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Depth-structured lineages in the coral *Stylophora pistillata* of the Northern Red Sea

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Coral reefs are biodiversity hotspots, where new species continue to be discovered. *Stylophora pistillata*, a depth-generalist coral, is widely distributed throughout the Indo-Pacific and has long been considered the poster child for phenotypic plasticity. It occupies a wide range of reef habitats and exhibits a myriad of gross morphologies. Here, we used reduced representation genome sequencing (nextRAD) to assess the genetic structure of adults and recruits of *S. pistillata* across shallow and mesophotic populations in the northern Red Sea (Gulf of Aqaba). Across analytical approaches, we observed a complex genetic structure with at least four genetically divergent lineages occurring sympatrically with little to no admixture and structured by depth. Morphological and physiological differences previously documented suggest that the long-considered ecological opportunism of *S. pistillata* in the Red Sea may, in fact, have a genetic basis. Assessment of both adult colonies and recruits within each of the lineages also revealed the prevalence of local recruitment and genetic structuring across the eight-kilometer section of the Israeli Red Sea coastline. Overall, the observed patterns confirm the presence of undescribed diversity within this model organism for coral physiology and corroborate a broader pattern of extensive undescribed diversity within scleractinian corals.

Corals reefs are biogenic structures that support over 25% of marine fauna despite occupying less than 0.1% of the ocean floor[1]. These three-dimensional ecosystems, primarily constructed by scleractinian corals, holds a biodiversity comparable to rain forests and offers shelter, nursery grounds, and food resources for thousands of reef-associated species[2]. Encompassing 1613 species, corals of the order Scleractinia are distributed globally, occurring in both shallow and deep waters[3]. However, coral reefs globally have experienced significant declines driven by local and global environmental stressors, with an extensive reduction in their global cover during the past decades[4–6]. Considering that new species of scleractinian coral are still being discovered and that species are being lost at an unpresented rate[7], some of them before being known to science, a deeper knowledge on our biodiversity is urgent.

The genus *Stylophora* (Scleractinia, Pocilloporidae) is recognized to encompass nine valid species as of 2023[8], albeit with a convoluted taxonomic history. To date, six species have been described to occur in the Red Sea, including *S. pistillata*, *S. danae*, *S. subseriata*, *S. kuehlmanni*, *S. wellsi*, and *S. mamillata*[9]. However, the validity of these classifications has been called into question in several studies[10–13]. A significant factor contributing to the controversy is the morphological variability and phenotypic plasticity frequently observed in scleractinian corals, which complicate species delineation[14]. This complexity is exacerbated by the presence of cryptic species, which are morphologically indistinguishable but genetically distinct[11,15–18]. Moreover, hybridization is hypothesized to be a pivotal mechanism in Scleractinia evolution, introducing further challenges to coral taxonomy[19–21]. Over recent decades, numerous reviews have focused on the

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systematics of the order, leveraging molecular data to elucidate species relationships and describe new taxa[22–33]. Despite these efforts, the systematics of *Stylophora* remains an ongoing debate.

Stylophora pistillata (Esper, 1792) is a brooding species, releasing larvae that settle mainly within the first 48 h[34–36]. It is one of the most well-studied scleractinian coral, distributed throughout the Indo-Pacific Ocean and occurring down to 70 m depth[37]. Brooding corals usually have a short planktonic larvae duration (PLD), since larvae are competent to settle upon release, a feature that can lead to reduced gene flow between intraspecific populations[38]. Thus, short dispersion and reduced gene flow could promote genetic subdivision through genetic drift and ecological adaptation to the local environment[39]. While several factors can influence dispersion and connectivity in the marine environment, high levels of population structure have been previously observed for brooding corals, indicating a strong influence of local recruitment, in contrast to high levels of gene flow frequently observed for broadcast spawning species (i.e., species that release gametes for external fertilization)[40–46]. Indeed, previous studies have shown that *S. pistillata* has an intricate population structure both among and within reefs along the Arabian coast, consistent with localized recruitment[47]. Recent studies also suggest that *S. pistillata* represents a species complex on the Great Barrier Reef[48].

For depth-generalist species such as *S. pistillata*, populations can be structured both geographically among sites and within sites, along their depth range[49–51]. Distinct patterns of species composition and genetic structure within a depth gradient have been recorded for fishes[52,53] and corals such as *Seriatopora hystrix*, *Montastraea cavernosa* and *Agaricia fragilis*[49,51]. This is particularly important for discussions regarding the potential of mesophotic coral ecosystems, defined as tropical reefs found at depths of ~30–150 m[54,55], to act as refuge zones for depth-generalist species (Deep Reef Refuge Hypothesis[49,56,57]) and potential sources of new colonizers for shallow reefs, as the combined effects of global warming and local stressor such as pollution and overfishing pose significant threats to shallow water reefs (see refs. 52,53 for discussion on the impacts in mesophotic ecosystems). However, genetic differentiation over depth seems to be common in scleractinian corals, challenging a broader refuge potential[52,57].

In this study, we utilize nextRAD sequencing to elucidate patterns of recruitment, genetic differentiation, and gene flow of *S. pistillata* at shallow and mesophotic depths in the Gulf of Aqaba, situated in the northern Red Sea. *S. pistillata* is considered a model species to study phenotypic plasticity in scleractinian corals, but surprisingly genetic assessments to investigate whether phenotypic differences have a genetic basis are lacking. The Gulf of Aqaba fosters a vibrant coral reef community that spans shallow regions (less than 30 m) to mesophotic zones (30–150 m), showcasing peak biodiversity at a depth of 30 m[58,59]. *S. pistillata* stands as one of the most abundant and well-studied reef-building species in the region. The locality naturally experiences high sea surface temperatures (SST) and elevated salinity levels[60], thereby presenting a unique environment with the resident coral species displaying an unusual high bleaching threshold[61]. Moreover, the area is exposed to a series of anthropogenic stressors such as eutrophication, and light pollution[62,63]. The biological rhythms of coral and cnidarians including their metabolic state, physiological processes, reproductive cycles, and behavioral activities are significantly regulated by the duration and intensity of exposure to light[35,64,65]. An incursion of light pollution has been linked to adverse effects such as reduced settlement success and impaired photosynthetic efficiency, as well as unsynchronized gamete release[62,66,67]. This underscores the pressing need for a detailed understanding of how environmental factors, notably the gradient of local pollutants along the coastline of Eilat[63], influence the life cycles of corals. Our research focused on determining the genetic structure and connectivity patterns of *S. pistillata* in the Gulf of Aqaba, emphasizing the critical role of our precise sampling regime. By studying populations that are exposed to varying levels of pollutants from north to south along this stretch, we aim to shed light connectivity pathways and recruitment, fostering a critical resource for future conservation strategies.

Results

Population structure

A total of 181 adults and 105 recruits were collected along a light pollution gradient and across a depth gradient in the Gulf of Aqaba (Fig. 1) and retained with a total of 38,835 SNPs after quality filtering. The tree-based model, ordination, and clustering approaches all revealed a complex genetic structure of *S. pistillata*, consisting of at least four major lineages, as shown by the neighbor-joining tree, and substantial sub-structure (Fig. 2, Dark Red, Red, Yellow, and Blue). Three genetic clusters (Dark Red, Red, and Yellow) were composed almost exclusively by shallow-water samples, except for three mesophotic samples from Katza and Natural Reserve (KAT45_AD_S09, within the Red cluster, and KAT45_AD_S06 and JAP45_AD_S23 within Yellow cluster), while the Blue genetic cluster was composed almost exclusively by mesophotic samples, except for three shallow-water specimens from Kissosky and Natural Reserve (KIS10_AD_S03, KIS10_SP_1, and NAT10_AD_S05) (Fig. 2). The PCA in Supplementary Fig. S1 also shows clustering according to depth. While all genetic clusters were comprised of individuals from more than one sampled site, a few patterns could be observed. Most samples from Kissosky ($n = 21$, or 70%), IUI ($n = 31$, or 77.5%), and Princess ($n = 25$, or 86.2%) were identified in the Red cluster, while most samples from Katza ($n = 27$, or 73%), Katza polluted ($n = 31$, or 77.5%) and Natural Reserve ($n = 30$, or 78.9%) were identified in the Yellow cluster. Under a K larger than three, the blue cluster is subdivided in three and four distinct clusters (Fig. 2, K = 6 and $K = 9$), with most samples from Katza ($n = 12$, or 66.7%) and Dakel ($n = 12$, or 70.6%) recovered within clusters Blue1 and Blue2, respectively. Within the Red and Yellow clusters, most samples from Kissosky and Natural Reserve form separate clusters under a larger K (Fig. 2, $K = 7$ and $K = 8$, Red2 and Yellow2).

When two lineages (with the largest number of samples) were investigated separately, a geographic pattern from north to south was identified using both PCA and STRUCTURE (Figs. 3 and 4). Kissosky and Natural Reserve were found to be clearly differentiated from the IUI and Princess group within the Red cluster and from Katza group within Yellow cluster (Figs. 3 and 4). No pattern of isolation-by-distance was observed (Supplementary Fig. S2). Nevertheless, since IBD analysis were performed within each lineage, the low number of samples might have reduced its statistical power. Although recruits generally seemed to cluster together with adults (indicating localized recruitment), in both lineages a proportion of recruits grouped separately indicating unsampled source populations (Figs. 3 and 4).

Recruitment pattern

The number of spats ranged from a mean of 16 spats/m^2 (mostly at Kissosky, all time points) to 652 spats/m^2 (at Katza, July 2018) (Fig. 5). Recruitment rate (as the number of spats) was significantly higher at Katza for most sampled months (except Sep and Nov 2017), while in Kissosky recruitment was significantly lower in three out of eight sampling months (Fig. 5A). At each site, no consistent recruitment pattern was found across time (Fig. 5B). The number of polyps per spat were more homogeneous among sites, although Katza had significantly larger numbers in July, September and November of 2018 (Supplementary Fig. 3, $p < 0.001$ for all comparisons). The ration between polyp and spats shows the average of the colony increase, with the lowest values found mainly in Kissosky (Supplementary Fig. 4).

Discussion

Stylophora pistillata is the poster child for ecological opportunism through phenotypic plasticity, however, here we show that this variation has a strong underlying genetic component by observing distinct (cryptic) lineages/species found to be associated with shallow/mesophotic depths. Furthermore, a strong genetic structuring within each of the lineages was found with much of it related to location, indicating distinct populations along the coast of Eilat (albeit with indications of occasional longer distance migration and some gene flow). Most of the recruits seem to have a local origin (i.e., they are closely related to the local adult population), suggesting that local dispersal

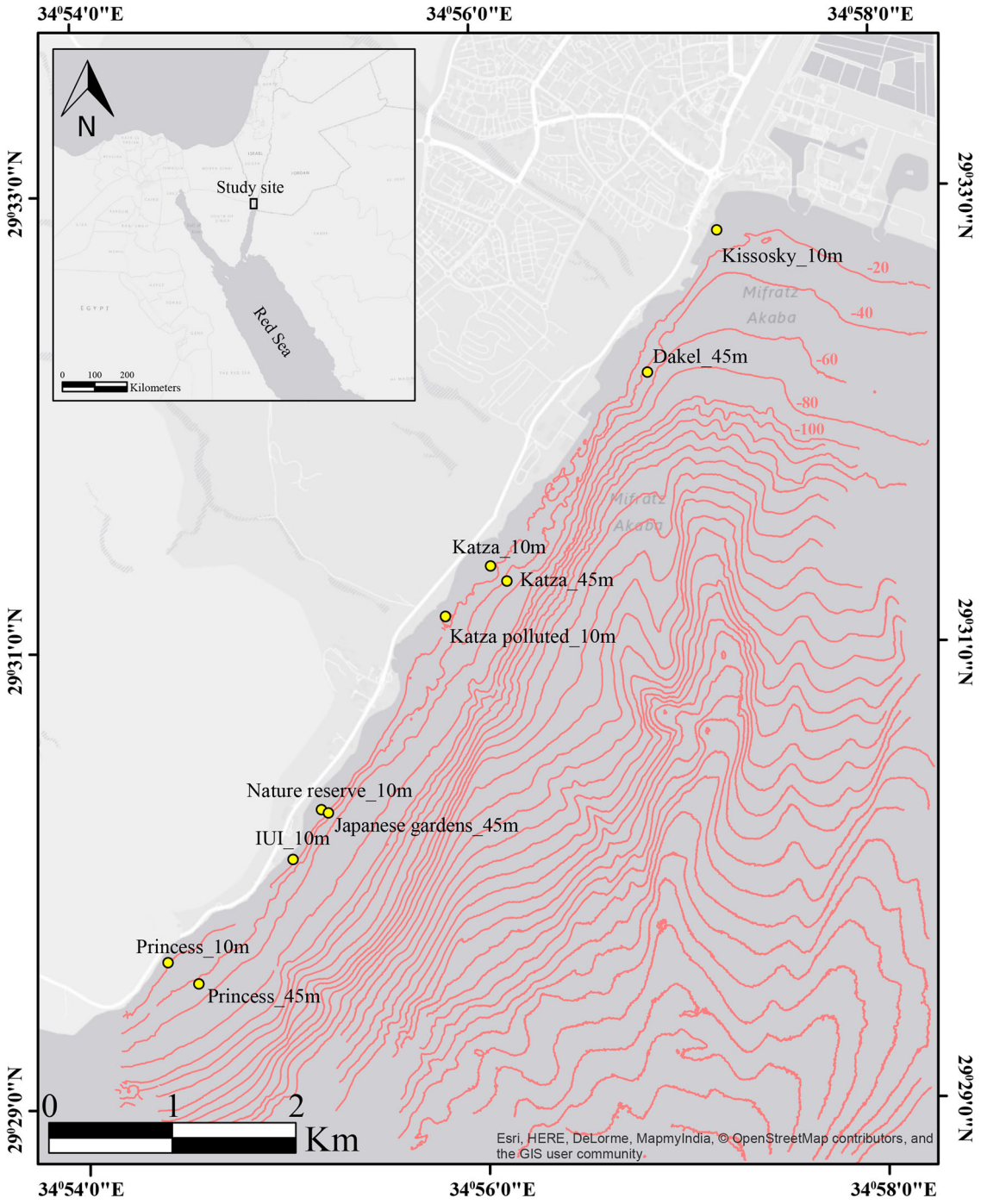

Fig. 1 | Sampling map. Sampling sites of adult fragments and juvenile spats *Stylophora pistillata* along the shoreline of Eilat, Red Sea. Sites are indicated by yellow dots, with name and depth of collection. Red line contours indicate isobaths of 20 m depth intervals. For further images, Japanese gardens_45m is referred as Natural reserve_45 (NAT45).

plays an important role in the observed structuring (although selection / local adaptation may still play an important additional role). The results provide valuable insights for the development of effective conservation strategies, highlighting the need to formulate targeted plans that incorporate diverse environments to safeguard the different genetic lineages.

With six recognized species, the Red Sea have been proposed as an important biodiversity center for *Stylophora*[9]. Based on morphological and molecular data, Stefani et al.[12] suggested that *S. danae*, *S. kuehlmanni*, and *S. subseriata* are ecomorphs of *S. pistillata*, and that the observed morphological variability is a result of differences in the environmental conditions, such as wave movement and light intensity. Similarly, Arrigoni et al.[13] found one single lineage for the Red Sea, indicating that *S. mamillata*, *S. wellsi*, and *S. pistillata* are either ecomorphs or early divergent lineages with a strong gene flow signal. Keshavmurthy et al.[10] identified four distinct lineages along the species' distribution of *S. pistillata*, with an estimated divergence of 51.5-29.6 million year ago, however identified only a single lineage in the Red Sea-Persian/Arabian Gulf-Kenya. Nevertheless, those studies were based on few traditional molecular markers, which have generally very low resolution to resolve intricate phylogenetic patterns[68]. Our findings reveal the presence of at least four cryptic lineages within *S. pistillata*, with no gene flow, shedding new light on the complex taxonomic issues and supporting the hypothesis of a species complex likely in the early stages of speciation for *Stylophora* in the

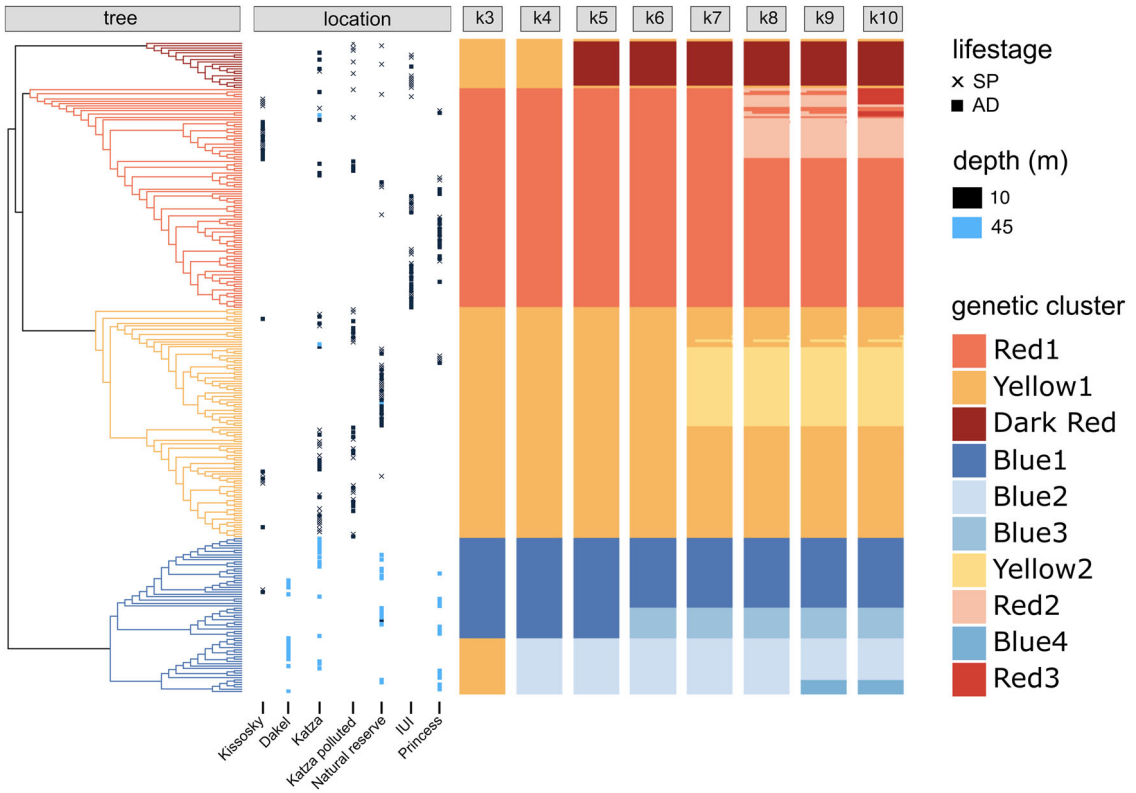

Fig. 2 | Overall genetic structure of *Stylophora pistillata*. Neighbor joining tree (based on 281 individuals and 38,836 SNPs) shows at least four major lineages and structure analysis (based on five replicate datasets with random SNPs separated by at least 2500 bp, each containing 281 individuals and 7185 SNPs) sowing *K* from three to 10. Colors indicate distinct genetic clusters, with each individual represented by a vertical bar with different colors indicating the relative proportion of each genetic cluster. Location shows original sites where samples were collected, with different colors and shapes indicating sampling depth and life stage, respectively.

Red Sea[13]. Similar results with distinct genetic lineages occurring in sympatry between 5- and 10-m depth were found by Buitrago-López et al.[47] along ~1500 km of the Saudi Arabian coast. Within the Great Barrier Reef, Mezieri et al.[48] found five distinct sympatric taxa at different stages of speciation, highlighting that the selection associated with the environment might have an important role on the evolution of *Stylophora*.

As currently recognized, *S. pistillata* displays high phenotypic plasticity[69], and notable morphological and physiological variations observed between specimens from shallow and mesophotic reefs. In light of the observed genetic structuring found in this study, these may represent specific adaptations that have evolved to thrive under distinct light conditions[70–72]. In the Gulf of Aqaba, the primary morphological disparities observed in *S. pistillata* between shallow and mesophotic reefs are calyx diameter, theca height, and corallite marginal spacing, all of which are closely linked to photosynthetic performance[70]. Furthermore, in scleractinian corals, adaptation to local environmental conditions can by influenced by the coral host genotype and their endosymbiotic community, as evidenced by previous observations of an association between the environment and the microbiome community within the Red Sea[47,73,74]. *S. pistillata* relies on a symbiotic relationship with dinoflagellate algae from the family Symbiodiniaceae[75] that supply the coral host with photosynthetic products. In addition to morphological disparities, shallow and mesophotic *S. pistillata* within the Gulf of Aqaba also differ in their symbiont composition (dominated by *S. microadriaticum* and *Cladocopium* sp. in shallow and deeper reefs, respectively[13,71]), photosynthetic traits[71,76,77], and green fluorescence protein (GFP) expression (higher on shallow colonies, where they act as photo-protection[78]). Consequently, an individual displaying specialized characteristics for deeper waters may struggle to survive in shallow water conditions and vice versa. Indeed Roberty et al.[71] observed strong photoinhibition when mesophotic colonies of *S. pistilata* were exposed to a high light regime. Here, we found at least one lineage almost exclusively on MCE, with no evidence of gene flow with shallow populations, corroborating previous observations of depth segregation within octocorals and scleractinian species (i.e., *Eunicea flexuosa* from the Caribbean[79], *Montastraea cavernosa*[80]; but see ref. 46), and indicating a genetic basis to previously observed morphological and physiological diferences in *S. pistillata*.

In addition to the depth segregation, results recovered three well supported lineages within shallow waters that occurred sympatrically (i.e., were not geographically partitioned). These results rekindle the taxonomic discussion regarding *Stylophora* and highlights the need of a thorough revision of the genus combining morphological, ecological and molecular data. Morphological similarities between putative species might be a result from recent speciation or morphological convergence/stasis, and have been highlighted as a confounding factor for coral taxonomy in several genera (e.g., *Pachyseris*[81]; *Acropora*[82]; *Stylophora*[11]).

Despite occurring on multiple reef sites, there appears to be a variation in the abundance of distinct lineages and a substructure within lineages. Most samples within the Yellow lineage are from sites geographically closer (Katza, Katza polluted [artificial light at night from the Eilat Oil Port Jetty] and Natural Reserve), but results recovered individuals from the Natural Reserve, and Princess as a separated cluster (Fig. 4). Curiously, there are signs of admixture only in one direction, in the cluster comprised by Kissosky, Katza, and Katza polluted. The Red lineage is mainly composed by samples from the northernmost (Kissosky) and the two southernmost sites (IUI and Princess). It is important to note that when a larger *K* is considered, Kissosky are nested within the Red lineage and separate as a subgroup under larger *K*. This pattern holds when the Red lineage was analyzed separately, with signs of admixture on the intermediary region. Among the sampled sites, Kissosky exhibits the highest levels of light pollution within the shallow sampling area (measured irradiance in the 589-nm wavelength channel of 4.6×10^{-4} μW cm^{-2} nm^{-1}; Tamir et al. 2017). Artificial light at night, also

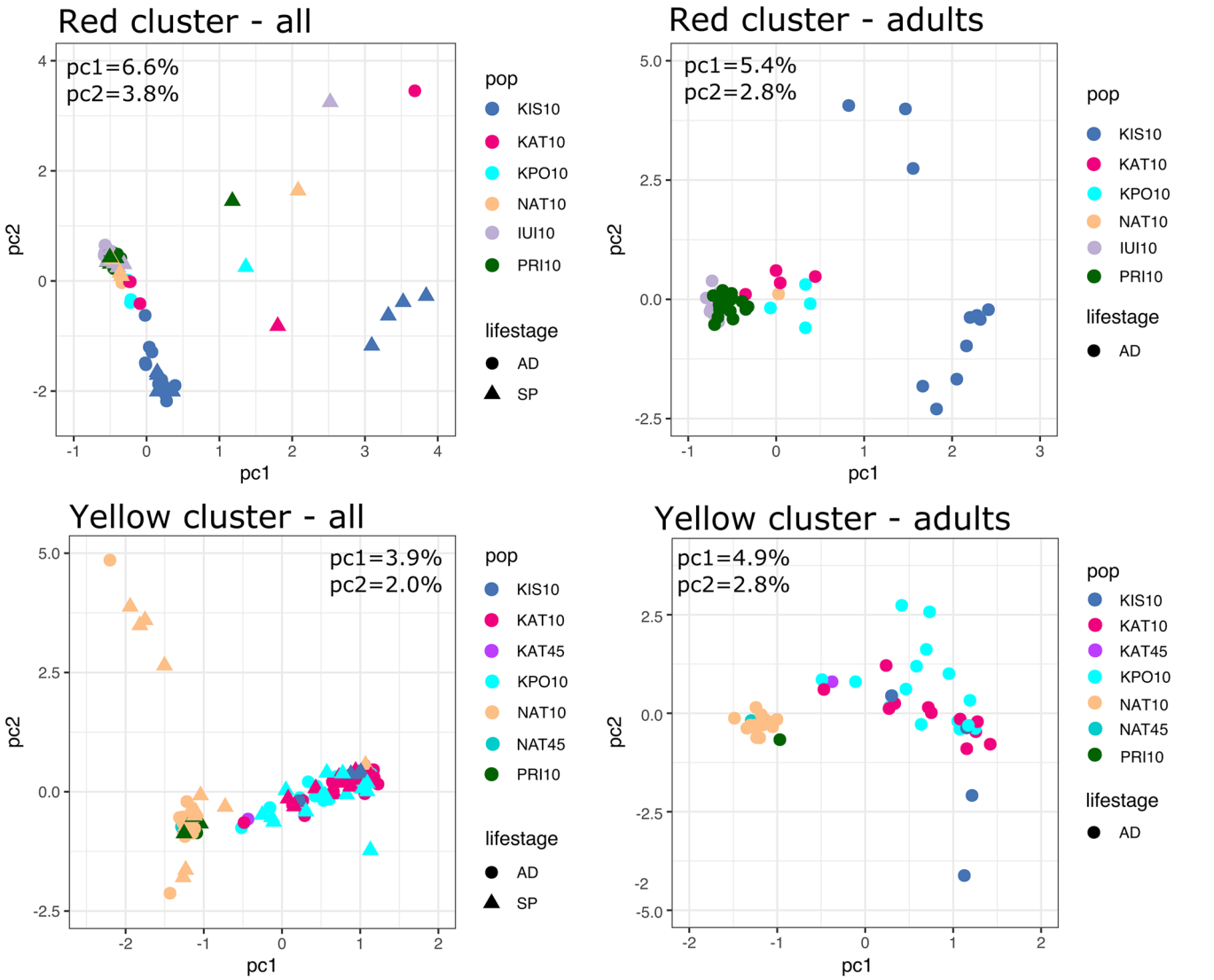

Fig. 3 | Principal component analysis for red and yellow clusters. Principal Component Analysis (PCA) based on 24,151 SNPs for the Red cluster and 29,617 SNPs for the Yellow cluster of all sampled individuals (left; 94 and 100 individuals for the Red and Yellow clusters, respectively) and only adults (right; 56 and 50 individuals for the Red and Yellow clusters, respectively) for the two major genetic lineages, Red and Yellow. Populations (pop) indicates site and depth of sampling. KIS Kissosky, KAT Katza, KPO Katza polluted, NAT Natural Reserve, IUI IUI, PRI Princess. Numbers 10 and 45 indicates samples collected from 7 to 10 and at 45 m depth, respectively. Life stage indicates adults (AD) and recruits (SP). Percentages of variance explained by the illustrated PCs are shown.

known as ecological light pollution (ELP), is currently considered one of the major global change issues[83]. However, it remains as one of the most understudied threats on coral reefs[84]. *S. pistillata* is a model species and it has been extensively used in stress response studies, including the impacts of light pollution (reviewed in Meziere et al.[85]). Here we observed the lower recruitment rate in Kissosky, corroborating previous findings that show a diminished settlement success for *S. pistillata* when exposed to light pollution[67]. Furthermore, light pollution is known to cause high oxidative stress and lead to lower photosynthetic efficiency for *S. pistillata* in the Gulf of Aqaba[67,86]. While further research is needed to investigate the putative substructure and its association to the stressful conditions, conservations strategies focusing on preserving the reefs on the northern portion of the Gulf of Aqaba are needed.

The observed tendency of local settlement among new recruits indicates that local recruitment plays a crucial role in the population dynamics of each genetic lineage or species within the Gulf of Aqaba, supplemented by occasional long-distance dispersal. Reproduction mode has been known to influence gene flow in scleractinian species, with broadcast spawners exhibiting higher connectivity. For example, *Montastraea cavernosa* and *Siderastrea siderea* spanning 1200 km in Brazil[42], *Acropora digitifera* within three atolls in northeast Australia[43], and *Pocillopora damicornis* in the Red Sea[47]. In contrast, high level of population structure and local recruitment are observed in brooding species such as, *Isopora brueggemanni* within three atolls in northeast Australia[43]. Furthermore, we assume that environmental stressors may influence coral settlement patterns in complex ways, potentially accelerating settlement even as they reduce survivorship. Here we found evidence of sub-structuring within the three main lineages (Red, Yellow and Blue) that could result from local recruitment since *Stylophora* is a brooding species and the majority of its larvae settle within the first 48 h[36]. Short dispersion and reduced gene flow could promote genetic subdivision through genetic drift and ecological adaptation to the local environment[39], which is hypothesized to be an important driver of *Stylophora* speciation[48]. Environmental features such as temperature, turbidity, currents and depth are known to influence corals physiology and morphology[57,87], and were identified as significant drivers of genetic differentiation among the distinct taxa recently discovered in the Great Barrier Reef[48].

Species are being lost before they are known by science at an unprecedent rate[7]. Within scleractinian corals, high phenotypic variation might

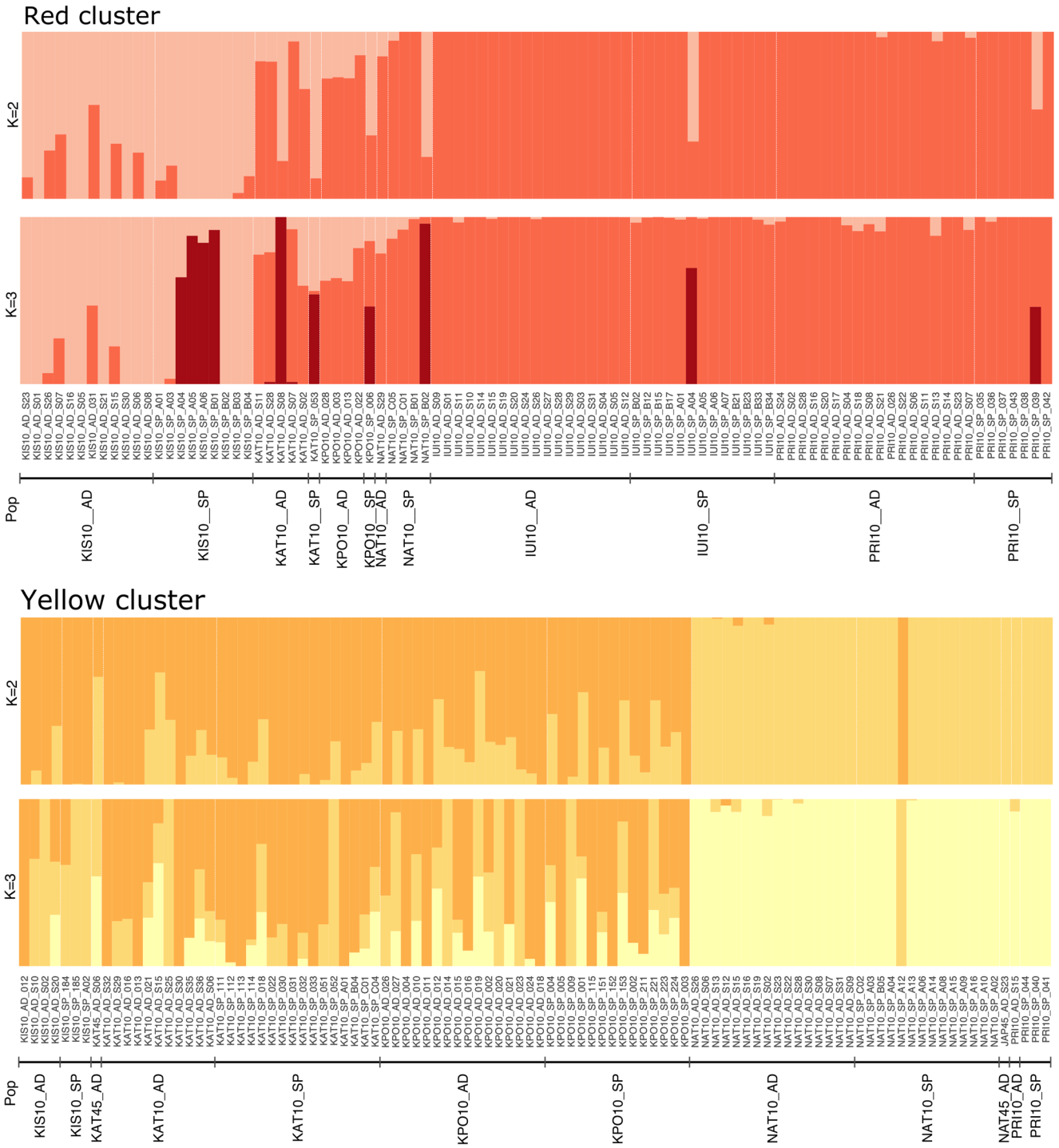

Fig. 4 | Genetic structure for Red and Yellow clusters. Genetic structure performed with the software ADMIXTURE of the Red (93 individuals and 24,151 SNPs) and Yellow (100 individuals and 29,617 SNPs) clusters for *K* equal two and three. Each individual is represented by a vertical bar with different colors indicating the relative proportion of each genetic cluster. Populations (pop) indicates site, depth of sampling and life stage. KIS Kissosky, KAT Katza, KPO Katza polluted, NAT Natural Reserve, IUI IUI, PRI Princess. Numbers 10 and at 45 indicates samples collected from 7 to 10 and 45 m depth, respectively. AD adults and SP recruits.

obscure interspecific diversity, and many new species have been uncovered since the advent of next-generation sequencing approaches. Here we found at least four distinct genetic lineages of *Stylophora pistillata* within the Gulf of Aqaba, suggesting that they represent a complex of species occurring in sympatry but with partitioning across depths. These findings corroborate that depth plays an important role on the genetic structure and speciation process of *Stylophora* and highlights the importance of recognizing this diversity in both research and management.

Methods

Sampling of adults and recruits

In March 2017, we deployed three sets of arrays, each consisting of 12 terracotta settlement tiles measuring 25 × 25 cm. These arrays were positioned at a depth of 7 m across six stations, resulting in a total of 36 tiles per site and 216 tiles in total. These stations were strategically located along the Eilat shoreline, spanning from the northern to the southern regions, and encompassing varying degrees of light pollution

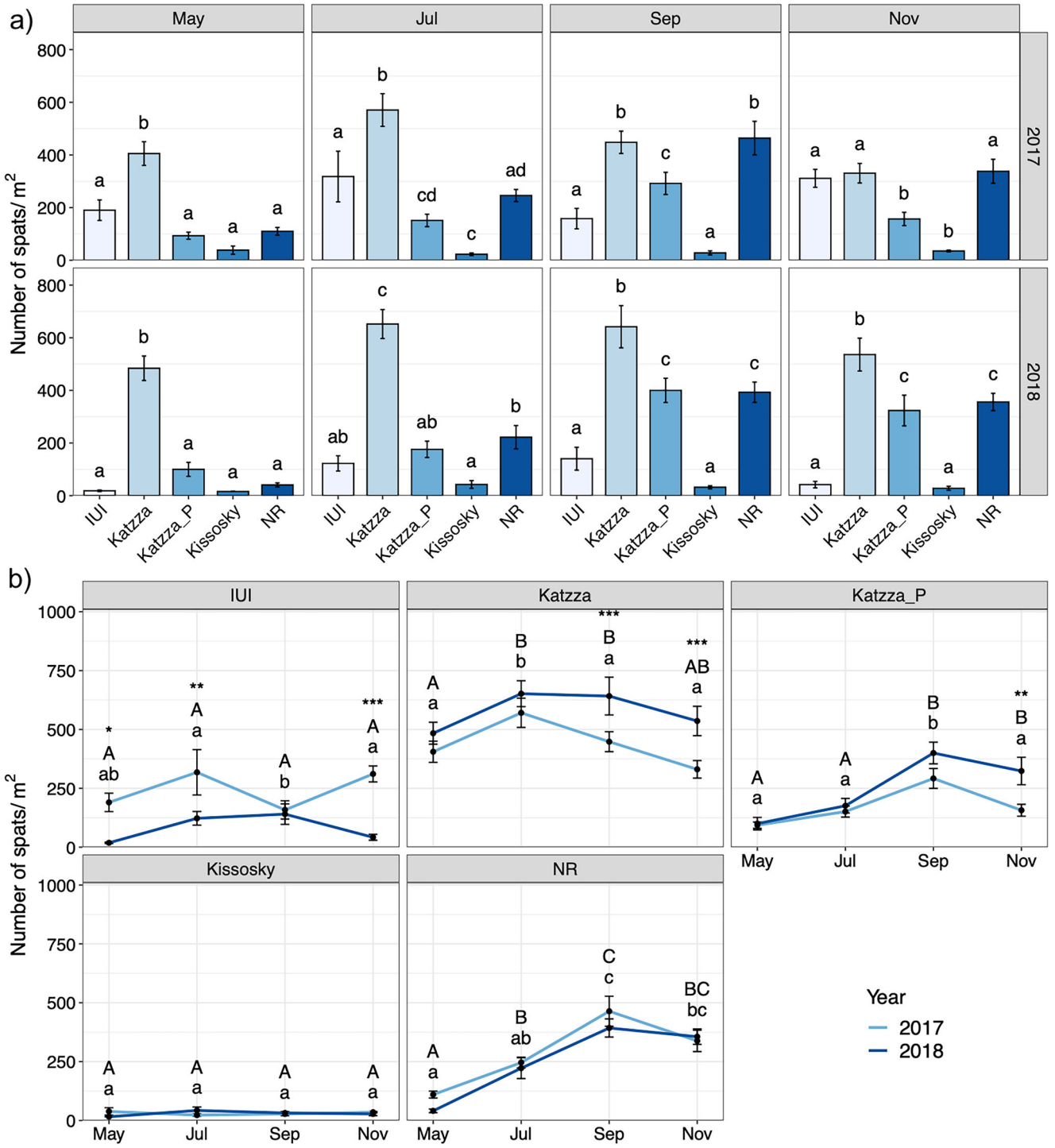

Fig. 5 | Spat count per m^2 at different locations and periods. Spat counts expressed as mean ± SEM Standard Error of the Mean) ($n = 4–12$) per location and sampling period. **a** Comparison between locations. Different lowercase letters indicate significantly different mean values between locations for each period ($p < 0.05$). **b** Comparison between periods. Different lowercase/ uppercase letters indicate significantly different mean values between months in 2017 and 2018 respectively ($p < 0.05$). Asterisks indicate significantly different mean values between measurements in 2017 and 2018 for each month (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Statistical significance was determined by a three-way ANOVA, followed by pairwise comparisons with FDR correction.

according to Tamir et al.[88] (Fig. 1). Starting in May 2017, we collected nine tiles from each station every two months, under permit number 2017/41,658 given by Israeli National Park Authority, NPA. The number of *Stylophora* recruitment spats (<2.5 cm) on each tile was counted using a binocular and some of these spats were carefully detached from the tiles and submerged in 100% ethanol for subsequent DNA analysis (Table 1).

Adult colonies were sampled under permit number 2017/41,658 by scuba diving from shallow (7–10 m depth) and mesophotic (45 m depth) reefs. A total of 181 fragments from adult colonies were sampled within a radius of approximately 20 m around the settlement tiles, for the shallow reef, and from nearby sites for the mesophotic reefs (Table 1). Fragments were stored in ziplock bags and later transferred to vials with 100% Ethanol for DNA analysis.

Table 1 | Number of adults and spats successfully sequenced at each location and depth

Location	Depth (m)	N. adults	N. spats
Kissosky	10	17	13
Dakel	45	17	0
Katza	10	19	18
	45	18	0
Katza polluted	10	20	20
Natural Reserve	10	18	20
	45	16	0
IUI	10	19	21
Princess	10	19	10
	45	16	0
Total		179	102

DNA extraction, library preparation and sequencing

DNA from adult coral fragments was extracted using a DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions with the addition of 6 µl of Rnase A. DNA concentration was determined by Qubit 2.0 fluorometer (Invitrogen). Since coral spats average size was 0.5–2.5 cm, DNA extraction using a commercial kit yielded very low or no DNA product. Therefore, a two steps process was conducted at the Forensic Biology Laboratory of Israel Police Head Quarters, Jerusalem. First, each spat was washed, rinsed twice using double-distilled water, and crushed using a mortar and pestle. Genomic DNA from each spat was then extracted at 56 °C for 2 h using a Chelex extraction[89], followed by a second extraction using the PrepFiler Express Forensic DNA Kit (Applied Biosystems, Foster City, CA, USA) according to the manufacturer's protocol[90] with the Auto-Mate Express DNA Extraction System.

Genomic DNA was converted into nextRAD genotyping-by-sequencing libraries (SNPsaurus, LLC) as in Russello et al.[91]. Genomic DNA was first fragmented with Nextera reagent (Illumina, Inc), which also ligates short adapter sequences to the ends of the fragments. The Nextera reaction was done at a 1/5 reaction, with 7 ng of genomic DNA used for input. Fragmented DNA was then amplified for 26 cycles at 73 degrees, with one of the primers matching the adapter and extending 9 nucleotides into the genomic DNA with the selective sequence GTGTAGAGG. Thus, only fragments starting with a sequence that can be hybridized by the selective sequence of the primer will be efficiently amplified. The nextRAD libraries were sequenced on Illumina HiSeq 4000 with one lane of 150 bp reads (University of Oregon) per plate of samples (95 samples per lane).

Population genetic analysis

Read trimming, quality filtering and mapping was conducted using BBMap tools (http://sourceforge.net/projects/bbmap/), with all reads mapped to the *Stylophora* reference genome[92] with an alignment identity threshold of 0.9. Genotype calling was done using callvariants (BBMap tools) (using the following settings: ploidy = 2 multisample = t rarity = 0.05 minallelefraction = 0.05 usebias = f ow = t nopassdot = f minedistmax = 5 minedist = 5 minavgmapq = 15 minreadmapq = 15 minstrandratio = 0.0 strandedcov = t), and the vcf was filtered to only retain genotypes with a minimum of 10X coverage, and SNPs for which less than 50% of samples were genotyped.

Pairwise genetic distance was calculated between all samples using vcf_gdmatrix script (in https://github.com/pimbongaerts/radseq), including two replicate pairs (99.0–99.8% similarity), which identified three potential clonal pairs for which one sample per pair was retained. Genetic structure was assessed using a neighbor-joining tree (following the gdmatrix2tree scripts script in https://github.com/pimbongaerts/radseq, with 281 individuals and 38,836 SNPs), principal components analysis (performed with the R package adegenet, with a reduced dataset of SNPs separated by at least 2500 bp containing 281 individuals and 7185 SNPs)[93,94], and the maximum-likelihood approach with snapclust[95]. For the latter, five replicate datasets were used with random SNPs separated by at least 2500 bp, using 50 iterations of the EM algorithm across the replicates, with a BIC optimum at 6 clusters (each containing 281 individuals and 7185 SNPs). Given the observed cryptic genetic structure, we then split the two largest clusters into separate datasets (94 and 101 individuals respectively), which were filtered for SNPs genotyped for at least 80% of samples and assessed for adults-only and both adults and recruits using Principal Component Analysis (PCA) from the R package adegene)[93,94]. A first analysis indicated the presence of outliers, which were then removed (KAT45_AD_S09 was removed from the Red Cluster and SP_KPO10_SP_007 was removed from the Yellow cluster), resulting in a dataset with 94 individuals and 24,151 SNPs for the Red cluster and 100 individuals and 29,617 SNPS for the Yellow cluster. Two PCAs were then performed, one with all individuals and a second one with adults only. The subset with adults only had 56 and 50 adult individuals for Red and Yellow clusters, respectively (individuals SP_KAT10_AD_S08 and SP_KI-S10_AD_S23 were outliers in the Red subset and not included in the PCA). Mantel's test for isolation-by-distance (IBD) was used for the same two largest clusters (Red and Yellow) with all individuals (also excluding the outliers) and only for the adults using the Nei's standard genetic distance (Nei[96]; 1978) with 999 replicates in the R package adegenet 2.1.10[93]. To check for intra-lineage structure for the two largest clusters, a maximum likelihood estimation of individual ancestries was performed in the software ADMIXTURE[97] ($K = 2$ to $K = 4$).

Statistical analysis

Three-way ANOVA analyses were performed to test the effect of site (IUI, Katza, Katza Polluted, Kissosky and Natural Reserve), year (2017–2018) and month (May, July, September and November) on the mean number of spats, polyps and the polyps per spat ratio. Specifically, multiple linear models were estimated. Post-hoc analysis was performed as pairwise comparisons defined by linear contrasts, and *p*-values were adjusted for multiple comparisons with the Benjamini–Hochberg (FDR) procedure.

Data availability

Recruitment data is provided as supplementary information files. Molecular data will be made available on request.

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Author contributions

I.A. and O.L. designed the research. I.A, N.S.B, A.Z, G.E and O.L collected the samples and performed the recruitment experiment. N.B.S, A.Z. J.R, and I.A performed the DNA extractions. K.C.C.C, I.A., P.B. and IC.J.B. performed the statistical and molecular analyses. K.C.C.C, I.A, D.A, G.E, O.L., P.B, and A.Z wrote the manuscript. All authors revised and contributed to the final version of the manuscript.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Additional information

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