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Coral spawning in the Gulf of Oman and relationship to latitudinal variation in spawning season in the northwest Indian Ocean

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Despite a wealth of information on sexual reproduction in scleractinian corals, there are regional gaps in reproductive records. In the Gulf of the Oman in the Arabian Sea, reproductive timing was assessed in four common species of broadcast spawning corals using field surveys of gamete maturity and aquarium observations of spawning activity. The appearance of mature gametes within the same month for *Acropora downingi*, *A. hemprichii*, *Cyphastrea microphthalma* and *Platygyra daedalea* ($\geq 75\%$ of colonies, $n = 848$) indicated a synchronous and multi-specific spawning season. Based on gamete disappearance and direct observations, spawning predominantly occurred during April in 2013 (75–100% of colonies) and May in 2014 (77–94% of colonies). The difference in spawning months between survey years was most likely explained by sea temperature and the timing of lunar cycles during late-stage gametogenesis. These reproductive records are consistent with a latitudinal gradient in peak broadcast spawning activity at reefs in the northwestern Indian Ocean which occurs early in the year at low latitudes (January to March) and progressively later in the year at mid (March to May) and high (June to September) latitudes.

Sexual reproduction in scleractinian corals can occur in a variety of forms but the majority of species ($>60\%$) are simultaneous hermaphrodites that spawn both eggs and sperm into the water column^{1,2}. Broadcast spawning allows cross-fertilization between individuals and development of planktonic larvae allows new coral genotypes to disperse across short and large distances^{3,4}. Recruitment of coral larvae is critical to the persistence and recovery of coral assemblages^{5,6} and enhances adaptive potential by increasing local genetic variation^{7–9}.

Broadcast spawning in most individual corals occurs during one or a few nights per year following an annual cycle of gametogenesis². Synchronous spawning within populations enhances their reproductive success and proposed environmental cues including sea temperature and lunar phase promote spawning during discrete seasons and nights¹⁰. Numerous studies of coral reproductive patterns demonstrate coral spawning around the warmest months of the year, yet the duration of spawning seasons and the extent of synchronicity among species and individuals can vary considerably among locations (see reviews by^{1,2,9,11}). Consequently, localised investigations are required to determine precise spawning months and nights in data deficient regions.

The aim of our study was to record spawning behaviour in corals from the Gulf of Oman, Arabian Sea, for which there were no previous records. We investigated the seasonal and lunar timing of spawning for 4 locally abundant scleractinian species using a combination of 2 years of field surveys and aquarium observations. Locally, these data provide important baseline information for monitoring the health of coral communities in the Gulf of Oman which are periodically impacted by damage from fishing gear and anchors¹², cyclones¹³, outbreaks of predatory crown-of-thorns starfish¹², oil pollution^{14,15} and harmful algal blooms¹⁶. More broadly, these data contribute to a growing number of records of coral spawning activity in the northwest Indian Ocean^{17–22} which allowed us to examine latitudinal patterns in spawning behaviour and their underlying environmental drivers.

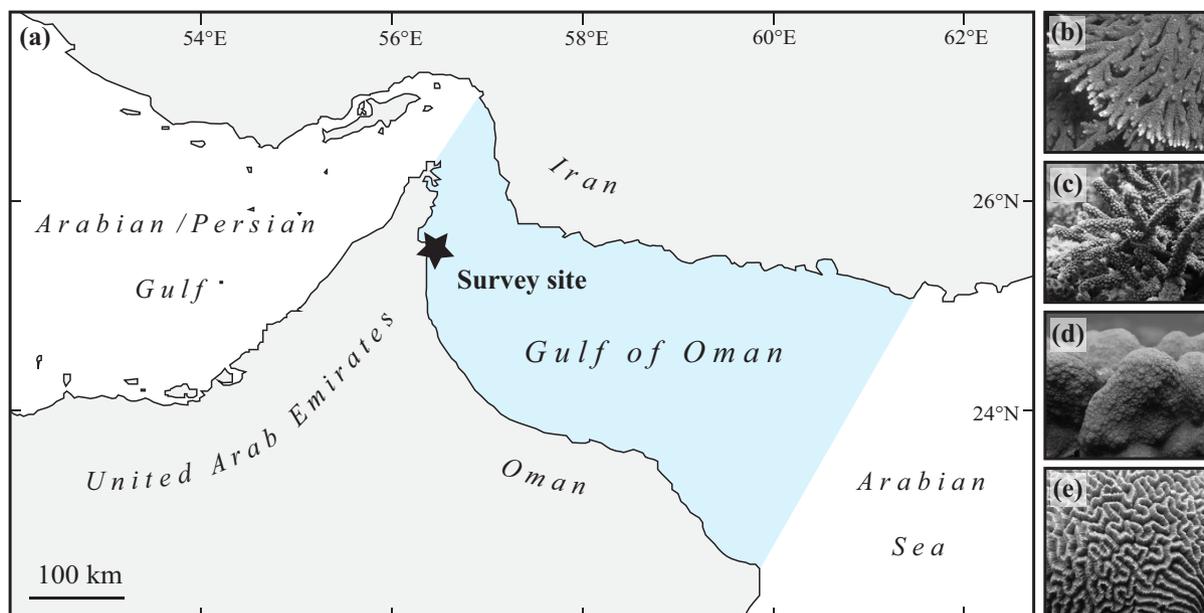


Figure 1 | Location of reproductive surveys in the Gulf of Oman (a) for the scleractinian corals *Acropora downingi* (b), *Acropora hemprichii* (c), *Cyphastrea microphthalma* (d), *Platygyra daedalea* (e). Map created by using Adobe Illustrator CS5.

Results

Sexual reproduction was seasonally synchronous in the scleractinian corals *Acropora downingi*, *A. hemprichii*, *Cyphastrea microphthalma* and *Platygyra daedalea* common to the Gulf of Oman²³ (Fig. 1). Mature gametes developed in $\geq 75\%$ of colonies of each species prior to one of the spring full-moons and disappeared by the following month, indicating that spawning had occurred (Fig. 2a). In 2013, the majority of colonies belonging to each species (75 to 100%) developed mature gametes by the April full moon (25th), whereas in 2014, gamete maturation did not occur in most colonies (77 to 94%) until prior to the May full moon (14th). This inter-annual variation in spawning timing corresponded with lower monthly average sea temperatures in the lead up to the 2014 spawning, including average sea temperature preceding the April full moon that were 1.5°C lower in 2014 compared with 2013 (Fig. 2b).

Additional field and aquarium observations of Gulf of Oman corals demonstrated variation in the lunar phase of spawning among the coral species being studied. The merulinids (formerly favids²⁴) *C. microphthalma* and *P. daedalea* spawned around the full moon, as indicated by the timing of disappearance of mature eggs between 4 days before and 12 days after the full moon in May 2014 (Table 1). The percentage of colonies with mature eggs declined from 88% ($n = 25$) to 23% ($n = 21$) in *C. microphthalma* and from 56% ($n = 41$) to 0% ($n = 42$) in *P. daedalea*. A small proportion (22%) of *P. daedalea* colonies had mature gamete bundles 7 days before the full moon in April. These colonies likely began spawning after the April full moon and may have still been releasing by the next survey 10 days after the full moon. Thus, the high proportion of colonies found with mature bundles 10 days after the April full moon may reflect colonies that were still spawning as well as those colonies with bundles mature enough to be released after the May full moon. This interpretation is supported by an extended spawning window observed in fragments from individual *P. daedalea* colonies ($n = 10$) kept in aquaria in April 2013. These colonies released gametes for up to 10 consecutive nights. Spawning occurred from 19:45 to 21:30 (1:00 to 2:45 hours after sunset) from 2 nights before the full moon to 9 nights after the full moon (when observations ceased), with a spawning peak 3 nights after full moon when all colony fragments released gametes.

In contrast, field surveys of the acroporids *A. downingi* and *A. hemprichii* indicated that the majority of colonies spawned later in

the lunar cycle or around the new moon. Between 10 nights after the April full moon and 4 nights before the May full moon in 2014, the percentage of colonies with mature gametes sharply declined from 81% ($n = 53$) to 5% ($n = 58$) in *A. downingi* and from 95% ($n = 41$) to 33% in *A. hemprichii*. This reproductive timing is supported by aquarium spawning of *A. downingi* ($n = 8$) which occurred in all colony fragments on 13 and/or 14 nights after the full moon (i.e. new moon) in April 2013.

Discussion

Patterns of sexual reproduction in corals from the Gulf of Oman demonstrate that coral communities in the northern Arabian Sea engage in seasonally synchronous spawning events, such as those that have been observed in numerous other tropical and temperate reef ecosystems (e.g. refs. 10, 25, 26). The April to May timing of spawning in acroporid and merulinid corals observed in the Gulf of Oman is consistent with spawning months of corals from these families at latitudes (22–27°N) from nearby regions of the Arabian/Persian Gulf¹⁷ and the Red Sea^{20,27}. At lower latitude (13°N) in the southern Arabian Sea, surveys of egg maturity indicate that at least half of the acroporid corals spawn in February and March²² which is consistent with the peak of spawning activity in acroporid and merulinid corals from equatorial reefs in the Indian Ocean^{18,19}. In contrast, at higher latitude (30°N), broadcast spawning in most coral species occurs from June to September (northern Red Sea²⁸). These results combined show a latitudinal gradient in seasonality of peak broadcast spawning activity in corals from the northwest Indian Ocean with spawning earlier in the year close to the equator and later in the year with increasing northward latitude ($r=0.75$, $p < 0.01$, Fig. 3).

Coral spawning during annual periods of sea temperature rise has been well documented²⁹. Latitudinal differences in spawning seasons in the northwest Indian Ocean are likely due to variation in temperature profiles and are consistent with latitudinal trends in coral reproduction in the northwest Pacific³⁰. For example, sites closer to the equator (<13°N; sites 10, 12–13 in Fig. 3) reach their annual maximum temperatures earlier in the year (March to May) compared with higher latitude sites (>22°N; sites 5–9 in Fig. 3) which reach their maximum later in the year (July to August). The delayed spawning peak at the highest latitude and coolest region of the Red

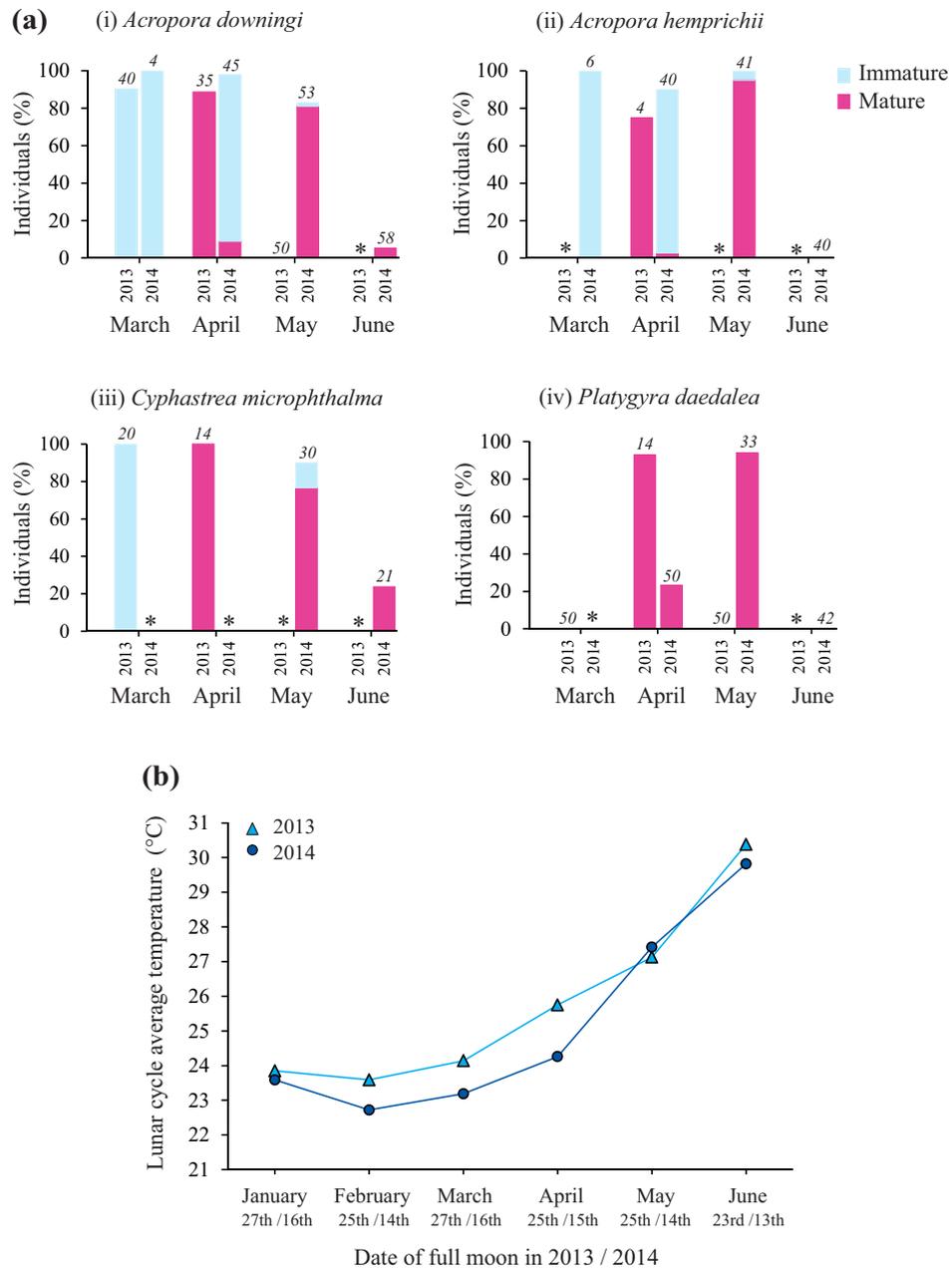


Figure 2 | Percentage of coral colonies in the Gulf of Oman with visibly immature and mature eggs (a) and sea temperatures (b) during 2013 and 2014. Coral species surveyed were *Acropora downingi* (i), *Acropora hemprichii* (ii), *Cyphastrea microphthalma* (iii), *Platygyra daedalea* (iv). Note that for (iv), immature eggs could not be distinguished from an absence of eggs. Sample sizes are provided in italicized text above columns and asterisks indicate months when no surveys were undertaken. Sea temperatures are the monthly average preceding each full moon during the coral spawning season in 2013 and 2014 in the Gulf of Oman. Monthly minimum and maximum values and annual trends are provided in the Electronic Supplementary Material.

Table 1 | Field (a) and aquarium (b) observations of the lunar phase of spawning in the Gulf of Oman. Sample sizes are provided in italicized text in parentheses

Coral species	(a) Colonies with mature gametes in the field on nights relative to full moon in 2014				(b) Aquarium spawning on nights relative to full moon in April 2013
	-7 April	+10 April	-4 May	+12 May	
<i>Acropora downingi</i>	9% (45)	81% (53)	5% (58)	-	+13 to +14 (10)
<i>Acropora hemprichii</i>	3% (40)	95% (41)	33% (42)	0% (40)	-
<i>Cyphastrea microphthalma</i>	-	77% (30)	88% (25)	23% (21)	-
<i>Platygyra daedalea</i>	22% (50)	94% (33)	56% (41)	0% (42)	-2 to +9 (peak +3) (8)

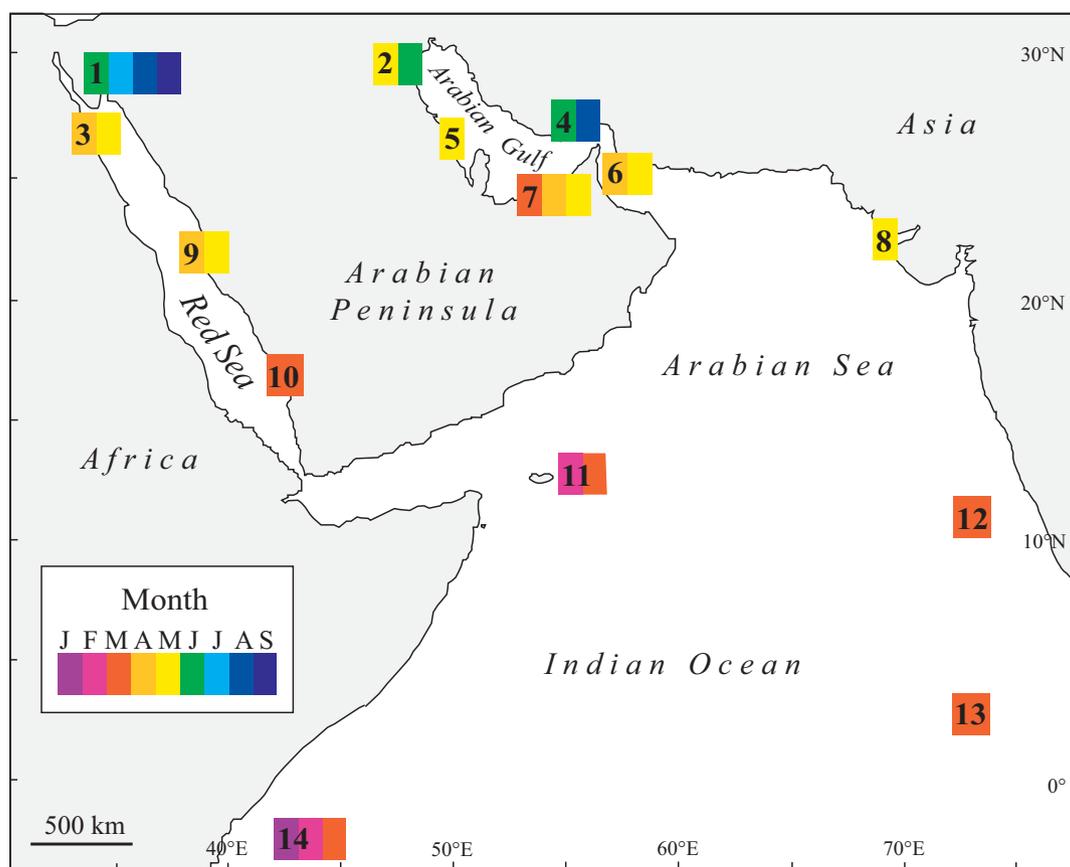


Figure 3 | Latitudinal trends in peak broadcast spawning activity in corals from the northwest Indian Ocean. Peak activity from January (J) to September (S) was classed as the month(s) when the majority of individuals and species were directly observed or inferred (from spawn slicks or assays of gamete maturity) to have spawned. 1: Eilat²⁸, 2: Kuwait⁴², 3: Hurghada²⁰, 4: Kish and Larak (pers. comm M. Shokri, M. Moradi), 5: Tarout³⁷, 6: Fujairah (this study), 7: Dubai¹⁷, 8: Gujarat⁴³, 9: Thuwal²¹, 10: Farasan⁴⁴, 11: Socotra²², 12: Lakshadweep (pers. comm S. Subburaman), 13: Maldives⁴⁵, 14: Mombassa^{18,19}. The correlation co-efficient between site latitude and spawning month, r , is 0.75 ($p < 0.01$). Map created by using Adobe Illustrator CS5.

Sea (sites 1–2, 4 in Fig 3) may reflect a lag in reaching temperatures that are optimal for reproduction (i.e. cross-fertilization and embryogenesis^{31,32}). In the Gulf of Oman, variation in the predominant spawning month between survey years is likely due to entrainment of spawning activity to the optimal temperature window¹. When the full moon falls early in the month^{29,33} and/or if the onset of seasonal warming is delayed, gamete maturation and spawning (in all or some corals in the population) is often delayed until the consecutive lunar cycle^{29,33,34}. Additionally, corals that have been moved to warmer or cooler environments during their gametogenic cycle often have accelerated or delayed spawning^{35,36} further supporting temperature as a strong driver of spawning month.

Species-specific variation in the lunar phase of spawning in the Gulf of Oman corresponded to the spawning nights previously reported for the investigated merulinid species but was relatively unusual for the acroporid species. Spawning of *Cyphastrea microphthalma* and *Platygyra daedalea* within 5 days of the full moon has been observed in the nearby Arabian Gulf¹⁷ as well as distant Indo-Pacific localities^{10,29}. However, the observation that individual *P. daedalea* colonies from the Gulf of Oman release gametes for up to 10 consecutive nights suggests an extended spawning period for this species compared to other localities (ref. 10, personal observations), although we cannot exclude the possibility that spawning behaviour was altered by aquarium conditions. Earlier records of spawning in *A. downingi* (Red Sea²¹, Arabian Gulf³⁷ (as *A. clathrata*, see ref. 38)) and *A. hemprichii* (Red Sea²¹) document gamete release within 4 nights of the full moon. This is in contrast to our observations of

A. downingi spawning around the new moon and *A. hemprichii* possibly also spawning at this time. Consequently, further observations are required to confirm the lunar phase of spawning in acroporids from the Gulf of Oman.

The data presented provide the first records of sexual reproduction in corals from the Gulf of Oman. Broadcast spawning in four common species of scleractinian corals occurs during the same month(s) of April to May but is spread across different phases of the lunar cycle. While the timing of coral spawning in the Gulf of Oman is seasonally consistent with regions of the Indian Ocean at similar latitude, further work is required to investigate the extent of reproductive synchrony among additional coral species and localities in the Gulf of Oman and the wider Arabian Sea.

Methods

Reproductive behaviour was surveyed in *A. downingi*, *A. hemprichii*, *Cyphastrea microphthalma* and *Platygyra daedalea* in the Gulf of Oman (Fig. 1). The survey area was located on shallow inshore reefs (< 6m depth) spanning a 15 km stretch of the coastline of Fujairah in the United Arab Emirates. Specifically, surveys were conducted at 25°36'11.84"N/56°21'2.70"E, 25°29'32.74"N/56°21'48.92"E and 25°28'56.61"N/56°21'56.14"E. To determine the lunar cycle(s) during which coral species were spawning, surveys were conducted in the week prior to each full moon from March to June in 2013 and 2014 during the transition between winter and summer as spawning typically occurs during a period of sea temperature rise or fall^{29,39}. Within the survey area, average sea temperatures across each lunar cycle were calculated from 30-minute readings from a temperature logger (HOBO® pendant, Onset®) attached to the reef substrate at Al Aqah reef.

A total of 848 colonies (>20 cm diameter) were haphazardly surveyed across the duration of the study and the sample sizes for each of four species and eight survey



months are provided in Fig. 2. Reproductive timing was inferred from the appearance and disappearance of mature eggs within the population following the methodology and categories of Baird et al.⁴⁰. Coral colonies with pigmented eggs were scored as reproductively mature and likely to spawn during the current or following lunar cycle. Corals with very pale or white eggs were scored as reproductively immature and likely to spawn during the following 1–2 lunar cycles. Corals with no visible eggs were either very immature and unlikely to spawn during the next 2 lunar cycles, had recently spawned, or did not reproduce during the survey year. In *A. downingi* and *A. hemprichii*, egg maturity was assessed by removing one branch from the center of each colony for *in situ* examination of gametes at the branch base well below their expected sterile zone⁴¹. In instances where no eggs were observed, two additional branches were sampled to confirm that the coral colony did not contain any visible eggs. In *C. microphthalma* and *P. daedalea*, egg pigmentation was assessed by removing 3 cm² sections of coral tissue from the center of each colony with a hammer and chisel. *C. microphthalma* samples were examined *ex situ* under a microscope and *P. daedalea* samples were examined *in situ* using a magnifying glass. In *P. daedalea*, we were unable to distinguish between immature eggs and the absence of eggs.

To identify the lunar phase (or nights) during which coral species were spawning, a combination of field and laboratory observations were undertaken. During the month when the proportion of pigmented eggs were highest in 2014, an additional field survey of gamete maturation was conducted in the week prior to the new moon to determine whether eggs were disappearing (i.e. being spawned) around the new or full phases of the moon. Additionally, fragments from 8 colonies of *A. downingi* and 10 colonies of *P. daedalea* containing pigmented eggs were collected one week before the April full moon in 2013 and observed nightly for spawning activity (gamete “setting” and/or release). Fragments were maintained in recirculating aquaria at New York University Abu Dhabi with daylight illumination and isolation in darkness at sunset each evening.

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Author contributions

E.J.H. designed the study. E.J.H., D.A. and G.O.V. collected data. E.J.H. wrote the manuscript with contribution from D.A. and J.A.B.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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