

Environmental optima for an engineer species: a multidisciplinary trait-based approach

Authors

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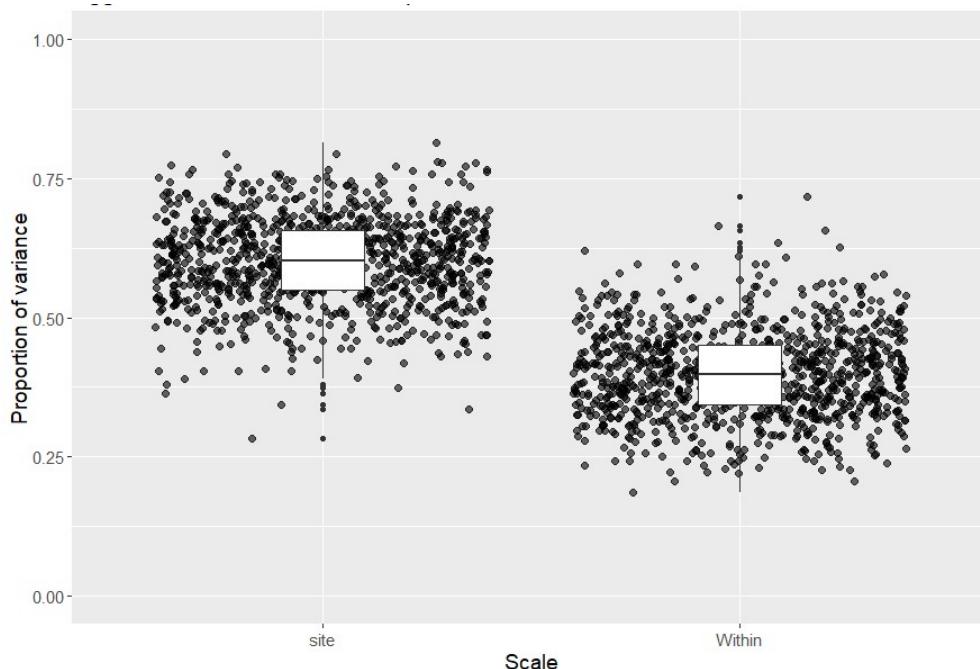
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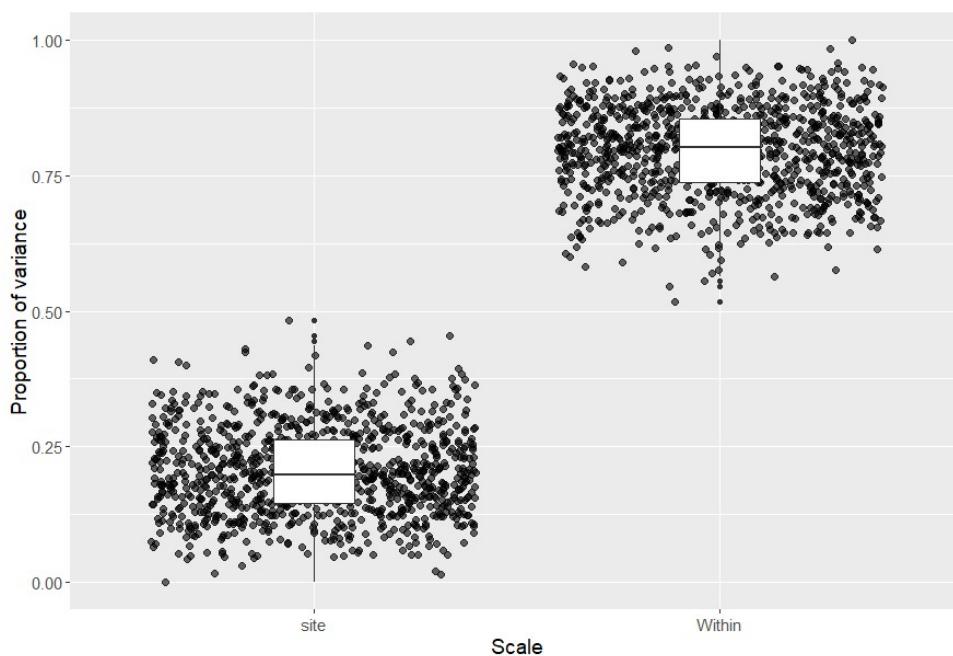
Supplementary Figure S1

Boxplots of variance component analyses across two nested scales using a decomposition (`varcomp` function) of variance on restricted maximum likelihood (REML) method (`lme` function) on 1000 resampling of 5 individuals per site for a) total egg diameter in Summer 2017 b) total egg diameter in Winter 2018 c) relative fecundity in Summer 2017 and d) relative fecundity in Winter 2018. See Messier et al. 2010 for more information).

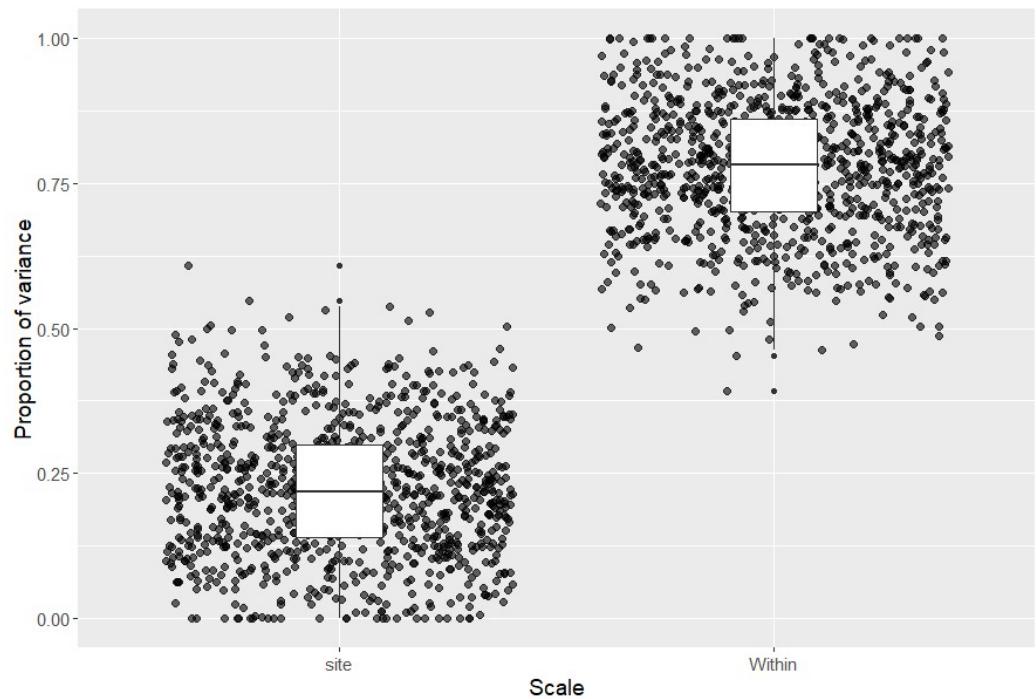
a) Total egg diameter, Summer 2017, 1000 resampling, 60% site, 40% intra-site



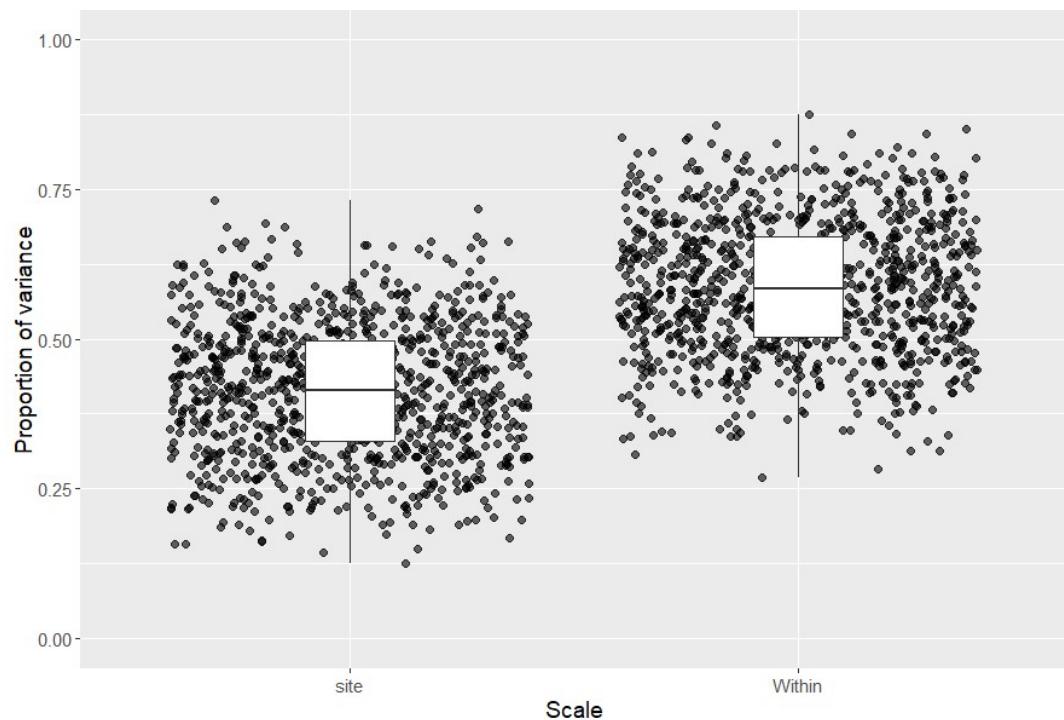
b) Total egg diameter, Winter 2018, 1000 resampling, 21% site, 79% intra-site



c) Relative Fecundity, Summer 2017, 1000 resampling, 22% site, 77% intra-site

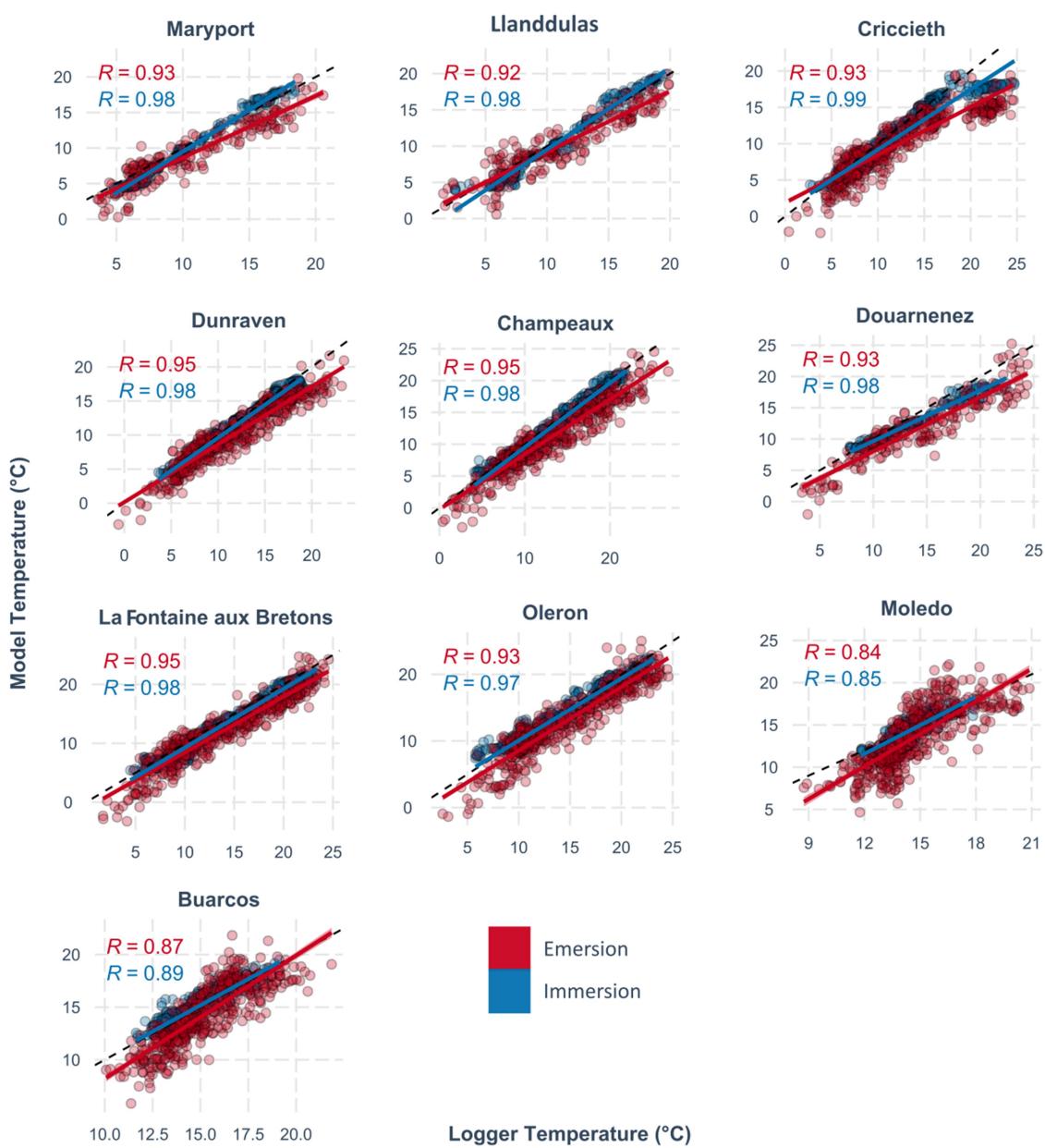


d) Relative Fecundity, Winter 2018, 1000 resampling, 41% site, 59% intra-site



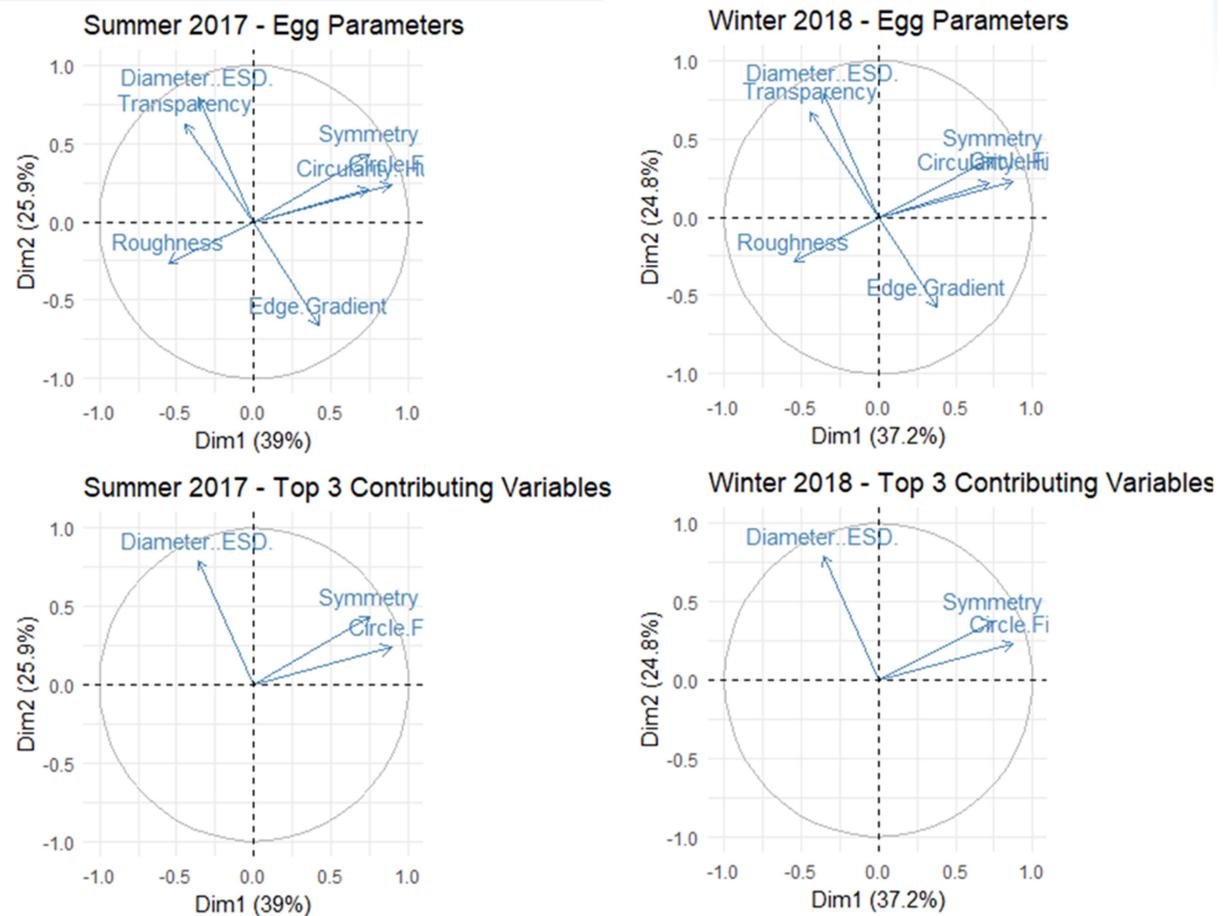
Supplementary Figure S2

Correlations between the *in-situ* temperature loggers and the environmental models over the 30-day period prior to sampling, for all project sampling dates (2016-2018 summer and winter, winter 2019). Please note that Maryport and Llanddulas loggers were not retrieved in summer 2017, and Maryport, Llanddulas and Douarnenez loggers were not retrieved in winter 2018. The red points and line, labelled "Emersion", represent the correlation between the ARPEGE model air temperature variable daily average and the logger readings at low-tide. The blue points and line, labelled "Immersion", represent the correlation between the CMEMS model seawater surface temperature daily average and the logger readings at high-tide. All correlations were significant at the $p < 0.001$ level.



Supplementary Figure S3

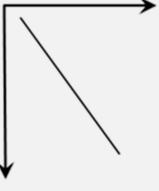
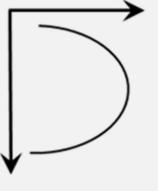
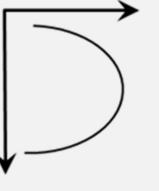
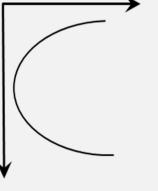
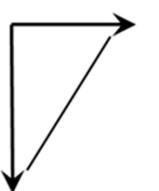
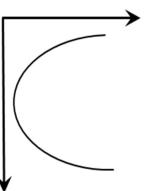
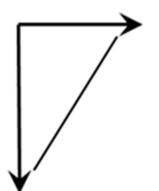
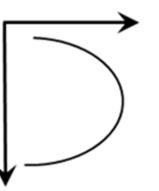
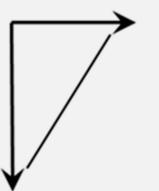
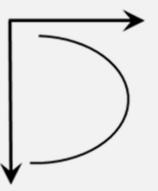
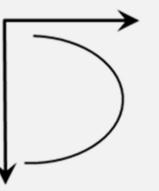
Principal Component Analysis (PCA) plot of 440,000 *Sabellaria alveolata* eggs and FlowCAM parameters for both sampling periods. The first two dimensions of the PCA express 64.9% of the total dataset inertia in summer 2017, and 62% of the total dataset inertia in winter 2018. PCA calculated using the PCA function of the package factoextra (Kassambara and Mundt, 2019).

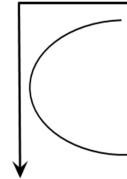
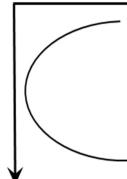
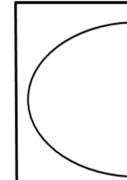
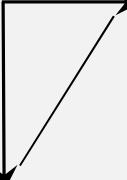
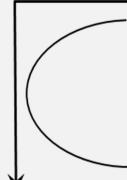


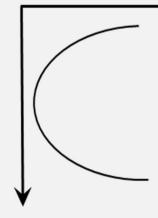
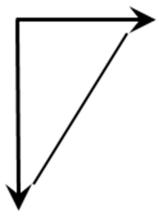
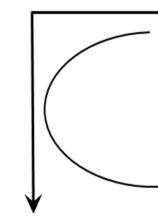
Supplementary Table S1. Key reproductive, environmental and biochemical variables and their relationship with either linear, or linear and quadratic, latitude. Graphical depictions of the regressions are presented. All variables are averaged at the site level (9 sites in summer, 10 sites in winter). Regression equations are given (lat1 = linear latitude; lat2= second degree polynomial of latitude) as well as p-values and adjusted R². Significant regression equations, when p ≤ 0.05, are in bold. *** = p ≤ 0.001, ** = p ≤ 0.01, * p ≤ 0.05. All fitted models were validated by checking that residuals were independent and normally distributed with mean zero and a constant variance.

| | Summer 2017 | | Winter 2018 | | |
|---|--|--|--|---|------------|
| | 58° N | Linear | Quadratic | Linear | Quadratic |
| 58° N | | | | | |
| 40° N | | | | | |
| | | ~lat1 | ~lat1+lat2 | ~lat1 | ~lat1+lat2 |
| Response variables | (n=9) | | | (n= 10) | |
| Total egg diameter μm | p=0.18 Adj. R ² =0.14 | p=0.06 Adj. R ² =0.60 | p=0.03* Adj. R²=0.38 | p=0.12 Adj. R ² =0.29 | |
| | | | | | |
| | S17_ESD $\hat{=}$ 78.43+14.29 (lat1) | S17_ESD $\hat{=}$ 77.31 +13.25(lat1)+19.66 (lat2) | W18_ESD $\hat{=}$ 85.37-10.85 (lat1) | W18_ESD $\hat{=}$ 85.42 -10.82(lat1)-0.98 (lat2) | |
| Relative fecundity nb eggs.mm^{-1} | p=0.15 Adj. R ² =-0.16 | p=0.17 Adj. R ² =0.26 | p=0.58 Adj. R ² =-0.08 | p=0.09 Adj. R ² =-0.36 | |
| | | | | | |
| | S17_rel_fecund $\hat{=}$ 21720.1+4081 3.86(lat1) | S17_rel_fecund $\hat{=}$ 23861.76+42797.0 1(lat1)-37577.84 (lat2) | W18_rel_fecund $\hat{=}$ 10551.81-9962. 52(lat1) | W18_rel_fecund $\hat{=}$ 12643.29-8796.2 5(lat1)-39056.23 (lat2) | |
| Circle Fit [0-1] | p=0.28 Adj. R ² =0.05 | p=0.09 Adj. R ² =0.38 | p=0.05* Adj. R²=0.31 | p=0.09 Adj. R ² =0.34 | |
| | | | | | |

| | | | | |
|---|---|--|--|--|
| | S17_circle^ =0.91+0.04(lat1) | S17_circle^=0.92 +0.05(lat1)-0.08 (lat2) | W18_circle^ =0.91-0.05(lat1) | W18_circle^ =0.91-0.04(lat 1)-0.03(lat2) |
| Symmetry [0-1] | p=0.41 Adj. R ² =-0.03 | p=0.21 Adj. R ² =0.21 | p=0.09 Adj. R ² =0.23 | p=0.05 Adj. R²=0.44 |
| | | | | |
| | S17_symmetry^ =0.92+0.04(lat1)- 0.08(lat2) | S17_symmetry^=0. 92+0.04(lat1)- 0.08(lat2) | W18_symmetry^ =0.93-0.04(lat1) | W18_symmetry^ =0.93-0.04(lat 1)-0.04(lat2) |
| Env. variables | (n=9) | | (n=10) | |
| Mean Air Temperature Degrees Celsius | p=0.02** Adj. R²=0.50 | p=0.01*** Adj. R²=0.71 | p=0.02* Adj. R²=0.46 | p=0.004** Adj. R²=0.74 |
| | | | | |
| | air_mean_S17^ =17.11-14.81 (lat1) | air_mean_S17^ =17.72-14.25 (lat1)-10.6(lat2) | air_mean_W18^= 6.68-18.05(lat1) | air_mean_ W18^=5.87 -18.5(lat1) +15.23(lat2) |
| Air Temperature SD Degrees Celsius | p=0.46 Adj. R ² =-0.05 | p=0.02* Adj. R²=0.65 | p=0.11 Adj. R ² =0.20 | p=0.03* Adj. R²=0.52 |
| | | | | |
| | air_sd_S17^ =2.1+1.98(lat1) | air_sd_S17^=2.47+ 2.33(lat1)-6.51 (lat2) | air_sd_W18^ =2.78+4.02(lat1) | air_sd_W18^ =3.05+4.17(lat 1)-5.12(lat2) |
| Mean Seawater Temperature Degrees Celsius | p=0.50 Adj. R ² =-0.07 | p=0.09 Adj. R ² =0.38 | p<0.001*** Adj. R²=0.94 | p<0.001*** Adj. R²=0.93 |
| | | | | |
| | swtemp_mean_ S17^=18.38+4.0 8(lat1) | swtemp_mean_S17 ^=19.08+4.73(lat1)- 12.35(lat2) | swtemp_mean_ W18^=8.12-26.5 5 (lat1) | swtemp_mean_ W18^=8.09-26. 57(lat1)+0.43(la t2) |
| Seawater Temperature SD Degrees Celsius | p=0.11 Adj. R ² =-0.23 | p=0.25 Adj. R ² =0.16 | p=0.08 Adj. R ² =0.26 | p=0.04* Adj. R²=0.51 |

| | | | | |
|---|---|---|--|---|
| |  |  |  |  |
| swtemp_sd_S17 ^=0.76-1.65 (lat1) | swtemp_sd_S17^ =0.72-1.69(lat1)+0. 72(lat2) | swtemp_sd_W18^ =0.53+1.28(lat1) | swtemp_sd_ W18^=0.6+1.3 2(lat1)-1.34(la t2) | |
| Mean Chlorophyll a $\mu\text{g.m}^{-3}$ | p=0.01** Adj. R²=0.57* | p=0.003** Adj. R²=0.81 | p=0.32 Adj. R ² =0.01 | p=0.35 Adj. R ² =0.05 |
| chla_mean_S1 7^=2.64+11.1(la t1) | chla_mean_S17^ =2.19+10.69(lat1) +7.87(lat2) | chla_mean_W18^ =2.06+3.44(lat1) | chla_mean_W18^ =1.83+3.32(lat1)+ 4.18(lat2) | |
| Chlorophyll a SD $\mu\text{g.m}^{-3}$ | p=0.22 Adj. R ² =0.09 | p=0.24 Adj. R ² =0.18 | p=0.58 Adj. R ² =-0.08 | p=0.84 Adj. R ² =-0.22 |
| |  |  |  |  |
| chla_sd_S17^ =0.77+1.8(lat1) | chla_sd_S17^=0.66 +1.7(lat1)+1.88 (lat2) | chla_sd_W18^=0. 55+0.83(lat1) | chla_sd_W18^=0. 53+0.82(lat1)+0.4 (lat2) | |
| Mean Salinity psu | p=0.60 Adj. R ² =-0.10 | p=0.78 Adj. R ² =-0.23 | p=0.25 Adj. R ² =0.05 | p=0.44 Adj. R ² =-0.02 |
| |  |  |  |  |
| salinity_mean_S 17^=32.41+2.7 (lat1) | salinity_mean_S17^ =32.25+2.55(lat1) +2.96(lat2) | salinity_mean_W1 8^=31.29+8.15(lat 1) | salinity_mean_W1 8^=31.58+8.3(lat1) -5.29(lat2) | |
| Mean Suspended Particulate Inorganic Matter mg.m^{-3} | p=0.37 Adj. R ² =-0.01 | p=0.50 Adj. R ² =-0.06 | p=0.66 Adj. R ² =-0.10 | p=0.29 Adj. R ² =0.10 |
| |  |  |  |  |
| spim_mean_S1 7^=5.42+15.29 (lat1) | spim_mean_S17^ =6.3+16.11(lat1) -15.52(lat2) | spim_mean_W18^ =22.85+29.74 (lat1) | spim_mean_W18^ =28.93+33.13 (lat1)-113.5(lat2) | |

| | | | | |
|---|---|--|---|--|
| Wave exposure $(m.s^{-1})^2$ | $p=0.31$ Adj. $R^2=0.03$  | $p=0.51$ Adj. $R^2=-0.07$  | $p=0.09$ Adj. $R^2=0.24$  | $p=0.04^*$ Adj. $R^2=0.49$  |
| wave_exp_mean_S17 [^] $=4.4+11.83(lat1)$ | wave_exp_mean_S17 [^] $17=3.94+11.4(lat1)+8.2(lat2)$ | wave_exp_mean_W18 [^] $W18=13.8-52.91(lat1)$ | wave_exp_mean_W18 [^] $W18=10.75-54.61(lat1)+56.96(lat2)$ | |
| Biochemical variables (n=10) | | | | |
| CS $mU.mg^{-1}$ | $p=0.34$ Adj. $R^2=-0.01$  | $p=0.03^*$ Adj. $R^2=0.51$  | | |
| SOD $U.mg^{-1}$ | $p=0.05^*$ Adj. $R^2=0.31$  | $p=0.05^*$ Adj. $R^2=0.44$  | | |
| Polar Lipid Arachidonic Acid % of total phospholipids | $p=0.30$ Adj. $R^2=0.03$  | $p=0.47$ Adj. $R^2=-0.04$  | | |
| Polar Lipid EPA % of total phospholipids | $p=0.77$ Adj. $R^2=-0.11$  | $p=0.73$ Adj. $R^2=-0.17$  | | |

| | | |
|--|--|--|
| |  |  |
| Polar Lipid DHA <i>% of total phospholipids</i> | $PL_EPA = 21.67 + 1.01(lat1)$ $p=0.93$ $Adj.R^2=-0.12$ | $PL_20_5n.3^\wedge = 21.83 + 1.11(lat1) - 3.11(lat2)$ $p=0.05^*$ $Adj. R^2=0.43$ |
| |  |  |
| | $PL_DHA^\wedge = 5.66 + 0.45(lat1)$ | $PL_DHA^\wedge = 5.02 + 0.1(lat1) + 11.92(lat2)$ |

Supplementary Table S2. Field locations and sampling dates. Numbers in italic represent the number of viable individuals retained after FlowCAM quality controls (>50 measurable eggs per 0.5mL subsample).

| Site name | Site abbreviations | GPS coordinates (decimal degrees) | Summer 2017 Sampling dates & No. of viable ind. | Winter 2018 Sampling dates & No. of viable ind. |
|-----------------------------|--------------------|--------------------------------------|---|---|
| Maryport | MAR | 54.718869 -3.507036 | 21/08/2017 24 | 17/03/2018 6 |
| Llanddulas | LLA | 53.294723 -3.634655 | 21/08/2017 13 | 17/03/2018 5 |
| Criccieth | CRI | 52.916712 -4.230685 | 21/08/2017 28 | 17/03/2018 9 |
| Dunraven | DUN | 51.444295 -3.608907 | 11/06/2017 - | 17/03/2018 5 |
| Champeaux | CHA | 48.732365 -1.552953 | 25/07/2017 28 | 01/03/2018 31 |
| Douarnenez- plage du Ris | RIS | 48.098813 -4.294829 | 24/07/2017 24 | 04/03/2018 31 |
| La Fontaine aux Bretons | LFB | 47.09958 -2.072538 | 22/07/2017 34 | 03/03/2018 29 |
| Oléron | OLE | 45.970809 -1.393057 | 21/07/2017 28 | 02/03/2018 28 |
| Moledo do Minho | MOL | 41.8417722 -8.9 | 25/07/2017 24 | 29/03/2018 16 |
| Buarcos | BUA | 40.1787 -8.9068 | 23/07/2017 2 | 30/03/2018 6 |

Supplementary Table S3. Environmental variable sources, units and horizontal resolution. All data were calculated over the thirty day period prior to the sampling dates.

| Variable | Abbreviated variable name | Unit | Source | Horizontal resolution |
|----------------------|----------------------------------|--------------------------------------|-----------------------|------------------------------|
| Air temperature | air | Degrees C | ARPEGE* | ~10km |
| Cold spells – air | arp_cs_n_event | No. of events over the 30-day period | HeatwaveR | ~10km |
| Heatwaves – air | arp_hw_n_event | No. of events over the 30-day period | HeatwaveR | ~10km |
| Seawater temperature | swtemp | Degrees Celsius | CMEMS [†] | ~3km |
| Cold spells – water | cop_cs_n_event | No. of events over the 30-day period | HeatwaveR | ~3km |
| Heat waves – water | cop_hw_n_event | No. of events over the 30-day period | HeatwaveR | ~3km |
| Seawater Salinity | salinity | psu | CMEMS | ~3km |
| Current Velocity | current_velocity | m.s ⁻¹ | CMEMS | ~3km |
| Tidal amplitude | tide_amp | Meters | OTIS-OSU [‡] | ~9km (1/12°) |

Suspended Particulate Inorganic Matter spim mg.m⁻³ OC5 ~1km

Chlorophyll *a* chla µg.m⁻³ OC5 ~1km

Wave exposure index wave_exposure (m.s⁻¹)² Adapted from Burrows et al. 2008 ~10km

* = Météo-France European Centre for medium-range Weather Forecasts (ECMWF) atmospheric model (Déqué et al., 1994) † = EU Copernicus Marine Environment Monitoring Service (CMEMS) operational IBI (Iberian Biscay Irish) Ocean Physics Analysis and Forecast Product (IBI_ANALYSIS_FORECAST_PHYS_005_001) ‡= Oregon State University Tidal Inversion Software - Regional Tidal Solution (Egbert & Erofeeva, 2010).

References

- Déqué, M., Dreveton, C., Braun, A., Cariolle, D., 1994. The ARPEGE/IFS atmosphere model: a contribution to the French community climate modelling. *Climate Dynamics* 10, 249–266. <https://doi.org/10.1007/BF00208992>
- Egbert, G.D., Erofeeva, S.Y., 2002. Efficient Inverse Modeling of Barotropic Ocean Tides. *Journal of Atmospheric and Oceanic Technology* 19, 183–204. [https://doi.org/10.1175/1520-0426\(2002\)019<0183:EIMOBO>2.0.CO;2](https://doi.org/10.1175/1520-0426(2002)019<0183:EIMOBO>2.0.CO;2)
- Kassambara, A., Mundt, F., 2019 *factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. R package version 1.0.6. <https://CRAN.R-project.org/package=factoextra>