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*Supplement of*

# Structural complexity and benthic metabolism: resolving the links between carbon cycling and biodiversity in restored seagrass meadows

**Theodor Kindeberg et al.**

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**Table S1 Deployment of eddy covariance and benthic chambers.** Coordinates are latitude and longitude in decimal degrees (WGS84) of the eddy covariance (EC) frame. Benthic chambers were deployed within five meters downstream of the EC. Start and end indicates the date and time (m-d-yy hh:mm, Central European Time) when deployments and incubations occurred, and Time is the duration (hh:mm).

| | | Eddy covariance | | | Benthic chambers | | |
|---|---|---|---|---|---|---|---|
| **Site** | **Coordinates** | **Start** | **End** | **Time** | **Start** | **End** | **Time** |
| **Bare** | N 58.231996<br>E 11.400655 | 7-5-22 16:30 | 7-7-22 17:30 | 49.00 | 7-7-22 13:32 | 7-7-22 17:25 | 3.01±0.03 |
| **3 yr** | N 58.231746<br>E 11.400830 | 7-16-22 13:30 | 7-18-22 11:30 | 46.00 | 7-17-22 13:02 | 7-17-22 16:17 | 3.08±0.02 |
| **7 yr** | N 58.231611<br>E 11.400667 | 7-8-22 13:30 | 7-10-22 09:30 | 44.00 | 7-8-22 13:32 | 7-8-22 16:52 | 2.85±0.02 |
| **Nat** | N 58.231669<br>E 11.399889 | 7-18-22 13:30 | 7-20-22 09:30 | 44-00 | 7-19-22 12:20 | 7-19-22 15:37 | 2.91±0.01 |

**Table S2 Abiotic conditions at the different sites.** Mean and standard deviation in parenthesis (*sd*) of photosynthetic active radiation (PAR), temperature, flow velocity, ambient dissolved oxygen (DO), salinity and turbidity. NTU refers to nephelometric turbidity unit. Letters in superscript indicate Tukey's HSD post hoc test ($p<0.05$) following one-way ANOVA.

| Site | PAR | Temp | Flow | DO | Sal | Turbidity |
|---|---|---|---|---|---|---|
| | µmol $m^{-2}$ $s^{-1}$ | °C | cm $s^{-1}$ | µM | - | NTU |
| **Bare** | 233.09[a] | 17.95[a] | 3.09[a] | 303.96[a] | 24.7[a] | 1.67[a] |
| | (*251.75*) | (*0.73*) | (*1.00*) | (*22.13*) | (*0.0*) | (*2.48*) |
| **3 yr** | 201.70[a] | 18.85[b] | 3.75[b] | 260.09[b] | 28.8[b] | 0.97[a] |
| | (*235.25*) | (*0.48*) | (*1.51*) | (*36.90*) | (*0.1*) | (*2.91*) |
| **7 yr** | 239.76[a] | 18.89[b] | 8.33[c] | 263.47[bc] | 24.8[a] | 0.50[a] |
| | (*257.00*) | (*0.68*) | (*3.25*) | (*30.37*) | (*0.00*) | (*0.82*) |
| **Nat** | 207.61[a] | 19.83[c] | 8.24[c] | 281.14[c] | 28.8[b] | 16.2[b] |
| | (*233.82*) | (*0.73*) | (*3.19*) | (*47.88*) | (*0.10*) | (*8.86*) |

**Table S3 Ambient seawater chemistry conditions at each site measured at the onset of incubations.** Temperature (Temp) is in °C whereas salinity (Sal), pH and aragonite saturation state ($\Omega_{Ar}$) are unitless. Dissolved oxygen (DO), total alkalinity (TA), dissolved inorganic carbon (DIC), dissolved inorganic nitrogen (DIN), total nitrogen (TN) and dissolved organic carbon are in µmol $kg^{-1}$ seawater. Dissolved $PO_4^{3+}$ was below detection limit in all samples and is not shown. Values are site mean±SE, n=6 per site.

| Site | Sal | Temp | DO | TA | pH | DIC | $\Omega_{Ar}$ | DIN | TN | DOC |
|---|---|---|---|---|---|---|---|---|---|---|
| **Bare** | 24.8±0.0 | 19.3±0.0 | 183±7 | 2098±4 | 8.35±0.03 | 1779±19 | 3.7±0.2 | 10.8±0.1 | 20.3±1.6 | 280±18 |
| **3 yr** | 29.9±0.0 | 19.1±0.0 | 260±2 | 2217±1 | 8.26±0.02 | 1891±11 | 3.7±0.1 | 11.7±0.2 | 14.0±0.7 | 241±8 |
| **7 yr** | 24.8±0.0 | 19.4±0.0 | 255±2 | 2099±3 | 8.38±0.02 | 1762±13 | 3.9±0.1 | 10.9±0.1 | 13.2±0.3 | 240±8 |
| **Nat** | 28.7±0.0 | 19.8±0.0 | 274±2 | 2191±1 | 8.11±0.01 | 1953±3 | 2.8±0.1 | 11.7±0.1 | 16.3±0.9 | 259±20 |

**Table S4 Trait-by-species matrix using fuzzy coding.** Feeding modes are suspension feeder (SuspFed), surface detritivore (SurfDet), burrowing detritivore (BurrDet), Predator (Pred), grazer/herbivore (GrazHerb) and omnivore (Omni). Bioturbation modes are biodiffusors (Biodiff), upward conveors (Upconv), downward conveyors (Downconv), surficial modifier (Surfmod), Regenerator (Reg) or not relevant (NotRel). Living habits are free living (Free), burrow dwelling (BurrDwell), tube dwelling (TubeDwell) or attached (Attach). Regarding the calcification trait, species with exoskeletons mostly comprised of chitin (e.g. shrimps and amphipods) are assigned a score of 1.5 in each mode whereas species with a high proportion of $CaCO_3$ in their shells are assigned full score.

| | **Feeding mode** | | | | | | **Bioturbation mode** | | | | | | **Movement mode** | | | | | **Living habit** | | | | **Env. Position** | | **Calcification** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Susp Fed | SurfDet | BurrDet | Pred | GrazHerb | Omni | Biodiff | Upconv | Downconv | Surfmod | Reg | NotRel | Sessile | Burrower | Crawler | Swimmer | Drifter | Free | BurrDwell | TubeDwell | Attach | Epifaunal | Infaunal | Calc. | Non-calc. |
| Ascidiacea spp. | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 3 |
| *Athanas nitescens* | 0 | 0.75 | 0 | 0.75 | 0.75 | 0.75 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 |
| Balanidae sp.1 | 2.5 | 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 3 | 0 |
| *Bittium reticulatum* | 0 | 3 | 3 | 3 | 3 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| Bryozoa | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 3 | 0 |
| *Capitella capitata* | 0 | 1.5 | 1.5 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 |
| *Carcinus maenas* | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 1.5 | 1.5 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Cerastoderma edule* | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1.5 | 1.5 | 0 | 0 | 1.5 | 1.5 | 0 | 0 | 0 | 3 | 3 | 0 |
| Chironomida | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 |
| *Ericthonius difformis* | 1.5 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1.5 | 1.5 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Eualus cranchii* | 0 | 1.5 | 0 | 0 | 1.5 | 0 | 1.5 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 1.5 | 1.5 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Eurytemora* sp. | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Gammarus locusta* | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Gobius niger* | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| Halacaridae sp.1 | 0 | 1.5 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| *Hydrobia neglecta* | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Hydrobia* sp.1 | 0 | **3** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Lepidonotus squamatus* | 0 | 0 | 0 | 1.5 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0.5 | 2.5 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| *Littorina* sp.1 | 1.5 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Marshallora adversa* | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Microdeutopus gryllotalpa* | 0 | 1 | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Monocorophium insidiosum* | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Musculus subpictus* | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 3 | 0 |
| *Mysis relicta* | 1.5 | 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1.5 | 1.5 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 |
| *Mytilus edulis* | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 3 | 0 |
| *Nassarius reticulatus* | 0 | 1.5 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| Nematoda | 0 | 1.5 | 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | | 3 | 1.5 | 1.5 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 |
| Nereididae | 0.2 | 1.8 | 0 | 0.5 | 0 | 0.5 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 |
| *Pagurus bernhardus* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Palaemon adspersus* | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 1.5 | 1.5 |
| Phyllodocidae sp.1 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 |
| *Platynereis dumerilii* | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.5 | 1.5 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| *Pusillina inconspicua* | 0 | 1.5 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Pusillina sarsii* | 0 | 1.5 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Rissostomia membranacea* | 0 | 1.5 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0.75 | 0.75 | 0.75 | 0.75 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| *Sagartiogeton viduatus* | 1.5 | 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 1.5 | 0 | 0 | 1.5 | 3 | 0 | 0 | 3 |
| *Scoloplos armiger* | 0 | 1.5 | 1.5 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 |
| *Spirorbis* sp.1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 3 | 0 |

**Table S5 Model output of linear mixed-effects model.** Model output parameters of linear mixed-effects model of absolute oxygen flux as a function of abiotic factors.

Model: |O2_flux| ~ Seabed_PAR + Flow_vel + Temp + Turbidity + (1 | Site)

| *Fixed effects* | Estimate | SE | df | *t* | p |
|---|---|---|---|---|---|
| Intercept | 3.35 | 1.01 | 2 | 3.30 | 0.06 |
| Seabed_PAR | 0.35 | 0.20 | 174 | 1.77 | 0.08 |
| Flow_vel | 1.02 | 0.28 | 176 | 3.63 | $3.7 \times 10^{-4}$ |
| Temp | -0.19 | 0.31 | 138 | -0.60 | 0.55 |
| Turbidity | -0.82 | 0.32 | 111 | -2.56 | 0.01 |
| *Random effects* | Variance | SE | | LRT | |
| Site | 3.97 | 0.15 | | 20.93 | $4.8 \times 10^{-6}$ |
| Residual | 6.54 | 0.19 | | | |

**Table S6 Taxonomic and functional diversity metrics for benthic fauna.** Biomass is dry weight of pooled samples in g $m^{-2}$ and Abundance is individuals $m^{-2}$. Taxonomic and functional diversity indices are transformed to effective numbers such that $H_{eff}$ = log(H') and $FD_{eff}$ = 1/(1-RaoQ). Note that the division between infauna and epifauna depends on sampling method, see main text for details. All values except for biomass are site mean±SE, n=6 per site for infauna and n=3 per site for epifauna. Biomass is pooled per site and values represent total biomass per site.

| | Site | Biomass | Abundance | Species | $H_{eff}$ | J' | FGR | FRic | FEve | $FD_{eff}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Bare** | 1.14 | 2093±951 | 2±0 | 2.14±0.40 | 0.92±0.03 | 2±0 | 0.03±0.03 | 0.84±0.10 | 1.01±0.01 |
| I | **3 yr** | 3.17 | 17593±3470 | 6±1 | 2.35±0.30 | 0.47±0.08 | 4±1 | 0.51±0.19 | 0.57±0.06 | 1.03±0.01 |
| N | **7 yr** | 3.96* | 5735±1305 | 7±1 | 4.87±0.95 | 0.81±0.03 | 5±1 | 0.48±0.10 | 0.71±0.03 | 1.05±0.00 |
| F | **Nat** | 2.37 | 7983±2661 | 7±1 | 4.41±0.57 | 0.80±0.05 | 5±1 | 0.54±0.13 | 0.61±0.06 | 1.04±0.01 |
| | **Bare** | n.d. | n.d. | n.d. | n.d. | n.d. | n.d. | n.d. | n.d. | n.d. |
| E | **3 yr** | 6.47 | 816±38 | 15±1 | 8.88±0.59 | 0.80±0.01 | 11±0 | 0.22±0.03 | 0.59±0.02 | 1.04±0.00 |
| P | **7 yr** | 5.88 | 1145±180 | 15±3 | 7.38±1.07 | 0.75±+0.02 | 11±2 | 0.19±0.09 | 0.63±0.01 | 1.03±0.00 |
| I | **Nat** | 15.53 | 1113±398 | 18±3 | 10.93±2.35 | 0.83±0.02 | 12±3 | 0.32±0.20 | 0.68±0.02 | 1.04±0.01 |

* A disproportionally large gastropod specimen contributing 86% of total biomass was removed from this number. With this specimen included, the biomass in 7 yr was instead 27.69 g/m2.

**Table S7 Photosynthetic parameters.** Photosynthetic parameters at the different sites, including maximum photosynthesis ($P_m$), initial slope (alpha), irradiance at compensation ($I_k$), respiration (R) and the adjusted $R^2$ of the fitted curves.

| Site | $P_m$ | α | $I_k$ | R | Adj. $R^2$ |
|---|---|---|---|---|---|
| **Bare** | 2.52 | 0.007 | 379.70 | 0.93 | 0.74 |
| **3 yr** | 8.26 | 0.024 | 345.60 | 3.47 | 0.45 |
| **7 yr** | 6.68 | 0.069 | 96.54 | 3.52 | 0.59 |
| **Nat** | 9.33 | 0.088 | 106.30 | 4.88 | 0.58 |

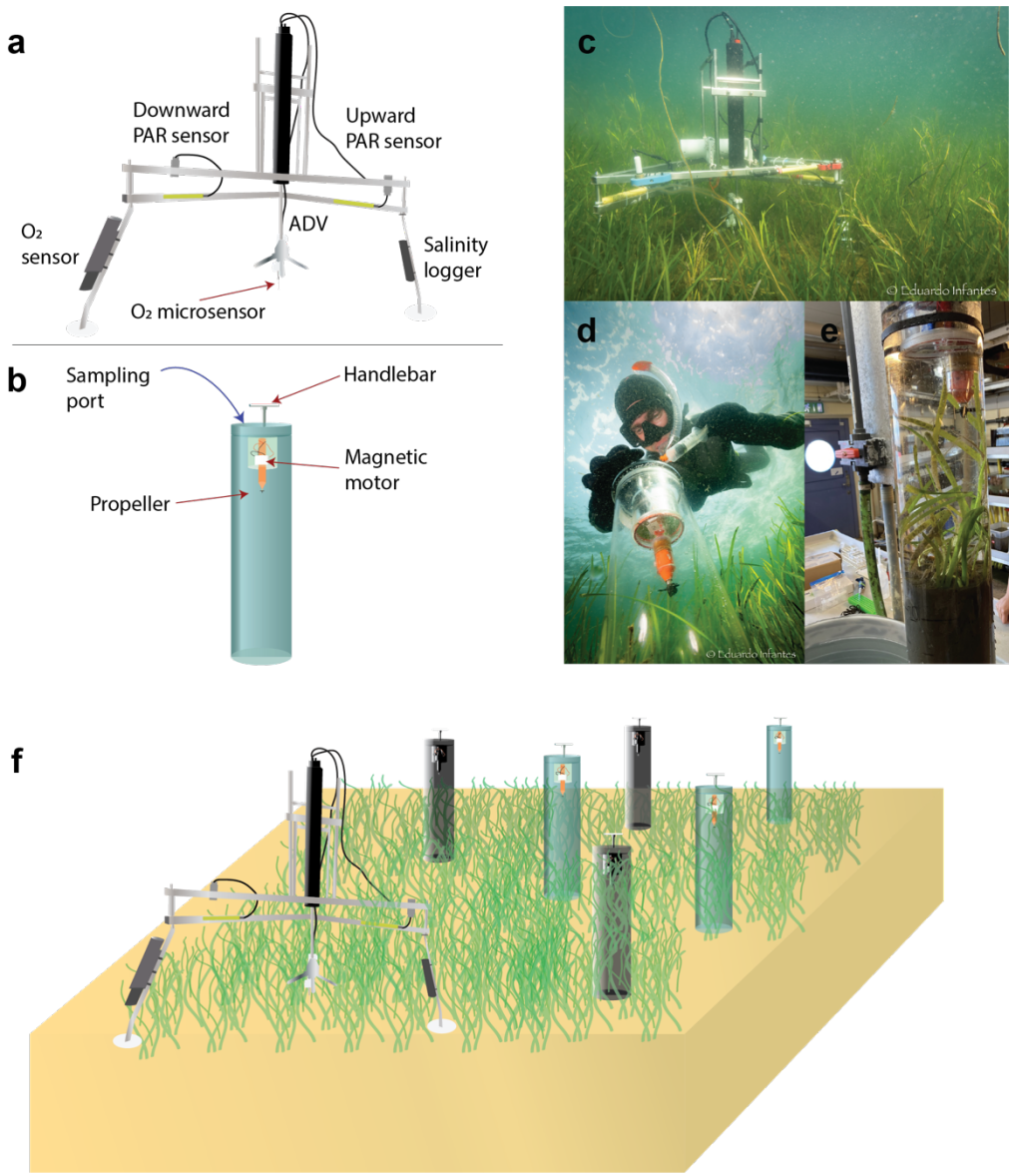


**Figure S1 Schematic illustration of benthic flux measurements.** a) eddy covariance (EC) outlining the most important components and b) benthic chambers (BC) showing a transparent chamber used for light incubations. c) shows the EC system deployed in the Natural meadow; d) shows the first author drawing a seawater sample from a BC in the field; e) shows an intact BC core used for lab incubations and f) shows the approximate deployment of EC and BC in the field. Light (n=3) and dark (n=3) benthic chambers were randomly distributed with 1 m distance of each other. Chambers were deployed less than 5 meters downstream of the EC as to not influence the footprint of the EC.

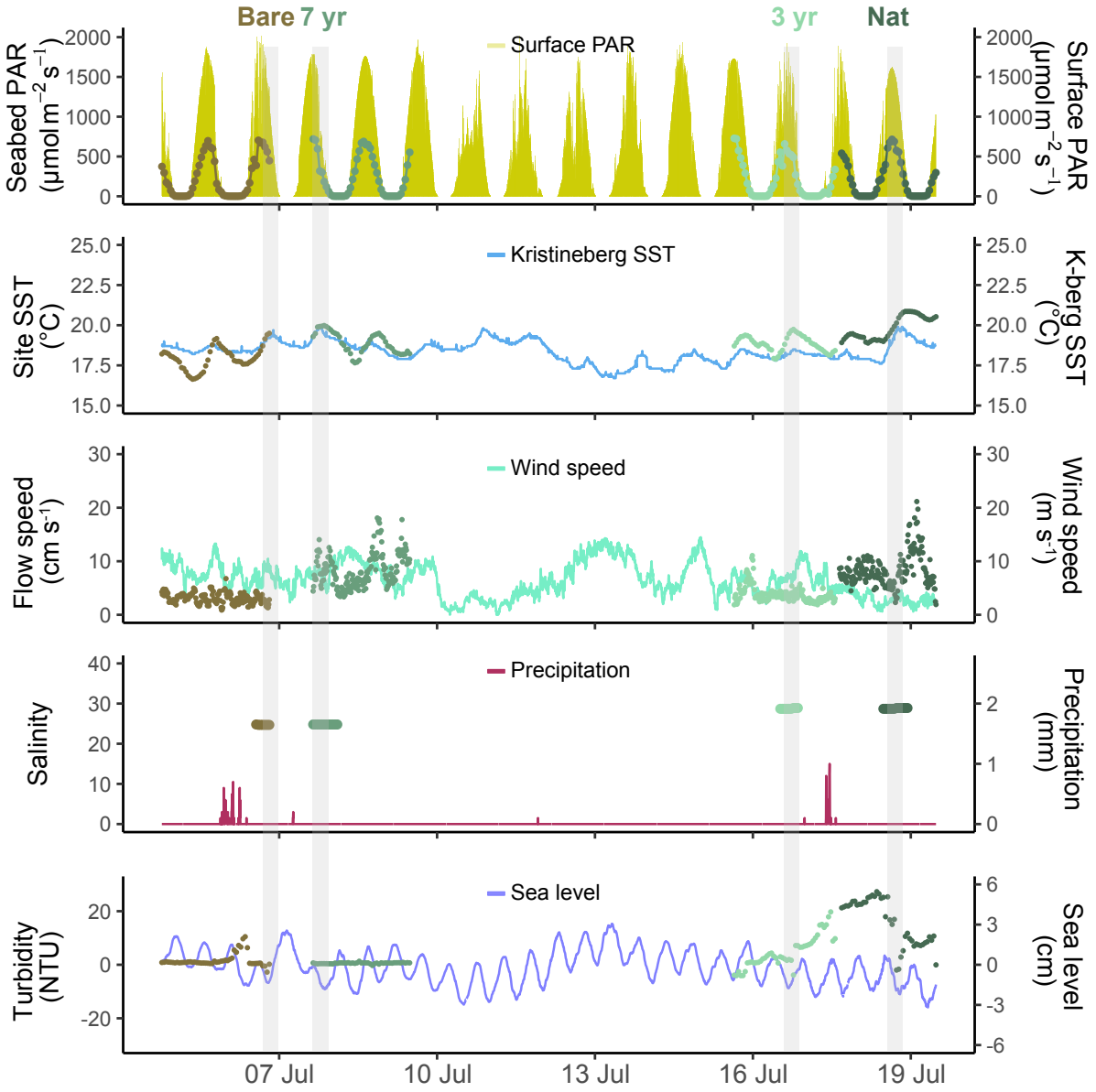


**Figure S2 Weather and continuous abiotic measurements.** Measurements during EC deployments (left y axes) and weather and oceanographic data (right y axes). Weather and oceanographic data were obtained from the weather station located at Kristineberg Marine Research Station (https://www.weather.loven.gu.se/kristineberg/en/data.shtml). Grey areas indicate benthic chamber deployments.

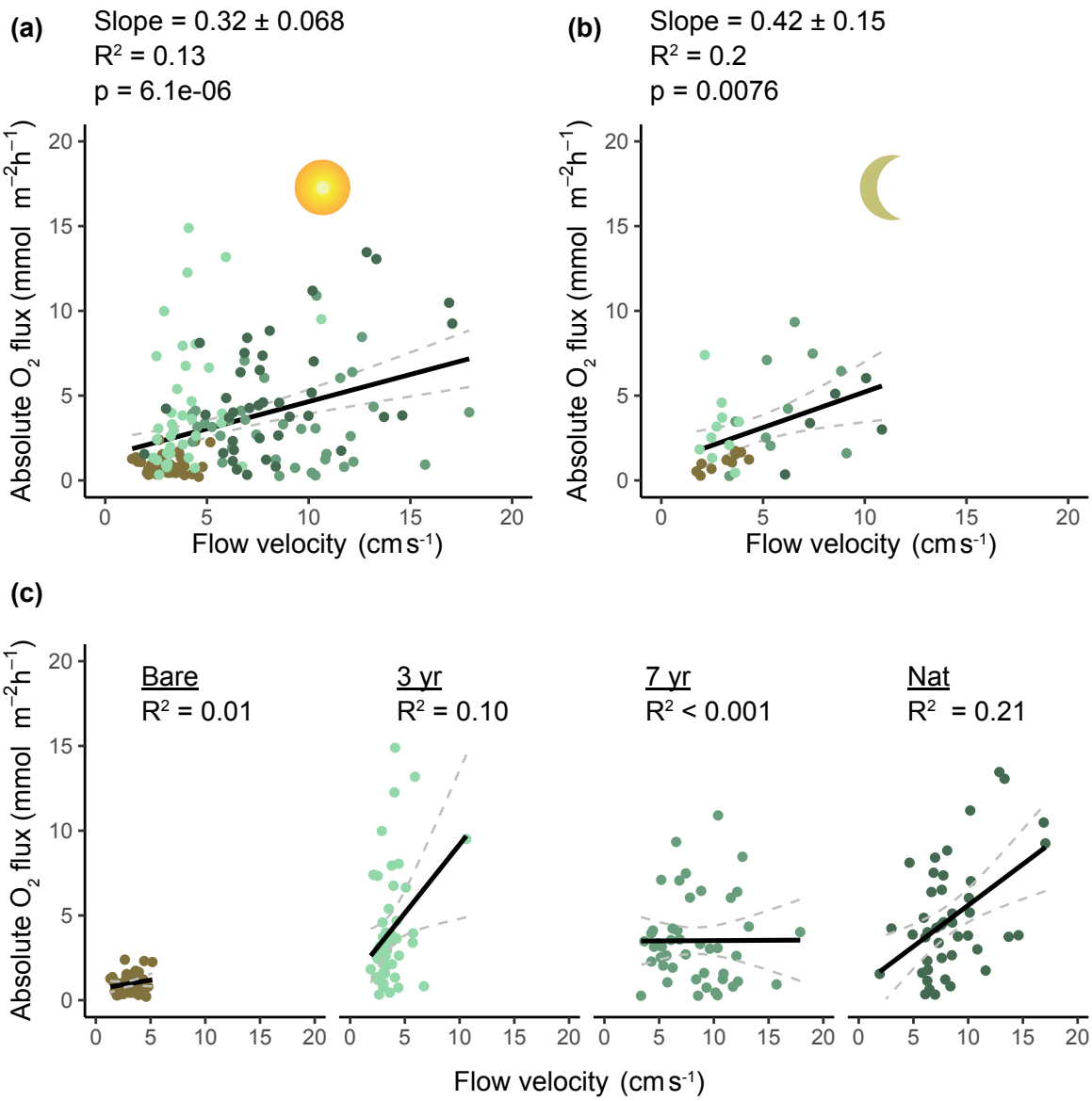


**Figure S3 Linear regression analyses of flow velocity and absolute oxygen fluxes.** a) shows daytime values and b) shows night time. c) shows linear regression analyses for each site with the $R^2$ of the fitted slope. Black line is linear fit and dashed grey lines illustrate the 95% confidence interval of the slope. There was only a significant correlation in the 3 yr and Natural meadow ($p<0.05$).

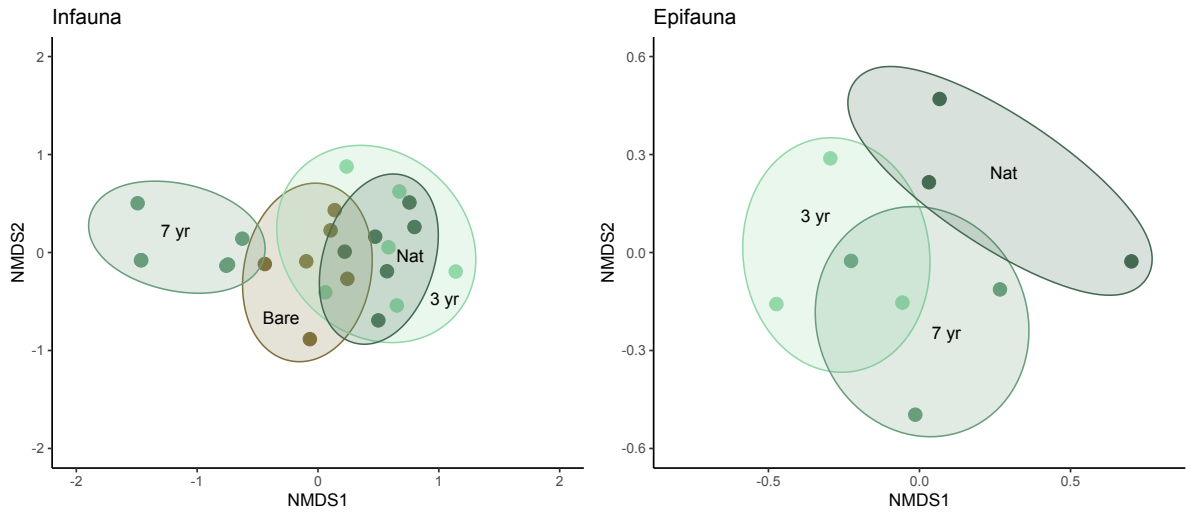


**Figure S4 NMDS of benthic fauna.** Non-metric multidimensional scaling (NMDS) of infauna (left) and epifauna (right). 2D stress level is 0.15 and 0.11, respectively.

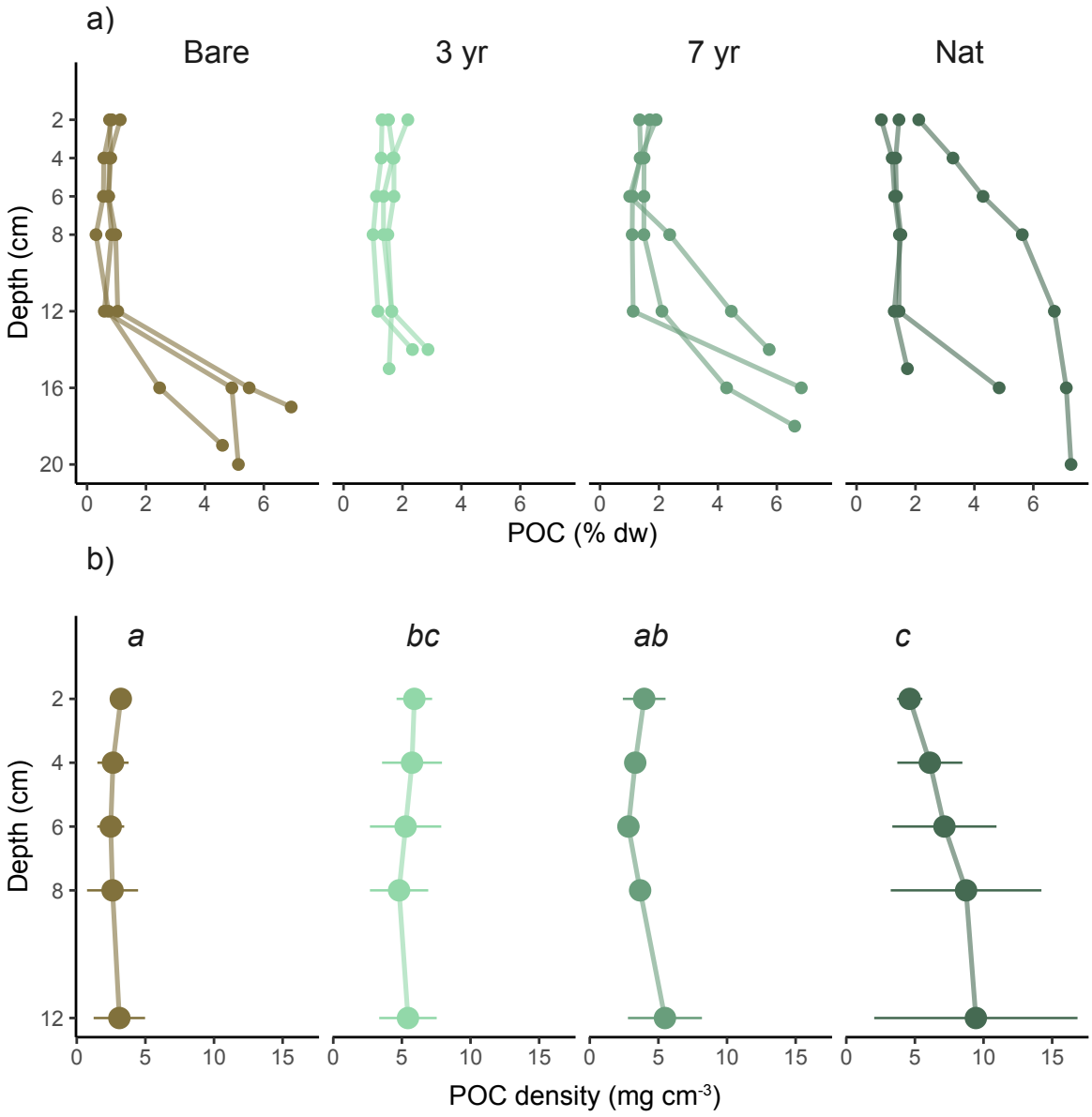


**Figure S5 Sediment POC profiles.** Sediment depth profiles of a) particulate organic carbon concentration (POC % dry weight) from all sediment core slices and b) the average 0-12 POC density. Letters in italics indicate between-site differences in POC density between 0-12 cm based on Tukey's post hoc test ($\alpha$=0.05).

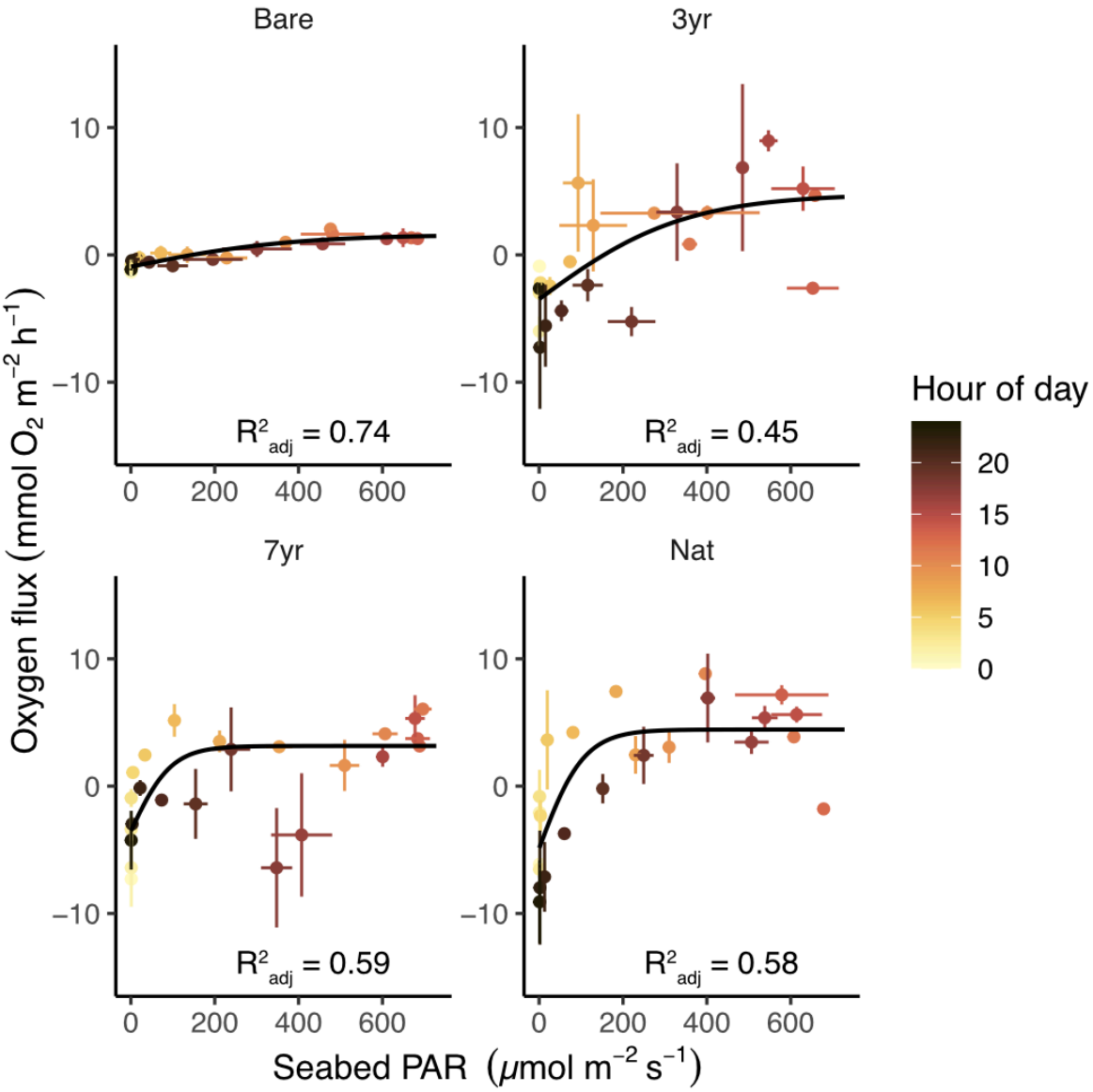


**Figure S6 P-I curves.** Photosynthesis-Irradiance (P-I) relationships fitted with hyperbolic tangent functions. Points indicate mean±SE between deployment days.