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5   Article type   : Research Paper

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8   **Predation as an explanation for a latitudinal gradient in arm number among featherstars**

9   **Running title**: Latitude and arm number in featherstars

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14   Handling editor: Marcelo Rivadaneira

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19

20   **Abstract**

21   *Aim*

22   The role of biotic interactions in generating broad patterns in organismal phenotypes is a

23   central question in macroecology. We investigate global patterns in feeding morphology among

24   featherstars, a globally widespread group of suspension-feeding echinoderms whose evolutionary

25   history has been demonstrably shaped by predators.

26   *Location*

27   World's oceans.

Major taxon studied

Crinoidea.

Methods

We tested for global patterns in the featherstar suspension feeding apparatus, a filter made up of five to 200 arms which is the main interface with predators. We investigate a geospatial dataset of 23,950 occurrences in 442 species using statistical analyses including quantile regression and a new permutation-based phylogenetic comparative approach appropriate for testing for a broad range of patterns in non-normal data.

Results

We find that featherstars exhibit a latitudinal gradient in arm number: arm number is both greater on average and more variable between species at lower latitudes. This pattern holds across depths and hemispheres and is not a spurious result of either the latitudinal diversity gradient or phylogenetic autocorrelation. Tropical featherstars that conceal themselves have fewer arms, and also appear to experience less intense predation.

Main conclusions

Temperature, primary productivity, and substrate type do not adequately explain the latitudinal gradient in arm number. We attribute it instead to a corresponding gradient in predation intensity: many-armed featherstars can withstand more intense arm loss to predators. Concealment and other alternate solutions to the problem of predation, along with reproductive costs associated with having many arms, explain why the trend is wedge-shaped rather than linear. Our findings constitute a latitudinal gradient in functional diversity, paralleling recent findings in other taxa. The gradient may be a consequence of shallow tropical reefs; inasmuch as reefs as centers of biotic interactions promote functional richness, changes in the distribution of reefs through deep time probably entailed shifts in the global deployment of ecological diversity.

Keywords: ecological diversity, functional morphology, latitude, macroecology, phylogenetic comparative methods, Crinoidea

Introduction

The role of biotic interactions in structuring macroecological patterns is of central interest to biologists. Despite the obvious importance of organism-organism interactions at the ecosystem

scale, the broadest spatial and temporal phenomena in biology are typically attributed to abiotic causes like climate or continental configuration (Antell et al., 2020; Barnosky, 2001; Benton, 2009). Nevertheless, biotic interactions demonstrably leave some signals in global phenotypic patterns. For example, increased intensity of predation and biological disturbance of the shallow seafloor throughout the Phanerozoic appears to have nonrandomly restricted some kinds of organisms to the deep sea (Bottjer & Jablonski, 1988), and driven others into the infauna (Thayer, 1983). There is also direct evidence for a latitudinal gradient in the intensity of predation in some systems (Klompmaker et al., 2019; Schemske et al., 2009; Vermeij, 1978), and anti-predatory adaptations are more common among tropical representatives of many groups: tropical molluscs are apparently more resistant to shell-crushing predators (Palmer, 1979; Vermeij, 1978), and toxicity/unpalatability is more common closer to the equator in marine worms, caterpillars, and various plant groups (Levin, 1976; Schemske et al., 2009). Beyond constituting good explanations for natural phenomena like these, predation and other biotic interactions form the core of a general evolutionary principle, albeit a contentious one (Dietl & Vermeij, 2006; Madin et al., 2006): escalation, the hypothesis that some of the most conspicuous evolutionary trends are the result of natural selection on organisms by their ecological 'enemies' (Vermeij, 1993, 2008). It is worthwhile to tease apart the degree to which evolution is driven by biotic interactions as opposed to abiotic factors, as these correspond to quite different histories of life on Earth.

Crinoids are a useful study system with which to consider the evolutionary role of biotic interactions because some of the major features of crinoid evolution appear to correlate with changes in the role of predators in marine ecosystems through time (Meyer & Macurda, 1977). Despite being some of the most diverse and conspicuous members of shallow marine ecosystems during much of the Paleozoic and Mesozoic (Kammer & Ausich, 2006), these suspension-feeding echinoderms are today restricted to deep waters (Bottjer & Jablonski, 1988) – with one conspicuous exception. Featherstars, those crinoids in the order Comatulida that shed their entire stalk during development, make up most of modern crinoid diversity and are common in shallow and deep water (Messing, 1997). These stalkless forms have a number of features that have been interpreted as antipredatory adaptations: they are more mobile than stalked crinoids (Meyer & Macurda, 1977), most can swim (Janevski & Baumiller, 2010), they regenerate arms rapidly (Baumiller & Stevenson, 2018), and many have toxic flesh (Meyer, 1985; Slattery, 2010). The

90   restriction to deep water of stalked but not stalkless crinoids occurred synchronously with the
91   radiation of crinoid predators in shallow water during the so-called Mesozoic Marine Revolution
92   (Vermeij, 1977), and is thought to reflect the respective success and failure of stalkless and
93   stalked crinoids to persist in spite of increased intensity of predation (Meyer & Macurda, 1977).
94   Even before the Mesozoic, morphological features that enhanced resistance to predation and
95   parasitism were common in crinoids (Syverson & Baumiller, 2014; Syverson, Brett, Gahn, &
96   Baumiller, 2018). Regenerating arms, thought to result in most cases from predation (Meyer,
97   1985), are prevalent among extant featherstars and in some populations can be found on virtually
98   every individual (Baumiller & Stevenson, 2018). They have even been identified in one fossil
99   featherstar (Baumiller & Fordyce, 2018). Predation is therefore a plausible and compelling agent
100 in crinoid evolution.

101   We explored and attempted to explain global patterns in arm number among living
102 featherstars. The feeding apparatus of extant crinoids consists of a system of particle-intercepting
103 tube feet lining one side of a set of five (rarely ten) sets of arms that bifurcate to varying degrees
104 and that bear unbranched "pinnules" at regular intervals (Hess & Messing, 2011). Like other
105 passive suspension-feeders, crinoids do not create their own feeding currents, and the rate at
106 which they encounter food-laden water is a function of local flow conditions and feeding
107 morphology (Baumiller, 1997). In particular, crinoids with dense filtration fans can only feed
108 effectively in fast-flowing water (Baumiller, 1993), and the most dense fans are found among the
109 crinoids with the most arms (Kitazawa, Oji, & Sunamura, 2007). However, beyond simply
110 reflecting fluid dynamic constraints, the crinoid feeding apparatus is also the animals' main
111 interface with predators: the arms make up much of a typical crinoid's biovolume [most of it in
112 featherstars (Janevski & Baumiller, 2010)] and recorded predation events typically involve the
113 arms (Baumiller & Gahn, 2013; Meyer, 1985). This study treats variation in arm number
114 between featherstar species (Fig. 1). Because the featherstar feeding apparatus is relatively
115 stereotyped – all branching occurs near the base of the arms, and all species bear pinnules (Oji &
116 Okamoto, 1994) – arm number captures the better part of its morphological variation, whereas
117 across the crinoid tree of life the feeding apparatus varies considerably in terms of the
118 distribution of branching points along the arms, the thickness of the arms, the length and spacing
119 of pinnules and tube feet, and the presence or absence of pinnules (Baumiller, 1993; Cole, 2019;
120 Kammer & Ausich, 1987). Variation in arm number within featherstar species is not sufficiently

121 documented across taxa to be treated here but exceeds a factor of three in some species and
122 seems to vary more in many-armed taxa (Clark, 1967). This within-species variability is worth
123 investigating further, not least because it may correspond to differences in microhabitat: Messing
124 (1994) reported that featherstars living in shallower water and exposed to more energetic flow
125 regimes had more and shorter arms than their deeper-water conspecifics, suggesting that crinoid
126 feeding morphology exhibits phenotypic plasticity. Here we investigate an apparent relationship
127 between absolute latitude and arm number among featherstars, and explore predation and abiotic
128 factors as possible causes.

129

130   **Methods**

131   *Occurrence data*

132   We downloaded all available species-level occurrences of featherstars (order Comatulida
133 minus the 'bourgueticrinid' families Bathycrinidae, Bourgueticrinidae, Guillecrinidae,
134 Phrynocrinidae, Porphyrocrinidae, and Septocrinidae) available from the Ocean Biogeographic
135 Information System (OBIS) in August 2019. Although the stalkless featherstars have historically
136 been identified with the order Comatulida, recent phylogenetic analyses have recovered several
137 lineages of the stalked 'bourgueticrinids' within the Comatulida (Hemery et al., 2013; Rouse et
138 al., 2013). Importantly, our study relies on featherstars sharing some basic ecological similarities,
139 but not on their monophyly. Forty-five 'rogue' terrestrial data points were removed from the
140 dataset, resulting in 23,853 total occurrences. Depth data were available for 14,844 (62%) of
141 these. Depth ranges for each species were supplemented with ranges recorded in the World
142 Register of Marine Species (WoRMS). Our dataset includes 442 species of featherstar,
143 encompassing 79% of the 556 species of featherstar recorded in the WoRMS. Many 'nodes'
144 around the world contribute to OBIS and the geographic and bathymetric data vary in precision
145 and accuracy. We recorded the latitudinal midpoint of each species, and tested for two potential
146 features of the dataset that would make the use of midpoints problematic: geographic biases in
147 sampling intensity, and a relationship between latitudinal range size and arm number (see
148 Results).

149   *Arm number and habit*

150   We gathered arm number data from the literature for 435 species of featherstar
151 (Supplementary Information). For species with variable arm number – the case for most many-

152 armed species – we recorded arm number as the midpoint between the maximum and minimum

153 number reported. Arm number varies by a factor of over 30 and is strongly right-skewed, with a

154 clear mode at 10 (Fig. 1). All Jurassic and Cretaceous featherstars that preserve the crown have 5

155 or 10 arms (Hess & Messing, 2011), so the few-armed state is probably primitive in this group.

156 Arm number varies substantially between species in many featherstar clades, and the many-

157 armed condition appears to have been derived many times (Fig. 1).

158   As an attempt to understand arm number in the context of other putative anti-predatory

159 adaptations, we combined our dataset with habit data from Schneider (1988), who scored 30

160 tropical featherstar species as feeding either diurnally or nocturnally and as feeding while fully

161 exposed or while fully or partly cryptic. These modes of concealment are thought to be

162 adaptations for avoiding predators (Meyer, 1985; Slattery, 2010). [nocturnality and concealment

163 as anti-predatory adaptations] Schneider (1988) also pulled together data on the frequency of arm

164 regeneration among 406 featherstar populations in the same 30 species, which we coded into

165 four variables: (1) the mean number of regenerating arms per individual, (2) the mean proportion

166 of regenerating arms per individual (the number of regenerating arms divided by the number of

167 arms checked by the investigator for each individual, averaged across the population), (3) the

168 proportion of individuals in a population with at least one regenerating arm, and (4) number of

169 individuals examined.

170   The proportion of regenerating arms in a population does contain information on the rate

171 of arm-loss events, but this information is indirect. A fully-regenerated arm is typically

172 indistinguishable from one that was never lost in the first place; individuals that fully regenerate

173 lost arms more rapidly will therefore exhibit fewer apparent injuries, and an investigator might

174 spuriously infer that those individuals encountered fewer predators (Baumiller, 2013). To our

175 knowledge only a few studies have attempted to use information on both regeneration rate and

176 the proportion of regenerating arms to estimate predator encounter rate; we combined their

177 findings ("Predator encounter rates.xlsx," Supplementary files) with our dataset.

178   Lastly, colorful toxic secondary metabolites make some crinoids less palatable to

179 potential predators (Slattery, 2010), and have made them the target of intense pharmacological

180 research (Feng et al., 2017). We combined our dataset with two recent experimental studies of

181 the palatability of 16 featherstar species to their fish predators.

182   *Analysis 1*

183   Arm number is visibly right-skewed (nonparametric skew = 0.46; Fig. 2), so we investigated its

184   relationship with absolute latitude using rank correlation with Spearman's ρ. A biplot of arm

185   number against absolute latitude is noticeably wedge-shaped (Fig. 2); we used quantile

186   regression to investigate this feature. Unlike least-squares linear regression, which estimates the

187   mean of a response variable conditional on one or more predictors, quantile regression estimates

188   conditional quantiles of a response variable – for example, the median – by minimizing the sum

189   of absolute distances between observations and the regression line, weighted to estimate the

190   appropriate quantile (Koenker & Hallock, 2001). Quantile regression was implemented with the

191   R package 'quantreg' v. 5.36 (Koenker et al., 2018). We also tested the latitude – arm number

192   relationship for subsets of the dataset based on depth (species with or without occurrences above

193   200 m) and hemisphere (northern or southern). Quantile regression fits were assessed in an

194   Akaike Information Criterion (AIC) framework: the likelihood of quantile regression conditional

195   on absolute latitude was compared to that of unconditional quantile regression (i.e., a regression

196   model without latitude as a variable), and the former was considered well-supported if it had a

197   lower AIC score. In other words, this test asks whether adding information on latitude improves

198   estimates of upper or lower quantiles of arm number enough to justify the extra parameter.

199   An apparent latitudinal gradient in maximum arm number might appear spuriously as a

200   result of the increase in species richness toward the equator, even if the underlying arm number

201   distribution was uniform across latitude. To screen for this kind of bias, we re-evaluated the

202   dataset after subsampling such that each 10° bin of absolute latitude had as many species as the

203   least-sampled bin (50° - 60°, N = 13).

204   We tested whether temperature, a close correlate of latitude, could explain geographic

205   patterns in arm number better than latitude itself. Temperature and absolute latitude can be

206   analytically pulled apart because they do not correspond perfectly: ocean gyres cause sea surface

207   temperature (SST) at the same latitude to differ on the east and west sides of oceans, and mean

208   annual SST changes non-linearly with latitude, decreasing gradually from the equator to the

209   tropics and then declining steeply in the higher latitudes. To generate comparable metrics of

210   temperature and latitude, we randomly drew one occurrence above 100 m depth for each species

211   with shallow-water occurrences, and matched these occurrences with SST using the *lookup_xy*

212   function in the R package 'obistools' v.0.0.9 (Bosch et al., 2018). We assessed correlations

213   between arm number and both absolute latitude and SST for these randomly-drawn occurrences,

214   and repeated the procedure many times.

215   *Analysis 2: Phylogenetic permutation*

216   The previous section comprises "equilibrium analyses" (Lauder, 1982): they assume

217   there is no historical phylogenetic component to the variation in trait values, effectively treating

218   each data point as independent and at equilibrium with its environment. We devised a new

219   permutation-based approach to investigate the properties of a comparative dataset with respect to

220   the phylogenetic history on which it evolved. We generated a timetree with penalized likelihood

221   (Sanderson, 2002) – implemented with the program *treePL* (Smith & O'Meara, 2012) – using the

222   molecular phylogeny inferred by Saulsbury & Zamora (2019). Two fossil calibrations were used

223   to scale the tree to units of time (Appendix). Both absolute latitudinal midpoint (Blomberg's K =

224   0.6355, p < 0.001) and arm number (K = 0.4673, p = 0.004) exhibit moderate, statistically

225   significant phylogenetic signal with respect to the resulting timetree. The phylogeny and trait

226   values were visualized simultaneously with the *phylomorphospace* function in the R package

227   'phytools' v. 0.6.99 (Revell, 2012).

228   The problem with interpreting comparative data at face value is that species share

229   phylogenetic history, and the resulting phylogenetic autocorrelation among trait values may

230   violate the assumptions of most standard tests. Phylogenetic comparative methods like

231   independent contrasts (Felsenstein, 1985) and its generalization, phylogenetic generalized least

232   squares (PGLS; Grafen 1989), get around the problem of non-independence of species by

233   considering trait differences at phylogenetic splits as independent observations. These

234   approaches have proven to be quite powerful, but are inappropriate for our data for two reasons:

235   1. The "shape" of our data thoroughly violates the assumptions of least-squares

236   regression. Arm number is strongly right-skewed, left-bounded, and characterized by

237   some features peculiar to crinoid biology – for example, about half of the species in

238   the dataset have exactly 10 arms, and there are no species with 0 to 4 or 6 to 9 arms

239   (Fig. 2). The residuals in a PGLS regression of arm number on absolute latitude are

240   right-skewed and gappy even when arm number is singly or doubly log-transformed

241   (Fig. A9), violating the assumption of normally distributed residuals. Kolmogorov-

242   Smirnov tests confirm that the residuals in PGLS regressions of arm number, log arm

243   number, and log log arm number on absolute latitude clearly depart from normality (p

244   < 1E-10 in all cases). No less problematic is the visible heteroskedasticity in our

245   dataset (Fig. 2): variance of arm number in the lowest bin of absolute latitude (0-10°,

246   var = 479.1, N = 155) is roughly sixty times that in the highest bin (60-70°, var = 8.2,

247   N=16). A Bruesch-Pagan test for heteroskedasticity, which regresses the squared

248   residuals of a response variable on a predictor, recovers statistically significant

249   departures from homoskedasticity in the PGLS residuals of arm number and singly

250   and doubly-logged arm number on absolute latitude [$\alpha = 0.05$; using a standard

251   correction for non-normality (Koenker, 1981)]. The consequences of

252   heteroskedasticity for the validity of PGLS are poorly-understood, but potentially

253   severe (Mundry, 2014).

254   2. PGLS, and least-squares regression more generally, are meant to detect a narrow

255   subset of biologically interesting patterns – namely, relationships between one or

256   more predictors and the *mean* value of a response variable. They therefore lack the

257   flexibility to explore other features of datasets, including trends in variance, trends in

258   quantiles of a response variable, or other patterns in trait space occupation.

259 Here we introduce a non-parametric phylogenetic comparative approach to evaluate the

260 possibility that the statistics associated with our dataset could have been generated if the traits

261 under consideration were independent, given the phylogenetic structure underlying the dataset.

262 This method generates a set of nulls that can be used to understand how the phylogenetic signal

263 in the data affects the range of patterns the data can potentially generate given no relationship,

264 and how those patterns compare with the empirical signal.

265   An investigator could generate a set of phylogenetically-informed nulls using either

266 simulations or permutations. A simulation approach would be straightforward to implement for

267 normally distributed data, as Mahler *et al.* (2013) did in their study of convergence in *Anolis*, but

268 the features of our data already described would make simulating comparable data difficult.

269 Instead, we generate a set of nulls using a phylogenetically-informed permutation approach:

270 empirical patterns are compared to the subset of permuted datasets in which the phylogenetic

271 signal of the permuted data on the empirical tree matches the phylogenetic signal in the empirical

272 data. In practice, one phylogenetic permutation of a single trait is generated by shuffling the

273 species labels on the data and then iteratively swapping pairs of observations via a simple hill-

274 climbing algorithm until a specified metric of phylogenetic signal (in our case, Blomberg's K or

275 Pagel's λ) is within a specified tolerance (for this study, 0.01) of the empirical signal (Fig. 3A-B;

276 Appendix). Note that this hill-climbing approach was taken for the sake of expediency only;

277 phylogenetic permutations could also be obtained by permuting many times and only considering

278 those permutations whose phylogenetic signal was within the specified tolerance, though this

279 could be far more computationally intensive. Statistics associated with the set of phylogenetic

280 permutations are then compared with empirical statistics, and can yield a p-value in the same

281 way as an ordinary permutation test. The distribution of phylogenetic permutations can also be

282 compared to that of ordinary permutations to understand the effect of the phylogeny on the range

283 of possible patterns. This approach is distinct from the "phylogenetic permutations" approach

284 introduced by Lapointe & Garland (2001). This simple frequentist test has two chief virtues.

285 First, like all permutation tests it is nonparametric and therefore appropriate for highly non-

286 normal datasets like ours. Second, it can be used to explore the phylogenetic component of any

287 statistics applied to a comparative dataset as such, rather than using transformations that may

288 remove information and limit the range of patterns that can be considered. Phylogenetic

289 permutation successfully rejects apparent trait associations induced solely by shared

290 phylogenetic history: it yields a nonsignificant result for Felsenstein's (1985) "worst case"

291 scenario in which a spurious correlation appears between two traits that evolved independently

292 on a tree of two polytomous clades separated by a long span of evolutionary time (Appendix).

293 Importantly, the phylogenetic permutation approach is similar to the restricted permutation test

294 (Anderson, 2001), in which shuffling only occurs within sets of exchangeable data points. In

295 fact, in the case of Felsenstein's worst case, phylogenetic permutation is equivalent to a restricted

296 permutation test in which exchanges only occur within the two polytomous clades.

297   We analyzed our dataset using phylogenetic permutation, considering Spearman's ρ and

298 the slopes of the 90th and 95th conditional percentiles. We generate phylogenetic permutations

299 with Blomberg's K, but our results are statistically indistinguishable from those obtained with

300 Pagel's λ (Appendix). The distribution of statistics for phylogenetic permutations differs slightly

301 depending on whether the predictor, response variable, or both are permuted. We present results

302 in which both variables are permuted, but results are qualitatively identical for all three methods

303 (Appendix).

304

305   **Results**

306   We detect a pervasive latitudinal gradient in the mean and spread of arm number (Fig. 2).

307 Arm number among featherstars decreases from the equator to the poles (ρ = -0.276), even when

308 analyzing northern (ρ = -0.183) and southern (ρ = -0.349) hemispheres or deep (ρ = -0.275) and

309 shallow-water (ρ = -0.266) species separately. All correlations are statistically significant [or

310 statistically clear, after Dushoff *et al.* (2019)] at the p < 0.01 level. The relationship between

311 absolute latitude and arm number is visibly wedge-shaped, and this is borne out by quantile

312 regression: the 5th and 10th conditional percentiles had slopes near zero (-0.08 and -7.9E-18,

313 respectively), and neither had a better (lower) AIC score than the corresponding unconditional

314 quantile. Conversely, the 90th and 95th conditional percentiles had quite negative slopes (-0.49

315 and -0.74, respectively) and received overwhelming AIC support, with ΔAIC values in excess of

316 70 in both cases. In other words, information about latitude improves estimates of upper but not

317 lower quantiles of arm number. The latitudinal gradient in arm number therefore reflects an

318 increased maximum arm number toward the equator without corresponding changes in the

319 minimum. Arm number also declines steeply with depth (ρ = -0.360; Figs. 2, A3), and the

320 variance among species with shallow-water occurrences (< 200 m) is 15 times greater than for

321 deep-water species.

322   The negative relationship between absolute latitude and arm number is apparent even

323 when the dataset is randomly subset such that each 10° bin has the same number of species. Arm

324 number was significantly negatively correlated with absolute latitude in all 10,000 subsets

325 (median p = 4.8E-8), with a median effect size of ρ = -0.358. Likewise, regression fits of the 95th

326 quantile had comparable slopes (median slope = -0.579) to quantile regression fits for the raw

327 dataset, and AIC tests favored them in all but 3 of 10,000 replicates (median ΔAIC = 42.6).

328 Thus, the latitudinal gradient in arm number is not a spurious result of the greater diversity of

329 featherstars in the tropics.

330   Midpoints are a convenient summary statistic for latitudinal ranges, but there are

331 important caveats to interpreting them at face value (Colwell & Hurtt, 1994), two of which we

332 deal with here. First, geographically biased sampling could systematically shift midpoints. For

333 example, if marine biological research were more intense in the northern hemisphere, it could

334 "pull" latitudinal midpoints north. However, we recover no such northern-hemisphere bias in our

335 occurrence dataset [N, northern hemisphere = 10803 (45%); N, southern hemisphere = 13050

336 (55%)]. A plot of per-species sampling intensity across latitude (Fig. A7) exhibits no clear

latitudinal trends, and the number of samples per species in each 5° latitudinal bin is not correlated with either latitude (Pearson's r = 0.0853, p = 0.637) or absolute latitude (r = 0.276, p = 0.12) As such, geographic bias in sampling intensity probably does not pose a serious problem for the use of latitudinal midpoints. Second, if many-armed featherstars had greater latitudinal ranges, it would tend to pull their latitudinal midpoints toward the equator, potentially engendering a spurious relationship between latitudinal midpoint and arm number. We do detect a weak but statistically perceptible relationship of this kind (Spearman's ρ = 0.168, p = 4.326E-4), so it is necessary to demonstrate that this alone does not cause the latitudinal gradient in arm number that we observe. For each species, we drew one latitude from a uniform distribution bounded by the observed latitudinal range limits of that species. We then calculated the correlation between arm number and those randomly drawn latitudes, and repeated this procedure many times. Absolute latitude was significantly correlated with arm number in all 1000 replicates (median ρ = -0.220, median p = 3.40E-6), indicating that the use of latitudinal midpoints does not induce a gradient in arm number where none truly exists. This finding is corroborated by a plot of arm number against the observed latitudinal range of each species (Fig. A1) and a boxplot of arm number for all species in each 10° bin of absolute latitude (Fig. A2).

Temperature and latitude at one randomly-selected occurrence per species were compared as predictors of arm number (see Methods). Arm number exhibited a stronger relationship with latitude (median ρ = 0.152) than with temperature (median ρ = 0.110) in 494/500 replicates, with a median difference in rhos of 0.0411 (Fig. A8).

With the phylogenetic comparative approach adopted here, we show that Spearman's ρ (p < 0.001) and the slope of the 90th (p = 0.017) and 95th (p = 0.009) conditional percentiles are more negative for the empirical dataset than in nearly all phylogenetic permutations (Fig. 3). The distributions of statistics for phylogenetically permuted datasets are visually similar to those associated with ordinary permutations, but have greater variance in all three cases (ex., the ratio of variances for ρ is 1.46; Appendix). Thus, phylogenetic gives the dataset a tendency to produce stronger correlations, but not enough to explain the strongly negative relationships we observe.

Arm number is greater on average among diurnal vs. nocturnal featherstars (difference in means = 24.01; Welch's t-test, p < 0.005; Fig. 4) and among exposed vs. cryptic and semicryptic forms (difference = 9.9; p = 0.315), although only the former is statistically significant. No nocturnal species has over 37 arms, whereas 10 of 19 of diurnal species have between 38 and 90

368   arms. Among the 21 out of 30 species in the concealment dataset with phylogenetic information,

369   the difference in arm number between diurnal and nocturnal species is not clearly distinguishable

370   from the set of phylogenetic permutations (two-tailed test; p = 0.166). However, this is also true

371   for the set of ordinary permutations (p = 0.1904), and therefore probably results from reduced

372   sample size.

373   All three measures of the prevalence of regenerating arms were lower on average for

374   cryptic and semi-cryptic or nocturnal species (Fig. 4). Individuals of exposed species were found

375   regenerating significantly more arms on average (difference in means = 2.06) than cryptic and

376   semi-cryptic forms [controlling for a false discovery rate of 0.05 following Benjamini and

377   Yekutieli (2001)]. Exposed forms were also regenerating a significantly greater proportion of

378   their arms (difference = 0.0619), and a significantly greater proportion of individuals were

379   regenerating at least one arm (difference = 0.358). Diurnal species also had higher values of all

380   three metrics than nocturnal species, but no differences were statistically significant.

381   Significance was basically identical when tested with ordinary and phylogenetic permutations:

382   the difference in all three regeneration metrics between exposed and concealed species was

383   significantly greater than in sets of 1000 phylogenetic permutations (number of regenerating

384   arms per individual, p = 0.003; proportion of regenerating arms per individual, p = 0.001;

385   proportion of individuals with at least one regenerating arm, p = 0.034).

386   The rate at which featherstars lose arms to predators decreases toward the poles among 5

387   shallow-water populations spanning 40° of latitude in the northern hemisphere (Fig. A14). All

388   individuals in a population of *Cenometra bella* in the Philippines were found regenerating at

389   least one arm and were estimated to suffer an attack from a predator every 9 days, whereas

390   individuals in two mid- to high-latitude populations of *Florometra serratissima* encounter

391   predators at about one-sixth that rate. No statistical significance is associated with this finding.

392   Among five featherstars from the Great Barrier Reef that feed in exposed positions,

393   species with more arms are apparently less palatable to the reef fish *Chaetodon* and *Canthigaster*

394   (Fig. A4; Slattery 2010). However, another experimental study of 8 shallow-water tropical

395   featherstars from Southern Vietnam recovered the greatest palatability to the sergeant-fish

396   *Abudefduf* among the two species with at least 95 arms (Tinkova *et al.*, 2014). Importantly,

397   palatability within species appears to be quite variable, either between fish or between localities:

398 palability as measured by Slattery (2010) is inversely related to palatability as measured by
399 Tinkova *et al*. (2014) among the three species considered in both studies.

400

401   **Discussion**

402   *Predation*

403   We demonstrate a latitudinal gradient in the mean and spread of arm number that appears
404 in shallow and deep water and on either side of the equator, and that cannot be plausibly
405 attributed to the effects of phylogenetic autocorrelation (for example, the coincidental
406 diversification of one or a few clades of many-armed featherstars at low latitudes). We take the
407 increase in maximum arm number toward the equator as the most biologically interesting feature
408 of our dataset. As such, we attempt to explain why many-armed featherstars are restricted to the
409 tropics, but few-armed featherstars are everywhere.

410   We argue that predation is the most plausible explanation for the latitudinal and
411 bathymetric trends in arm number described here. All else being equal, a crinoid with more arms
412 will be able to encounter more predators without losing too many arms to feed effectively.
413 Predation would therefore constitute a selective agent with a consistent latitudinal signal if
414 tropical featherstars encounter predators more frequently. Predators are not universally more
415 ecologically important or prevalent toward the equator (Klompmaker et al., 2019; Schemske et
416 al., 2009), but this does seem to be the case for marine durophages (Vermeij, 1978). Moreover,
417 the teleost fish and echinoid predators that matter most to crinoids (Baumiller et al., 2010;
418 Meyer, 1985) have their greatest region-scale diversity and (at least for fishes) abundance in the
419 tropics (Edgar et al., 2017; Stuart-Smith et al., 2013). The estimated waiting times between
420 predator encounters decreases monotonically toward the equator among 5 featherstar populations
421 (Fig. A14), corroborating the existence of a latitudinal gradient in predation intensity. More
422 ecological studies are needed to definitively establish this pattern. Importantly, the predation
423 hypothesis predicts both "first-order" spatial patterns in feeding morphology: the decrease in
424 maximum arm number toward the poles and with depth. There is good evidence for a decrease in
425 the intensity of predation on crinoids with depth (Baumiller, 2013; Oji, 1996); the relationship
426 between latitude and predation intensity should be investigated further.

427   If arm number has evolved as a result of predation, it is not the only aspect of crinoid
428 morphology to do so. Both the configuration of arm branching and the spacing of articulations

429 specialized for autotomy in the arms of featherstars match theoretical predictions for a predator-
430 resistant feeding apparatus (Oji & Okamoto, 1994). Featherstar arms branch close to the base,
431 minimizing arm loss in the event of an attack but covering the filtration area less efficiently.
432 Conversely, branching points are distributed more evenly along the arms of isocrinids –
433 exclusively deep-sea stalked crinoids that encounter fewer predators than shallow-water stalkless
434 forms (Meyer & Macurda, 1977; Oji, 1996). The spacing of autotomy articulations along the
435 arms in both stalked crinoids and featherstars very closely approximates an anti-predatory
436 theoretical optimum, but the arms of featherstars have more autotomy articulations (Oji, 1996).
437 The placement of crinoid gametes on arms and pinnules close to the center of the body, or on
438 arms concealed in the substrate, has also been cited as an anti-predatory adaptation (Vail, 1987).
439 It therefore does not stretch the imagination to suggest that spatial patterns in arm number are the
440 result of corresponding patterns in predation intensity.

441 If the latitudinal arm number gradient is caused by a corresponding gradient in the
442 intensity of predation, then the few-armed featherstars at low latitudes should have other ways of
443 coping with predators. Two such strategies have been documented extensively among
444 featherstars: concealment (defined broadly here to include species nocturnal feeding and cryptic
445 or semi-cryptic feeding positions) and toxicity. Our findings are consistent with concealment as
446 an alternative to high arm number as an anti-predatory adaptation: featherstars that emerge to
447 feed at night, when their predators are probably less active (Meyer & Macurda, 1977; Vail,
448 1987), have significantly fewer arms (Fig. 4). Moreover, all metrics of the prevalence of
449 regenerating arms are lower for both forms of concealment (though only with statistical
450 significance for crypsis), corroborating their effectiveness as anti-predatory strategies. Results
451 for palatability are less clear: Slattery (2010) found exposed species to be uniformly less
452 palatable (more toxic) than cryptic ones, but the three most palatable species studied by Tinkova
453 *et al.* (2014) were exposed. Combining the data from Slattery (2010) with our own, many-armed
454 featherstars appear to be the least palatable, but the experimental results of Tinkova *et al.* (2014)
455 support the opposite conclusion. Palatability of a single species can clearly be variable, but
456 whether this is due to genuine within-species variability or to differences in taste among
457 predators is not yet clear.

458 High arm number is probably just one among many solutions to the problem of intense
459 predation at low latitudes. We are not aware of any tropical reef species without any of the

solutions discussed in this paper – arm number, toxicity, or concealment – and we suggest more intense predation may favor a combination of these strategies, and perhaps others not mentioned here. Some strategies may not be available to members of some groups: for example, arm number appears exceptionally conserved within the Antedonidae (Fig. A3). A survey of ecology across latitude among ten-armed featherstars would allow an investigator to isolate and study apparent anti-predatory adaptations besides arm number like concealment or toxicity, and would be a productive complement to this study.

If many-armed featherstars are better able to cope with intense predation, then why do few-armed featherstars occur at all latitudes and constitute most of the extant species diversity (Fig. 2)? The predominance of few-armed featherstars would make sense if many-armed forms were at a relative disadvantage in terms of their ability to feed or reproduce, all else being equal. Featherstars typically increase arm number above 10 by autotomizing free arms close to the base and regenerating two in their place in a process known as augmentative regeneration, so growing more arms temporarily reduces food intake and sets an individual back the resources required to grow and maintain two new arms (Moore & Teichert, 1978; Shibata & Oji, 2003). However, featherstars with more arms can potentially harvest more food, so it is not clear how arm number ultimately affects feeding efficiency. Instead, growing many arms could push back the onset of sexual maturity. The 40-armed featherstar *Anneissia japonica* does not begin to augmentatively regenerate arms until roughly 8 months of age (Shibata et al., 2008), and at a year old is still far from reaching its terminal arm number (Shibata & Oji, 2003)Although developmental data are excruciatingly scarce, the many-armed featherstars *Lamprometra klunzingeri* and *Anneissia japonica* reach sexual maturity later (1.5 years and 2 years old, respectively) than the few-armed featherstars *Antedon bifida* and *Florometra serratissima* (both one year) (Holland, 1991; Shibata et al., 2008). Moreover, those many-armed featherstars appear to attain sexual maturity before reaching their adult arm number (Shibata et al., 2008), so further growth must involve wasting reproductive tissues. The cost of reproduction could therefore explain why many-armed phenotypes are rare in general, and are only present in the shallow and tropical waters where intense predation makes them necessary. The issue cannot be settled without more data on reproduction and development and should be treated as an open question.

If predation intensity on crinoids increases toward the equator, an interesting possibility is that phenotypic plasticity can account for some part of the latitudinal arm number gradient.

491 Phenotypically plastic responses to predation (inducible defenses) have not been documented in
492 crinoids but are widespread in marine invertebrates, with six cases of inducible defenses
493 identified among non-crinoid echinoderms (Padilla & Savedo, 2013). Featherstars that repeatedly
494 autotomize arms in response to predators might be induced to augmentatively regenerate more
495 frequently. If hypothetically the ocean were suddenly made free of predators, a new generation
496 of featherstars might exhibit a weaker latitudinal arm number gradient, even without any
497 evolutionary change. The degree to which arm number exhibits a reaction norm controlled by
498 predation intensity is not known, but could be tested with aquarium experiments in which the
499 frequency of autotomy is manipulated by an investigator.

500 Although not considered in this study, stalked crinoids are thought to have been gradually
501 excluded from shallow water by the ecological expansion of durophagous predators in the
502 Mesozoic (Bottjer & Jablonski, 1988). We predict that predation on shallow-water stalked
503 crinoids should exhibit predictable trends with both time and latitude, and that it became
504 prohibitively intense in the tropics first and only later in higher latitudes. Such a prediction is
505 consistent with recently described shallow-water stalked crinoids from Paleogene and earliest
506 Neogene localities across high southern latitudes (Whittle et al., 2018), but could be more readily
507 addressed by an attempt to comprehensively survey fossil occurrences across depth and latitude.

508   *Temperature, productivity, and substrate*

509 A latitudinal gradient in the intensity of predation on featherstars is a plausible
510 explanation for the global phenotypic patterns documented here, and we have suggested several
511 tests of this explanation in the preceding section, but the evidence is not conclusive. Here we
512 discuss three essentially abiotic correlates of latitude that could conceivably underlie the patterns
513 in arm number: water temperature, food supply, and coral reefs.

514 Like mean and maximum arm number among featherstars, temperature increases toward
515 the equator in shallow water and declines with depth. However, the mechanistic link between
516 temperature and arm number is unclear. There is a well-documented relationship between sea-
517 surface temperature and the frequency of cyclones (Knutson et al., 2010), and the possibility that
518 periodic intense tropical storms could select for more arms among exposed featherstars is worth
519 exploring. Nevertheless, arm loss due to intense storms is apparently easy to distinguish
520 anatomically from predator-induced arm loss: instead of being shed at articulations specially
521 adapted for autotomy, arms are broken off randomly by storms (Mizui & Kikuchi, 2013). Thus,

522 studies of predation are unlikely to have been misled by damage from storms. Moreover, arm

523 number is more weakly correlated with temperature than with latitude (Fig. A8). We studied

524 temperature as a predictor of arm number among shallow-water species, but the relationship is

525 likely even weaker in deep water, where arm number increases toward the equator but

526 temperature is nearly constant (Webb, 2019). The latitudinal temperature gradient may be

527 causally 'upstream' of many hypothesized latitudinal patterns in biology, including the

528 latitudinal diversity gradient (Willig et al., 2003) and the importance of predators at low latitudes

529 (Schemske et al., 2009). Nevertheless, if global differences in temperature have left an imprint in

530 the distribution of arm numbers across the globe, they have probably done so indirectly.

531   Primary productivity also exhibits latitudinal trends, with peaks in high latitudes (Yoder

532 et al., 2001), and could be implicated in latitudinal patterns of feeding morphology. Suspended

533 phytoplankton makes up much of the crinoid diet, and the amount and kind of phytoplankton is

534 surely important for crinoid feeding ecology (Kitazawa et al., 2007). However, the amount of

535 particulate organic carbon that reaches the seafloor decreases toward the equator and with depth

536 (Lampitt & Antia, 1997), whereas arm number increases toward the equator and decreases with

537 depth (Figs. 2, A4). Moreover, phytoplankton abundance, and the availability of suspended

538 particulate food more generally, is extremely heterogeneous geographically, and varies more

539 across time and with terrestrial nutrient input than it does across latitude (Yoder et al., 2001).

540 The correspondence between food supply and arm number is probably not analytically tractable

541 with our dataset: the most consistent spatial correlate of particulate organic carbon supply is

542 depth [e.g. the amount of particulate organic carbon reaching 2000 m depth represents less than

543 1% of surface production (Lampitt & Antia, 1997)], but we only have ready access to estimates

544 of surface productivity. Most of the occurrences in our dataset are from deep water (e.g. 66%

545 from below 100 m), where ocean color estimates of surface productivity correspond only weakly

546 with the amount of particulate organic carbon encountered by the benthos. Finally, neither a

547 positive nor a negative relationship between arm number and food supply is predicted by crinoid

548 biology: increased arm number and denser filtration fans are relatively well-suited to fast-

549 flowing water (Baumiller, 1993), but have no obvious implications for fitness in productive or

550 unproductive waters. Increasing arm number should increase maximum food intake, but also

551 increases energy requirements (see previous paragraph). Global patterns in productivity can be

552 safely rejected as causes of patterns in arm number on both pattern-based and mechanistic
553 grounds.

554   The unique physical environment created by tropical coral reefs may facilitate the
555 evolution of feeding morphologies not possible further toward the poles. High-flow
556 microhabitats that can support featherstars with dense, many-armed filtration fans might be
557 especially common on coral reefs. Local flow regime has clear consequences for the
558 effectiveness of different crinoid feeding morphologies (Baumiller, 1993; Kitazawa et al., 2007;
559 Leonard et al., 1988). A number of distinct microhabitats can be found across a coral reef (e.g.
560 Zmarzly 1984), and both crinoid feeding postures (e.g. arcuate vs. parabolic vs. radial fan
561 postures; Meyer and Macurda 1980) and aspects of morphology (Meyer, 1973) seem to
562 correspond to particular microhabitats. In theory, the role of coral reefs in facilitating the
563 latitudinal gradient in arm number could be tested by comparing arm number among featherstars
564 along the East Pacific and East Atlantic, where tropical reefs are rare to absent, with species
565 along the reef-rich West Atlantic and Indo-West Pacific. However, while reef-poor continental
566 margins do not exhibit latitudinal gradients in arm number (Fig. A6), they are also extremely
567 species-poor: the Tropical East Pacific marine province [(following Spalding et al. (2007)] and
568 the tropical east Atlantic (the Western African Transition and Gulf of Guinea marine provinces)
569 have occurrences from 2 and 4 featherstar species, respectively. The question is therefore not
570 amenable to a simple macroecological approach. Nevertheless, the physical properties of coral
571 reef microhabitats are unlikely to directly account for the latitudinal arm number gradient alone.
572 Arm number increases toward the tropics among shallow- and deep-water species alike (Fig. 2),
573 but zooxanthellate scleractinian reefs are exclusively found in shallow water. Moreover,
574 although coral reefs present a unique physical environment, the high-energy flow regimes that
575 favor many-armed filtration fans are not unique to the tropics: there are probably many habitats
576 in temperate and polar regions in which many-armed featherstars could feed effectively. Lastly,
577 some of the featherstars in our dataset with the greatest number of arms have been recorded
578 living on soft bottoms (e.g. *Phanogenia multibrachiata* – 150 arms, Mekhova and Britayev 2012;
579 *Zygometra microdiscus* – 83 arms, Messing et al. 2006), indicating that coral reef substrates are
580 not a prerequisite for the many-armed condition.

581   Physical factors and biotic interactions do not constitute mutually exclusive (or
582 collectively exhaustive) explanations for the broad spatial patterns in functional morphology

583 outlined here. A more holistic conception of the evolution of arm number is that intense

584 predation in the shallow tropics promotes the relative success of many-armed featherstars, and

585 the reefs that are there help facilitate their ecological disparification by creating unique

586 microhabitats and flow regimes. Reefs also provide the deep infrastructure in which cryptic

587 forms hide from predators (Meyer, 1985), and they recruit fish and echinoid predators (Baumiller

588 & Stevenson 2018). Thus, the greatest diversity of featherstar ecologies seems to be made

589 possible by corals. Throughout the Phanerozoic, widespread reefs have not always been strictly

590 tropical, made of photosymbiont-bearing coral, or even present (Kiessling et al., 1999).

591 Inasmuch as reefs facilitate ecological disparification, changes in the global assembly of reefs

592 probably correspond with changes in the deployment of ecological diversity around the globe.

593

594 **Conclusions**

595 We demonstrate a latitudinal gradient in mean and maximum arm number among

596 featherstars that is symmetrical on either side of the equator, present in shallow and deep water,

597 and distinct from the latitudinal diversity gradient. Concurrently, we introduce a new non-

598 parametric phylogenetic comparative approach appropriate for non-linear trends in non-normal

599 datasets, and use it to reject the possibility that the patterns we observe result solely from

600 phylogenetic autocorrelation of arm number and latitude. We also present evidence against

601 several plausible abiotic agents as causes of this gradient. Instead, consilient evidence from

602 crinoid ecology and functional morphology, indicates that a latitudinal gradient in the intensity of

603 predation is a plausible and readily testable cause of the wedge-shaped relationship between arm

604 number and absolute latitude. Many-armed featherstars are not only more predator-resistant, but

605 are also characterized by several unique ecologies, especially on tropical coral reefs. Crypsis and

606 toxicity are additional ecologies that characterize the tropical reefs where predators make them

607 necessary. Inasmuch as these ecomorphological roles are only or most viable in the face of

608 intense predation, predators act as an "enabling factor" sensu Vermeij (2020), expanding the

609 range of viable ecologies. Conceptually, ecological diversity is typically linked with opportunity

610 (e.g., unfilled niches), but we suggest that predation, typically thought of as a "constraint," may

611 just as readily promote functional innovation.

612 To the degree that arm number corresponds to feeding ecology, the wedge-shaped

613 relationship between arm number and latitude implies a latitudinal gradient in functional richness

(the number of unique ecologies) that is independent from the latitudinal diversity gradient. Similar patterns in functional richness have been reported in bats, birds, bivalves, and shallow-water fish (Schumm et al., 2019; Stevens et al., 2003; Stuart-Smith et al., 2013). Notably, the proposed mechanisms for such a pattern in these taxa involve abiotic factors – for example, latitudinal gradients in temperature, with downstream effects on resource abundance/stability – whereas our explanation emphasizes predation as a causal/selective agent. Biotic interactions like competition have been incorporated by other authors into explanations for latitudinal gradients in species richness and evolutionary innovation (Schemske et al., 2009). Pianka (1966) implicated predation in the latitudinal diversity gradient, but to our knowledge a model in which predation facilitates functional diversification is novel. The generality of latitudinal gradients in ecological diversity remains to be explored, but when they exist they need not be linked with ecological opportunity or resource availability.

Figures

Fig. 1. Arm number among featherstars. *A*, An unidentified 10-armed featherstar perched on an octocoral. Photo © Paul Humann. *B*, The large, many-armed (average: 55 arms) featherstar *Comaster schlegelii* (Comatulidae). Photo © James A. Maragos. *C*, Phylogeny of featherstars and the distribution of arm number within major clades. Phylogeny shown is a summary of the relationships recovered by Hemery *et al.* (2013), with nodes without support values collapsed into polytomies. There are no featherstars with between 0 and 4 arms, or between 6 and 9 arms. There are 109 10-armed antedonid featherstars in the dataset [although "Antedonidae" is non-monophyletic (Hemery et al., 2013)].

Fig. 2. Arm numbers among extant featherstars show a wedge-shaped relationship with latitude. Absolute value of latitude against arm number, with Spearman rank correlations shown for the entire dataset and subsets including deep-water (no occurrences above 200 m) and shelf taxa. All correlations shown are significant at the $p < 0.0005$ level. 5th and 95th conditional percentiles shown for the entire dataset. Marginal histograms for latitude (bin width = 10°) and arm number (bin width = 10) plotted at top and right, respectively.

Fig. 3. Comparing empirical relationships with a set of 1000 "phylogenetic permutations" in which both the predictor and response variable have been randomly rearranged such that their

phylogenetic signal (here, Blomberg's K) on the phylogeny is approximately equal to that of the observed data. *A*, Arm number against absolute latitude for the 122 species represented in the phylogeny, with the phylogeny connecting tip values with ancestral state estimations for internal nodes. *B*, Three sets of phylogenetic permutations. *C-E*, Histograms of summary statistics of phylogenetic permutations, with empirical statistics plotted as an orange bar. One-sided p-value shown. *C*, Spearman's ρ. *D*, Slope of the conditional 90th percentile estimated with quantile regression. *E*, Slope of the conditional 95th percentile.

Fig. 4. Arm loss and arm number in populations of tropical shallow-water featherstar species with differing habits. Differences in means are shown, along with p-values for Welch's unequal variances t-tests. Jittered points are species; larger points represent greater sample sizes. Statistically significant differences [controlling for a false discovery rate of 0.05 following Benjamini and Yekutieli (2001)] shown in bold. See text for habit details. 19 species are diurnal and 11 are nocturnal; 15 species are scored as concealed and 15 exposed.

Data availability

The species-level dataset including latitude, depth, arm number, habit, and literature sources, the time-calibrated phylogeny used in the phylogenetic comparative analyses, a table aggregating information on predator encounter rate, all code needed to replicate analyses and generate select figures, and an appendix including additional information on "phylogenetic permutation" and the relationships between habit, depth, phylogeny, and arm number are available as supplementary files on a Dryad Digital Repository at https://doi.org/10.5061/dryad.ht76hdrcp.

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915   **Biosketch**

916   **James G. Saulsbury**'s research interests include functional morphology, invertebrate zoology,

917   paleobiology, and marine macroecology. James approaches these topics through direct

918   qualitative and quantitative study of living and fossil organisms, phylogenetic inference and

919   comparative methods, and evolutionary simulations and modeling.

920   **Tomasz K. Baumiller**'s research focuses on functional morphology, biomechanics, taphonomy,

921   and the Phanerozoic history of biotic interactions. In addition to studying fossils in the field and
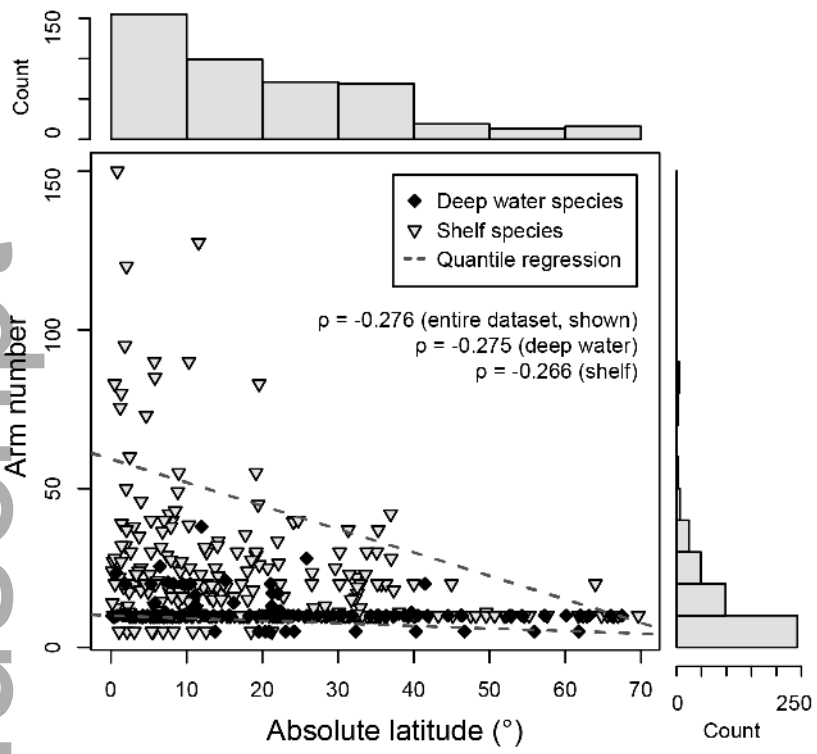
922 in museums, Tomasz also studies modern organisms using scuba and submersible observations,

923 laboratory experiments, and computer and physical modeling.
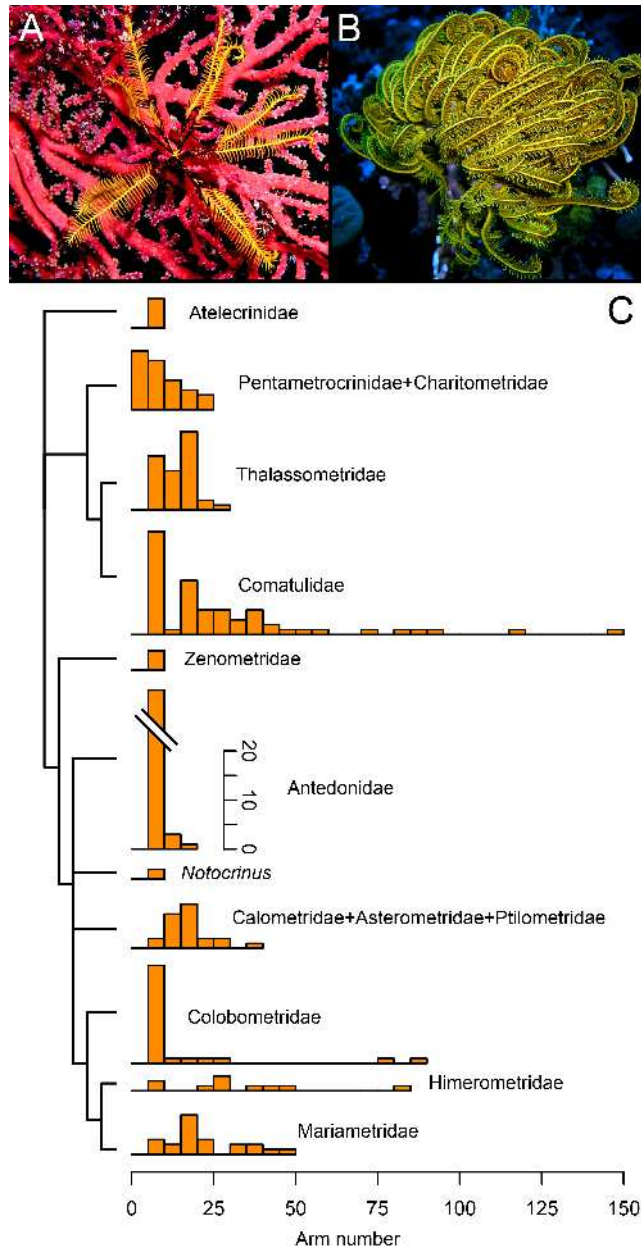
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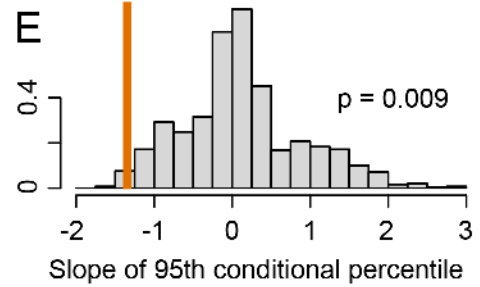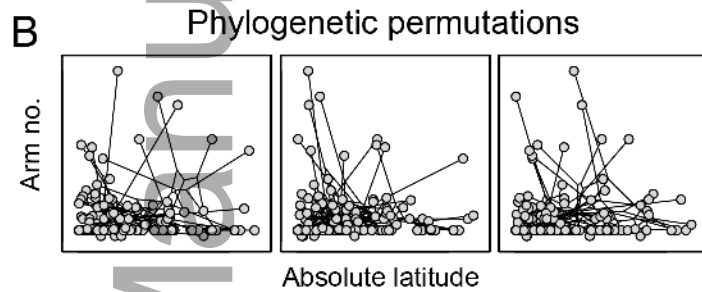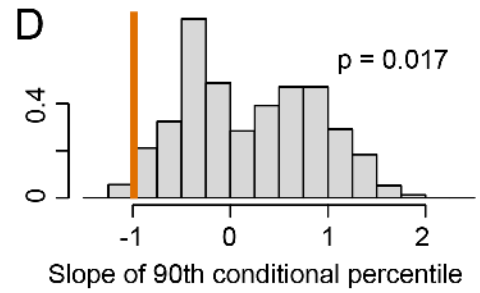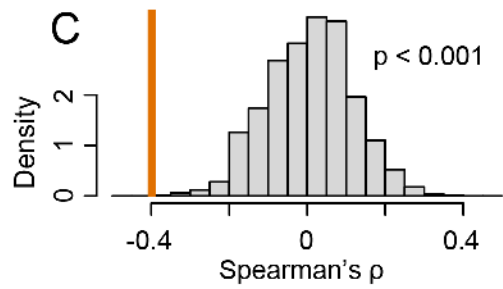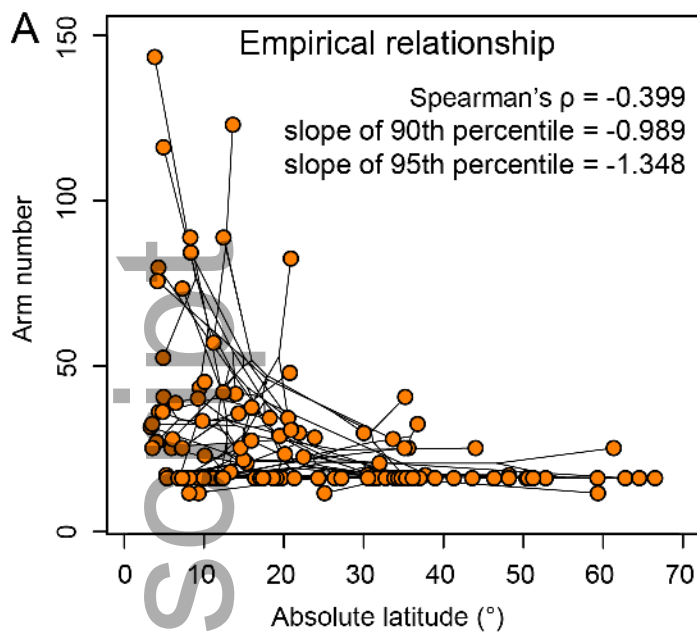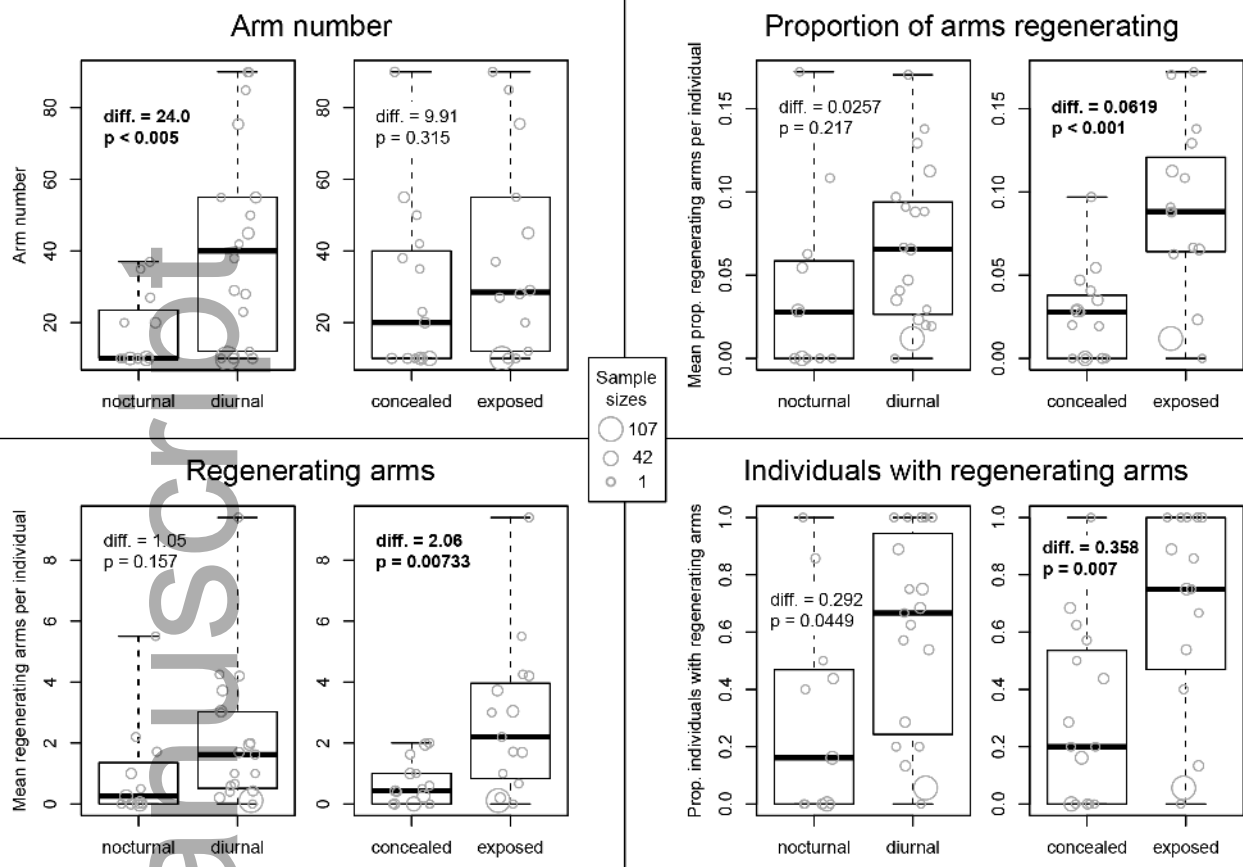
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