

Multiyear trend in reproduction underpins interannual variation in gametogenic development of an Antarctic urchin.

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1 Article to *Scientific Reports*

2 Demi-decadal trend in reproduction underpins inter-annual
3 variation in gametogenic development of an Antarctic
4 urchin.

5

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13 **ABSTRACT**

14 Ecosystems and their biota operate on cyclic rhythms, often entrained by
15 predictable, small-scale changes in their natural environment. Recording and
16 understanding these rhythms can detangle the effect of human induced shifts
17 in the climate state from natural fluctuations. In this study, we assess long-
18 term patterns of reproductive investment in the Antarctic sea urchin,
19 *Sterechinus neumayeri*, in relation to changes in the environment to identify
20 drivers of reproductive processes. Polar marine biota are sensitive to small
21 changes in their environment and so serve as a barometer whose responses
22 likely mirror effects that will be seen on a wider global scale in future climate
23 change scenarios. Our results indicate that seasonal reproductive periodicity
24 in the urchin is underpinned by a demi-decadal trend in reproductive
25 investment beyond and in addition to, the previously reported 18-24 month
26 gametogenic cycle. Our model provides evidence that annual reproductive
27 investment could be regulated by an endogenous rhythm since environmental
28 factors only accounted for a small proportion of the residual variation in gonad
29 index~~Chlorophyll concentration and the large-scale climate metric, the~~
30 ~~Southern Oscillation Index, were also identified as significant factors~~
31 ~~explaining some of the residual variability observed in gonad index.~~ This
32 research highlights a need for multi-year datasets and the combination of
33 biological time series data with large-scale climate metrics that encapsulate
34 multi-factorial climate state shifts, rather than using single explanatory
35 variables to inform changes in biological processes.

- 36 Key words: Echinoderm, ecological pattern, El Niño, endogenous rhythm,
37 [Southern Oscillation Index](#), temporal series

38 1. INTRODUCTION

39 Reproduction is a fundamental process for all life. Reproductive periodicities
40 are often intrinsic rhythms entrained by external cues that aid synchronicity in
41 reproduction, as well as timing the arrival of vulnerable early life-stages with
42 favourable conditions ^{1,2}. To understand environmental influences on
43 reproductive processes, innate reproductive periodicities must be detangled
44 from environmental fluctuations, both for regular seasonal variation and
45 isolated events.

46 Seasonal and annual reproductive periodicities have been well documented in
47 marine invertebrates. Evidence suggests that local environmental cues
48 including photoperiod ^{3,4}, water temperature ^{5,6}, food availability ^{7,8}, and lunar
49 cycles ^{6,7,9}, play roles in regulating gametogenesis. However, reproductive
50 cycles and their drivers still remain challenging to interpret, since they are
51 often regulated by the interplay of multiple climate variables ¹⁰.

52 Changes to the climate state can affect populations at local, regional and
53 global scales ¹¹⁻¹³. For example, the large-scale climate metric, Southern
54 Oscillation Index (SOI), is most known for its regional impacts on the tropical
55 Pacific ^{11,14}. However, strong links have been found between El Niño-
56 Southern Oscillation (ENSO) and extreme events such a heat waves and
57 storms, across the globe⁻¹⁵. SOI and extreme events drive ecological
58 processes ^{16,17}, and more specifically, reproductive processes ^{18,19}, with some
59 impacts reaching as far as Antarctica ^{20,21}. Multi-factorial indices, rather than
60 single variables, instead provide a context for large-scale oceanographic

61 variation, and hence integrate both locally measured components of weather
62 and rarer, infrequent, extreme events ¹⁰.

63 Although regulation of gametogenesis, reproductive cycles and
64 synchronisation of spawning events are undoubtedly influenced by
65 environmental factors, temporal patterns in some species are largely
66 regulated by endogenous rhythms that govern not only reproduction, but other
67 developmental and biological functions such as growth and seasonal activity
68 ^{22,23}. These rhythms may be caused by an internal oscillator, allocating energy
69 based on life history requirements on seasonal, annual or decadal cycles ²².

70 To understand how climate interacts with fundamental biological processes
71 such as reproduction, we first need to identify these innate internal rhythms
72 ^{24,25}, especially for slow paced species, including many Antarctic taxa.
73 Antarctic marine invertebrates have adapted *in situ* over millennia to unique
74 conditions characterised by low and stable temperatures and extreme
75 seasonality in light and food availability ²⁶. Many species have adapted to
76 control and minimise energy expenditure ^{2,27}, and exhibit extended
77 reproductive cycles, where gametogenesis often takes 18-24 months to
78 complete instead of ~~the~~ 6-12 months ~~characteristic of their~~ temperate
79 counterparts ^{28,29}.

80 The Antarctic sea urchin, *Sterechinus neumayeri*, is one of the most
81 functionally important Antarctic shallow marine species. It has a circumpolar
82 distribution and is the most dominant echinoid in the near-shore benthic
83 community, having recorded abundances up to 223 individuals m⁻² ³⁰.
84 *Sterechinus neumayeri* is an important predator and grazer. It is also a model

85 research species due to its ease of husbandry, including laboratory spawning
86 and larval culture^{31,32}. The urchin also has an extended 18-24 month
87 gametogenic cycle²⁸.

88 This study aims to document the reproductive ecology of *S. neumayeri* across
89 multiple years, characterising seasonal and inter-annual variability and the
90 key factors underpinning reproductive allocation. To this purpose, we
91 investigated the reproductive cycle of *S. neumayeri* over a seven-year period
92 (2012-2018). Seasonal and inter-annual variations in reproductive condition
93 were explored in relation to locally measured environmental variables (e.g.,
94 temperature, chlorophyll a, etc.) and the regional climate metrics SOI and
95 SAM due to their influence in the Southern Ocean and connection with
96 extreme events.

97 **2. RESULTS**

98 The total number of female urchins collected each year exceeded the number
99 of males. Overall, the sex ratio was significantly skewed towards females at
100 1.32:1 (chi-squared = 13.38, $p < .001$, $n = 718$) (Supplementary information,
101 Table S1). The gonad index was significantly higher in females ($t(661) =$
102 2.26, $p = 0.024$) however there was no significant difference in animal size
103 between the sexes (Supplementary information, Table S2).

104 **Seasonal cycles**

105 Males and females exhibited seasonal cycles in gonad index (GI), oocyte
106 size, nutritive phagocyte proportions and male maturity (Fig. 2), where both
107 males and females presented synchronous cycles, although there was

108 considerable individual variability. GI peaked in June and September for both
109 males (12.8 ± 1.97 S.E. and 9.54 ± 1.48 S.E., respectively) and females (11.1
110 ± 1.05 S.E. and 12.6 ± 1.24 S.E., respectively). In both cases, GI then
111 decreased to a minimum in January (5.74 ± 0.59 S.E. for males, and $5.67 \pm$
112 0.40 S.E. for females, Fig. 2A). For females, mean oocyte size, measured as
113 equivalent circular diameter (ECD; μm), increased from January to peak in
114 July ($74.4 \mu\text{m} \pm 0.57 \mu\text{m}$ S.E.), followed by a decline and a subsequent
115 increase again in September ($71.8 \mu\text{m} \pm 0.68 \mu\text{m}$ S.E.). Mean ECD then
116 decreased from September to a minimum in January ($46.3 \mu\text{m} \pm 0.31 \mu\text{m}$
117 S.E., Fig. 2B). The proportion of gonad area dedicated to nutritive phagocytes
118 (NPs) was inversely related to average oocyte size (ECD) ($r^2 = 0.45$, p
119 $< .001$), where, as oocytes matured, relative proportions of NPs decreased
120 (Fig. 2C). However, as a proportion of GI, NPs increased in April to $60.8\% \pm$
121 2.1% S.E. of GI, and then again in December to $79.6\% \pm 2.0\%$ S.E. of GI. At
122 its lowest, the proportion of GI accounted for by NPs declined to $49.5\% \pm$
123 2.8% S.E. of GI in August (Fig. 3). The overall GI pattern with 2 peaks
124 resulted from the combined variation in oocyte and NPs.

125 The proportion of males in spent and recovering maturity stages peaked in
126 January ($52.0\% \pm 13.2\%$ S.E.), followed by increasing proportions of
127 individuals transitioning to growing stages of maturity, peaking in May (75.7%
128 $\pm 7.0\%$ S.E., Fig. 2D). Following this peak, proportions of mature males
129 increased from May to October/November (peaking at $87.7\% \pm 10.3\%$ S.E. of
130 individuals), from which point the proportion of spent and recovering
131 individuals increased again until January (Fig. 2D).

132 **Changes in Gonad Index**

133 The partials plot analysis revealed co-linearity between temperature and
134 chlorophyll-a (Chl-a) (Pearson's $r = 0.73$) and between salinity and
135 temperature (Pearson's $r = 0.54$). Therefore, based on a weighted importance
136 analysis, only Chl-a ~~one of these variables~~ was included in the model. The
137 starting model fit (null model) was as per equation (1).

138
$$\text{Gonad Index} = f(\text{Time}) + \epsilon \quad (1)$$

139 Where f is the smoothing function. This model had an AIC of 1368. Initially,
140 single environmental variables considered as potentially ecologically
141 influential, were added to the model. Following automated comparisons of all
142 possible model variations, Chl-a was identified as the main environmental
143 predictor of GI variation, with sex as a factor and as an interaction with the
144 smoothed functions of time and Chl-a. Since other single environmental
145 variables were not considered significant, the large-scale climate metrics, SOI
146 and SAM, ~~was/were~~ included as ~~an~~ additional factors to Chl-a and sex. There
147 is some evidence that SOI and the SAM can influence each other³³. However,
148 the partials plot in our time-series did not reveal co-linearity between SAM and
149 SOI. Other studies have also reported weak relationships between these
150 metrics^{34,35}. As such, we included both metrics in our model since both were
151 significant factors in explaining some of the remaining variance in GI and
152 together, improved the model AIC. It should however be noted that the SAM
153 had the lowest relative importance comparative to other variables in the model
154 (Supplementary information, Fig. S1). ~~The addition of SOI was considered a~~
155 significant factor in explaining some of the remaining variance in GI, and
156 ~~hence the~~The final model resulted as per equation (2).

157 Gonad Index= $f(\text{Time, by= Sex}) + f(\text{Chlorophyll, by Sex}) +$ (2)
158 $f(\text{SOI, by Sex}) + f(\text{SAM}) + \text{Sex} + \varepsilon$

159 This model had an AIC of 125974, compared to the null model. This model
160 was ranked highest with regards to AIC, and explained 419.42% of the
161 variance in GI. Model predictions fitted well with the raw data and aside from
162 the functions of time and sex, environmental covariates, Chl-a ~~and~~ SOI and
163 SAM, were considered the best predictors of variance in GI, explaining 12.4%
164 of the variance. The model met the assumptions of homogeneity of variance
165 and model residuals were normally distributed. All Cooks distance values
166 were < 0.034 and were not considered influential ³⁶.

167 The estimated covariate smoothers (Fig. 4) show there was a positive
168 relationship for the smooth function of time, where both male and female GI
169 increased from mid-2013 to mid-2016. Male GI then declined until the end of
170 the time series suggesting a demi-decadal trend. The variation in GI explained
171 by the model was limited by the individual GI variability within each month
172 sampled. However, the model captures the overall increasing and decreasing
173 trend observed over time.

174 For the covariate SOI, there were limited data for extreme negative SOI
175 values of < -15 , and so over-interpretation of the model predictions at this tail
176 end was avoided. In comparison, data collected for SOI values > -5 were
177 comprehensive and showed a negative association between GI and SOI for
178 females when SOI was positive. This was not the case for males, where the
179 relationship was not significant. For the covariate SAM, there was evidence of
180 a bell-shaped curve in the relationship, with GI values peaking at SAM values

181 of 0. Negative and positive SAM values resulted in lower GI. There was less
182 certainty in the negative association between GI and positive SAM values due
183 to the increase in the 95% confidence interval (CI) and the poor fit between
184 the data points and the model prediction. As such, over-interpretation of this
185 association was avoided.

186 There was good data coverage at low Chl-a concentration because of the
187 highly seasonal productivity. However, the association of GI with Chl-a
188 concentration was negative for males from concentrations exceeding 1.5 mg
189 m⁻³. This downward trend followed an initial increase in GI for both males and
190 females at low Chl-a concentrations. This inverse relationship was also
191 evident from the decomposition analysis, where seasonal cycles were
192 extracted from both GI and Chl-a (~~Supporting information, Fig. 5S4~~).

193 Chlorophyll and temperature trends, extracted by decomposition analysis,
194 showed positive linear relationships with SOI, where positive values of SOI
195 (La Niña) correlated with high temperature ($R^2 = 0.20742$, $p < .001$) and Chl-a
196 concentrations ($R^2 = 0.226$, $p < .001$) (Supplementary information, Fig. ~~S25~~
197 ~~S6S3~~). Other variables ~~did not have~~ lacked significant linear relationships,
198 lagged or unlagged, with the SOI trend.

199 **Oocyte growth and maturation**

200 Oocyte mean diameters varied significantly ~~between months (permutation~~
201 ~~ANOVA, $df = 11$, $p < .001$) and~~ between years for the months March-August
202 and also for November and December, with March having the most

203 interannual variability. For all other months, the mean ECD was not
204 significantly different between years (Supplementary information, Table S32).
205 Size distributions of developing oocytes within individual females were
206 bimodal for most months of the year (i.e., from February/March, through to
207 October). In December oocyte sizes were mostly 6–80 μm . The oocyte
208 distribution then broadened, with bimodal peaks appearing from January to
209 February/March, and oocyte sizes ranging from 12–122 μm . In July, the
210 frequency of large oocytes (80–135 μm), peaked at 51.1 % \pm 4.9 % S.E., and
211 steadily decreased until November, when they almost disappeared from the
212 distribution accounting for 9.6 % \pm 2.5 % S.E. of the distribution. Over this
213 period, a cohort of small oocytes (12–80 μm) increased in frequency from
214 49.0 % \pm 4.9 % S.E. in July, through to 90.4 % \pm 2.5 % S.E. in December
215 (Supplementary information, Fig. S47).

216 **Male maturity**

217 Males varied in reproductive maturity on both seasonal and interannual
218 scales. Substantial individual variation was evident since the maturity
219 categorisation was broad, with 105 \pm 20 S.D. individuals in each category
220 emphasising the large variation. Across the time-series, from March 2012–
221 2017, there were periodicities in the proportion of maturity stages present
222 (Fig. 56). A distinct bell curve in the proportion of mature males occurred from
223 March 2012–2015, peaking in March 2013. This distribution overlapped almost
224 simultaneous bell curves in spent/recovering and growing stages, which
225 peaked in March 2015 and November 2015, respectively.

226 3. DISCUSSION

227 Data presented here comprise the longest reproductive time series of an
228 Antarctic benthic marine invertebrate to date and are the first to provide
229 evidence that reproductive allocation may be accumulated across a demi-
230 decadal scale with no evidence for an environmental link. Where multi-year
231 studies have been conducted, evidence is building that some marine
232 invertebrates have endogenously driven growth and reproductive cycles, in
233 which environmental variation is independent, or interacts with this internal
234 rhythm to regulate reproductive investment and growth over time ^{1,22}. Our
235 model outcomes suggest a demi-decadal trend in reproductive investment
236 which could suggest an innate endogenous rhythm. [Owed to the number of](#)
237 [years comprising the time series,](#) ~~r~~Repetition of this trend has not been
238 captured in our dataset and therefore it is necessary to interpret these results
239 with caution. However, several studies have recorded multi-year cycles of
240 similar periodicities in a range of Antarctic species. For the crab-eater seal
241 around the Antarctic Peninsula, the juvenile leopard seal at Macquarie Island,
242 and the Weddell seal in McMurdo Sound, 4-5 year intervals for both
243 reproduction and population peaks have been identified (Testa et al. 1991).
244 Other Antarctic research has shown that some bivalves exhibit endogenous
245 growth cycles, with a 9.06 year cycle present for *Aequiyoldia eightsi*, and two
246 endogenous cycles of 5 and 6.6-years [reported infor](#) *Laternula elliptica*
247 (Román-González et al. 2017). There is therefore evidence for a temporal
248 mediator of growth and reproductive investment in Antarctica, possibly
249 because of low temperature effects on biological rates [and extreme](#)
250 [seasonality](#), where it may take multiple years to build reserves, with seasonal

251 spawning and growth taking place against a backdrop of long-term investment
252 over several years.

253 The ~~general lack of~~ very small number of multi-year investigations suggests
254 endogenous cycles in growth and reproduction may be more common than
255 previously identified. A similar trend to ~~that identified in~~ GI was also evident
256 in our male maturity data, where we observed a single peak in each maturity
257 stage across a 5 year period, with the 'growing' phase of maturity, matching
258 the shape of the curve for variation in male GI. Extreme inter-annual variation
259 in reproductive condition and a circaseptennial rhythm (7-year cycle) has
260 been previously proposed for *S. neumayeri*²⁸ based on studies of the Pacific
261 purple sea urchin, *Strongylocentrotus purpuratus*³⁷.

Commented [RDL1]: Halberg et al 1987 reference has been added to this sentence as suggested.

262 Alongside the temporal signal in GI, our data also indicate that there is
263 environmental entrainment of this periodicity as the whole population builds
264 gonad and spawns synchronously across the cycle. This entrainment likely
265 arises from a combination of factors. ~~H,~~ however, our analysis identified a
266 negative relationship in female GI when the SOI signal is positive (La Niña)
267 and negative relationship in both male and female GI when the SAM signal is
268 negative. Climate coupled atmospheric-oceanic-sea-ice processes, like SOI
269 and SAM, are known to impact ecosystem variability in Antarctica, especially
270 for the Antarctic Peninsula ³⁸⁻⁴⁰. These effects could result from direct links
271 caused by changes in physical factors including ocean temperature, or else
272 indirect links resulting from altered primary productivity and food web
273 dynamics ^{35,41,42}. Effects could also result from a combination of, or synergistic
274 interactions between, factors. Isolating a single cause and effect of these

Commented [RDL-B2]: References added here and throughout to include SAM

275 large-scale climate indices is challenging, when many environmental factors
276 are closely linked and the consequences of change in one variable cascades
277 through multiple physical and biological pathways ⁴³.

278 Relationships between SOI and climate parameters in Antarctica are non-
279 linear, but there is strong evidence that El Niño and La Niña signals are
280 translated widely across the southern hemisphere ^{12,44}. Here La Niña
281 episodes have been correlated with warm SST anomalies and decreased
282 sea-ice extent, while El Niño episodes produce opposite effects ^{20,45}. Our time
283 series encapsulates El Niño years up to values of -20, and La Niña values of
284 +10. Our model predictions indicate a negative association with reproductive
285 investment for females when SOI is positive (La Niña), and a positive
286 association when SOI is negative (El Niño). Reasons for this are unclear,
287 however our regression analysis of Chl-a and temperature against SOI,
288 suggest that positive SOI ~~related to~~correlated with higher temperatures and
289 higher chlorophyll concentrations, outside the usual seasonal variation. These
290 relationships would likely have implications for sea-ice cover and water
291 column stratification ^{17,46}. Because of this interaction of factors, the SOI can
292 be used to highlight extremes in the environment and multifactorial shifts,
293 rather than that of a single mechanism driving an ecological response.

294 The drop in GI at positive SOI (La Niña) is only present in females. Reasons
295 for this could be owed to a higher energy requirement for oocyte development
296 ^{47,48}. Therefore, reproductive costs for females may be higher and trade-offs in
297 energy allocation to reproduction may be necessary during periods of
298 environmental change ⁴⁹. Possible changes in environmental variables as a

299 result of La Niña events may then result in a reduction of GI indices for
300 females only.

301 Impacts of large-scale climate metrics on Antarctic biodiversity have been
302 identified across a range of taxa. Mammals including Weddell seals and
303 Elephant seals have reproductive rates in phase with the SOI ^{21,42}. Other
304 studies have shown strong links with plankton population abundance and krill
305 reproductive recruitment success ³⁸, and seasonal vertical migration
306 behaviour ¹³. Abundance of the planktonic tunicate, *Salpa thompsoni* has
307 also been correlated with SOI ⁴⁶, as well as 5-year cycles in abundance peaks
308 for krill, *Euphausia superba*, where high abundance was associated with
309 greater sea-ice extent ⁵⁰. The authors are unaware of any studies that
310 demonstrate such correlations for Antarctic benthic species or SOI effects on
311 species or ecosystems this far south.

312 Interestingly, studies have shown that the SAM is more closely linked to
313 interannual sea surface temperature variability around the WAP, compared
314 toative with SOI³⁵. Our model exploration shows that the SOI accounts for
315 more of the variability in the GI of *S. neumayeri* than the SAM, and both
316 temperature and SAM had low relative importance in predicting GI. These
317 results further suggest that temperature is likely not the most important or only
318 driver of reproductive processes in these ~~ordinarily~~ thermally sensitive
319 species, and instead there is more complexity underlying the interaction
320 between ~~these~~ large-scale climate metrics, local environmental drivers, and
321 biological functioning.

322 Temperature and Chl-a variation can be seasonal drivers of reproductive
323 cycles ^{7,8}. Our results show that Chl-a concentration co-varies with
324 reproductive condition in *S.neumayeri*, where the negative relationship
325 between GI and Chl-a alludes to spawning being correlated with Southern
326 Ocean summer phytoplankton characteristics ^{51,52}. Model predictions show
327 that when Chl-a concentrations increase, GI declined, which is indicative of
328 spawning. The relationship between GI and Chl-a may be indirect, whereby
329 spawning is initiated prior to the bloom either by a trigger associated with
330 early phytoplankton increase to facilitate feeding of planktonic larval stages ³¹
331 or another environmental factor co-varying with Chl-a. This hypothesis would
332 also result in a negative association between trends in GI and Chl-a. Again,
333 we see different responses for males and females to high Chl-a
334 concentrations. Since the GI relationship with Chl-a is likely a result of
335 spawning, it may be that we observe a smaller reduction in GI in females
336 following spawning due to the presence of nutritive phagocytes (NPs). We
337 provide evidence that NPs are still present in the gonad following spawning,
338 and hence will contribute to the higher post-spawning GI. Although we do not
339 have NP data for males in this study, for the temperate sea urchin,
340 *Strongylocentrotus droebachiensis*, the volume of NP in males was lower than
341 in females throughout the gametogenic cycle ⁵³. If NPs contribute less to the
342 GI in males, it is reasonable that we would see a larger decline in GI following
343 spawning.

344 Seasonal patterns in *S. neumayeri* reproduction were evident in GI, male
345 maturity and oocyte size distributions, all of which exhibited periods of
346 maturation and growth, followed by phases that implied spawning across

347 several months (e.g. decreasing GI, decreasing mean oocyte size for
348 females, or increasing spent/recovering stages for males). Monthly changes in
349 GI during the year highlight this reproductive seasonality. However, for
350 urchins, gonad tissue comprises both germ cells (gametes) and ~~nutritive~~
351 ~~phagocytes~~ (NPs)^{54,55}. Our data demonstrate that fluctuations in female GI
352 are caused by both the maturation of gametes and changes in gonad
353 proportions dedicated to NPs. These changes are clearest in April, where GI
354 increases significantly from March. However, this GI increase is due primarily
355 to larger NP increases, rather than oocytes. The April GI peak for females
356 follows the end of the summer phytoplankton bloom and suggests the
357 resultant phytodetrital pulse to the seafloor is the primary nutritional source for
358 this species. This explanation is further supported by fluctuations in *S.*
359 *neumayeri* gut mass during the season. Gut mass decreases during the first
360 half of the austral winter, when feeding activity ceases, followed by
361 stabilisation until the onset of feeding in November³⁰. Gut index data for *S.*
362 *neumayeri* in 2017/18 also supports this finding (Supplementary information,
363 Fig. S85). ~~NPs~~~~nutritive phagocytes~~ accumulate in late summer and early
364 winter. andDuring the period of cessation of feeding in winter NPs transfer
365 nutrients to developing gametes. NP stores are also used to meet the urchin's
366 energy requirements for metabolic maintenance ; where reduced food
367 availability during the austral winter is subsidised by NP stores to meet the
368 urchin's energy requirements for metabolic maintenance and gamete
369 development during this time⁵⁶. Our results suggest these nutrient stores are
370 important reproductive reserves in *S. neumayeri* as proportions vary inversely

371 with mean oocyte size and NPs are depleted as reserves are mobilised to
372 maturing gametes.

373 This research demonstrates the need for long-term multi-year studies that
374 encapsulate endogenous and environmentally driven reproductive investment
375 against a backdrop of seasonal change. Relationships between reproductive
376 cycles and single environmental ~~variables~~ ~~parameters~~ are well reported,
377 where spawning often coincides with seasonal changes (e.g., in temperature
378 and chlorophyll). However, gradual environmental shifts over several years
379 are rarely encompassed by single variable studies. Furthermore, it is more
380 likely that such change occurs from alterations in multiple interacting
381 ~~parameters~~ ~~variables~~. Large-scale climate metrics (~~e-g-e.g.~~, SOI and SAM),
382 can capture shifts in multifactorial environmental states and highlight how
383 environmental alterations translate into ecological processes.

384 Identifying endogenous rhythms for growth and reproduction enables the
385 partitioning of these processes from the effects of small-scale environmental
386 change and large-scale environmental cycles on marine biodiversity, ~~which is~~
387 ~~essential for predicting future climate impacts. Observations like this for~~
388 ~~sensitive polar marine taxa can be used to inform our understanding of how~~
389 ~~species might respond on a global scale to the predicted change in the~~
390 ~~coming decades. We have identified a potential demi-decadal trend in~~
391 ~~reproduction in a polar sea-urchin, *Sterechinus neumayeri*, from a seven year~~
392 ~~dataset. There may be even longer cycles, and cycles like these may be~~
393 ~~cumulative across decades or multi-decadal timescales. To identify such~~
394 ~~long-term trends requires very long sampling and monitoring programmes, but~~

395 [these would be invaluable when assessing the impacts of the current](#)
396 [environmental change that is occurring over decadal to centennial scales](#)

397 **4. METHODS**

398 **Study site and sampling**

399 *Sterechinus neumayeri* were collected from Hangar Cove (67°33'54.2"S
400 68°07'13.1"W), located near the British Antarctic Survey's Rothera Research
401 Station on the Western Antarctic Peninsula (Fig. 1). Adult urchins (19-51 mm
402 diameter; n=16) were collected monthly (weather permitting) from 2012 to
403 2018 by SCUBA divers (13-21 m depth), with the exception of a 6-month gap
404 from August 2015 to January 2016, when thin ice prohibited access to the
405 collection site. Specimens were preserved in 10% buffered formalin solution
406 until analysis.

407 **Measuring reproductive condition**

408 ~~Gonad index (GI)~~, oocyte size and tissue composition in females and maturity
409 stage in males were used to describe urchin reproductive condition. Total
410 gonad wet mass was measured and water content and dry gonad mass
411 obtained from subsamples of gonad tissue. GI was used instead of direct
412 gonad mass to allow for [differences in](#) animal size, and was derived by
413 calculating the gonad mass as a proportion of total body size according to
414 equation (3), following Bronstein et al. (2016):

$$415 \quad GI = \frac{\text{Total gonad dry mass (mg)}}{\text{Test diameter (mm)}} \quad (3)$$

416 A subsample of wet gonad tissue was examined for oocyte size and tissue
417 composition for females, or maturity stage for males following standard wax
418 histology procedures⁵⁸. In brief, tissue was dehydrated in a graded
419 isopropanol series, cleared in XTF clearing agent, embedded in paraffin wax,
420 sectioned at 7 µm and stained with haematoxylin and eosin.

421 Individuals were sexed and female tissue sections viewed under a light
422 microscope (Olympus BHS (BH-2)) at x10 magnification and photographed
423 using a Nikon D5000 camera (Supplementary information, Fig. S64). To
424 obtain oocyte size data, outlines were drawn around representative oocytes in
425 images using imaging software, Fiji (image-J v2)^{59,60}. Only oocytes with a
426 visible nucleus or nucleolus were measured to ensure oocytes were centrally
427 sectioned and maximum circumferences measured. Where possible, at least
428 5 females were analysed each month and 100 oocytes measured at random
429 per female. Subsamples of 100 oocytes were used to calculate an average
430 oocyte size distribution²⁸. Oocyte area (A) was used to calculate the
431 ~~Equivalent Circular Diameter (ECD)~~ according to equation (4), used in
432 previous studies^{61,62} to determine the size of a spherical oocyte with an
433 equivalent area.

434
$$ECD = \sqrt{\frac{4A}{\pi}} \quad (4)$$

435 Male tissue sections observed under light microscope at x10 magnification
436 were staged for maturity based on the development of the testes. Testis
437 maturity level (Supplementary information, Fig. S72) was categorised from
438 representative images following Brockington et al. (2007):

439 Stage 1: Spent/Recovering: Lumen empty. Nutritive phagocytic tissue lining is
440 of variable thickness and possibly a thin layer of spermatogonia on the
441 germinal epithelium.

442 Stage 2: Growing: Spermatogonia visible on germinal epithelium;
443 spermatozoa present at moderate density in lumen.

444 Stage 3: Mature: Lumen densely packed with mature spermatozoa in swirls.
445 Lumen stains intense blue. Spermatid production may still be evident.
446 Nutritive tissue generally highly reduced.

447 To visualise changes in male maturity as a continuous variable, both
448 seasonally and across years, the occurrence of each stage was converted to
449 a percentage frequency for each month ((number of individuals at given stage
450 / number males sampled in month) x100). Percentage frequency of maturity
451 stage was then modelled as a smoothed function for month, using the local
452 regression smoother (LOESS) method ⁶³.

453 **Nutritive phagocytes (NPs)**

454 Sea urchin gonad tissue serves two functions. Tissues contain both the
455 developing gametes and nutritive phagocytes (NPs), a storage tissue.
456 Variation in GI is thus a product of variation in both tissue types and not
457 limited to maturing gametes. Understanding how the proportions of these
458 tissues change seasonally is important to understanding gonad function and
459 interpreting seasonal GI variation. Images taken for oocyte size were,
460 therefore, used to quantify proportions of NPs to oocytes in female gonads.
461 For this purpose, three females from each month were selected at random,

462 where for each, three images of histological sections from different areas in
 463 the gonad were used to provide a representative assessment. The relative
 464 areas occupied by germ cells and NPs were calculated using Fiji (image-J v2)
 465 'Area' tool. This process involved first selecting only NPs as defined by
 466 specific colour thresholds and converting these areas to a mask. The mask %
 467 area relative to the image was then calculated. This process was also applied
 468 to oocytes. Gonad tissue was almost exclusively formed from oocytes and
 469 NPs, hence % area of NPs and oocytes was calculated relative to the total
 470 gonad tissue area in each image.

471 To relate NP and oocyte % areas to gonad size, and inform how these
 472 proportions contribute to seasonal GI variation, NP and oocyte proportions in
 473 the gonad were averaged across individuals for each month using images that
 474 were of highest quality from across the time-series. Following this, NP and
 475 oocyte percentages were scaled to represent relative proportions of the
 476 corresponding GI (averaged for all females for each month). Gonad oocyte
 477 and NP proportions were calculated based on % area tissue coverage
 478 estimates from image analysis according to equation (5).

$$479 \quad \left(\frac{A_o}{A_o + A_{np}} \right) = AA_o; \quad \left(\frac{A_{np}}{A_o + A_{np}} \right) = AA_{np} \quad (5)$$

$$480 \quad \overline{AA_o} \times \overline{GI} = \text{Oocyte proportion of the gonad}$$

$$481 \quad \overline{AA_{np}} \times \overline{GI} = \text{Nutritive phagocyte proportion of the gonad}$$

482 Where A_o = Percentage area of oocytes; A_{np} = Percentage area of nutritive
 483 phagocytes; AA_o = adjusted area of oocytes relative to gonad tissue total
 484 area; AA_{np} = adjusted area of nutritive phagocytes relative to gonad tissue

485 total area; \overline{AAo} = monthly mean of AAo; \overline{AAnp} = monthly mean of AAnp; \overline{GI} =
486 monthly mean of female GI.

487 **Environmental covariates**

488 Environmental data were collected weekly from Ryder Bay (67°34'12.0"S
489 68°13'30.0"W), ~ 4km west of Hangar Cove. This oceanographic sampling
490 regime is an on-going part of the Rothera Oceanographic and Biological Time
491 Series (RaTS) that has run continuously since 1997^{64,65}. Data from March
492 2012 to March 2018 were obtained for physiological drivers including
493 temperature and salinity (at 15m depth), as well as sea-ice extent and
494 ~~chlorophyll a~~ (Chl-a) concentration (a proxy for food availability). The regional
495 climate metrics, SOI and SAM, ~~were~~ also considered as a covariate
496 measure. SOI and was represented as the standardised anomaly of the mean
497 atmospheric sea level pressure (MSLP) difference between Tahiti and Darwin
498 (Australian Bureau of Meteorology), calculated according to equation (6).

$$499 \quad \text{SOI} = 10 \frac{P_{\text{diff}} - P_{\text{diffav}}}{\text{SD}(P_{\text{diff}})} \quad (6)$$

500 Where P_{diff} = (average Tahiti MSLP for the month) - (average Darwin MSLP
501 for the month); P_{diffav} = long-term average of P_{diff} for each month, $\text{SD}(P_{\text{diff}})$
502 = long-term standard deviation of P_{diff} for the month in question.

503 SAM was represented as the standardized 3-month running mean value of
504 the Antarctic Oscillation index, reported by NOAA National Weather Service
505 Climate Prediction Centre.

506 **Data analysis**

507 Data were initially tested for normality and homogeneity of variance, and
508 identification of outliers and between-variable relationships, as per Zuur et al.
509 (2007). ~~A chi-squared test was used to assess whether sex ratios deviated~~
510 ~~from 1:1. When data were non-normal, the non-parametric Kruskal-Wallis A t-~~
511 ~~test was used, e.g., to determine differences in size differences (i.e. test~~
512 ~~diameter and whole animal mass) and GI between males and females. This~~
513 ~~test~~ An analysis of variance (ANOVA) -was also used to determine differences
514 in oocyte size between months of comparable gametogenic maturation/ stage
515 across the time series (i.e., between years) between years. Where significant
516 difference were found (p <0.05), the ANOVA was followed by a post-hoc
517 Tukey pair-wise test. Gonad maturation was assessed using GI and inter-
518 annual differences were assessed as above. A chi-squared test was used to
519 assess whether sex ratios deviated from 1:1. Interannual differences in oocyte
520 ECD were assessed using analysis of variance (ANOVA), where each month
521 of the year was separately compared between years.

522 An initial linear regression model of GI with time revealed patterns in the
523 residuals, indicating an underlying non-linear relationship. Following this, a
524 generalised additive model (GAM) was used to examine factors influencing
525 reproductive state⁶⁶. The response variable, GI, was used as a measure of
526 reproductive state and modelled against smoothed ecological and
527 environmental variables. Time, Chl-a, temperature, fast ice concentration,
528 salinity, SAM and SOI were considered in the model as continuous predictors.
529 Month and season were considered as factors accounting for seasonal
530 periodicities and modelled as main effect predictors using cyclic cubic
531 regression splines, and finally sex was considered both as an interactive and

532 main effect predictor. In order to meet the assumptions of normality, GI was
533 square root transformed.

534 An initial pair's plot was constructed to determine co-linearity between
535 predictor variables before adding them to the model. Of the explanatory
536 variables that correlated (threshold correlation for inclusion = 0.50), the most
537 ecologically relevant variable was included in the initial model. If both
538 variables were ecologically relevant, then the weakest predictor was removed.
539 Penalised cubic regression splines were used to estimate the smooth function
540 for each non-cyclic predictor variable and with knots limited to 5 which was
541 deemed adequate to explain the data, without over-fitting ⁶⁷. Using the
542 "FSSgam" package in R ⁶⁸ a full-subsets information theoretical approach was
543 used to compare a complete model set of all predictor variables from the
544 environmental and ecological data available. Other relevant R packages for
545 the model included the "MuMin" and "mgcv" packages ⁶⁹.

546 All candidate predictors were considered during the initial model exploration
547 and ranked in order of conditional probability, calculated by the Akaike
548 Information Criterion' (AIC). Variable weights were ranked by importance and
549 predictors ranking low were excluded. Residuals from the 'best' model were
550 checked for normality and homogeneity of variance using the "gam.check"
551 function in the "mgcv" package.

552 Decomposition analysis was carried out on the gonad index time series data
553 as an alternative method, to identify any overall trends and seasonal
554 components. This analysis produced results very similar to the GAM model
555 and did not provide any additional information. However, this additional

556 analysis did substantiate the GAM model results (Supplementary information,
557 [Fig. S83](#)). Decomposition of the environmental variables was also explored
558 and trends, seasonal cycles and residual variations were observed in relation
559 to the GI trend. Decomposition of the environmental variables allowed the
560 trends observed for each factor to be regressed against SOI to determine how
561 this large-scale climate metric might relate to single variables measured in our
562 time series. Lag effects were also considered and incorporated where
563 visualisation of the trends alluded to a delay in biological response. The R
564 code for this analysis is given in the Supplementary information
565 ([Supplementary information, Text S1](#)).

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574 paper.

575 **AUTHOR CONTRIBUTIONS**

576 L.S.P and L.J.G conceived and designed the study. R.D carried out the
577 practical work and data processing. R.D, L.J.G and L.S.P analysed the data,
578 drafted the manuscript and approved its publication'

579 **COMPETING INTERESTS**

580 The authors declare no competing interests.

581 **DATA AVAILABILITY**

582 Data available from the Dryad Digital Repository

583 <https://doi.org/10.5061/dryad.6q573n5z1>⁷⁰

584 **FIGURES**

585 Figure 1: Location of Hangar Cove study site at Rothera Point, Adelaide
586 Island, Antarctica (67°33'54.2"S 68°07'13.1"W) and insert map showing
587 Rothera Point on Western Antarctic Peninsula. Marine environmental data are
588 collected at the site south west of Rothera Point as part of the British Antarctic
589 Survey Rothera Time Series monitoring programme (RaTS). Large-scale map
590 indicates the position of Rothera Research Station on Adelaide Island, on the
591 Western Antarctic Peninsula. Figure modified from Grange et al. (2011).

592 Figure 2: Monthly changes for *Sterechinus neumayeri* in a) gonad index for
593 males (blue) and females (red); b) mean equivalent circular diameter (ECD) of
594 oocytes present in female gonads; c) percentage (%) of gonad tissue in
595 females composed of nutritive phagocytes; d) percentage frequency (%) of
596 male gonad maturity stages where frequencies are smoothed by the function
597 $y \sim x$ using the local regression smoother (LOESS) method. The smoothing
598 span was chosen to reflect seasonal changes. Data as box plots are
599 displayed with the central line in the boxes representing the median value, the
600 upper and lower hinges representing the 25th and 75th percentiles, and the

601 upper/lower whiskers representing the largest/smallest value, no further than
602 1.5 times the interquartile range from the hinge. All data outside these ranges
603 are plotted as points.

604 Figure 3: Monthly female gonad index as proportional area of nutritive
605 phagocytes (NP) and oocytes. Monthly data for proportions are \pm the standard
606 error of the NP or oocyte equivalent GI based on replicate months.
607 Chlorophyll data are represented on the secondary y-axis and have been
608 averaged from the time series (2012 – 2018), \pm standard error.

609 Figure 4: Smoothers of the effect of the three non-parametric terms: time,
610 Southern Oscillation Index (SOI) ~~and~~, chlorophyll and Southern Annular Mode
611 (SAM), on the gonad index of *Sterechinus neumayeri*, from the optimal GAM
612 model. Shaded area represents a 95% confidence interval and data points
613 represent raw gonad index data. The magnitude of change in gonad index as
614 a response to the change in the x-variable is represented on the y-axis as the
615 square-root transformed gonad index. For the axis 'time', year intervals are
616 plotted on every 1st January. Green represents males and yellow represents
617 females.

618 Figure 5: Seasonal cycle of gonad index for males (solid green line) and
619 females (solid yellow line), extracted from decomposition analysis, overlaid on
620 seasonal cycle of chlorophyll (dotted black line) extracted from decomposition
621 analysis.

622 Figure 65: Long-term changes in the percentage frequency (%), represented
623 as a density plot, of maturity stages in the male sample population from March
624 2012 - March 2017. Frequency densities derived from (LOESS) method. The

625 smoothing span was chosen to reflect long-term changes rather than
626 seasonal variability.

627 **LITERATURE CITED**

- 628 1. Takemura, A., Rahman, M. S. & Park, Y. J. External and internal
629 controls of lunar-related reproductive rhythms in fishes. *J. Fish Biol.* **76**,
630 7–26 (2010).
- 631 2. Brockington, S. & Clarke, A. The relative influence of temperature and
632 food on the metabolism of a marine invertebrate. *J. Exp. Mar. Bio. Ecol.*
633 **258**, 87–99 (2001).
- 634 3. Kelly, M. S. Environmental parameters controlling gametogenesis in the
635 echinoid *Psammechinus miliaris*. *J. Exp. Mar. Bio. Ecol.* **266**, 67–80
636 (2001).
- 637 4. Muthiga, N. A. The reproductive biology of a new species of sea
638 cucumber, *Holothuria (Mertensiothuria) arenacava* in a Kenyan marine
639 protected area: The possible role of light and temperature on
640 gametogenesis and spawning. *Mar. Biol.* **149**, 585–593 (2006).
- 641 5. Emilio, L. *et al.* Is the Orton's rule still valid? Tropical sponge fecundity,
642 rather than periodicity, is modulated by temperature and other proximal
643 cues. *Hydrobiologia* **815**, 187–205 (2018).
- 644 6. St.Gelais, A. T., Chaves-Fonnegra, A., Moulding, A. L., Kosmynin, V. N.
645 & Gilliam, D. S. *Siderastrea siderea* spawning and oocyte resorption at
646 high latitude. *Invertebr. Reprod. Dev.* **60**, 212–222 (2016).
- 647 7. Zhadan, P. M., Vaschenko, M. A. & Ryazanov, S. D. Assessing the
648 effect of environmental factors on the spawning activity of the sea
649 urchin *Strongylocentrotus intermedius* through video recording
650 observations. *Mar. Ecol. Prog. Ser.* **588**, 101–119 (2018).
- 651 8. Grange, L. J., Tyler, P. A., Peck, L. S. & Cornelius, N. Long-term
652 interannual cycles of the gametogenic ecology of the Antarctic brittle
653 star *Ophionotus victoriae*. *Mar. Ecol. Prog. Ser.* **278**, 141–155 (2004).
- 654 9. Balogh, R., Wolfe, K. & Byrne, M. Gonad development and spawning of
655 the vulnerable commercial sea cucumber, *Stichopus herrmanni*, in the
656 southern Great Barrier Reef. *J. Mar. Biol. Assoc. United Kingdom* **99**,
657 487–495 (2019).
- 658 10. Stenseth, N. C. *et al.* Studying climate effects on ecology through the
659 use of climate indices: The North Atlantic Oscillation, El Niño Southern
660 Oscillation and beyond. *Proc. R. Soc. B Biol. Sci.* **270**, 2087–2096
661 (2003).
- 662 11. Wood, S. *et al.* El Niño and coral larval dispersal across the eastern
663 Pacific marine barrier. *Nat. Commun.* **7**, (2016).
- 664 12. Turner, J. The El Niño-Southern Oscillation and Antarctica. *Int. J.*
665 *Climatol.* **24**, 1–31 (2004).

- 666 13. La, H. S. *et al.* Zooplankton and micronekton respond to climate
667 fluctuations in the Amundsen Sea polynya, Antarctica. *Sci. Rep.* **9**, 1–7
668 (2019).
- 669 14. Xuebin, Z. & Mcphaden, M. J. Eastern equatorial Pacific forcing of
670 ENSO sea surface temperature anomalies. *J. Clim.* **21**, 6070–6079
671 (2008).
- 672 15. Oliver, E. C. J. *et al.* Longer and more frequent marine heatwaves over
673 the past century. *Nat. Commun.* **9**, 1–12 (2018).
- 674 16. Ryan, J. P. *et al.* Causality of an extreme harmful algal bloom in
675 Monterey Bay, California, during the 2014–2016 northeast Pacific warm
676 anomaly. *Geophys. Res. Lett.* **44**, 5571–5579 (2017).
- 677 17. Conde, A. & Prado, M. Changes in phytoplankton vertical distribution
678 during an El Niño event. *Ecol. Indic.* **90**, 201–205 (2018).
- 679 18. Santidrián Tomillo, P. *et al.* The impacts of extreme El Niño events on
680 sea turtle nesting populations. *Clim. Change* (2020).
681 doi:10.1007/s10584-020-02658-w
- 682 19. Wilson, S. K. *et al.* Climatic forcing and larval dispersal capabilities
683 shape the replenishment of fishes and their habitat-forming biota on a
684 tropical coral reef. *Ecol. Evol.* **8**, 1918–1928 (2018).
- 685 20. Welhouse, L., Lazzara, M., Keller, L., Tripoli, G. & Hitchman, M.
686 Composite analysis of the effects of ENSO events on Antarctica. *J.*
687 *Clim.* **29**, 1797–1808 (2016).
- 688 21. Testa, J. W. *et al.* Temporal variability in Antarctic marine ecosystems:
689 periodic fluctuations in the phocid seals. *Can. J. Fish. Aquat. Sci.* **48**,
690 631–639 (1991).
- 691 22. Román-González, A. *et al.* Analysis of ontogenetic growth trends in two
692 marine Antarctic bivalves *Yoldia eightsi* and *Laternula elliptica*:
693 Implications for sclerochronology. *Palaeogeogr. Palaeoclimatol.*
694 *Palaeoecol.* **465**, 300–306 (2017).
- 695 23. Brown, M. *et al.* Long-term effect of photoperiod, temperature and
696 feeding regimes on the respiration rates of Antarctic Krill (*Euphausia*
697 *superba*). *Open J. Mar. Sci.* **3**, 40–51 (2013).
- 698 24. Ainley, D. G. *et al.* Decadal trends in abundance, size and condition of
699 Antarctic toothfish in McMurdo Sound, Antarctica, 1972 – 2011. *Fish*
700 *Fish.* **14**, 343–363 (2013).
- 701 25. Doney, S. C. *et al.* Climate Change Impacts on Marine Ecosystems.
702 *Ann. Rev. Mar. Sci.* **4**, 11–37 (2012).
- 703 26. Peck, L. S. Antarctic Marine Biodiversity: Adaptations, Environments
704 and Responses to Change. *Oceanogr. Mar. Biol. An Annu. Rev.* **56**,
705 105–236 (2018).
- 706 27. Peck, L. S. A Cold Limit to Adaptation in the Sea. *Trends Ecol. Evol.* **31**,
707 13–26 (2016).
- 708 28. Brockington, S., Peck, L. S. & Tyler, P. A. Gametogenesis and gonad
709 mass cycles in the common circumpolar Antarctic echinoid *Sterechinus*
710 *neumayeri*. *Mar. Ecol. Prog. Ser.* **330**, 139–147 (2007).

- 711 29. Grange, L. J., Tyler, P. A. & Peck, L. S. Multi-year observations on the
712 gametogenic ecology of the Antarctic seastar *Odontaster validus*. *Mar.*
713 *Biol.* **153**, 15–23 (2007).
- 714 30. Brockington, S. The seasonal ecology and physiology of *Sterechinus*
715 *neumayeri* (Echinodermata; Echinoidea) at Adelaide Island, Antarctica.
716 PhD thesis The Open University. (2001).
- 717 31. Bosch, I., Beauchamp, K. A., Steele, M. E. & Pearse, J. S.
718 Development, metamorphosis, and seasonal abundance of embryos
719 and larvae of the Antarctic sea urchin *Sterechinus Neumayeri*. *Biol. Bull.*
720 **173**, 126–135 (1987).
- 721 32. Stanwell-Smith, D. & Peck, L. S. Temperature and embryonic
722 development in relation to spawning and field occurrence of larvae of
723 three Antarctic echinoderms. *Biol. Bull.* **194**, 44–52 (1998).
- 724 33. Fogt, R. L., Bromwich, D. H. & Hines, K. M. Understanding the SAM
725 influence on the South Pacific ENSO teleconnection. *Clim. Dyn.* **36**,
726 1555–1576 (2011).
- 727 34. Kwok, R. & Comiso, J. C. Spatial patterns of variability in Antarctic
728 surface temperature: Connections to the Southern Hemisphere Annular
729 Mode and the Southern Oscillation. *Geophys. Res. Lett.* **29**, 2–5 (2002).
- 730 35. Santamaría-Del-ángel, E. *et al.* Interannual climate variability in the
731 west antarctic peninsula under austral summer conditions. *Remote*
732 *Sens.* **13**, (2021).
- 733 36. Montgomery, D. & Peck, E. *Introduction to linear regression analysis*.
734 (Wiley, 1992).
- 735 37. Halberg, F., Shankaraiah, K. & Giese, A. . The chronobiology of marine
736 invertebrates: methods of analysis. in *Reproduction of marine*
737 *invertebrates, Vol IX. General aspects: seeking unity in diversity* 331–
738 384 (The Boxwood Press, 1987).
- 739 38. Loeb, V. J., Hofmann, E. E., Klinck, J. M., Holm-Hansen, O. & White, W.
740 B. ENSO and variability of the antarctic peninsula pelagic marine
741 ecosystem. *Antarct. Sci.* **21**, 135–148 (2009).
- 742 39. White, W. B., Chen, S. C., Allan, R. J. & Stone, R. C. Positive
743 feedbacks between the Antarctic Circumpolar Wave and the global El
744 Niño-Southern Oscillation wave. *J. Geophys. Res. C Ocean.* **107**, 29–1
745 (2002).
- 746 40. Saba, G. K. *et al.* Winter and spring controls on the summer food web of
747 the coastal West Antarctic Peninsula. *Nat. Commun.* **5**, 1–8 (2014).
- 748 41. Cavanagh, R. D. *et al.* A synergistic approach for evaluating climate
749 model output for ecological applications. *Front. Mar. Sci.* **4**, (2017).
- 750 42. Vergani, D. F., Labraga, J. C., Stanganelli, Z. B. & Dunn, M. The effects
751 of El Niño-La Niña on reproductive parameters of elephant seals
752 feeding in the Bellingshausen Sea. *J. Biogeogr.* **35**, 248–256 (2008).
- 753 43. Clark, G. F. *et al.* Light-driven tipping points in polar ecosystems. *Glob.*
754 *Chang. Biol.* **19**, 3749–3761 (2013).
- 755 44. Schneider, D. P., Okumura, Y. & Deser, C. Observed Antarctic

- 756 interannual climate variability and tropical linkages. *J. Clim.* **25**, 4048–
757 4066 (2012).
- 758 45. Yuan, X. ENSO-related impacts on Antarctic sea ice: A synthesis of
759 phenomenon and mechanisms. *Antarct. Sci.* **16**, 415–425 (2004).
- 760 46. Loeb, V. J. & Santora, J. A. Population dynamics of *Salpa thompsoni*
761 near the Antarctic Peninsula: Growth rates and interannual variations in
762 reproductive activity (1993-2009). *Prog. Oceanogr.* **96**, 93–107 (2012).
- 763 47. Moran, A. L., McAlister, J. S. & Whitehill, E. A. G. Eggs as energy:
764 Revisiting the scaling of egg size and energetic content among
765 echinoderms. *Biol. Bull.* **224**, 184–191 (2013).
- 766 48. Gómez-Robles, E. & Saucedo, P. E. Evaluation of quality indices of the
767 gonad and somatic tissues involved in reproduction of the pearl oyster
768 *Pinctada mazatlanica* with histochemistry and digital image analysis. *J.*
769 *Shellfish Res.* **28**, 329–335 (2009).
- 770 49. Gómez-Valdez, M., Ocampo, L., Carvalho-Saucedo, L. & Gutiérrez-
771 González, J. Reproductive activity and seasonal variability in the
772 biochemical composition of a pen shell, *Atrina maura*. *Mar. Ecol. Prog.*
773 *Ser.* **663**, 99–113 (2021).
- 774 50. Steinberg, D. K. *et al.* Long-term (1993-2013) changes in
775 macrozooplankton off the Western Antarctic Peninsula. *Deep. Res. Part*
776 *I Oceanogr. Res. Pap.* **101**, 54–70 (2015).
- 777 51. Rozema, P. D. *et al.* Interannual variability in phytoplankton biomass
778 and species composition in northern Marguerite Bay (West Antarctic
779 Peninsula) is governed by both winter sea ice cover and summer
780 stratification. *Limnol. Oceanogr.* **62**, 235–252 (2017).
- 781 52. Starr, M., Himmelman, J. H. & Therriault, J. Direct coupling of marine
782 invertebrate spawning with phytoplankton blooms. *Science (80-.)*. **247**,
783 1071–1074 (1990).
- 784 53. Harrington, L. H., Walker, C. W. & Lesser, M. P. Stereological analysis
785 of nutritive phagocytes and gametogenic cells during the annual
786 reproductive cycle of the green sea urchin, *Strongylocentrotus*
787 *droebachiensis*. *Invertebr. Biol.* **126**, 202–209 (2007).
- 788 54. Magniez, P. Reproductive cycle of the brooding echinoid *Abatus*
789 *cordatus* (Echinodermata) in Kerguelen (Antarctic Ocean): changes in
790 the organ indices, biochemical composition and caloric content of the
791 gonads. *Mar. Biol.* **74**, 55–64 (1983).
- 792 55. Pérez, A. F., Morriconi, E., Boy, C. & Calvo, J. Seasonal changes in
793 energy allocation to somatic and reproductive body components of the
794 common cold temperature sea urchin *Loxechinus albus* in a Sub-
795 Antarctic environment. *Polar Biol.* **31**, 443–449 (2008).
- 796 56. Hernandez, E., Vázquez, O. A., Torruco, A. & Rahman, M. S.
797 Reproductive cycle and gonadal development of the Atlantic sea urchin
798 *Arbacia punctulata* in the Gulf of Mexico: changes in nutritive
799 phagocytes in relation to gametogenesis. *Mar. Biol. Res.* **16**, 177–194
800 (2020).

- 801 57. Bronstein, O., Kroh, A. & Loya, Y. Reproduction of the long-spined sea
802 urchin *Diadema setosum* in the Gulf of Aqaba - Implications for the use
803 of gonad-indexes. *Sci. Rep.* **6**, 1–11 (2016).
- 804 58. Alturkistani, H. A., Tashkandi, F. M. & Mohammedsaleh, Z. M.
805 Histological Stains: A Literature Review and Case Study. *Glob. J.*
806 *Health Sci.* **8**, 72–79 (2015).
- 807 59. Schindelin, J. *et al.* Fiji: An open-source platform for biological-image
808 analysis. *Nat. Methods* **9**, 676–682 (2012).
- 809 60. Rueden, C. T. *et al.* ImageJ2: ImageJ for the next generation of
810 scientific image data. *BMC Bioinformatics* **18**, 1–26 (2017).
- 811 61. Lau, S. C. Y., Grange, L. J., Peck, L. S. & Reed, A. J. The reproductive
812 ecology of the Antarctic bivalve *Aequiyoldia eightsii* (Protobranchia:
813 Sareptidae) follows neither Antarctic nor taxonomic patterns. *Polar Biol.*
814 **41**, 1693–1706 (2018).
- 815 62. Reed, A. J., Morris, J. P., Linse, K. & Thatje, S. Reproductive
816 morphology of the deep-sea protobranch bivalves *Yoldiella ecaudata*,
817 *Yoldiella sabrina*, and *Yoldiella valettei* (Yoldiidae) from the Southern
818 Ocean. *Polar Biol.* **37**, 1383–1392 (2014).
- 819 63. Cleveland, W. S. Robust locally weighted regression and smoothing
820 scatterplots. *J. Am. Stat. Assoc.* **74**, 829–836 (1979).
- 821 64. Venables, H. J., Clarke, A. & Meredith, M. P. Wintertime controls on
822 summer stratification and productivity at the western Antarctic
823 Peninsula. *Limnol. Oceanogr.* **58**, 1035–1047 (2013).
- 824 65. Clarke, A., Meredith, M. P., Wallace, M. I., Brandon, M. A. & Thomas,
825 D. N. Seasonal and interannual variability in temperature, chlorophyll
826 and macronutrients in northern Marguerite Bay, Antarctica. *Deep. Res.*
827 *Part II Top. Stud. Oceanogr.* **55**, 1988–2006 (2008).
- 828 66. Zuur, A., Ieno, E. N. & Smith, G. M. Analyzing Ecological Data. in
829 *Analyzing Ecological Data* (ed. M. Gail, K. Krickeberg, J. Samet, A.
830 Tsiatis, W. W.) 23–47 (Springer-Verlag New York, 2007).
- 831 67. Burnham, K. P. & Anderson, D. R. *Model selection and multimodel*
832 *inference. A practical information-theoretical approach. Model Selection*
833 *and Multimodel Inference* (Springer, 2002). doi:10.1007/978-0-387-
834 22456-5_7
- 835 68. Fisher, R., Wilson, S. K., Sin, T. M., Lee, A. C. & Langlois, T. J. A
836 simple function for full-subsets multiple regression in ecology with R.
837 *Ecol. Evol.* **8**, 6104–6113 (2018).
- 838 69. Wood, S. Fast stable restricted maximum likelihood and marginal
839 likelihood estimation of semiparametric generalized linear models. *J. R.*
840 *Stat. Soc.* **73**, 3–36 (2011).
- 841 70. De Leij, R., Peck, L. S. & Grange, L. J. R code and csv. files. (2021).
842 doi:<https://doi.org/10.5061/dryad.6q573n5z1>
- 843 71. Grange, L. J., Peck, L. S. & Tyler, P. A. Reproductive ecology of the
844 circumpolar Antarctic nemertean *Parborlasia corrugatus*: No evidence
845 for inter-annual variation. *J. Exp. Mar. Bio. Ecol.* **404**, 98–107 (2011).

