Year-round high abundances of the world's smallest marine vertebrate (Schindleria) in the Red Sea and worldwide associations with lunar phases

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Title: Year-round high abundances of the world's smallest marine vertebrate (*Schindleria*) in the Red Sea and worldwide associations with lunar phases

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Abstract

Very little is known about the ecology and biology of the smallest marine vertebrates, fishes in the genus *Schindleria.* Even though over half of named *Schindleria* species have been described from the Red Sea, very few specimens have been identified. Here, we assessed abundance patterns of nearly two thousand Red Sea adults and found evidence for putative seasonal and spatial differences, likely related to differing habitat and environmental conditions. Within the Red Sea, the highest abundances were neither found during seasonal temperature extremes nor during peaks of coral reef fish recruitment. We also found evidence for global trends in abundances related to lunar cycles, for which data from a recently published large collection of specimens from the DANA Expedition (1928-1930) were included. The abundance of *Schindleria* in relation to lunar phases differed significantly, with most *Schindleria* being caught outside the full moon. Adult specimens in our Red Sea collections were most abundant during the new moon, while the 3rd quarter moon yielded the highest abundances in the DANA collection. We further suggest that the abundances of *Schindleria* at coral reefs may be related to reproductive cycles and that these cycles may be timed with the moon, since back-calculations of hatch dates from otoliths resulted significantly around the new moon. *Schindleria* may be the most numerous coral reef fish in the world, for which we encourage increased research.

Introduction

Schindleriidae is a small cryptic gobioid family, currently comprising only one described genus: *Schindleria*. These are the smallest vertebrates of the marine realm and the youngest reproducing vertebrates on the planet[1]. Due to their cryptic biology and the fact that, to our knowledge, apart from one photograph of an aggregation in the Hawaiian Islands taken by J. E. Randall documenting their residence over sand and rubble substrata during daytime[2], they have never been sighted in their natural habitat elsewhere, nor has it been possible to maintain them in aquaria[3]. Hence, very little is known about their biology, ecology, and exact distribution. Furthermore, since adult *Schindleria* are very small in size and have paedomorphic features (i.e., never undergoing metamorphosis and retaining a larval phenotype throughout their life[4]), specimens are generally overlooked; and most studies are based on very few samples or report the sighting of some of these individuals as bycatch of other research purposes, mainly from light traps and planktonic tows[5,6]. More recent sampling efforts[3,7] and the inspection of museum collections from plankton tows for the presence of *Schindleria*[8] have increased knowledge and attention on the presence and distribution of this genus, and high numbers of these fishes have more recently been studied. Ahnelt and Sauberer (2020) provide a complete overview of all currently published *Schindleria* sightings and the data available on its distribution[8]. Apart from the Caribbean and the tropical Atlantic, the family seems to be common across coral reefs worldwide.

Schindleria can be found throughout the Indo-Pacific[7–9] and are believed to be "lagoon-completers", remaining for their entire lifecycle in shallow coral reef lagoons[10,11]. However, some specimens have also been collected in coastal waters around volcanic islands with no lagoons (e.g., Easter Island[5]) as well as relatively distant from coral reefs and at depths of hundreds of meters[8,9,12–14]; but whether these findings are exceptions or strayed specimens,

individuals advected by strong currents, or whether deeper oceanic environments are also part of *Schindleria'*s habitat, still remains unanswered and highlights the need for more targeted and comprehensive sampling efforts. Data about their ecology and biology are also not available since no study reports observations of specimens in their natural habitat, which remains speculative. Some authors suggest that *Schindleria* may live in burrows in the sandy bottoms of the coral reef matrix[10] of which they come out at night, probably to feed and avoid visual predators. Many studies suggest that they retain a planktonic life (since they were mainly collected in plankton tows in the pelagic or neritic habitats[15–17] but are in close association with the reefs[6,7,11]), while Randall and Cea reported daytime aggregations over sand and rubble substrata in Hawaii[2], but whether this is a common behavior or aggregations are seasonally induced, still remains unknown.

To date, very few *Schindleria* species have been described. From the seven named species, four have been described from the Red Sea and only a handful of specimens were collected for the description of each of these Red Sea species[6,14,18–21]. Genetically, more than 40 different haplotypes have been identified in the eastern Indo-Pacific based on sequence data from the 16S mitochondrial rDNA gene region, suggesting that there may be a much higher number of species within the genus[3,7]. Morphologically, it has been very difficult to classify specimens or discriminate among haplotypes due to the lack of evident characteristic features. As a result, classification into two main types remains the most commonly used approach[8,22]: a long dorsal fin type (LDF; with the origin of the dorsal-fin anterior to the origin of the anal fin, by a minimum of six fin rays), which is also the most commonly sighted[8]; and a short dorsal fin type (SDF; with the origins of anal and dorsal fin more or less vertically aligned), which seems more rare and potentially comprises endemic species.

Our study assessed the abundance of adult LDF type specimens of *Schindleria* at three reefs along a cross-shelf environmental gradient in the central Red Sea of Saudi Arabia. We collected specimens at night, using LED light traps around the new moon of twelve consecutive months to measure potential changes related to spatio-temporal variations in abundances of *Schindleria* and assess during which season individuals may be more likely to surface and/or to be present in the shallow water column of the reefs' matrices. We further hypothesized that mature *Schindleria* specimens may be coming out of their putative diurnal hideaways and surface at night[6,11] forming aggregations to reproduce and should thus be more abundant in the catches around the new moon or darker moon phases, during which their translucent bodies are less likely to be visible to nocturnal predators. Many marine species show reproductive cycles linked to lunar patterns[23]. For this purpose, we also collected specimens at the same sites using the same light traps every day for an entire lunar month to assess whether or not specimens were rather absent in the catches around the full moon. Lastly, we used the recently published information on the presence of *Schindleria* in the plankton tows collections from the DANA Expedition 1928-1930[8] and assessed whether or not abundances of *Schindleria* related to lunar phases is a global trend. To further support putative links between the biology/reproduction of *Schindleria* and lunar cycles, we assessed the ages of the mature *Schindleria* specimens from the Red Sea using daily growth increments of their sagittal otoliths, inferred their hatch dates, and estimated the length of a putative reproductive cycle of this premature and extremely short-lived species. To our knowledge, our study is the first based on a collection of nearly two thousand specimens of *Schindleria* and provides first baseline information on putative temporal distribution patterns worldwide, as well as year-round abundances in the Red Sea.

Results

Sampling and data

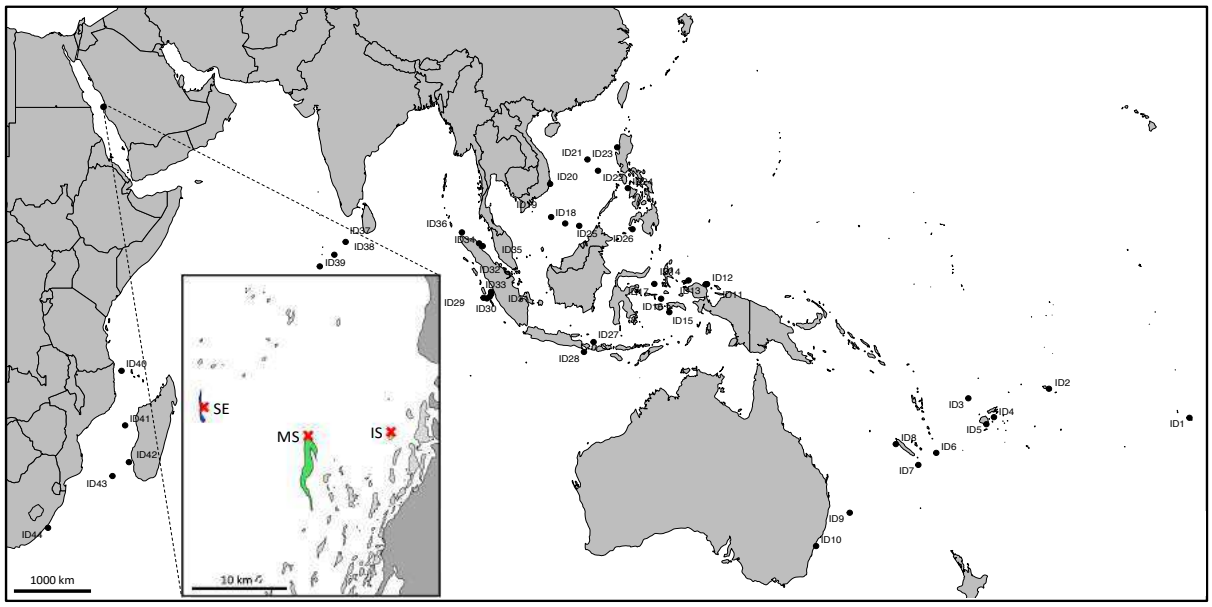


Fig. 1: Collection sites of *Schindleria:* from the DANA Expedition 1928-1930 (all sites represented by a "dot": ID1 – ID44, following Ahnelt and Sauberer 2020[8]); and from the Red Sea, with a zoomed-in section displaying the three reefs where collection took place using a LED powered light trap along a cross-shelf gradient from the shore to the shelf edge, near the coast of Thuwal, Saudi Arabia. Coral reefs within the zoomed-in Red Sea section are given in "light grey" while the land sections are in "dark grey" and the sampled reef sites are color coded, with the "yellow" reef inshore (IS), the "green" reef at the mid-shelf (MS), and the "blue" reef at the shelf edge (SE). The "red" crosses indicate the location of deployment of the LED powered light traps for this study.

A total of 1996 adult *Schindleria* specimens were collected for this study using LED light traps in the central Red Sea, Thuwal, Saudi Arabia (Fig. 1). From these, 44 specimens were selected for the extraction of otoliths, out of which 41 specimens were successfully aged by reading the number of daily growth increments of at least one sagittal otolith in order to assess lunar reproductive cycles (Fig. 2).

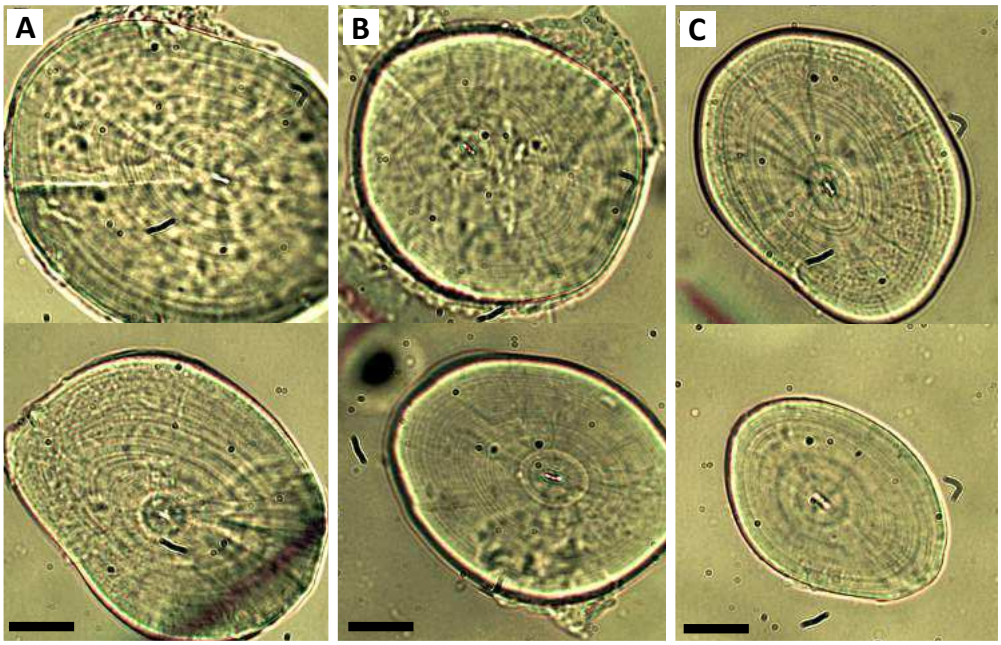


Fig. 2: Sagittal otoliths from mature *Schindleria* specimens sampled with light traps from an inshore (A), a mid-shelf (B), and a shelf-edge (C) reef in the Red Sea, near the coast of Thuwal, Saudi Arabia. These otoliths represent otoliths of ideal conditions (i.e., "C3" category) to count daily growth increments and yielded average numbers of increments (between 30-33) despite slightly differing shapes and sizes. All otoliths are to scaled, with the bar at the bottom (left) of each panel representing 20 μm. The otolith at the top of each panel represents a rounder and larger otolith while the otolith at the bottom a more oval-shaped and smaller otolith.

For the assessment of abundances in relation to moon phases, 204 specimens were collected during the daily sampling efforts within a lunar month (from the 16th October to the 16th November, 2014). For the yearlong spatio-temporal assessment of abundances in the Red Sea, a total of 1792 specimens were caught from February 2015 to January 2016.

Additionally, data on the temporal abundance of 502 specimens from the DANA Expedition were used to assess putative worldwide trends in abundances of *Schindleria* with moon phases (Table 1).

155

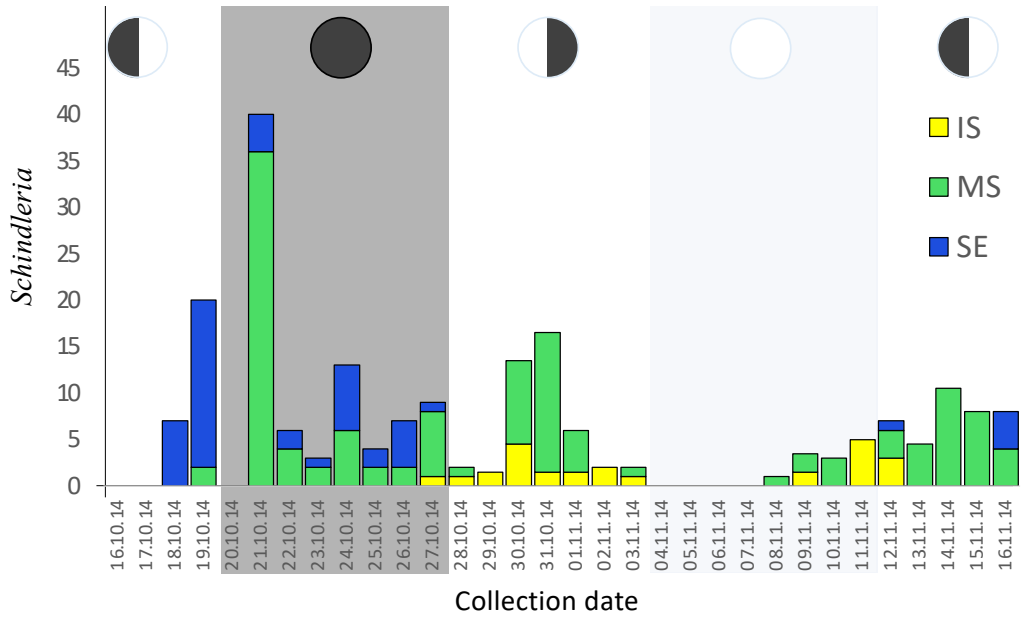
156 **Table 1:** Total abundances of *Schindleria* (All) observed in each of the four main moon
157 phases: the new moon (NM), the 1st quarter moon (1stQ), the full moon (FM), and the 3rd quarter
158 moon (3rdQ) comprising two different data sets: The Red Sea collections (at an inshore (IS:
159 22.3055 °N, 39.0493 °E), a mid-shelf (MS: 22.3054 °N, 38.9684 °E), and a shelf-edge (SE:
160 22.3415 °N, 38.8538 °E) reef) and the collection from the DANA Expedition from 1928-1930
161 (DANA).

Collection	Moon Phase			
	NM	***1stQ***	***FM***	***3rdQ***
All	200	139	35	332
DANA	116	97	15	274
Red Sea	84	42	20	58
Inshore (IS)	2	12	10	0
Mid-shelf (MS)	60	30	9	29
Shelf-edge (SE)	22	0	1	29

162

163 *Abundances of* Schindleria *related to lunar phases*

164 Out of the 204 specimens collected daily during a lunar month (Oct-Nov, 2014) in the Red Sea,
165 only 4 % were caught during the days around the full moon (±3 days), while more than 40 %
166 were caught during the days around the new moon (±3 days) (see Fig. 3). Similarly, during the
167 DANA Expedition, only 3 % of the 502 *Schindleria* specimens were caught during days around
168 the full moon (±3 days), while more than 33 % were caught during days around the new moon
169 (±3 days). In both cases there was a tenfold increase in *Schindleria* from full moon to new moon
170 catches (Table 1).



171

172 **Fig. 3:** Barplot representing the total abundances of *Schindleria* collected during one lunar cycle
173 in the Red Sea of Saudi Arabia. Total numbers of *Schindleria* specimens (y-axis) collected are
174 color-coded for the relative number caught at each of three sampling locations: an inshore reef
175 (IS) in "yellow", a reef at the mid-shelf (MS) in "green", and one at the shelf-edge (SE) in
176 "blue". Collections took place using three replicate LED powered light traps (collapsible
177 Bellamare model) at each sampling location for the period of 32 consecutive nights from the
178 16th October to the 16th November (2014; x-axis). Different moon phases are indicated with pie
179 charts on the top of each shaded section of the plot starting with the 3rd quarter moon, followed
180 by the new moon, the 1st quarter moon, the full moon, and ending again with the 3rd quarter
181 moon (from left to right).

182

183 Otolith counts revealed the median age of mature *Schindleria* specimens from the Red Sea to
184 be 33 days (± 3 days; Table 2, Fig. 2). Moreover, through the back-calculation of the hatch
185 dates using the age of the specimens and the collection date, we found a significant hatch pattern
186 with lunar periodicity (Rao's spacing test, $P < 0.01$), for which the angular mean was found a
187 few days after the new moon (Fig. 4). Together, the abundances of adult *Schindleria* and the

188 derived hatching events indicated that *Schindleria* may be approaching the reef around the new
189 moon for reproduction after which a couple of days later the eggs hatch, the larvae grow, and
190 the specimens mature to return to the reef matrix for reproduction on time for the next new
191 moon, from which their reproductive cycle starts over. The oldest two individuals in our sample
192 were 44 and 42 days old; all others were less than 40 days old. Females carried large eggs and
193 their ovaries were relatively full. Males had well developed urogenital papillae and all
194 specimens had similar body lengths, within the expected size range of adults. It thus seems
195 likely that *Schindleria* is completing its life cycle (i.e., one generation time) within a single
196 lunar cycle. Lastly, despite similar age, we found differences in the sizes and shapes of the
197 otoliths (Fig. 2), which may be indicative of the presence of different species among our
198 samples (Whittle 2003).
199
200 **Table 2:** Otolith data from 44 adult specimens of *Schindleria* from the Red Sea, collected
201 from May to July 2015 at three reefs along a cross-shelf gradient (one inshore "IN", one at the
202 mid-shelf "MS", and one at the shelf-edge "SE") near the coast of Thuwal, Saudi Arabia. The
203 last columns "L" and "R" indicate the qualitaty assigned (C1-C3) to each, left and right sagittal
204 otolith, respectively, where C1 represents poor/unreadable conditions, C2 conditions
205 sufficiently good for readings, and C3 ideal conditions.

N	Reef	Age	Sampling date	Hatch date	L	R
1	IN	-	28-05-2020	-	C3	-
2	IN	36	28-05-2020	22-04-2020	-	C1
3	IN	33	28-05-2020	25-04-2020	C3	C1
4	IN	34	28-05-2020	24-04-2020	C1	C1
5	IN	30	28-05-2020	28-04-2020	C1	C3
6	IN	36	28-05-2020	22-04-2020	C2	C3
7	IN	35	28-05-2020	23-04-2020	C2	C2
8	IN	42	28-05-2020	16-04-2020	C2	C2
9	SE	31	28-05-2020	27-04-2020	C2	C3

10	SE	-	28-05-2020	-	-	-
11	SE	29	28-05-2020	29-04-2020	-	C2
12	SE	31	28-05-2020	27-04-2020	C2	C3
13	SE	32	28-05-2020	26-04-2020	C3	C3
14	SE	30	28-05-2020	28-04-2020	C3	-
15	SE	32	28-05-2020	26-04-2020	C2	C2
16	SE	36	28-05-2020	22-04-2020	C2	C1
17	MS	34	28-05-2020	24-04-2020	C3	C2
18	MS	29	28-05-2020	29-04-2020	C3	C2
19	MS	33	28-05-2020	25-04-2020	C2	C1
20	MS	34	28-05-2020	24-04-2020	C3	C2
21	MS	29	28-05-2020	29-04-2020	C2	-
22	MS	33	28-05-2020	25-04-2020	-	C2
23	MS	29	28-05-2020	29-04-2020	C2	C2
24	MS	36	28-05-2020	22-04-2020	C2	C2
25	MS	19	28-05-2020	09-05-2020	C2	C2
26	MS	33	28-05-2020	25-04-2020	C2	C2
27	MS	29	28-05-2020	29-04-2020	-	C2
28	MS	44	28-05-2020	14-04-2020	C2	C1
29	MS	37	28-05-2020	21-04-2020	C2	C2
30	MS	27	28-05-2020	01-05-2020	C2	C2
31	MS	30	28-05-2020	28-04-2020	-	C1
32	MS	39	28-05-2020	19-04-2020	C2	C2
33	IN	16	28-05-2020	12-05-2020	C2	C2
34	IN	31	28-05-2020	27-04-2020	C2	-
35	IN	33	28-05-2020	25-04-2020	C2	C2
36	MS	32	28-05-2020	26-04-2020	C3	C2
37	MS	33	28-05-2020	25-04-2020	-	C1
38	MS	33	28-05-2020	25-04-2020	C3	C2
39	MS	30	28-05-2020	28-04-2020	C1	C2
40	MS	36	28-05-2020	22-04-2020	C2	C2
41	SE	31	28-05-2020	27-04-2020	C1	C3
42	SE	33	28-05-2020	25-04-2020	C3	-
43	SE	31	28-05-2020	27-04-2020	C2	C2
44	SE	-	28-05-2020	-	-	C2

206

207

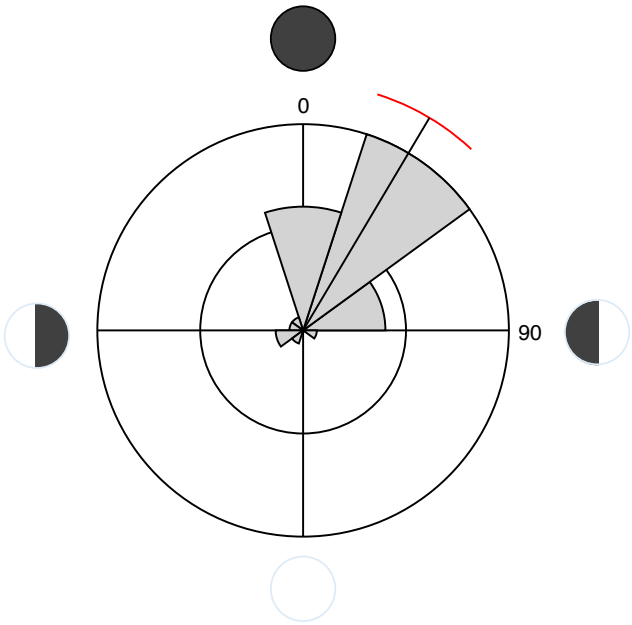


Fig. 4: Distribution of hatch frequencies of *Schindleria* from the Red Sea along a lunar cycle (indicated with the four different black and white pie charts). The new moon corresponds to 0 ° (top), the 1st quarter moon to 90 ° (right), the full moon to 180 ° (bottom), and the 3rd quarter moon to 270 ° (left). The "black" line gives the angular mean and the "red" arc the angular variance of the data and the pie sections within the circle, the number of hatch events during those lunar days.

From the linear regression models, the differences in the abundances of *Schindleria* in relation to the moon phases were most significant for the collections from the DANA Expedition, with the highest abundances caught in the 3rd quarter moon followed by the new moon; while in the Red Sea, it was the new moon, which yielded the highest abundances followed by the 3rd quarter moon (see Fig. 5A and Fig. 5B). However, in both datasets, the full moon yielded the lowest abundances, followed by the 1st quarter moon; and the differences between the full moon and the new moon abundances were always (i.e., in the linear regressions of both datasets) significant (Fig. 5A and Fig. 5B). Additionally, the global trend of relations between lunar phases and abundances of *Schindleria* was supported by the slope of the generalized linear

models of both datasets, which were similar and of which the means did not significantly differ (Fig. 5C)

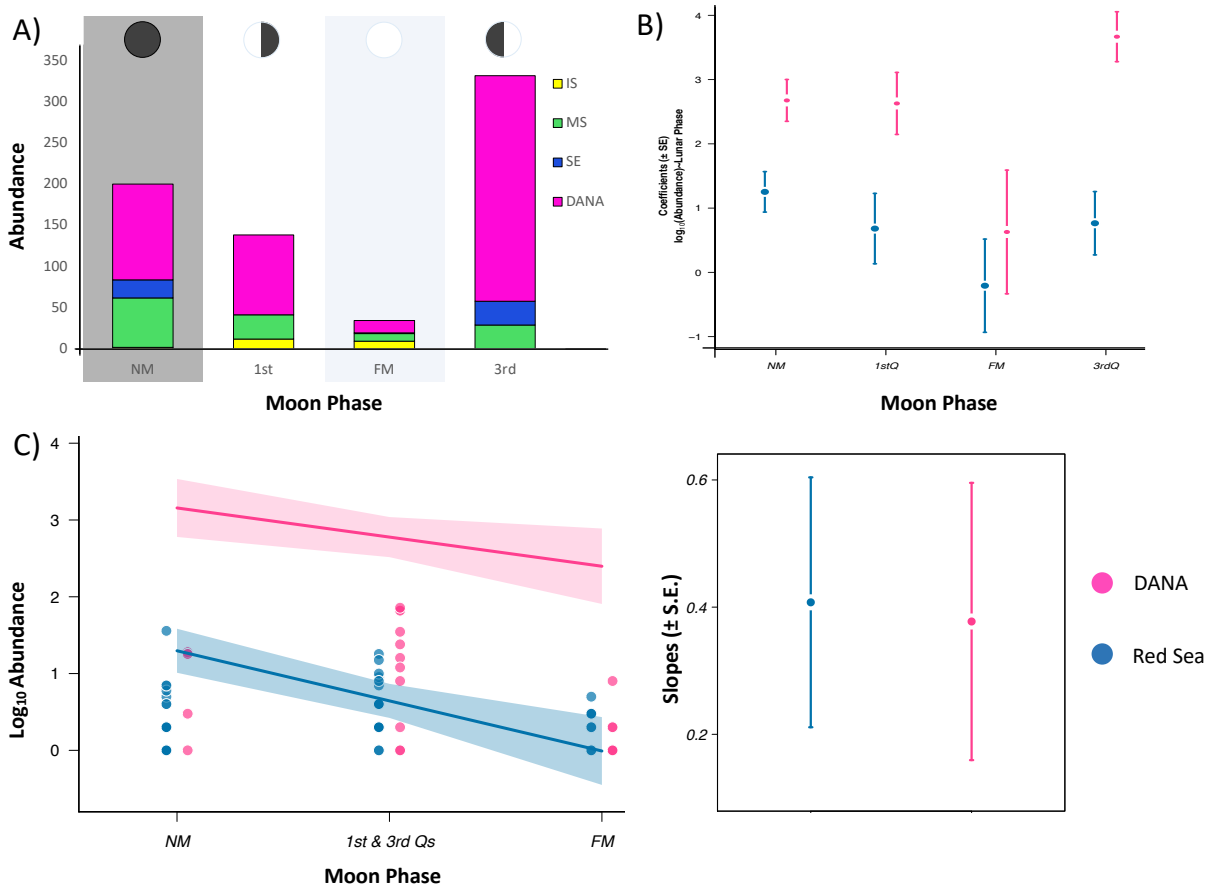


Fig. 5: Relations between abundances of *Schindleria* and the four main moon phases (the new moon "NM", the 1st quarter "1stQ", the full moon "FM", and the 3rd quarter "3rdQ") in two different datasets: one from an Indo-Pacific collection from the DANA Expedition 1928-1930 (DANA) and the other from a Red Sea collection (from the 16th Oct to the 16th Nov, 2014). Values from the DANA Expedition are always color-coded in "pink". Panel A displays the abundances in the Red Sea color-coded per sampling site: inshore/IS reef in "yellow", mid-shelf/MS reef in "green", and shelf-edge/SE reef in "blue". In Panel B and C, the Red Sea abundances are given as total values in "blue". Panel A displays the total abundances (y-axis) for each dataset per moon phase (x-axis). The moon phases are represented by the circles on

238 the top of the barplot and the brightest moon phase (FM) highlighted by a “light-blue” shaded
239 box, while the darkest moon phase (NM) by a “black” shaded box. Panel B displays the
240 coefficients of linear regression on the corrected Log_{10} Abundances (± SE; y-axis) of each moon
241 phase (x-axis) of the two main datasets (DANA vs. Red Sea). Panel C displays, on the left plot,
242 the abundances of each day of sampling (as dots) within a moon phase (on the x-axis; where
243 the moon phases are grouped by light intensity for which the 1stQ and the 3rdQ moons are
244 grouped in the middle of the regression) and on the right plot the respective slopes of the linear
245 regression of both datasets of which the mean does not differ significantly between the two data
246 sets. The lowest abundances of *Schindleria* were generally during the FM.
247
248 *Spatio-temporal abundances of adult* Schindleria *within the Red Sea*
249 The mid-shelf reef site near the coast of Thuwal, Saudi Arabia, had the highest abundances of
250 *Schindleria* among all our Red Sea sites. Seventy-five percent (1341 specimens) of the total
251 catches were collected at this site, followed by 366 specimens collected at the shelf-edge reef,
252 and only 85 at the inshore reef (Fig. 6). Plotting the year-round abundances of *Schindleria* for
253 all sites and their respective sea surface temperature (SST), it was evident that the highest
254 abundances of *Schindleria* were neither during the hottest season of the year, nor during the
255 coolest, but rather in between those two seasonal temperature extremes (Fig. 6A). Additionally,
256 in relation to the presence of larval fish recruits, peaks in abundances of adult *Schindleria* were
257 also temporally decoupled from the peaks of abundances in coral reef fish recruitment (Fig. 6B-
258 C).
259

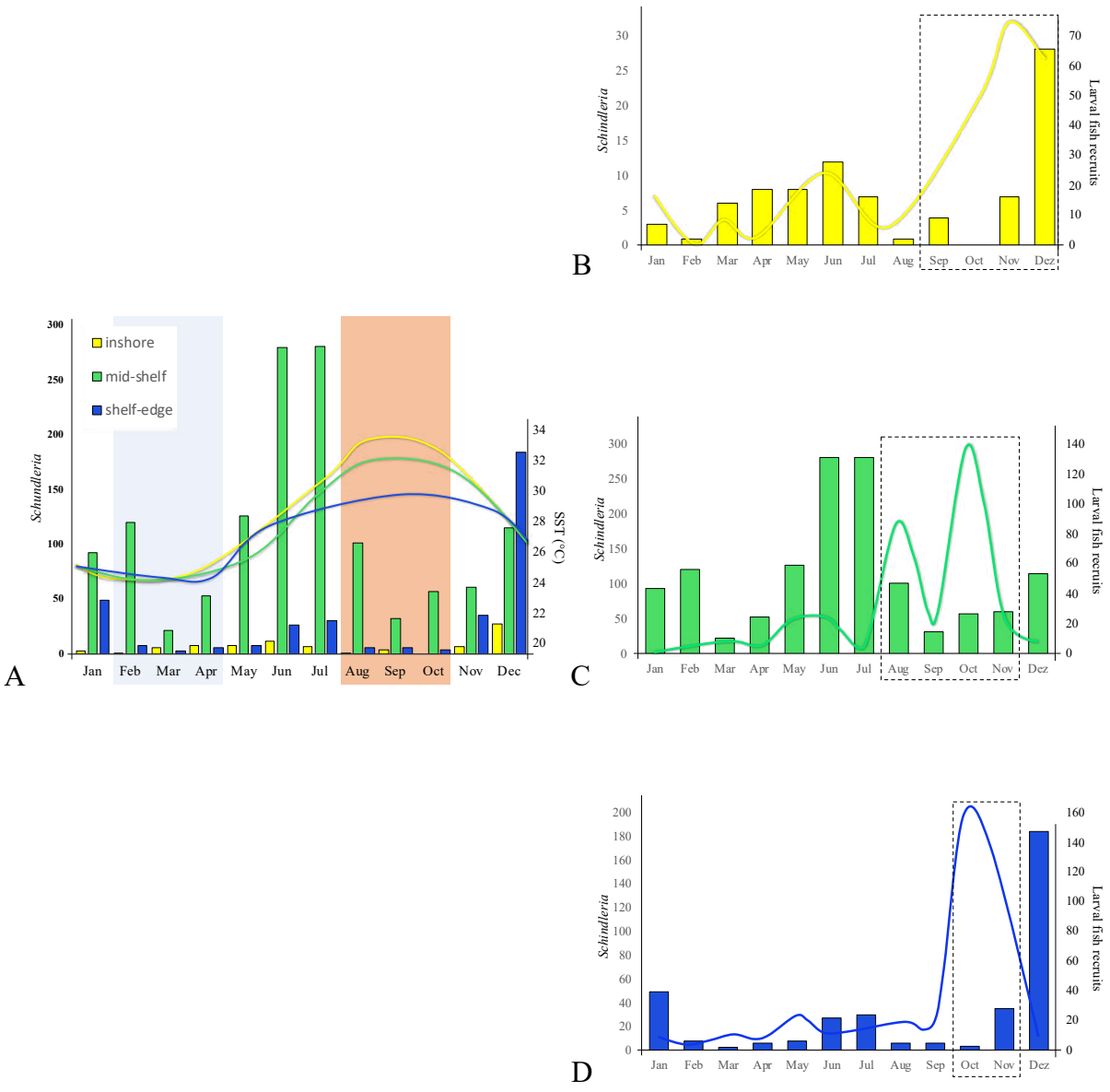


Fig. 6: Barplot of the year-round abundances of adult *Schindleria* (y-axis) from the Red Sea (Thuwal, Saudi Arabia) caught with LED powered light traps (from February 2015 to January 2016) at three different reefs along a cross-shelf gradient: one inshore ("yellow"), one at the mid-shelf ("green"), and one at the shelf edge ("blue"). Panel A: *Schindleria* abundances in relation to sea surface temperatures (SST, in °C). The total number of individuals for each sampling site collected each month is given as vertical bars (values correspond to the y-axis to the left). Temperature (SST) profiles per reef are also color-coded and given as a continuous line (values correspond to y-axis to the right). A "light-blue" shaded box indicates the months

with temperature minima (February to April) and an “orange” shaded box indicates the months with temperature maxima (August to October). Peaks of abundances are observed outside both boxes. Panel B to D: *Schindleria* abundances in relation to the abundance of larval fish recruits, color-coded per reef site as in Panel A. The total number of *Schindleria* individuals collected at each sampling site is given by vertical lines and their values correspond to the left y-axis. Profiles of the abundances of larval fish recruits are given by continuous lines and their scale is given by the right y-axis. Dashed boxes indicate the months with peaks in recruitment of coral reef fish larvae (*sensu* Robitzch et al. 2020). Peaks of abundances of *Schindleria* do not generally coincide with peaks of larval fish recruitments.

Linear regression models were used to corroborate these observations. Initial models of the abundances of *Schindleria* were created for the entire data set (i.e., SST, number of larval fish recruits, reef site, and month as explanatory variables). However, the best fitting model only included the reef site as the most significant explanatory parameter, having a relative importance of 0.62 among all variables of the initial model (which explained 65.2 % of the total variance). Hence, linear regression models on the abundance of *Schindleria* were also performed per reef site. At the inshore reef, the initial model, including SST and the number of larval fish recruits, was the best fitting model and was able to explain 43.9 % of the total variance of the data with a relative importance of 0.77 for SST, and of 0.24 for the number of larval coral reef fish recruits. Contrastingly, the same initial model did not fit well neither at the mid-shelf reef nor at shelf-edge reef. In both latter cases, only very little of the variance was explained by this model (14.8 % and 2.9 %, respectively) and the number of larval fish recruits was relatively more important (0.67 - 0.99) compared to SST (0.001 - 0.33).

Discussion

Schindleria, the smallest coral reef fish in the world, potentially has the largest populations of any reef associated fish. With high turnover rates, these populations may have a substantial ecological role in reef ecosystems. Unfortunately, due to its cryptic biology and very few available studies, little is known about its basic biology and population dynamics. Putative migrations with lunar cycles may also represent an important carbon route from the pelagic into the trophic niches of the highly populated and oligotrophic coral reef matrix. We used a large collection of *Schindleria* specimens from the Red Sea (nearly two thousand specimens) and data from a recently published collection of more than 500 adult *Schindleria* from the DANA Expedition in 1928-1930[8] in order to access more information on the biology and reproductive behavior of this fish.

Even though over half of named *Schindleria* species have been described from the Red Sea, further research on the biology and ecology of this taxon is still missing, and prior to our study, only 44 adult specimens had so far been collected and documented in the Red Sea (El-Regal *pers. comm.).* In our study, we found evidence for seasonal and spatial differences in abundances likely related to differing habitat and environmental conditions among the sampled reef sites, and we also found global trends related to lunar cycles likely linked to reproductive cycles. We hypothesized that *Schindleria* would be most abundant during environmentally moderate conditions (i.e., not the hottest seasons in the Red Sea, nor those with peaks in coral reef fish recruitment) and at the darker moon phases, since these tiny paedomorphic fishes will prefer to emerge and/or approach the reef matrix in the absence of light (from the moon) to protect themselves from nocturnal visual predators; and that the collection of primarily mature specimens at the reefs may indicate trends in reproductive behavior. Back-calculations of hatch dates from the Red Sea based on otolith microincrements corroborated that *Schindleria* larvae

317 hatched a couple of days after their abundance peak during the new moon. Hence, our results
318 supported our hypotheses of reproductive cycles of *Schindleria* being linked to the moon phases
319 and the completion of one generation time occurring in a single lunar cycle; in addition,
320 *Schindleria* appear to have greater success/abundances during more suitable environmental
321 conditions. In the following we will discuss in detail our two major findings: The global trend
322 of low abundances of *Schindleria* around the full moon and the generally high year-round
323 abundances of *Schindleria,* yet decreased during seasonal temperature extremes and
324 recruitment peaks of larval coral reef fishes in the Red Sea.
325
326 The Red Sea collection and that from the DANA Expedition had significant differences in the
327 abundance of *Schindleria* in relation to moon phases. *Schindleria* was mostly absent in catches
328 during the full moon, while peaks of abundances were during the 3rd quarter (i.e., collections
329 from DANA Expedition) and the new moon (i.e., Red Sea collections), with a tenfold increase
330 compared to full moon catches, in both collections.
331 In the Red Sea, the specimens caught were all mature and females carried large eggs. Hence,
332 we suggested that high abundances during the darker moon phases may serve to reduce
333 predation but may also be related to reproductive cycles. *Schindleria* are thought to be lagoon
334 completers that live within the coral reef matrix[11]. However, recent studies have found evidence
335 for the presence of a substantial number of adult *Schindleria* specimens far away from coral
336 reefs (between 320 km to 360 km) in the tropical Indo-Pacific or in deeper pelagic waters (up
337 to 1000 m depth) close to or in between coral reefs[8]. Hence, *Schindleria* may not be staying for
338 their entire life-cycle within the reef matrix and may be timing their association to reefs with
339 lunar cycles. For instance, Isari et al.[24] found *Schindleria* within plankton tows taken in pelagic
340 waters close to our Red Sea sampling sites (a couple of km away from the reef). The authors

mainly sampled in the days prior or around the full moon, had two differing sampling sites (inshore vs. offshore), where oblique tows sampled substantially different depths (50 m depths inshore vs. 500 m depth offshore), and did not provide information on the abundances of *Schindleria* among the sampling sites, dates, or depths. However, overall, the study mainly collected juvenile *Schindleria* (S. Isari, pers. comm.), which may indicate that the abundances, distribution, and habitat or location of *Schindleria* also differs with ontogeny and that their presence at the reef matrix may be periodic, induced by seasonality of the region and lunar cycles.

Schindleria are very short-lived (max. age of 42 to 60 days [1,5]) and reach maturity at an extraordinarily early age for a vertebrate (23 days[1]). Hence, we speculated that the specimens may be reaching maturity at a certain moon phase at which they aggregate at the reefs to reproduce and spawn after which the eggs hatch (within a couple of days), larvae disperse, and the new cycle ends again with the return of the adults to the reef at the next new moon. In order to corroborate this hypothesis, we assessed the age of specimens collected at our Red Sea reef sites counting daily increments in their sagittal otoliths. Their average age was approximately 33 (± 3) days, which is close to the total length of a lunar cycle (29 days). More interestingly, the back-calculation of hatching dates for these Red Sea specimens were significantly occurring around the same lunar days and shortly after the new moon, thus supporting our hypothesis of a potential recurring reproductive aggregation during this moon phase. Hence, it may be that these specimens have generation times as short as one lunar cycle. It remains unclear why *Schindleria* evolved such a short generation time[25], but our results suggest that coupling with a lunar cycle may be a strategy that works on a global scale.

We observed a slight shift in lunar phase with the highest abundance of *Schindleria* between the two collections studied (i.e., 3rd quarter moon in the DANA Expedition vs. the new moon

365 in the Red Sea). This could be explained by the method, the exact location of the sampling, and
366 following the previous line of thought. The DANA specimens were not collected directly in the
367 reef matrix (as our Red Sea specimens were) but from more pelagic waters, and the sampling
368 method used during the DANA Expedition were plankton tows, which do not actively attract
369 specimens within the reef-matrix (as do the light traps used during the Red Sea sampling) but
370 capture those specimens present in the water column. Hence, while we were able to collect only
371 mature specimens that were already at the reef to reproduce, the DANA Expedition may have
372 collected adult specimens that were yet in the pelagic, on their way to the reef, but still a couple
373 of days away from reaching complete maturity. The observations from inshore in the Red Sea
374 were completely different, showing peak abundances during unexpected moon phases (the 1st
375 quarter and the full moon). However, this site had an extremely low overall abundance of
376 *Schindleria*, limiting the value in interpretation of these trends. Due to the small sample size, it
377 is difficult to assess whether these reflect biological patterns or variations due to other factors
378 (such as light intensity of the surroundings vs. the light trap, wave action, turbidity, and other
379 factors). For example, the inshore sampling site is very close to the coastal town of Thuwal and
380 the King Abdullah University of Science and Technology, which are both sources of noise and
381 light at night. Sound has proven to be negatively related to the abundance of *Schindleria*
382 (Whittle 2003). Specimens from the inshore site could have been affected by stronger coastal
383 lights more than sites further from shore, particularly during the darker new moon. Likewise,
384 predation risk may be increased inshore due to the stronger illumination[26].
385 Overall, we were able to support our hypothesis of the alignment of a generation time and
386 reproductive cycles with the lunar cycles in the Red Sea using data on abundances and ages of
387 the specimens from daily microincrements from otoliths. The same support was found among
388 abundance data of *Schindleria* from the DANA Expedition, which comprised a much wider

temporal and geographic range. Due to the preservation method used in the DANA collection (i.e., the samples had initially been placed in a formalin/ethanol mixture), the otolith structures were dissolved, precluding the estimation of age. Nonetheless, we hypothesize that the trends at other geographic locations will likely resemble results from the Red Sea. Other recent collection efforts using light traps at the shores of Rapa Nui/Easter Island, Chile, and in the Western Indian Ocean, also indicate higher presence of *Schindleria* during the new moon (V. Robitzch, unpubl. data).

Lastly, among the sampling sites within the Red Sea, we further concluded that the highest abundances of adult *Schindleria* were neither found during seasonal temperature extremes (i.e., maxima and minima) nor during the peaks of coral reef fish recruitment. Most specimens were caught outside of the hottest season, which can be related to the extraordinarily high sea surface temperatures of the Red Sea[24,27,28] and may not hold true outside the Red Sea. However, *Schindleria*'s peaks in abundance, although outside the seasons with highest temperatures, did not coincide with the peaks of abundance of recruiting coral reef fishes in the Red Sea, which is also outside of the hottest season[24,27]. We explain the difference in peaks with the longevity and biology of *Schindleria.* As opposed to longer-lived coral reef fishes, *Schindleria* cannot time reproduction or the termination of their PLD in the long term; the species' longevity demands monthly, year-round reproduction[29,30]. Nonetheless, its larvae are likely benefitting from the same conditions as are other coral fish larvae[27]. Hence, *Schindleria* may have a more successful PLD outside the periods of peaks in coral reef fish reproduction, since it will likely have less competition for resources, particularly within the extremely oligotrophic central Red Sea. The mortality of premature phases of *Schindleria* may also increase during abundance peaks of coral reef fish larvae as these may prey on tiny *Schindleria* leaving fewer adults that

survive the PLD. Due to the morphological similarity between adult *Schindleria* and fish larvae, both may have similar predators. Hence, the abundance of *Schindleria* may be seasonally reduced during periods of recruitment peaks of coral reef fish larvae because of associated higher abundances of predators adapted to feed on incoming larval recruiting cohorts. Nevertheless, we argue that *Schindleria*'s unique life history and short generation time forces it to start a new generation every month "despite the weather", which is why it is generally abundant year-round. The longevity and biology of *Schindleria* may also further explain why its behavioral cycles follow lunar cycles globally as environmental conditions become less important when periodicity needs to be established and a generation must be completed within a few weeks. Schindleriidae is yet a species-poor monogeneric family, likely due to the lack of data rather than the lack of biodiversity; and a large number of cryptic species are likely to be found within this taxon[7]. Hence, species-specific trends are yet far from understood and the differences in otoliths structures we found suggest the presence of several species at small scales[26]. With increased research on the species' diversity of this taxon, further discoveries of discrepancies and preferences in *Schindleria'*s ecology, biology, recurring cyclic behavior, and habitats will rise. Accordingly, some of the differences in the spatial yearlong abundances as well as in the site-specific temporal abundances we found in adult *Schindleria* may further be distinctive among species and their specific biological and ecological features.

Methods

Sampling and data

Schindleria samples were collected at three reefs: one reef inshore "IS", one at the mid-shelf "MS", and one at the shelf-edge "SE" off of the coast of Thuwal, Red Sea, Saudi Arabia (blue, green, and yellow reef, respectively, in the zoomed map section of Fig. 1), using a set of three

replicate light traps per reef (i.e., nine light traps total) attached to fixed moorings positioning the light trap ~2 m below the surface, at the northern end of the wave-protected (eastern) side of each reef, with a bottom depth of approx. 8 m to 14 m. Prior to each sampling night, the rechargeable batteries of the light traps were replaced with fully charged ones and each light trap and mooring were cleaned to assure the same starting conditions for each sampling period and to avoid sampling biases due to algal growth, reduced light intensity, or induced chemical cues. For all qualitative and quantitative analyses, the daily catches from all three light traps were pooled for each reef. This research was undertaken in accordance with the policies and procedures of the King Abdullah University of Science and Technology (KAUST). Permits for sampling in Saudi Arabian waters were obtained from the relevant Saudi Arabian authorities. The study did not involve live specimens or endangered or protected species. KAUST implemented its Institutional Animal Care and Use Committee in December 2016; the collections in this paper were concluded prior to that date.

Correlations of abundances of Schindleria *with lunar phases*

The collapsible LED light traps (Bellamare 500-micron mesh) were first deployed for 32 consecutive days (from the 16th October to the 16th November 2014) to capture variation in abundance related to lunar phases (within a complete lunar month). The daily light trap samples were assigned to one of four main moon phases depending on the date of their collection relative to the lunar day: the new moon "NM" (comprising the 26th-29th and the 1st-4th lunar day), the 1st quarter "1stQ" (from the 5th-11th lunar day), the full moon "FM" (from the 12th-19th lunar day), and the 3rd quarter "3rdQ" (from the 20th-25th lunar day).

To further assess the importance of moon phases on the abundance of *Schindleria* on a global scale, data on *Schindleria* abundances from sampling stations from the DANA Expedition

1928-1930 (i.e., all sampling points outside the Red Sea (ID1 – ID44)[8] in Fig. 1) were taken and categorized into the four main moon phases in the same way as the Red Sea data. The "moon phase" was then used as the explanatory variable (i.e., as a factor) for the abundance of *Schindleria* from the DANA Expedition and from the Red Sea in two separate linear regression models (generalized linear models in R, *glm* function, R Core Team[31]). The linear regression models were then compared to one another. Due to overdispersion observed in both data sets (evaluated by using the dispersion test in the *AER* R package[32,33]) we used the quasi-poisson family distribution in the *glm* function to fit the model. An ANOVA was then performed between the null-model and our alternative model. To compare the results of the glms of both data sets, we plotted the $\log_{10}$ coefficients of the linear regressions of the abundances in the different moon phases of both datasets in order to assess the significance of the differences of abundances of *Schindleria* among the different moon phases, and whether these changes in abundances were similar between the two data sets. In this regard, to compare the slopes of the linear regression models of the two datasets, the moon phases were converted to numeric ranks following the light intensity of each moon phase for which the "NM" was given the value "0", the FM the value "2" and the 1st and 3rd quarter moons (1stQ and 3rdQ) the value of "1", since both of them represent the value of one illuminated quarter of the moon. The *glm* function was then again applied using the quasi-poisson family to correct for overdispersion of the data; and the respective slopes of the models of each dataset (Red Sea vs. DANA) were plotted to check for significant differences in the correlations between moon phases and abundances of *Schindleria*.

As a last step to examine potential relations of *Schindleria* catches with moon phases, the age of mature *Schindleria* specimens (i.e., females with visibly developed ovocytes and males with distinctive urogenital papillae) collected in the three Red Sea locations (preserved

485 in 95% EtOH) were assessed by counting daily growth increments of the sagittal otoliths. Right
486 and left sagittal otoliths were removed under an Olympus SZ61 stereomicroscope equipped
487 with a polarized light filter. The pair of otoliths was completely immersed in epoxy resin and
488 fixed to a microscopy slide. The otoliths were then photographed under a Zeiss AXIO Lab.A1A
489 microscope equipped with an ATRAY camera. No further preparation was needed to reveal
490 daily increments. Additionally, the pictures taken from the otoliths for the counts of
491 microincrements were categorized with a qualitative scale (C1 – C3), where C1 had poor
492 resolution, were too damaged and/or in a state that made the readings of microincrements
493 impossible, and were thus discarded from the analysis; C2 had tissue remains or were broken
494 but provided enough resolution to assess numbers of microincrements; and C3 were in ideal
495 condition. Normality of the data was then tested using the Shapiro-Wilk test. Counts of the right
496 and/or the left sagittae were used, because both counts did not differ significantly (*Wilcoxon*-
497 test, $z = 0.30$, $P = 0.76$). Therefore, in cases where one of the two sagittae otoliths were broken
498 or too blurry to measure, the other available otolith was used. The otoliths were counted at least
499 three times by an independent reader (Camilo Rodríguez-Valentino), who lacked any
500 information on the samples or the study purpose in order to obtain unbiased estimates of the
501 age of each sample and its hatch date. To assess the hatch frequencies over the lunar cycle, the
502 hatch dates were back-calculated from the sampling date. Then, the "Lunar hatch day" (LHD)
503 was determined to transform the lunar cycle to an angle variable. Thus, the lunar cycle (of 29
504 days) was converted to a 360° cycle, setting the new moon as day 1. Thereby, LHD = the
505 number of days since the new moon*(360/29). A uniform distribution around the lunar cycle
506 was tested using Rao's spacing test[34] as it is a robust circular statistical test able to analyze bi-
507 and multimodal distributions. All statistical analyses related to otolith increments were
508 performed using the free software Past 4.0[35].

Relationships of abundances of Schindleria *with temporal and spatial conditions*

After the month of daily sampling of *Schindleria*, the same light traps were deployed during five consecutive nights around the new moon for twelve consecutive months at the same moorings, to assess variation in abundance related to seasonal environmental (i.e., temporal) conditions and habitat/site-related (i.e., spatial) differences among the reefs within the Red Sea (i.e., the "IS", the "MS", and the "SE" reef). Hence, sea surface temperatures (SST) at each reef were further recorded during the sampling period with an acoustic doppler current profiler (ADCP, Nortek AS, data available in Appendix S3[27]). The light traps also attracted larval fish recruits of which the abundances were measured and were spatio-temporally regulated by environmental conditions[27]. We included said abundances as a predictive variable for the abundance of *Schindleria,* since the abundance of these larval coral reef fish recruits already comprised/reflected a range of ecosystem and environmental parameters/conditions and was therefore considered as a good proxy to represent changes in the environment and habitat. Additionally, physiologically and morphologically, adult *Schindleria* strongly resemble fish larvae for which the relation between the abundance of said larvae and that of mature *Schindleria* is further interesting. While adult *Schindleria* are often mistaken for a larva, their ontogeny may lead to differing ecological and biological features, which may also be reflected in their abundance. Hence, the local abundances of larval coral reef fish recruits (as total counts) together with the sampling location (as the reef site), the SST (in °C), and the month of sampling were considered in the initial model to perform linear regression on the abundances of *Schindleria*.

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Competing interests' statement: The authors declare no competing interests.

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Figures

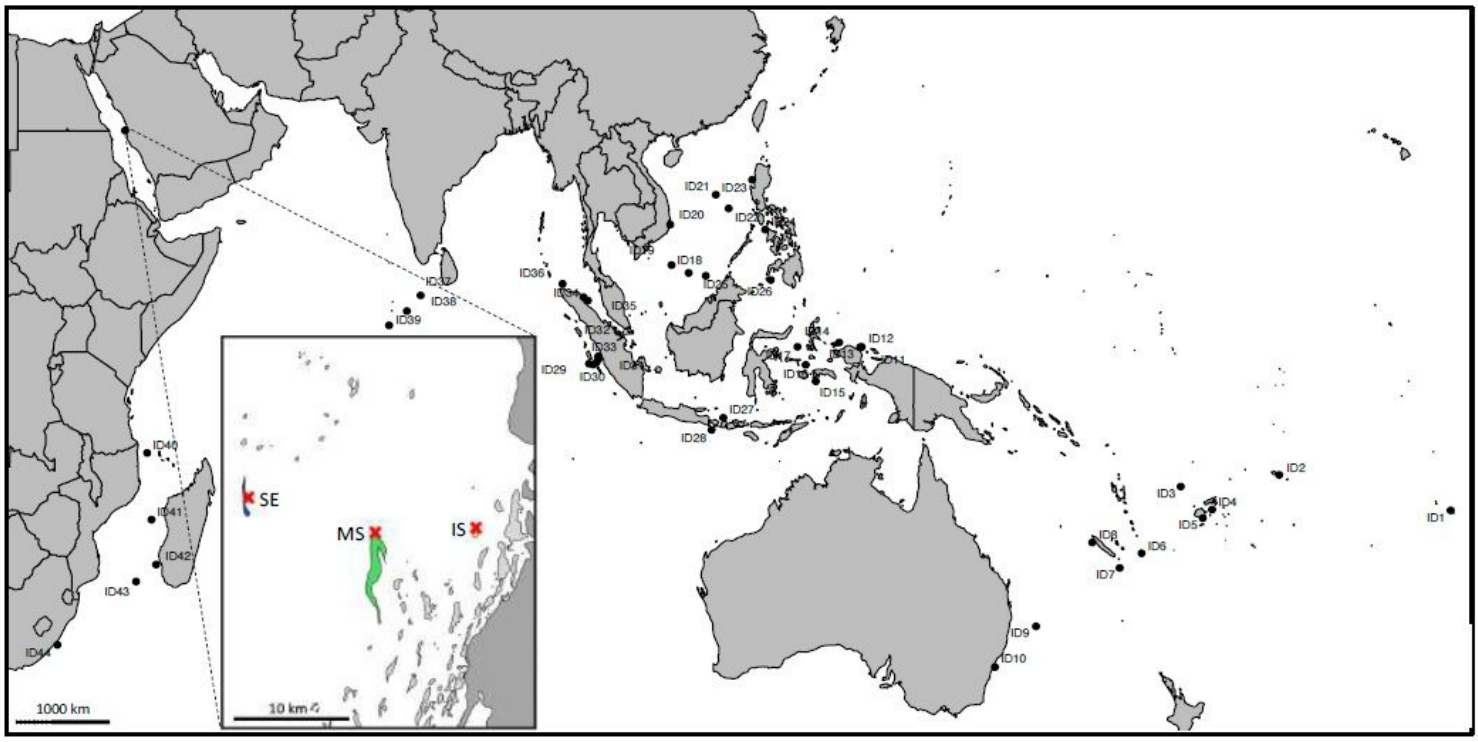

Figure 1

Collection sites of Schindleria: from the DANA Expedition 1928-1930 (all sites represented by a “dot”: ID1 – ID44, following Ahnelt and Sauberer 20208); and from the Red Sea, with a zoomed-in section displaying the three reefs where collection took place using a LED powered light trap along a cross-shelf gradient from the shore to the shelf edge, near the coast of Thuwal, Saudi Arabia. Coral reefs within the zoomed-in Red Sea section are given in “light grey” while the land sections are in “dark grey” and the sampled reef sites are color coded, with the “yellow” reef inshore (IS), the “green” reef at the mid-shelf (MS), and the “blue” reef at the shelf edge (SE). The “red” crosses indicate the location of deployment of the LED powered light traps for this study. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

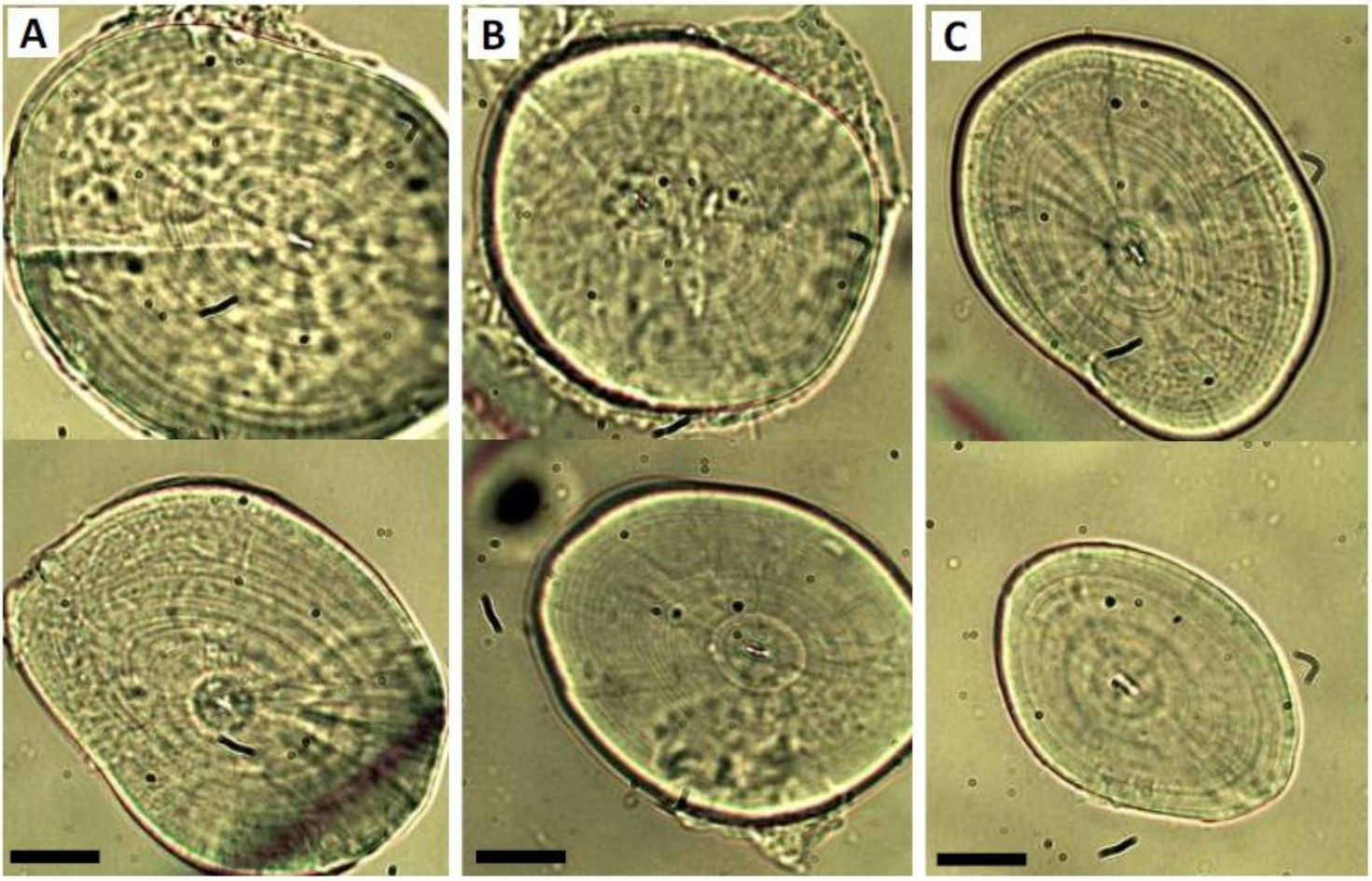

Figure 2

Sagittal otoliths from mature Schindleria specimens sampled with light traps from an inshore (A), a mid-shelf (B), and a shelf-edge (C) reef in the Red Sea, near the coast of Thuwal, Saudi Arabia. These otoliths represent otoliths of ideal conditions (i.e., “C3” category) to count daily growth increments and yielded average numbers of increments (between 30-33) despite slightly differing shapes and sizes. All otoliths are to scaled, with the bar at the bottom (left) of each panel representing 20 µm. The otolith at the top of each panel represents a rounder and larger otolith while the otolith at the bottom a more oval-shaped and smaller otolith.

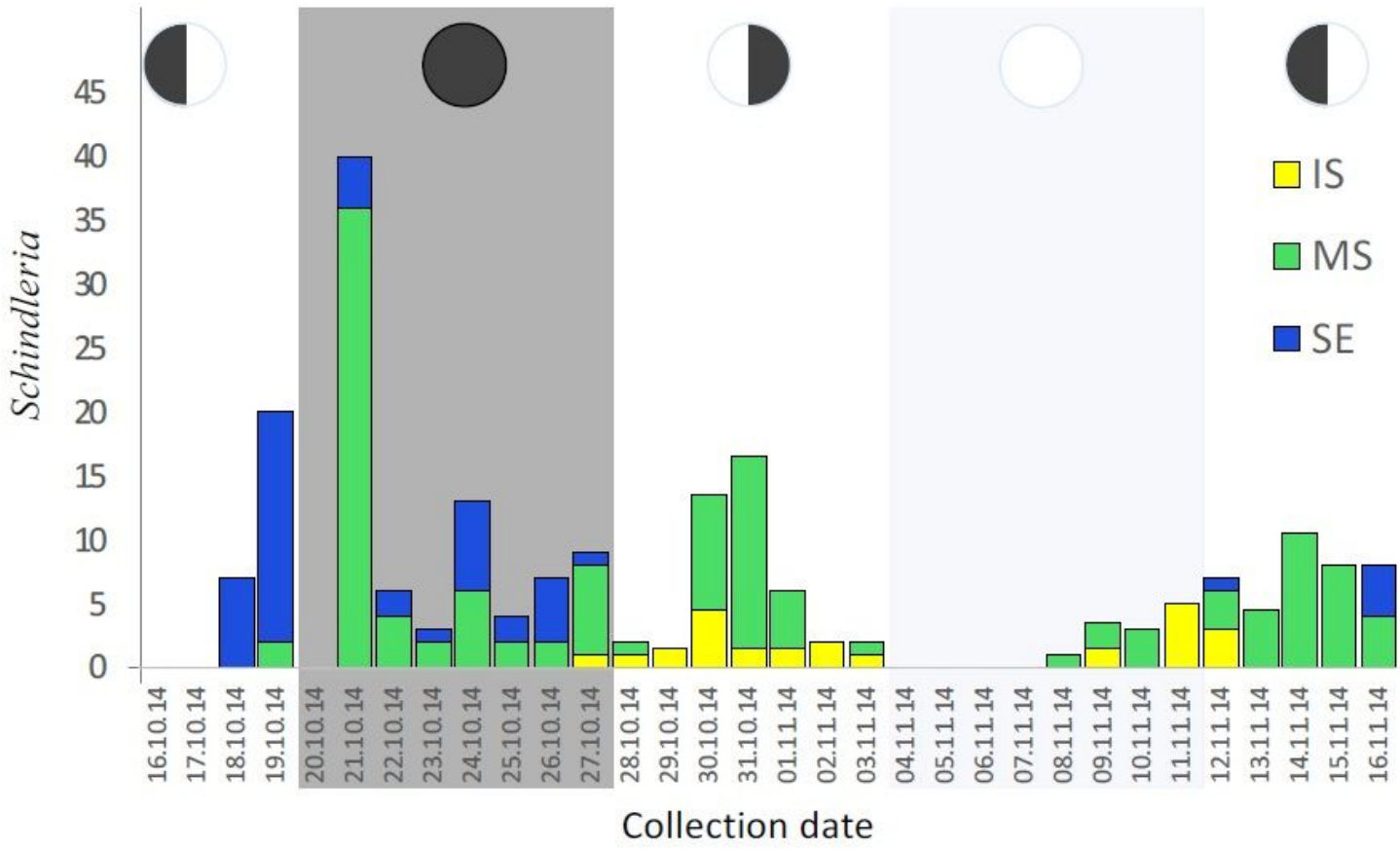

Figure 3

Barplot representing the total abundances of Schindleria collected during one lunar cycle in the Red Sea of Saudi Arabia. Total numbers of Schindleria specimens (y-axis) collected are color-coded for the relative number caught at each of three sampling locations: an inshore reef (IS) in “yellow”, a reef at the mid-shelf (MS) in “green”, and one at the shelf-edge (SE) in “blue”. Collections took place using three replicate LED powered light traps (collapsible Bellamare model) at each sampling location for the period of 32 consecutive nights from the 16th October to the 16th November (2014; x-axis). Different moon phases are indicated with pie charts on the top of each shaded section of the plot starting with the 3rd quarter moon, followed by the new moon, the 1st quarter moon, the full moon, and ending again with the 3rd quarter moon (from left to right).

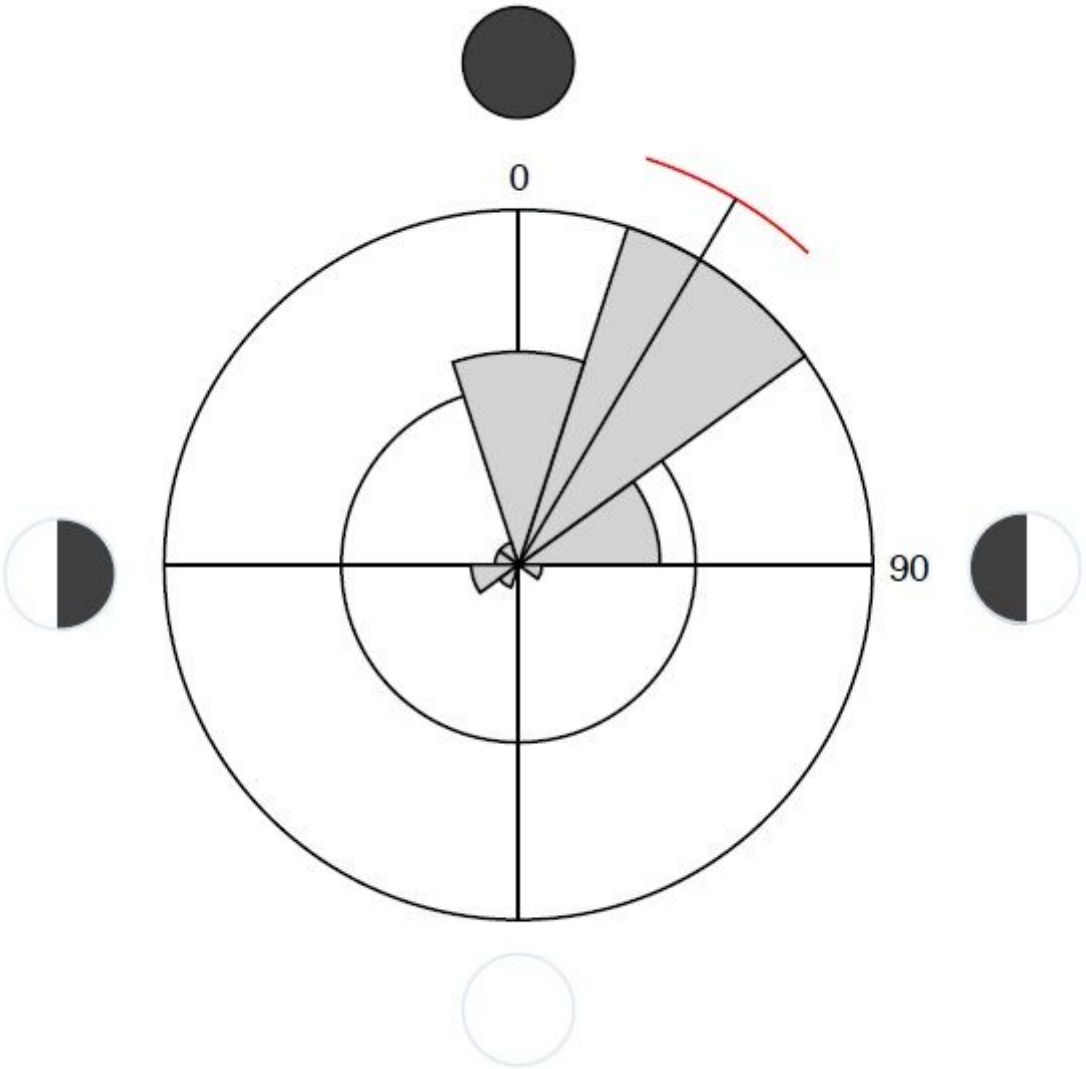

Figure 4

Distribution of hatch frequencies of Schindleria from the Red Sea along a lunar cycle (indicated with the four different black and white pie charts). The new moon corresponds to 0 ° (top), the 1st quarter moon to 90 ° (right), the full moon to 180 ° (bottom), and the 3rd quarter moon to 270 ° (left). The “black” line gives the angular mean and the “red” arc the angular variance of the data and the pie sections within the circle, the number of hatch events during those lunar days.

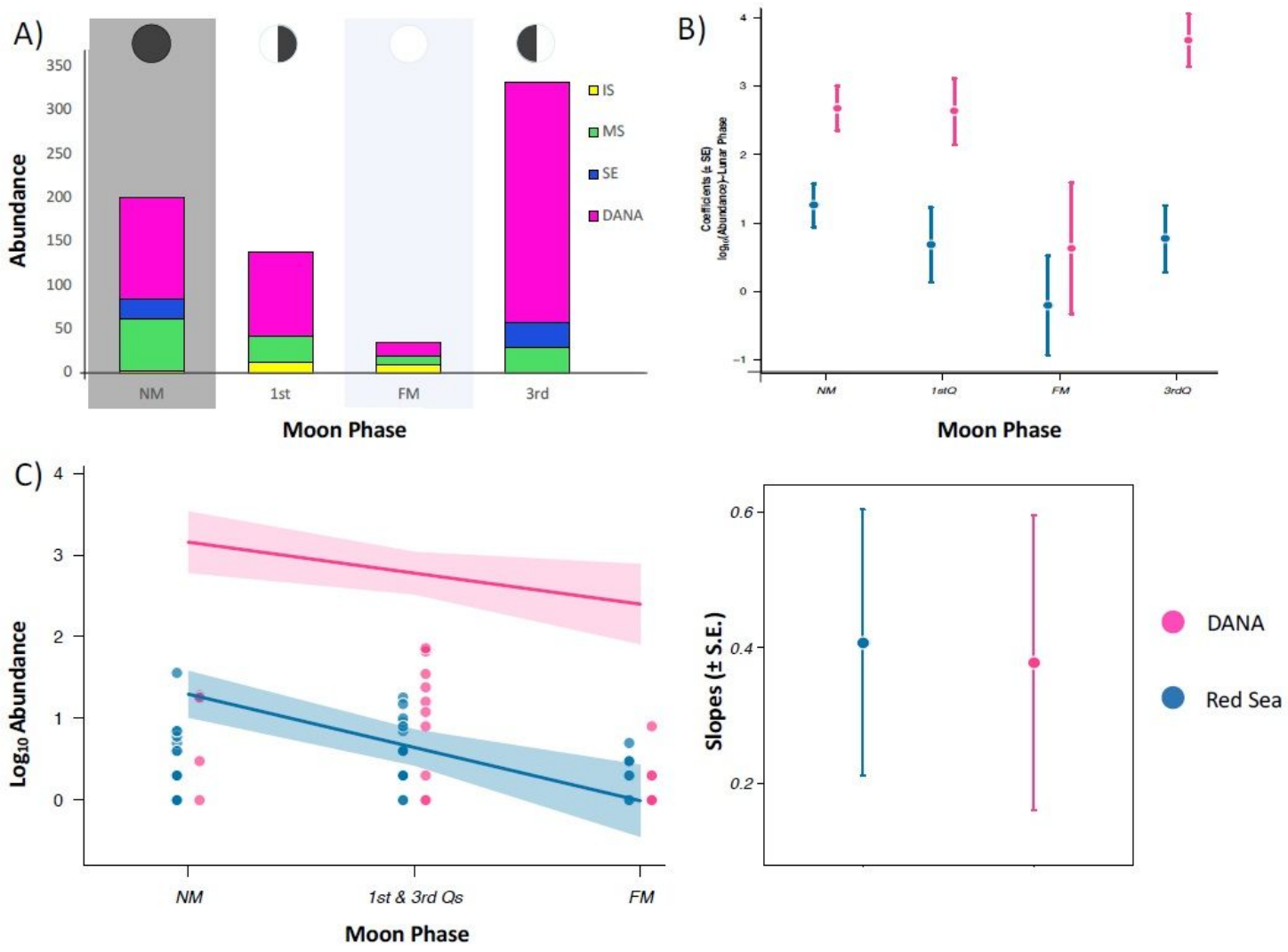

Figure 5

Relations between abundances of Schindleria and the four main moon phases (the new moon “NM”, the 1st quarter “1stQ”, the full moon “FM”, and the 3rd quarter “3rdQ”) in two different datasets: one from an Indo-Pacific collection from the DANA Expedition 1928-1930 (DANA) and the other from a Red Sea collection (from the 16th Oct to the 16th Nov, 2014). Values from the DANA Expedition are always color-coded in “pink”. Panel A displays the abundances in the Red Sea color-coded per sampling site: inshore/IS reef in “yellow”, mid shelf/MS reef in “green”, and shelf-edge/SE reef in “blue”. In Panel B and C, the Red Sea abundances are given as total values in “blue”. Panel A displays the total abundances (y-axis) for each dataset per moon phase (x-axis). The moon phases are represented by the circles on the top of the barplot and the brightest moon phase (FM) highlighted by a “light-blue” shaded box, while the darkest moon phase (NM) by a “black” shaded box. Panel B displays the coefficients of linear regression on the corrected Log10 Abundances (± SE; y-axis) of each moon phase (x-axis) of the two main datasets (DANA vs. Red Sea). Panel C displays, on the left plot, the abundances of each day of sampling (as dots) within a moon phase (on the x-axis; where the moon phases are grouped by light intensity for which the

1stQ and the 3rdQ moons are grouped in the middle of the regression) and on the right plot the respective slopes of the linear regression of both datasets of which the mean does not differ significantly between the two data sets. The lowest abundances of Schindleria were generally during the FM.

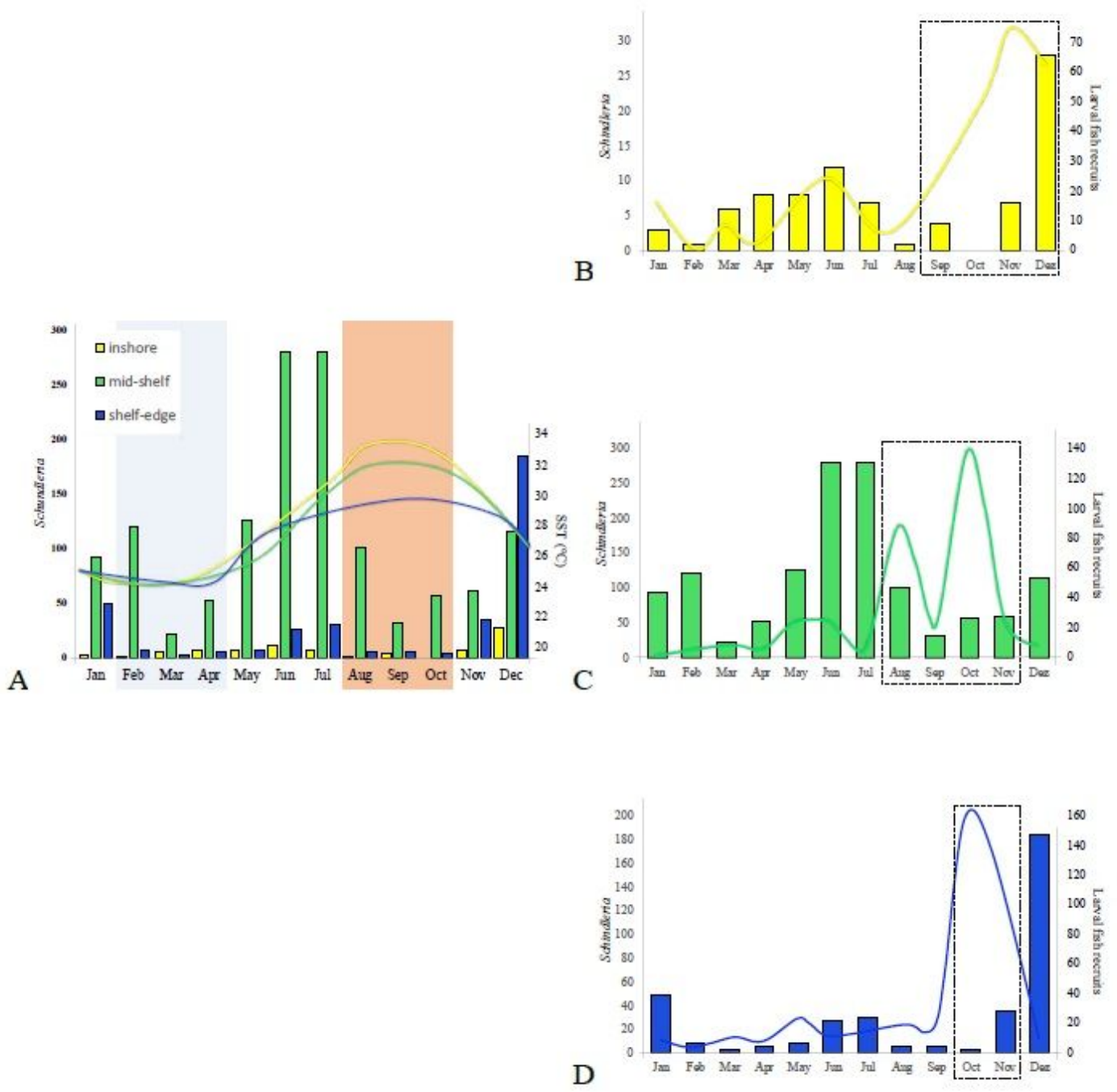

Figure 6

Barplot of the year-round abundances of adult Schindleria (y-axis) from the Red Sea (Thuwal, Saudi Arabia) caught with LED powered light traps (from February 2015 to January 2016) at three different reefs along a cross-shelf gradient: one inshore (“yellow”), one at the mid-shelf (“green”), and one at the shelf edge (“blue”). Panel A: Schindleria abundances in relation to sea surface temperatures (SST, in °C). The total number of individuals for each sampling site collected each month is given as vertical bars

(values correspond to the y-axis to the left). Temperature (SST) profiles per reef are also color-coded and given as a continuous line (values correspond to y-axis to the right). A “light-blue” shaded box indicates the months with temperature minima (February to April) and an “orange” shaded box indicates the months with temperature maxima (August to October). Peaks of abundances are observed outside both boxes. Panel B to D: Schindleria abundances in relation to the abundance of larval fish recruits, color-coded per reef site as in Panel A. The total number of Schindleria individuals collected at each sampling site is given by vertical lines and their values correspond to the left y-axis. Profiles of the abundances of larval fish recruits are given by continuous lines and their scale is given by the right y-axis. Dashed boxes indicate the months with peaks in recruitment of coral reef fish larvae (sensu Robitzch et al. 2020). Peaks of abundances of Schindleria do not generally coincide with peaks of larval fish recruitments.