay, Miyagi	38.3455	141.0808	<i>Undaria pinnatifida</i>	2020-10-18	2021-03-14	145	8.3	4.4	3254 (4)
Arikawa Bay, Nagasaki	32.9883	129.1184	<i>Sargassum</i> spp.	2017-04-09	2017-04-30	22	16.5	0.57	2473 (14)
Arikawa Bay, Nagasaki	32.9883	129.1184	<i>Sargassum</i> spp.	2017-10-01	2018-04-30	136	16.8	3.9	2473 (14)
Arikawa Bay, Nagasaki	32.9883	129.1184	<i>Sargassum</i> spp.	2018-10-08	2019-04-30	178	17.1	2.6	2473 (14)
Arikawa Bay, Nagasaki	32.9883	129.1184	<i>Sargassum</i> spp.	2019-10-01	2020-04-21	178	17.6	3.1	2473 (14)
Arikawa Bay, Nagasaki	32.9883	129.1184	<i>Sargassum</i> spp.	2020-10-01	2021-04-29	159	17.7	3.1	2473 (14)
Tainoura Bay, Nagasaki	32.9513	129.1096	isoyake	2017-04-09	2017-04-30	22	16.8	0.6	1016 (8)
Tainoura Bay, Nagasaki	32.9513	129.1096	isoyake	2017-11-01	2018-04-30	101	16.7	2.9	1016 (8)
Tainoura Bay, Nagasaki	32.9513	129.1096	isoyake	2018-10-01	2019-04-30	185	17.7	2.8	1016 (8)
Tainoura Bay, Nagasaki	32.9513	129.1096	isoyake	2019-10-01	2020-04-30	187	18.1	3.1	1016 (8)
Omura Bay, Nagasaki	32.8700	129.9735	<i>Sargassum</i> spp.	2015-04-17	2015-04-22	6	15.8	0.4	1584 (3)
Omura Bay, Nagasaki	32.8700	129.9735	<i>Sargassum</i> spp.	2015-10-14	2016-04-30	27	16.2	4.8	1584 (3)
Omura Bay, Nagasaki	32.8700	129.9735	<i>Sargassum</i> spp.	2016-11-02	2017-02-02	14	15.5	5.5	1584 (3)
Bise Point, Okinawa	26.7043	127.8597	<i>Cladosiphon okamuranus</i>	2021-01-15	2021-04-30	105	21.8	0.9	7336 (62)

To determine wind fetch, 108 vectors with an upper limit of 10,000 m were generated in a 2π radial pattern around each coordinate. Rows are ordered from north to south.

Light and Wind Speed

To determine daylength and to calculate the air-sea gas flux of oxygen, the photosynthetic photon flux density (S-LIA-M003, Onset Computer Corporation, Bourne, MA, USA) and wind speed (S-BPB-CM50, Onset Computer Corporation, Bourne, MA, USA) were recorded to a datalogger (USB Microstation, Onset Computer Corporation, Bourne, MA, USA) at a rate of one sample every ten minutes. One set of instruments were deployed at each site. At the natural ecosystems, the measurements were taken one meter above the seawater surface by placing the equipment on a floating raft; however, at the seaweed aquaculture farms, the instruments were placed 10 m above ground at nearby boat harbors. Data was recorded for four to twenty days (e.g., Hinode et al., 2020).

Estimating Productivity

The gross ecosystem production (GEP) rates and ecosystem respiration (ER) rates were estimated from the diurnal fluctuations of the dissolved oxygen concentration with the open-water method (Hanson et al., 2008; Staehr et al., 2010; Champenois and Borges, 2012; Berg et al., 2019; Hinode et al., 2020), therefore the data includes not only the physiological processes of photosynthetic organisms, but also includes the respiration of non-photosynthetic organisms (see Gallagher et al., 2022 for details on the processes occurring in open systems). Briefly, the net ecosystem production (NEP) rate can be defined as $NEP = GEP + ER$, where GEP are positive values and ER are negative values. NEP rates (NEP_t) with respect to sampling time (i.e., $\Delta t = 10$ minutes) are calculated

as the time rate-of-change of the dissolved oxygen concentrations ($NEP_t = \frac{\Delta O_2}{\Delta t} + F_{O_2,t}$) determined from a smoother fitted with a generalized additive model (GAM) and the calculated flux ($F_{O_2,t}$) at the air-sea interface (Wanninkhof, 1992). The smoother for the GAM was a thin-plate spline, and the distribution was assumed to be Gaussian (Wood, 2011). Physical flux of dissolved oxygen within the water column cannot be evaluated by this method, however given the relative size of our measurement sites, our experience shows that any concentration gradients that could affect the measurements tend to sum to zero. Hence, we define the daily rates of NEP as the sum of the flux-corrected NEP rates ($NEP = \sum NEP_t$), and are approximations to NEP. The daily rates of ER are the sum of flux-corrected NEP rates occurring during the night (H_n), which were then normalized to 24 hours ($ER = \frac{H_n}{24} \sum NEP_t$). We assume that ER occurring during the night is representative of ER occurring over 24 hours. It is important to note that at the spatial scale of this study, unmeasured processes such as the physical flux of oxygen and the calcium carbonate cycle should be expected to influence GEP estimates, regardless of methodology (Holtgrieve et al., 2010; Staehr et al., 2012; Smith, 2013; Macreadie et al., 2017). Nevertheless, after assuming a 1:1 relationship between O_2 production and CO_2 consumption (Gauthier et al., 2018), we refer to NEP interchangeably with carbon capture potential, where the conversion rate of O_2 to C was 0.375. Units normalized to unit depth, given the vertical position of the data loggers, and are presented in $[g\ m^{-2}\ d^{-1}]\ m^{-1}$. It is important to recall that the vertical position of the data loggers was designed to maximize the fidelity of the dissolved oxygen fluctuations caused by photosynthetic and respiratory activity in the study system.

The total yield and carbon content of *U. pinnatifida* and *C. okamuranus* was determined for the 2021 production season. The percent carbon content for the seaweeds were determined from 5 haphazardly selected thalli for each taxa collected on 30 April 2021 for *C. okamuranus*, 14 March 2021 for *U. pinnatifida* from Matsushima Bay, and 15 April 2021 for *U. pinnatifida* from Hirota Bay. The whole thalli was analyzed for the *C. okamuranus* specimens. However, due to the large size of the *U. pinnatifida* specimens, a 20 mm diameter section of the frond was excised from the widest portion of the frond and used in the carbon content analysis. The seawater on the samples were carefully removed from their surfaces by blotting with a paper towel. The samples were dried in an oven (EYELA WFO-500, Tokyo Rikakikai Co., Ltd., Tokyo, Japan) for 12 hours at 80 °C. The dried samples were pulverized with a mortar and pestle, and the carbon content was measured with a CHN analyzer (Flash 2000, Thermofisher Scientific, Waltham, MA, USA).

Data Analysis

Inclement weather conditions caused periods of missing light and wind data. In the case of missing wind values, wind speeds were interpolated by fitting a generalized additive model to the wind, gust, and barometric pressure measurements publicly available from the Japan Meteorological Agency (<https://www.jma.go.jp/>). The smoother for the generalized additive model was

a tensor smooth of the three variables (i.e., wind speed, gust speed, and barometric pressure) with a normal distribution and an identity link-function. The Matsushima Bay observations referenced the wind and gust speed data from the Shiogama station and the barometric pressure from the Ishinomaki station, the Hirota Bay observations referenced the wind and gust speed data from the Kesen'numa station and the barometric pressure from the Ishinomaki station, the Bise Point observations referenced Nago station, and Arikawa Bay and Tainoura Bay observations referenced the Fukue station. No interpolation was needed for the Omura Bay observations. Interpolating light values resulted in poor estimates; however, the light data was only required to estimate day length, therefore the crepuscule function from the R package *maptools* was used to calculate day length for each study site (Bivand and Lewkin-Koh, 2021).

The relative wind exposure of each site was estimated by calculating the wind fetch with the *fetchR* package (Blake, 2020). A total of 108 vectors radiating out from each GPS coordinate (**Table 1**) were initially generated in a 2π radial pattern (see Supplement for details). The upper limit of the vectors was initialized to 10,000 m. Vectors that reached an obstruction (i.e., shoreline) was truncated and the mean values of these vectors were determined. Vectors that were not truncated (i.e., 10,000 m), were included and the numbers of untruncated vectors recorded. The mean wind fetch and number of untruncated vectors is a proxy for the physical conditions (e.g., wind and wave exposure) of the sites.

A generalized linear model (GLM) was used to analyze the effect of site (i.e., Hirota Bay, Matsushima Bay, Arikawa Bay, Tainoura Bay, Omura Bay, and Bise Point) on the daily NEP rates. A Student's t-distribution with an identity-link function was applied to the GLM. The variance for each site was modeled separately using a log-link function. The Student's t-distribution with 3 degrees-of-freedom, a location of 0, and a scale of 2.5 was the prior distribution that was applied to all parameters of the GLM. However, and a Gamma distribution with a shape of 2 and an inverse scale of 0.1 was applied to the degrees-of-freedom parameter for the GLM.

A GLM was also used to analyze the effect of site (i.e., Hirota Bay, Matsushima Bay, Arikawa Bay, Tainoura Bay, Omura Bay, and Bise Point) on the frequency of autotrophic days (i.e., positive rates of net ecosystem production). A Bernoulli distribution with a logit-link function was applied to this model and the prior distributions for the model parameters were similar to those applied in the GEP analysis. We did not include temperature or wind fetch as predictors in either of the GLMs, since they would be confounded with site.

All analyses were done with R version 4.1.2 (R Core Team, 2021) and days with missing values or erroneous measurements were excluded from the analysis. We used the *brms* package (Bürkner, 2017; Bürkner, 2018) to fit the model and ran four Markov chains for at least 4000 iterations each. The posterior distribution and convergence of the Markov chains were assessed visually. We report the mean and standard deviation of the observed rates of GEP, NEP, and ER. These values are unconditional with respect to the model and hence are not

restricted to distributional assumptions. As the data was not normally distributed, our discussion focuses on the conditional means estimated by the GLM, which are conditional on the model and data, and minimize the influence of the outliers. The value of the unconditional and conditional mean may differ in sign and magnitude (especially for values near zero) and likely indicates the effect of the scaled t-distribution of the model on the conditional mean.

RESULTS

The mean temperature observed during the study period across the sites ranged from 8.3 to 21.8°C (**Table 1**) and was lowest at the northern sites; however, the mean temperatures do not reflect yearly means for the seaweed aquaculture farms, since they were only collected during production season of *Undaria pinnatifida* and *Cladosiphon okamuranus*. From the 1726 daily observations, 169 observations were excluded from the analyses if the calculated values of GEP was less than zero or ER was greater than zero. An examination of the daily NEP rates indicated a symmetrical distribution with long tails, hence the use of a scaled t-distribution to model the error term in the GLM. However, the observations for all sites, except for Hirota Bay, (**Figure 2**) had a light negative skew (i.e., long tails to the left) when compared to the results of the model.

In general, the mean daily NEP rates of the observations were negative in all seaweed farms, the natural ecosystem of Omura Bay, and the degraded site of Tainoura Bay (**Table 2**). The NEP rates were most positive at Arikawa Bay and most negative at the

C. okamuranus farm at Bise Point. The mean daily GEP rates of the observations were highest at Bise Point, whereas it was the lowest at the *U. pinnatifida* farm at Hirota Bay. Natural ecosystems and the *U. pinnatifida* farm at Matsushima Bay had intermediate values of GEP and ER and followed similar patterns. ER rates reflected the GEP observations.

The GLMs clearly indicated that NEP and the frequency of autotrophic days differed among sites.

Unlike the mean values of the observations, the conditional means of the NEP from the GLM analysis followed a slightly different pattern. Applying a scaled t-distribution generally made little to no differences between the unconditional mean of the observation and the conditional means of the GLM. However, the long tails in the observations for Matsushima Bay and Omura Bay lead to slightly negative unconditional means (**Table 2**), whereas controlling for extreme values led to positive conditional means (**Table 3**).

These effects are observed because a scaled t-distribution dampens the effect of relatively extreme observations. The GLM results of the NEP observations indicated that the *C. okamuranus* farm at Bise Point had the least positive conditional mean value while the natural *Sargassum* spp. ecosystem at Omura Bay had the most positive conditional mean value (**Figure 2**). Leave-one-out cross validation indicated that the difference in the expected log pointwise predictive density (elpd) between the NEP GLM and a null model (i.e., no explanatory variables) was 143.2 ± 19.9 (mean \pm one standard error), supporting the NEP GLM over the null model (Vehtari et al., 2017). The GLM of the frequency of autotrophy indicated that the *C. okamuranus* farm at Bise Point was most often heterotrophic (26%); the *U. pinnatifida* farm at

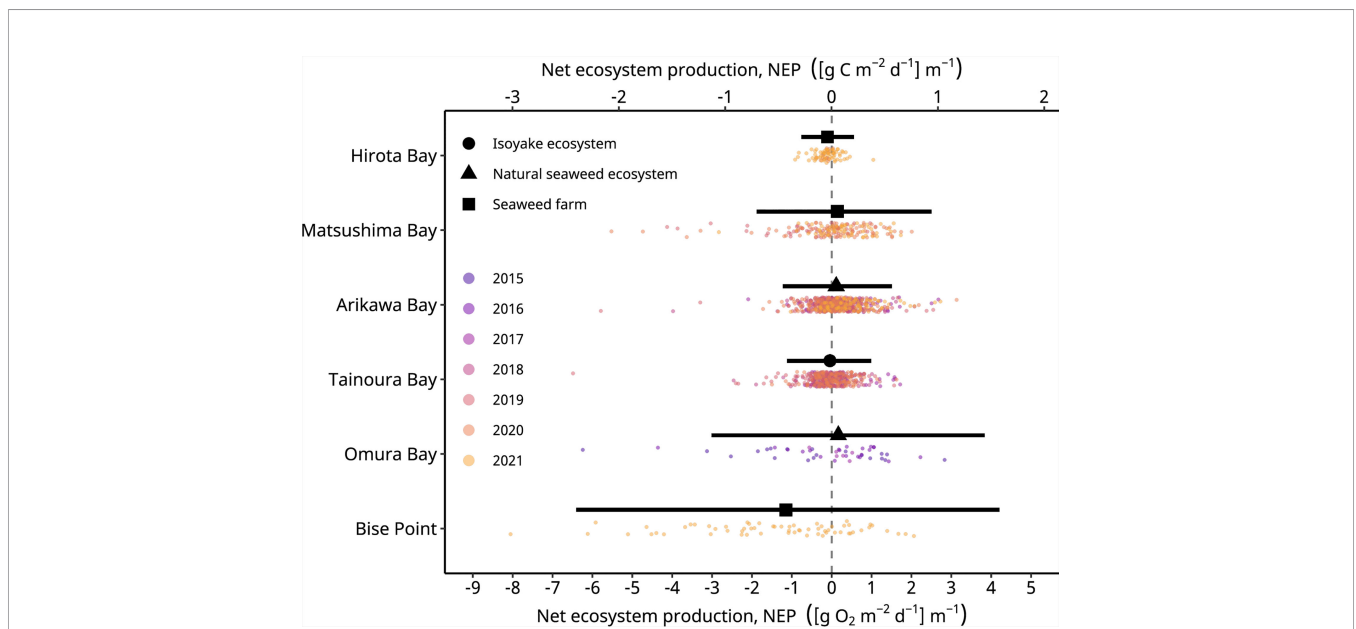


FIGURE 2 | The observed (colored points) and conditional mean of the net ecosystem production (black symbols) rates of the study sites. The black horizontal lines indicate the 95% highest density credible interval of the predicted values. Hirota Bay and Matsushima Bay are the *Undaria pinnatifida* aquaculture farms, Bise Point is the *Cladosiphon okamuranus* aquaculture farm, Arikawa Bay and Omura Bay are sites of the natural *Sargassum* spp. ecosystem, and Tainoura Bay is a site where a seaweed ecosystem has degraded into an isoyake state. The net ecosystem production in O₂ and C are calculated assuming a 1 to 1 molar ratio.

TABLE 2 | The mean and one standard deviation (SD) of the observed rates of gross ecosystem production (GEP), net ecosystem production (NEP), and the ecosystem respiration (ER) determined from three seaweed aquaculture farms (*Undaria pinnatifida* and *Cladosiphon okamuranus*) and three natural ecosystems in Japan.

Site	Species or State	GEP		NEP		ER	
		Mean	SD	Mean	SD	Mean	SD
Hirota Bay, Iwate	<i>Undaria pinnatifida</i>	0.39	0.39	-0.11	0.30	0.50	0.45
Matsushima Bay, Miyagi	<i>Undaria pinnatifida</i>	1.94	1.27	-0.05	1.12	1.98	1.70
Arikawa Bay, Nagasaki	<i>Sargassum</i> spp.	1.43	0.92	0.15	0.70	1.28	0.84
Tainoura Bay, Nagasaki	isoyake	0.77	0.54	-0.06	0.61	0.83	0.57
Omura Bay, Nagasaki	<i>Sargassum</i> spp.	3.73	1.91	-0.15	1.62	3.87	2.57
Bise Point, Okinawa	<i>Cladosiphon okamuranus</i>	3.87	3.01	-1.41	2.07	5.28	3.11

Rows are ordered from the north to south. Units of GEP, NEP, and ER are in $[g O_2 m^{-2} day^{-1}] m^{-1}$.

TABLE 3 | The mean and 95% highest density credible interval for the expectations of the generalized linear model (GLM) of the net ecosystem production (NEP) and the autotrophic frequency.

Site	State	NEP GLM			Autotrophic frequency GLM		
		Mean	Lower	Upper	Mean	Lower	Upper
Hirota Bay, Iwate	<i>Undaria pinnatifida</i>	-0.11	-0.16	-0.06	0.34	0.24	0.44
Matsushima Bay, Miyagi	<i>Undaria pinnatifida</i>	0.11	-0.01	0.22	0.56	0.49	0.63
Arikawa Bay, Nagasaki	<i>Sargassum</i> spp.	0.11	0.07	0.15	0.59	0.55	0.63
Tainoura Bay, Nagasaki	isoyake	-0.05	-0.09	-0.02	0.42	0.37	0.46
Omura Bay, Nagasaki	<i>Sargassum</i> spp.	0.16	-0.20	0.54	0.59	0.46	0.73
Bise Point, Okinawa	<i>Cladosiphon okamuranus</i>	-1.10	-1.59	-0.65	0.26	0.16	0.37

Rows are ordered from north to south. Units of NEP are in $[g O_2 m^{-2} day^{-1}] m^{-1}$.

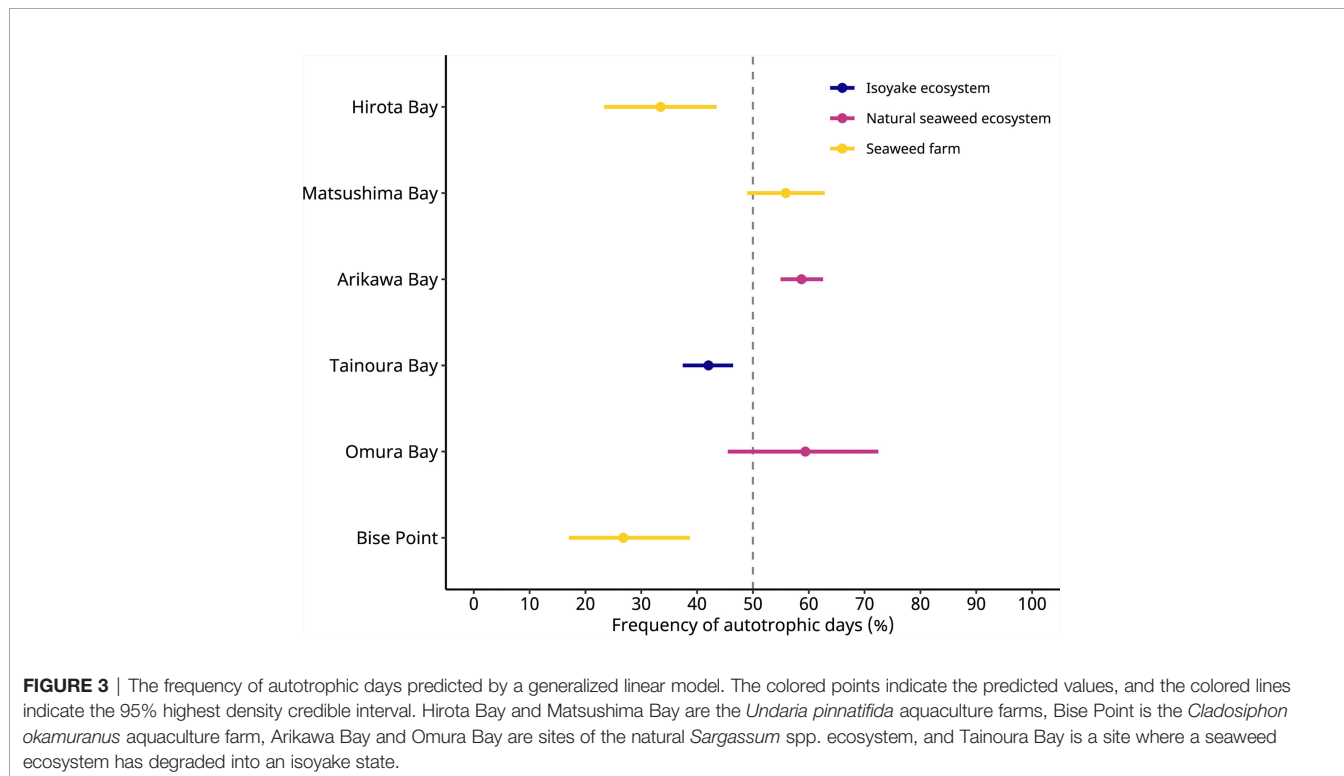


FIGURE 3 | The frequency of autotrophic days predicted by a generalized linear model. The colored points indicate the predicted values, and the colored lines indicate the 95% highest density credible interval. Hirota Bay and Matsushima Bay are the *Undaria pinnatifida* aquaculture farms, Bise Point is the *Cladosiphon okamuranus* aquaculture farm, Arikawa Bay and Omura Bay are sites of the natural *Sargassum* spp. ecosystem, and Tainoura Bay is a site where a seaweed ecosystem has degraded into an isoyake state.

Hirota Bay was the second most heterotrophic site (34%; **Figure 3** and **Table 3**). In contrast, the two *Sargassum* sp. ecosystems at Arikawa Bay and Omura Bay, and the *U. pinnatifida* farm at Matsushima Bay were most often autotrophic (> 50%). The GLM

of the autotrophic frequency had an elpd of 24.1 ± 7.6 , indicating support over the null model.

The total yield for each of the farms are known, and was 120, 40, and 6.8 tons for the *U. pinnatifida* farms in Hirota Bay,

Matsushima Bay, and the *C. okamuranus* farm at Bise Point, respectively (Table 4). The intensity of the carbon yield was calculated after determining the % carbon content of the cultivated seaweeds and ranged from 3.7 to 14.1 g C m⁻² (Table 4).

DISCUSSION

An ultimate goal would be to estimate the carbon sequestration rate of seaweed farms; however, without information regarding the export and import of carbon from allochthonous sources (see Gallagher et al., 2022), as well as the knowing the fate of cultivated seaweed, we can only estimate the carbon sequestration potential of our study sites. Nevertheless, we provide field estimates of the carbon sequestration potential of seaweed farm sites in Japan and also provide estimates of natural ecosystems and a degraded ecosystem for context. We expected NEP to be more positive in seaweed farms compared to the natural and degraded ecosystems, since natural ecosystems are expected to be primarily heterotrophic (Gallagher et al., 2022) and degraded ecosystem are deficient in primary producers, but our results were mixed and given the limitations of the data the model results provided should not be interpreted strictly as one system functioning more efficiently than the other. Nevertheless, the key finding of this study was that the field data clearly shows how seaweed aquaculture may not necessarily lead to carbon capture, and the potential to capture carbon may depend on taxa. For example, the conditional means of NEP for the *U. pinnatifida* farm at Matsushima Bay was 0.041 [g C m⁻² d⁻¹] m⁻¹ (Figure 2, Table 3). Among the seaweed farms, this site had the second highest rate of GEP (Table 2) and was autotrophic 56% of the time (Figure 3 and Table 3). In contrast, the *C. okamuranus* aquaculture farm at Bise Point had the highest rate of GEP among the aquaculture farms, however the NEP was most negative (Figure 1 and Tables 2, 3), and the aquaculture farm was only autotrophic 26% of the time (Figure 2 and Table 3).

Within taxa, the two *U. pinnatifida* seaweed farms clearly differed in NEP, where the conditional mean difference NEP between the Hirota Bay (-0.041 [g C m⁻² d⁻¹] m⁻¹) and Matsushima Bay (+0.041 [g C m⁻² d⁻¹] m⁻¹) differed by aquaculture farms was -0.083 (-0.13 to -0.038) [g C m⁻² d⁻¹] m⁻¹ (95% highest density credible interval). However, the intensity of carbon yield at Hirota Bay was 3.8 times greater than at Matsushima Bay (Table 4). We speculate that greater carbon yield intensities

occurring at the Hirota Bay farm stimulated the release of dissolved organic carbon and/or particulate organic carbon by *U. pinnatifida* (Wada et al., 2008; Chen et al., 2020). Although some of this material is exported out of the ecosystem (Krause-Jensen and Duarte, 2016), the release of this material can result in locally increased rates of ecosystem metabolism, through incorporation into the food-web (Sosik and Simenstad, 2013; Renaud et al., 2015; Paine et al., 2021). Additionally, it is unlikely that the *U. pinnatifida* produced at the aquaculture farms influenced the results, since both farms used the same cultivar provided by the authors (Sato et al., 2021a). Although the carbon yield intensity was also higher at Hirota Bay, compared to Matsushima Bay, evidence suggests that these differences were due to natural variation (Gao et al., 2014).

The GLM also indicated the *C. okamuranus* farm at Bise Point was heterotrophic (Table 3). In contrast to *U. pinnatifida*, which are cultivated on ropes, *C. okamuranus* are cultivated on nets (Sato et al., 2021b). However, the final yield intensity (i.e., 28 g m⁻²), was within the range of observed for *U. pinnatifida* at Hirota and Matsushima Bay (i.e., 52 g m⁻² and 15 g m⁻², respectively). Therefore, it is possible that stocking density may also influence the NEP of *C. okamuranus* farms, however since we could only examine one *C. okamuranus* farm site, the details remain to be revealed. Given that the *C. okamuranus* farm is deployed in the lagoon of a coral reef, characteristics of the ecosystem, such as the presence of corals and seagrasses nearby, may have led to a low NEP. Coral reef ecosystems were shown to be primarily heterotrophic in a number of studies (Falter et al., 2008; Miller et al., 2009; McGillis et al., 2011).

The potential for seaweed aquaculture farms to capture carbon from the environment and contribute to the mitigation of climate change was noted in a number of studies (Chung et al., 2017). It was suggested that seaweed aquaculture could potentially remove 1 g C m⁻² d⁻¹ from the environment based on aquaculture yields (Duarte et al., 2017; Froehlich et al., 2019), which is 1 to 2 orders of magnitude higher than our yield estimates (Table 4). A pioneering study on carbon flux in seaweed farms off the coast of the town Lidao, China, also suggested that seaweed farms could absorb 1.2 g C m⁻² d⁻¹ (Jiang et al., 2013). Based on the conditional mean of NEP from the GLM analysis, the potential carbon capture rate was -0.041, +0.041, -0.41 [g C m⁻² d⁻¹] m⁻¹, for Hirota Bay, Matsushima Bay, and Bise Point, respectively.

There is an important caveat to these estimates of the seaweed farms examined in our study. Recall that measurements are limited to the production season of the seaweed farms (i.e., October to April), and do not provide a range of rates that would

TABLE 4 | The total yield and estimated amount of carbon captured by the seaweed farms at Hirota Bay, Matsushima Bay, and Bise Point during their respective cultivation season.

Site	Species	Yield (ton dry)	Farm area (m ²)	% Carbon content	Carbon yield intensity (g C m ⁻²)	Production duration (days)	Carbon capture rate (g C m ⁻² d ⁻¹)
Hirota Bay	<i>Undaria pinnatifida</i>	120	2,292,480	27.0	14.1	129	0.110
Matsushima Bay	<i>Undaria pinnatifida</i>	40	2,721,800	25.2	3.7	145	0.026
Bise Point	<i>Cladosiphon okamuranus</i>	6.8	246,581	13.3	3.7	105	0.035

occur over a year. Inclusion of the off-season (i.e., summer to autumn), would likely lead to a decrease in the frequency of autotrophic days, since respiration rates are higher during this period (Bordeyne et al., 2020). Macroalgae ecosystems are generally heterotrophic (Gallagher et al., 2022), and the GLM examining the frequency of autotrophic days also provides some support to these observations (**Figure 3**). Hence, we suggest that the NEP of seaweed farms are not exceptionally superior to natural ecosystems. Moreover, the limited production period of seaweed aquaculture must be considered when estimating their potential as a carbon mitigating system.

Since we measured oxygen production did not assess lateral flux of carbon, calcification rates, or the production of dissolved organic carbon our estimates of the potential to capture carbon should be considered carefully. Consider that at Bise Point, metabolic activity of nearby seagrasses may have influenced our oxygen observations. In seaweed ecosystems a significant portion of captured carbon is expected to be exported to adjacent ecosystems or as far as the deep ocean (Duarte and Cebrián, 1996; Krause-Jensen and Duarte, 2016; Ortega et al., 2019). Indeed, up to 50% of carbon captured by a *Sargassum horneri* ecosystem is believed to be exported out of the ecosystem (Watanabe et al., 2020). Additionally, many calcifying species produce calcium carbonate, with a net release of CO₂ into the environment during the calcification process, which can affect the net flux of CO₂, but not O₂ into the atmosphere (Frankignoulle et al., 1994).

In terms of blue carbon strategies, seaweed farms provides a large opportunity to mitigate climate change, given that it is easier and cheaper to scale-up, in contrast to the restoration of ecosystems, such as seagrass ecosystems (Gattuso et al., 2018; Lovelock and Duarte, 2019; Wu et al., 2020) and seaweed ecosystems (Eger et al., 2022). The net flux of carbon into seaweed farms was demonstrated in a number of studies (Tang et al., 2011; Jiang et al., 2013). However, to serve as a mitigation strategy, the carbon captured by seaweed aquaculture must be stored over long time scales. If all the seaweed produced by the farms could have been protected from conversion to CO₂, 43,384 kg of carbon would have been stored during the 2021 season (**Table 4**). Although we support past studies that suggests seaweed ecosystems can play a significant role in the mitigation of climate change and provide enough carbon capture capability to be included in carbon offset mechanisms, there remains a number of key questions that must be addressed before governments rush to develop seaweed farms to mitigate and offset carbon emissions. Uninformed expansion of seaweed farms can potentially cause a negative effect on surrounding and underlying ecosystems (Campbell et al., 2019). For example, in shallow water seaweed farms, the cultivation of carrageenophytes (e.g., *Kappaphycus* and *Euclidean*) led to reductions in productivity and shoot density of the underlying seagrass ecosystems (Eklöf et al., 2005; Kelly et al., 2020; Moreira-Saporiti et al., 2021). Light reduction and the removal of nutrients by seaweed farms change the composition of phytoplankton (Jiang et al., 2020; Aldridge et al., 2021). Water flow and tidal exchange rates can decrease leading to increased

sedimentation rates and poor water exchange (Zeng et al., 2015). The expansion of seaweed farms can be associated with increased flux of plastic materials from discarded and lost equipment (e.g., synthetic polymer ropes) and plastic particles, exacerbating existing problems with marine plastic pollution (Derraik, 2002; Andrady, 2011; Krüger et al., 2020). An increase in the albedo of the sea surface may also occur, since seaweeds are better able to reflect short-wave radiation than the sea surface, enhancing local cooling of the environment (Bach et al., 2021). Steps towards a compromise between environmental disturbance and carbon capture *via* seaweed farms can be found in the proper site selection and monitoring of environmental conditions to optimize the timing of the grow-out period. For example, kelps cultured in exposed conditions exhibit the best growth performance with increased carbon content in their tissues (Peteiro and Freire, 2013; Visch et al., 2020). On the other hand, culturing seaweeds in nutrient limited waters leads to nutrient stress and a subsequent loss in seaweed biomass and a net increase in dissolved organic matter in the culture area (Yoshikawa et al., 2001; Paine et al., 2021). For temperate species, timing the grow-out and harvest phase is critical as warmer surface temperatures promote the growth of fouling organisms (Visch et al., 2020).

Reliable long-term field observations of carbon capture rates by macroalgae ecosystems remains scarce. Presently, most assessments of carbon capture rates rely on extrapolating from chambered photosynthesis experiments of using phytoelements or the whole thallus of macroalgae, measuring the CO₂ flux at the air-sea interface and the O₂ flux at the water-sediment interface using eddy covariance techniques (e.g., Berg et al., 2022), extrapolate from simulations and limited in temporal scope (e.g., Watanabe et al., 2020), extrapolate from O₂ mass-balances (e.g., Champenois and Borges, 2012; Hinode et al., 2020), measuring the O₂ flux at the water-sediment, and isotopic measurements (e.g., Holtgrieve et al., 2010; Staehr et al., 2012; Hoellein et al., 2013). All methods have both advantages and disadvantages, that must be considered prior to data interpretation. The method we used was comparatively inexpensive and can provide a long and continuous time-series of measurements, but introduces bias due to the assumptions used to estimate air-water flux of oxygen, the horizontal and vertical heterogeneity of dissolved oxygen concentrations and flux (Berg et al., 2022), and the assumption that night-time respiration adequately describes respiration rates during the day. However, all methods suffer from the inability to assess the carbon flux into and out of the system of interest and are unable to precisely assess whether or not the system is a carbon donor or carbon receiver (Hill et al., 2015). Methods to correct for advection and include more ecosystem level processes could enhance the accuracy of carbon flux estimates (Chung et al., 2013; Gruber et al., 2017; Gallagher et al., 2022). More critically, macroalgae can secrete organic carbon and about 18 to 62% of their productivity may be secreted as dissolved carbon, which can be respired by microbes (Wada et al., 2007; Wada et al., 2008; Paine et al., 2021).

The potential of seaweed farms to mitigate climate change remains to be determined. The effectiveness of aquaculture farms

to capture and remove carbon for relevant time-scales remains a challenge. Despite this, seaweed farms are still highly valuable for their contribution to the livelihood of coastal communities and have lesser detrimental impacts to the environment compared to other forms of aquaculture (Walls et al., 2017; Visch et al., 2020). We believe that the potential to capture carbon will not be homogenous across species and location, and that more studies to address carbon flux at organismal and ecosystem scales remain to be conducted. Despite these uncertainties, land-based aquaculture of seaweeds and the development of technology to lengthen the production season and yield should provide seaweed aquaculture with a unique opportunity to contribute to the mitigation of climate change (e.g., Sato et al., 2021a). However, the fate of the produced seaweeds will define the effectiveness of these strategies. Finally, detailed measurements of carbon capture from the aquaculture farms of carrageenophytes, chlorophytes such as *Ulva* spp. and *Monostroma* spp., some species of *Pyropia* spp., *Saccharina* spp., and *Sargassum* spp., are worthy of future investigation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

YS, GN, AT, RT, and HE conceptualized and supervised the research, YS, GN, AT, and RT acquired funding support, YS, GN,

and DB prepared the original draft of the manuscript, YS, GN, AT, RT, HE, and DB reviewed and edited the manuscript. YS, GN, AT, DB, AK, YI, KH, ST, YM, and KT conducted the research and collected data, YS, GN, DB, AK, YI, KH, ST, YM, and KT analyzed the model and prepared figures for the manuscript. GN administered the project. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.861932/full#supplementary-material>

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