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The blue octocoral *Heliopora* sp. as a subordinate competitor for space on Indonesian coral reefs

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Abstract

Octocorals of the genus *Heliopora* are known to be abundant and to be capable of building large mono-specific stands on Indo-Pacific coral reefs. They have a calcium carbonate skeleton and although they are zooxanthellate, they have been observed to resist threats that have a negative impact on other reef-building corals, such as long periods of elevated seawater temperatures, and population outbreaks of predators, such as corallivorous *Acanthaster* crown-of-thorns sea stars. On the other hand, *Heliopora* corals can be harmed by aggressive competitors for space, but how they attack *Heliopora* is not well documented. Here, we illustrate examples from Indonesia in which *Heliopora* corals are overgrown and overtopped by corals of *Porites rus* and the genus *Montipora*. The nature of these interactions is discussed, and a hypothetical future scenario is presented in which *Heliopora* may become a more successful competitor and a more common reef coral species than it is today.

The octocoral genus *Heliopora* is widely distributed in the Indo-West Pacific, where it can easily be recognized because of its blue calcium carbonate coral skeleton (Taninaka *et al.* 2021; Veron 2000; Zann and Bolton 1985). For many years, only a single species was recognized, *Heliopora coerulea* (Pallas, 1766), but recently two species were added, all showing overlapping distribution ranges with their congeners (Richards *et al.* 2018, 2020; Zhang *et al.* 2026). Thus previous reports dealing with '*Heliopora coerulea*' may actually concern one of its look-alike species, which show slightly different morphologies and reproduction seasons (Villanueva 2016). It is unclear whether they react in different ways to environmental stressors. Therefore, when no accurate identification can be made in the field, it is necessary to categorize them as '*Heliopora*' or '*Heliopora* sp.', depending on whether it concerns the genus or a single unidentified species, respectively.

Heliopora corals are usually found at shallow depths on corals reefs, down to 30 m but most commonly above 10 m (Zann and Bolton 1985), where they have been reported to be locally common, abundant, or even dominant, such as in Taiwan (Benayahu *et al.* 2004), the Seychelles (Latypov 2009), Japan (Satoh *et al.* 2026), and the Philippines (Azcuna *et al.* 2025). In some areas, extensive, monospecific stands have been observed, such as at 8–12 m depth in the Chagos Archipelago (Sheppard 1979) and at 3–4 m depth in the Lakshadweep Archipelago (Sreenath *et al.* 2021), both located in the central Indian Ocean. In addition, several large aggregations were reported from southern Japan, West Pacific, at depths from 1 to 14 m (Reimer *et al.* 2024; Takino *et al.* 2010; Yasuda *et al.* 2012).

The abundance and dominance of *Heliopora* on shallow Indo-Pacific reefs can partly be explained by its resistance to stressors that may locally cause mass mortality (75–100%) in other reef coral species, allowing *Heliopora* corals to survive, grow, and reproduce where other species cannot. Moreover, the surrounding dead corals can serve as settling area for its larvae, which have the tendency to remain close, up to 350 m away from their parent colonies (Atrigenio *et al.* 2017; Harii and Kayanne 2003; Taninaka *et al.* 2019). For example, *Heliopora* has been shown to grow faster at higher temperatures and resists bleaching at temperatures where scleractinian corals do bleach (Guzman *et al.* 2019; Harii *et al.* 2014; Kayanne *et al.* 2002; Ryan *et al.* 2019). Another cause of severe mortality in reef corals is population outbreaks by corallivorous sea stars of the genus *Acanthaster* (Foo *et al.* 2024; Garing *et al.* 2026), which does not appear to affect *Heliopora* (Tkachenko *et al.* 2022).

There is, however, a threat against which *Heliopora* corals do not have much defence, which is aggressive behaviour by neighbouring benthic organisms when competing for space (Dai 1990; Sheppard 1979). Healthy coral reefs are able to grow when they show a high cover of reef-building invertebrates, such as scleractinian corals, whereas soft-bodied organisms, such as algae and sponges, do not contribute to the stony reef structure (Smith *et al.* 2016). Since space for benthic organisms is limited, both reef-building and non-reef-building species compete for suitable places where they can settle and expand (Chadwick and Morrow 2011; de Voogd *et al.*

2003; McCook *et al.* 2001). Some aggressive corals are able to harm neighbouring opponents by using long mesenterial filaments or sweeper tentacles that contain toxic chemical compounds (Lapid and Chadwick 2006; Roff *et al.* 2009). Foliaceous and branching corals are able to outcompete adjacent competitors by overgrowing or overtopping them (Álvarez-Noriega *et al.* 2018; García-Hernández *et al.* 2017), whereas massive corals are more likely to engage in direct confrontations in which they block each other's expansion and one of them causes tissue damage in its neighbour (Chadwick and Morrow 2011; Lang 1973). The difference between overgrowing (as epibiosis) and overtopping is that overgrowing corals have direct contact with the subordinate or even use it as substrate for attachment and that overtopping corals keep a distance but harm the subordinate by overshading it. It is also possible that competitors have direct contact without causing harm to each other or they may remain at a distance from each other, which are considered neutral interactions or stand-off situations (Aerts and van Soest 1997; Hoeksema *et al.* 2024; Monchanin *et al.* 2025).

In relation to competing coral species, *Heliopora* corals have been documented to be subordinate (Dai 1990), neutral (Sheppard 1979; Zann and Bolton 1985), but also aggressive, depending on the interacting species and environmental stressors, such as eutrophication, sedimentation, and storms (Atrigenio *et al.* 2020; Rodriguez *et al.* 2020). These variable outcomes demand for further in-depth studies on the interactions between *Heliopora* and its competitors for space, which can tell us more about its future prospects as a reef builder. Here, we report on some detailed observations from Indonesia, which may help to better understand *Heliopora*'s role in Indo-Pacific reef coral communities.

During a coral reef survey in May 2015 at Pulau Weh, an island off North Sumatra (western Indonesia), several colonies of branching *Heliopora* were encountered in varying stages of being overgrown or overtopped by two encrusting colonies of *Porites rus* (Forskål, 1775). This species can be common and even dominant in various reef habitats, where it can be recognized by its smooth coenosteum with tiny white polyps in between ridges on its surface (Veron 2000). Colonies are known to display a large variety in sizes and growth forms, either laminar and encrusting, submassive, or massive, possibly with branches or columns (Lenz and Edmunds 2017; Padilla-Gamiño *et al.* 2012; Veron 2000). Both specimens were found in slightly murky water (7–10 m depth) near residential areas and a ferry port at the west side of the island. Although the reef communities here had been exposed to a strong tsunami in 2004, this caused no visible changes in their species composition (Baird *et al.* 2005). In 2010, a major bleaching event occurred in Southeast Asia (Guest *et al.* 2012; Hoeksema *et al.* 2012; Yeemin *et al.* 2013). In Pulau Weh, this caused much mortality (>50%) among branching corals of the genera *Acropora* and *Pocillopora* (Guest *et al.* 2012), and, as a consequence, corals of the genera *Heliopora* and *Porites* became more dominant (Rudi *et al.* 2012; Utama and Budiyanto 2017; Utama and Hadi 2018).

Porites rus corals competing with *Heliopora* were growing in lateral directions, around and over the nearest upright *Heliopora* branches, which had their tips still free (Figure 1). *Heliopora* corals without nearest-neighbour contact were not affected. One *Porites* colony was partly overgrown and killed by crustose coralline algae (CCA), which halted its expansion towards a nearby *Heliopora* coral and prevented it from becoming harmful (Figure 1b). The *Heliopora* corals showed either rounded branches (Figure 1a, b) or flattened branches (Figure 1b), suggesting that they may belong to different species (Richards *et al.* 2018, 2020; Zhang *et al.* 2026). *Heliopora* corals were either overgrown and in direct contact with the aggressor (Figure 1a) or were overtopped with some distance between the two competitors (Figure 1b).

In addition to underwater observations on *Heliopora* interacting with neigbouring corals, collection material was studied in which blue octocorals served as substrate for scleractinians. Two *Montipora* skeletons from Southwest Sulawesi (Indonesia) in the coral collection of Naturalis (catalogue numbers RMNH.COEL.15627 and RMNH.COEL.23241) were sampled with their substrate consisting of *Heliopora* corals (Figure 2). Both specimens were from Kudingareng Keke, an uninhabited island in the Spermonde Archipelago; the first one was collected in 1979 and the second one in 1994. This island is known for its high coral diversity and located in relatively clear water, 13 km offshore from a major river outlet and from Makassar, the largest city in eastern Indonesia (Hoeksema 2012, Polónia *et al.* 2015). The first colony, a *Montipora hispida* (Dana, 1846), had nearly encapsulated its host by tightly overgrowing it, leaving no space in between them and using it as a substrate (Figure 2a), whereas the other one (*Montipora hoffmeisteri* Wells 1954) kept a distance of a few millimetres from its living substrate while it was becoming overtopped (Figure 2b). This distance suggests that *Heliopora*'s very thin layer of soft tissue (Bouillon and Houvenaghel-Crevecoeur 1970; Moseley 1876), and its dense cover of tiny polyps (Liu *et al.* 2005; Toh *et al.* 2016) offered resistance against its aggressor, preventing direct-contact overgrowth.

These observations show that even *Porites* corals, otherwise known to range from intermediate to subordinate aggressive (Dai 1990; Monchanin *et al.* 2025; Sheppard 1979), can overgrow or overtop *Heliopora*. In this case, the aggressor is *P. rus*, which in various localities appeared to be the most abundant species among its congeners (Dai 1990; Idjadi and Karlson 2007; Rinkevich and Sakai 2001). In the present study (Figure 1b), a large area of *P. rus* was overgrown by a thin layer of CCA representing the so-called 'inhibitor' functional type (Buenau *et al.* 2012), which may be able to cover large parts of coral colonies (Hill *et al.* 2021). The CCA appears to have stopped the *P. rus* coral from reaching a *Heliopora*, which remained free from contact (Figure 1b). *Montipora* corals, on the other hand, have a reputation of showing weak degrees of aggression in interactions with their opponents, such as neutral (Sheppard 1979) and moderately to subordinate (Dai 1990). Despite this, they were able to smother *Heliopora* corals (Figure 2).

The four cases of the present study are consistent with *Heliopora*'s rank as a subordinate competitor for space in direct interactions with *Montipora* and *Porites*. The interactions consisted of the aggressors either overgrowing or overtopping *Heliopora* corals, which look very similar and probably have the same effect on the subordinate. In all observed interactions *Heliopora* branch tips had remained free, potentially leading to a situation in which they become covered, smothered, killed, and hidden from sight. Some recent studies suggest that *Heliopora* could become more dominant on degraded coral reefs that were exposed to warming sea water and eutrophication, either by overgrowing other corals (Atrigenio *et al.* 2020) or by preventing juvenile settlement of competing species (Rodriguez *et al.* 2020). In contrast to many other reef corals, *Heliopora* is able to resist bleaching during elevated seawater temperatures (Kayanne *et al.* 2002; Ryan *et al.* 2019). Among its opponents, *Montipora* corals have been reported to show modest to high mortality during bleaching events (Depczynski *et al.* 2013; McClanahan 2004), in contrast to *P. rus*, which appears to be more bleaching resistant and heat tolerant (Lenihan *et al.* 2008; Lenz and Edmunds 2017). Moreover, similar to *Heliopora* on shallow fore reefs, *P. rus* is also able to build monospecific stands, but these appear to be limited to

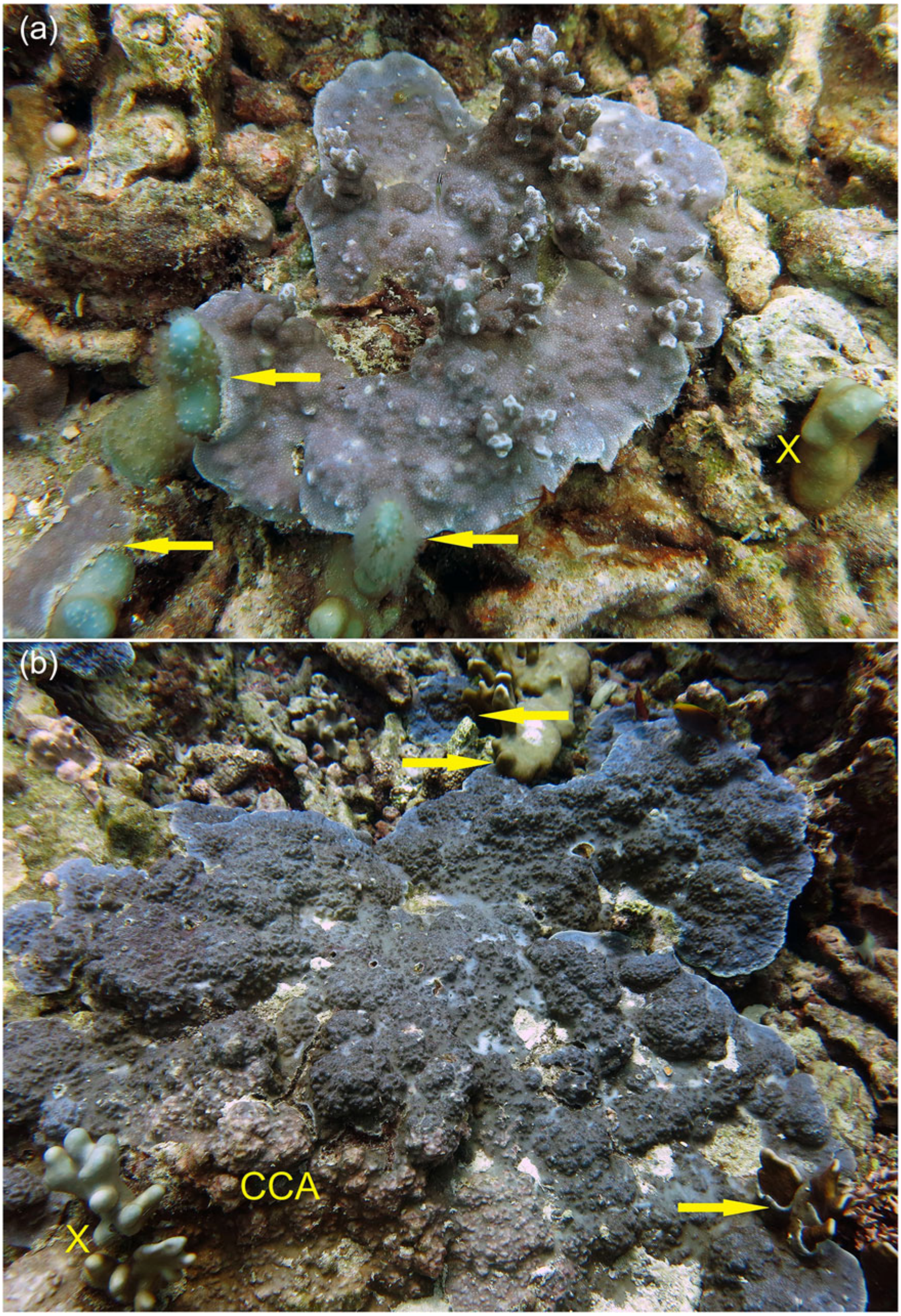

Figure 1. Competition for space between branching *Heliopora* colonies ($n = 4$) and encrusting *Porites rus* at Pulau Weh, Indonesia. Expanding *P. rus* colonies are in contact with *Heliopora* colonies and overgrowing or overtopping most of them (arrows). *Heliopora* not in contact with the aggressor are marked by an X. (a) Smallest colony of *P. rus* in interaction with three *Heliopora* corals with round branches. (b) Largest colony of *P. rus*, part of which is overgrown and smothered by pink crustose coralline algae (CCA), preventing further contact with *Heliopora* ($n = 4$). Three *Heliopora* corals show flat branches; the other one (X) shows round branches. The *P. rus* coral around the *Heliopora* with flat branches (right corner below) is overtopping Photo credit: Agus Budiyanto.

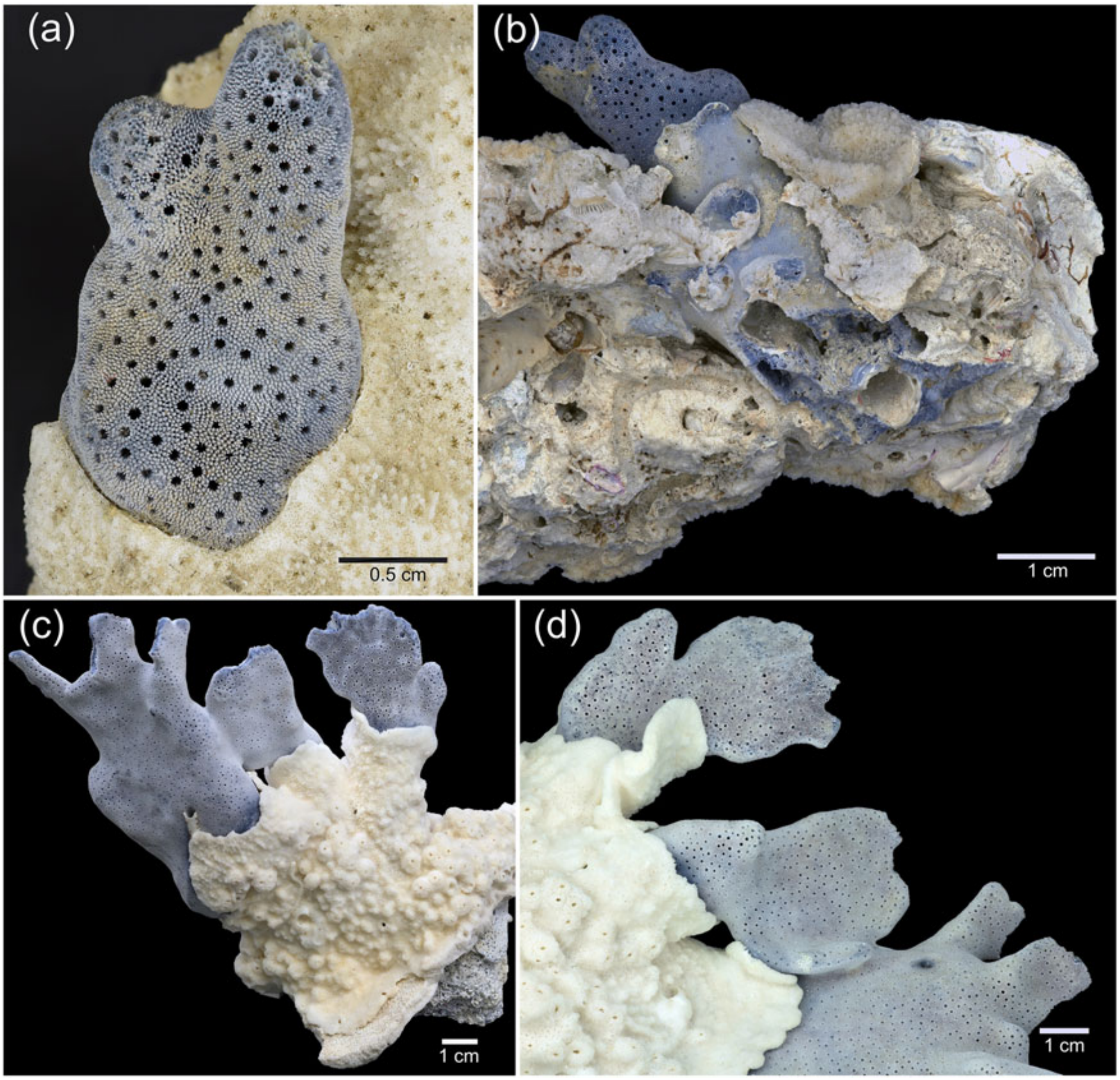

Figure 2. Coral skeletons of branching *Heliopora* sp. (blue colour) being overgrown by encrusting *Montipora* corals (white colour) off Southwest Sulawesi, Indonesia. Museum collection material: (a, b) Round branches of *Heliopora* sp. almost completely encapsulated by a *M. hispida* colony (RMNH.COEL.15627) collected in 1979 (leg. H. Moll), showing tight contact between the two corals; (c, d) Flat branches of *Heliopora* sp. with their base incorporated by a *M. hoffmeisteri* colony (RMNH.COEL.23241) collected in 1994 (leg. B.W. Hoeksema), keeping a few millimetres distance from its competitor. Photo credit: R.S.U.

sheltered lagoons (Brooks *et al.* 2007; Idjadi and Karlson 2007; Lenz and Edmunds 2017).

In future scenarios, many reef corals are expected to disappear because of warming seawater and other environmental stressors (Carpenter *et al.* 2008; Gutierrez *et al.* 2024), but *Heliopora* corals may become strong survivors (Atrigenio *et al.* 2020; Rodriguez *et al.* 2020). Among its competitors, the bleaching-resistant *P. rus* may also become more abundant and widespread. Hence, *Heliopora* and its opponent *P. rus*, both have the potential to become more important inhabitants of future coral reefs, increasing their chances to become engaged in battles for living space.

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References

Aerts LAM and van Soest RWM (1997) Quantification of sponge/coral interactions in a physically stressed reef community, NE Colombia. *Marine Ecology Progress Series* **148**, 125–134.

Álvarez-Noriega M, Baird AH, Dornelas M, Madin JS and Connolly SR (2018) Negligible effect of competition on coral colony growth. *Ecology* **99**, 1347–1356.

Atrigenio M, Aliño P and Conaco C (2017) Influence of the blue coral *Heliopora coerulea* on scleractinian coral larval recruitment. *Journal of Marine Biology* **2017**, 6015143.

Atrigenio MP, Conaco C, Guzman C, Yap HT and Aliño PM (2020) Distribution and abundance of *Heliopora coerulea* (Cnidaria: Coenothecalia) and notes on its aggressive behavior against scleractinian corals: Temperature mediated? *Regional Studies in Marine Science* **40**, 101502.

Azcuna MEM, Sanchez-Escalona K and Onda DF (2025) Reef assessments in the Verde Island Passage reveal *Heliopora* and *Galaxea* dominance in reefs with high coral cover. IOP Conference Series: Earth and Environmental Science 1496, 012003.

Baird AH, Campbell SJ, Anggoro AW, Ardiwijaya RL, Fadli N, Herdiana Y, Kartawijaya T, Mahyiddin D, Mukminin A, Pardede ST, Pratchett MS, Rudi E and Siregar AM (2005) Acehnese reefs in the wake of the Asian tsunami. *Current Biology* **15**, 1926–1930.

Benayahu Y, Jeng MS, Perkol-Finkel S and Dai CF (2004) Soft corals (Octocorallia: Alcyonacea) from southern Taiwan: II. Species diversity and distributional patterns. *Zoological Studies* **43**, 548–560.

Brooks AJ, Holbrook SJ and Schmitt RJ (2007) Patterns of microhabitat use by fishes in the patch-forming coral *Porites rus*. *Raffles Bulletin of Zoology* **14**, 245–254.

Bouillon J and Houvenaghel-Crevecoeur N (1970) Étude monographique du genre *Heliopora* de Blainville. *Annales Musée Royal de l Afrique Centrale (Series 8)* **178**, 1–83. pls. 1–12.

Buenau KE, Price NN and Nisbet RM (2012) Size dependence, facilitation, and microhabitats mediate space competition between coral and crustose coralline algae in a spatially explicit model. *Ecological Modelling* **237**, 23–33.

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzmán HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E and Wood E (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321**, 560–563.

Chadwick NE and Morrow KM (2011) *Competition among sessile organisms on coral reefs*. In Dubinsky Z and Stambler N (eds), *Coral Reefs: An Ecosystem in Transition*. Dordrecht: Springer, 347–371.

Dai CF (1990) Interspecific competition in Taiwanese corals with special reference to interactions between alcyonaceans and scleractinians. *Marine Ecology Progress Series* **60**, 291–297.

Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, Holmes TH, Moore JAY, Radford BT, Thomson DP, Tinkler P and Wilson SK (2013) Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. *Coral Reefs* **32**, 233–238.

de Voogd NJ, Becking LE, Hoeksema BW, Noor A and van Soest RWM (2003) Sponge interactions with spatial competitors in the Spermonde Archipelago. *Bollettino dei Musei e degli Istituti Biologici dell Universita di Genova* **68**, 253–261.

Foo SA, Millican HR and Byrne M (2024) Crown-of-thorns seastar (*Acanthaster* spp.) feeding ecology across species and regions. *Science of the Total Environment* **930**, 172691.

García-Hernández JE, van Moorsel GWNM and Hoeksema BW (2017) Lettuce corals overgrowing tube sponges at St. Eustatius, Dutch Caribbean. *Marine Biodiversity* **47**, 55–56.

Garing MR, McWilliam MJ, Tebbett SB, Levering LT and Pratchett MS (2026) Coral bleaching and crown-of-thorns starfish modulate long-term changes in coral cover and composition across reef zones at Lizard Island, northern Great Barrier Reef. *Coral Reefs* **45**, 649–663.

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA and Chou LM (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS One* **7**, e33353.

Gutierrez L, Polidoro B, Obura D, Cabada-Blanco F, Linardich C, Pettersson E, Pearce-Kelly P, Kemppinen K, Jose Alvarado J, Alvarez-Filip L, Banaszak A, Casado de Amezua P, Crabbe J, Croquer A, Feingold J, Goergen E, Goffredo S, Hoeksema B, Huang D, Kennedy E, Kersting D, Kitahara M, Kružić P, Miller M, Nunes F, Quimbayo JP, Rivera-Sosa A, Rodríguez-Martínez R, Santodomingo N, Sweet M, Vermeij M, Villamizar E, Aeby G, Alliji K, Bayley D, Couce E, Cowburn B, Nuñez Lendo CI, Porter S, Samimi-Namin K, Shlesinger T and Wilson B (2024) Half of Atlantic reef-building corals at elevated risk of extinction due to climate change and other threats. *PLoS One* **19**, e0309354.

Guzman C, Atrigenio M, Shinzato C, Aliño P and Conaco C (2019) Warm seawater temperature promotes substrate colonization by the blue coral, *Heliopora coerulea*. *PeerJ* **7**, e7785.

Harii S and Kayanne H (2003) Larval dispersal, recruitment, and adult distribution of the brooding stony octocoral *Heliopora coerulea* on Ishigaki Island, southwest Japan. *Coral Reefs* **22**, 188–196.

Harii S, Hongo C, Ishihara M, Ide Y and Kayanne H (2014) Impacts of multiple disturbances on coral communities at Ishigaki Island, Okinawa, Japan, during a 15 year survey. *Marine Ecology Progress Series* **509**, 171–180.

Hill CEL, Lymperaki MM and Hoeksema BW (2021) A centuries-old man-made reef in the Caribbean does not substitute natural reefs in terms of species assemblages and interspecific competition. *Marine Pollution Bulletin* **169**, 112576.

Hoeksema BW (2012) Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde Shelf, South Sulawesi. *Raffles Bulletin of Zoology* **60**, 183–212.

Hoeksema BW, Matthews JL and Yeemin T (2012) The 2010 coral bleaching event and its impact on the mushroom coral fauna of Koh Tao, western Gulf of Thailand. *Phuket Marine Biological Center Research Bulletin* **71**, 71–81.

Hoeksema BW, Samimi-Namin K and Vermeij MJA (2024) Neutral interactions among three nonindigenous coral species in a tropical marine fouling community. *Ecology* **105**, e4371.

Idjadi JA and Karlson RH (2007) Spatial arrangement of competitors influences coexistence of reef-building corals. *Ecology* **88**, 2449–2454.

Kayanne H, Harii S, Ide Y and Akimoto F (2002) Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. *Marine Ecology Progress Series* **239**, 93–103.

Lang J (1973) Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bulletin of Marine Science* **23**, 260–279.

Lapid ED and Chadwick NE (2006) Long-term effects of competition on coral growth and sweeper tentacle development. *Marine Ecology Progress Series* **313**, 115–123.

Latypov YY (2009) Species composition and distribution of scleractinians on the reefs of the Seychelles Islands. *Russian Journal of Marine Biology* **35**, 454–462.

Lenihan HS, Adjeroud M, Kotchen MJ, Hench JL and Nakamura T (2008) Reef structure regulates small-scale spatial variation in coral bleaching. *Marine Ecology Progress Series* **370**, 127–141.

Lenz EA and Edmunds PJ (2017) Branches and plates of the morphologically plastic coral *Porites rus* are insensitive to ocean acidification and warming. *Journal of Experimental Marine Biology and Ecology* **486**, 188–194.

Liu PJ, Fan TY and Dai CF (2005) Timing of larval release by the blue coral, *Heliopora coerulea*, in southern Taiwan. *Coral Reefs* **24**, 30.

McClanahan TR (2004) The relationship between bleaching and mortality of common corals. *Marine Biology* **144**, 1239–1245.

McCook L, Jompa J and Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* **19**, 400–417.

Monchanin C, de Jonge SK and Mehrotra R (2025) Differing competitive hierarchies between scleractinian corals on natural reefs and recruits on artificial reefs. *Marine Ecology* **46**, e70032.

Moseley HN (1876) On the structure and relations of the Alcyonarian *Heliopora coerulea*, with some account of the anatomy of a species of *Sarcophyton*; notes on the structure of species of the genera *Millepora*, *Pocillopora*, and *Stylaster*; and remarks on the affinities of certain Palaeozoic corals. *Proceedings of the Royal Society of London* **24**, 59–70.

Padilla-Gamiño JL, Hanson KM, Stat M and Gates RD (2012) Phenotypic plasticity of the coral *Porites rus*: Acclimatization responses to a turbid environment. *Journal of Experimental Marine Biology and Ecology* **434**, 71–80.

Polónia ARM, Cleary DFR, de Voogd NJ, Renema W, Hoeksema BW, Martins A and Gomes NCM (2015) Habitat and water quality variables as predictors of community composition in an Indonesian coral reef: A multi-taxon study in the Spermonde Archipelago. *Science of the Total Environment* **537**, 139–151.

Reimer JD, Mizukami I, Fourreau CJL, Abram A, Britta F, Sato T, Ueda K, Nakakouji H and Tamae M (2024) A large *Heliopora*-dominated reef off the east coast of Okinawajima Island, Japan. *Fauna Ryukyuana* **69**, 19–23.

Richards ZT, Yasuda N, Kikuchi T, Foster T, Mitsuyuki C, Stat M, Suyama Y and Wilson NG (2018) Integrated evidence reveals a new species in the ancient blue coral genus *Heliopora* (Octocorallia). *Scientific Reports* **8**, 15875.

Richards Z, Haines L, Scaps P and Ader D (2020) New records of *Heliopora hiberniana* from SE Asia and the Central Indian Ocean. *Diversity* **12**, 328.

Rinkevich B and Sakai K (2001) Interspecific interactions among species of the coral genus *Porites* from Okinawa, Japan. *Zoology* **104**, 91–97.

Rodriguez MVB, Segumalian CS, Lalas JAA and Maningas JMC (2020) Octocorals outcompete scleractinian corals in a degraded reef. *IOP Conference Series: Earth and Environmental Science* **420**, 012027.

Roff G, Dove SG and Dunn SR (2009) Mesenterial filaments make a clean sweep of substrates for coral growth. *Coral Reefs* **28**, 79.

Rudi E, Campbell SJ, Hoey AS, Fadli N, Linkie M and Baird AH (2012) The coral triangle initiative: What are we missing? A case study from Aceh. *Oryx* **46**, 482–485.

Ryan EJ, Hanmer K and Kench PS (2019) Massive corals maintain a positive carbonate budget of a Maldivian upper reef platform despite major bleaching event. *Scientific Reports* **9**, 6515.

Satoh N, Noda T, Hisata K, Yoshioka Y, Nagata T, Yamakawa E, Castelló GM and Reimer JD (2026) Inferring the distribution of octocorals *Nanipora* and *Heliopora* along the coast of the Kerama Islands, Okinawa, Japan, by eDNA metabarcoding. *Coral Reefs* **45**, 1421–1432.

Sheppard CRC (1979) Interspecific aggression between reef corals with reference to their distribution. *Marine Ecology Progress Series* **1**, 237–247.

Smith JE, Brainard R, Carter A, Grillo S, Edwards C, Harris J, Lewis L, Obura D, Rohwer F, Sala E, Vroom PS and Sandin S (2016) Re-evaluating the health of coral reef communities: Baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20151985.

Sreenath KR, Anto A, Raju AK, Jasmine S, Sreeram MP, Ranjith L and Joshi KK (2021) Extensive monospecific stand of Blue coral *Heliopora coerulea* (Pallas, 1766) in the Chetlat atoll of Lakshadweep Archipelago. *Indian Journal of Geo Marine Sciences* **50**, 759–761.

Takino T, Watanabe A, Motooka S, Nadaoka K, Yasuda N and Taira M (2010) Discovery of a large population of *Heliopora coerulea* at Akaishi Reef, Ishigaki Island, southwest Japan. *Galaxea, Journal of Coral Reef Studies* **12**, 85–86.

Taninaka H, Bernardo LPC, Saito Y, Nagai S, Ueno M, Kitano YF, Nakamura T and Yasuda N (2019) Limited fine-scale larval dispersal of the threatened brooding corals *Heliopora* spp. as evidenced by population genetics and numerical simulation. *Conservation Genetics* **20**, 1449–1463.

Taninaka H, Maggioni D, Seveso D, Huang D, Townsend A, Richards ZT, Tang SL, Wada N, Kikuchi T, Yuasa H, Kanai M, de Palmas S, Phongsuwan N and Yasuda N (2021) Phylogeography of blue corals (genus *Heliopora*) across the Indo-West Pacific. *Frontiers in Marine Science* **8**, 714662.

Tkachenko KS, Dung VV and Ha VT (2022) Phase shift from a stony-coral to a soft-coral community on a coral reef: A case study of an alternative state. *Marine Biology Research* **18**, 544–554.

Toh TC, Ng CSL, Toh BK, Afiq-Rosli L, Taira D, Loke HX and Chou LM (2016) Mass brooding of the blue octocoral, *Heliopora coerulea* on a sedimented equatorial reef. *Marine and Freshwater Behaviour and Physiology* **49**, 69–74.

Utama RS and Budiyanto A (2017) Kondisi dan keanekagaragaman karang batu di Perairan Sabang. *Oseanologi dan Limnologi di Indonesia* **2**, 69–82.

Utama RS and Hadi TA (2018) Recent coral reef conditions in Weh Island, Aceh Province, Indonesia. *Ocean Life* **2**, 47–53.

Veron JEN (2000) *Corals of the World*. Vols. **1–3**. Townsville: Australian Institute of Marine Science.

Villanueva RD (2016) Cryptic speciation in the stony octocoral *Heliopora coerulea*: Temporal reproductive isolation between two growth forms. *Marine Biodiversity* **46**, 503–507.

Yasuda N, Abe M, Takino T, Kimura M, Lian C, Nagai S, Nakano Y and Nadaoka K (2012) Large-scale mono-clonal structure in the north peripheral population of blue coral, *Heliopora coerulea*. *Marine Genomics* **7**, 33–35.

Yeemin T, Pengsakun S, Yucharoen M, Klinthong W, Sangmanee K and Sutthacheep M (2013) Long-term decline in *Acropora* species at Kut Island, Thailand, in relation to coral bleaching events. *Marine Biodiversity* **43**, 23–29.

Zann L and Bolton L (1985) The distribution, abundance and ecology of the blue coral *Heliopora coerulea* (Pallas) in the Pacific. *Coral Reefs* **4**, 125–134.

Zhang J, Hu Y, Yang L, Zhang Z, Wei S, Yu W, Luo H, Wei F and Zhou W (2026) Integrative phylogenetic and morphological approach for species delimitation of *Heliopora* corals, with the description of *H. chinensis* sp. nov. (Octocorallia: Helioporidae). *Journal of Systematics and Evolution* **64**. https://doi.org/10.1111/jse.70062