RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RE-NEW OPINION ARTICLE

Beneath the surface: the overlooked subtidal reef-building oysters of the east coast of Australia

Marina A. Richardson[1,2], John Healy[3,4], Nikolina Nenadic[1], Adam Boyle[1], Rod M. Connolly[1], Carmel McDougall[1,5]

Molecular and morphological evidence has reshaped our understanding of oyster diversity, distributions and phylogeny, revealing widespread misidentifications and undescribed species. On Australia's east coast the Sydney rock oyster, *Saccostrea glomerata*, traditionally thought to be reef-building both intertidally and subtidally, is likely a predominantly intertidal species. Examination of museum specimens and historical literature indicates that subtidal *S. glomerata* identifications are likely incorrect and instead represent multiple species, all with reef-building capacity. Broadly, clarifying species identities and distributions by tidal zone and depth will be an essential first step for guiding subtidal oyster reef restoration in tropical and subtropical areas. Given this re-interpretation, the threatened status of *S. glomerata* reefs should be re-assessed to reflect their true, predominantly intertidal distribution.

Key words: *Magallana dactylena*, oyster reef restoration, oyster taxonomy, *Saccostrea subtrigona*, subtidal oyster reef

Implications for Practice

- *Saccostrea glomerata* is likely an intertidal species which may explain why subtidal restoration attempts have been unsuccessful.
- Subtidal reef-building oysters historically identified as *S. glomerata* likely belonged to multiple different species.

Introduction

Once a common marine ecosystem worldwide, oyster reefs have now collapsed in many regions (Beck et al. 2011). There is an urgent need for their restoration, but efforts in many tropical and subtropical systems remain constrained by limited understanding of reef-building species and their ecology (Richardson et al. 2022). In these warmer regions molecular tools are essential for species identification, which has subsequently changed our understanding of oyster diversity, distributions and phylogeny, driving major taxonomic revisions (Salvi & Mariottini 2016; Sekino & Yamashita 2016). For example, *Saccostrea cuccullata*, once thought to occur across Australia and the Indo-Pacific, is now recognized as a species known only from Ascension Island in the Atlantic Ocean (Tan et al. 2025). While molecular work has begun to clarify the taxonomy of many intertidal species, the identity of subtidal oysters remains far less understood.

On the southeast coast of Australia, the Sydney rock oyster (*Saccostrea glomerata*) is the predominant reef-building species, and has previously been reported across tropical Australia (Ogburn et al. 2007). However, molecular work has shown that these past tropical identifications actually represent multiple species of *Saccostrea*, none of which are *S. glomerata* (Lam & Morton 2006; Snow et al. 2023; McDougall et al. 2024). Historical records also describe *S. glomerata* as occurring both intertidally and subtidally to depths of 10 m (Saville-Kent 1891), but modern observations reporting subtidal occurrences have been restricted to very shallow depths. For example, *S. glomerata* spat recruited subtidally in the Noosa River estuary at 0.7 m; however, recruitment was low, mortality was high, and no subtidal adults were observed in the system (Richardson et al. 2025b). Similarly, presumed *S. glomerata* spat recruited subtidally at 0.6 m in Pumicestone Passage, however, mortality was high and recruitment was hindered by sedimentation (Diggles 2017). Although *S. glomerata* may recruit to shallow subtidal depths, recruitment alone is not a reliable indication of species distributions as no naturally-occurring adult *Saccostrea* have been definitively identified subtidally. Following decades of intense overharvesting, the absence of subtidal *S. glomerata* reefs in the present day continues to be attributed to sedimentation, mudworm, and QX disease (Ogburn et al. 2007;

Author contributions: MAR, JH, RMC, CM conceptualized the study; MAR, NN, AB undertook all field work; MAR wrote the initial draft; all authors helped interpret results, edited the manuscript, and approved the submitted version.

[1]Coastal and Marine Research Centre, Australian Rivers Institute, School of Environment and Science, Griffith University, Brisbane 4111, Queensland, Australia
[2]Address correspondence to M. A. Richardson, email marina.richardson@griffith.edu.au
[3]Biodiversity and Geosciences Program, Queensland Museum, South Brisbane, Queensland 4101, Australia
[4]Negaunee Integrative Research Center, Field Museum of Natural History, Chicago 60605, IL, USA
[5]Scottish Oceans Institute, School of Biology, University of St Andrews, St Andrews KY16 8LB, UK

doi: 10.1111/rec.70382

Diggles 2013). However, the persistence of widespread intertidal *S. glomerata* reefs (see https://www.arcgis.com/apps/mapviewer/index.html?webmap=e81158f553324b12a3487dae4a4f6f22), suggests that environmental conditions no longer support subtidal reef formation across the entire range of the species (Diggles 2013; Gillies et al. 2015). Extrapolating results from recruitment studies conducted in highly modified seascapes in <1 m depths to support unconfirmed historical claims that *S. glomerata* formed reefs at 10 m depths is problematic. While environmental degradation is nevertheless a key problem for conservation and management regardless of the species, we present evidence which suggests that historical drift/dredge oysters may have been misidentified as *S. glomerata*.

The Overlooked Subtidal Reef-Builders

On Australia's east coast, intertidal ("bank") and subtidal ("drift" or "dredge") oysters were historically described as morphologically distinct, even when considered to be conspecifics (Tenison-Woods 1882; Cox 1883; Saville-Kent 1891). Given that species within the same genus are challenging to distinguish and require molecular tools for identification (McDougall et al. 2024; Richardson et al. 2024), it is unlikely that morphologically distinct subtidal morphs are *S. glomerata*. Indeed, early ecologists initially shared this notion. In 1871, *Ostrea subtrigona* (from "Australia") was described from two disparate syntype specimens, one elongate shell (now missing from collections) and one triangular-shaped specimen (paired valves) (Sowerby 1871). This species name was subsequently applied to the drift/dredge oyster of Moreton Bay and New South Wales, a subtidal reef-building species that occurred in moderately deep water below the zones of both *S. glomerata* and *Ostrea angasi* and was considered one of Australia's most important commercial oysters (Tenison-Woods 1882; Cox 1883).

While morphology alone is insufficient for definitive species identifications, certain characteristics can be useful for distinguishing different genera. For example, *Saccostrea* are generally characterized by thick, irregular shells with strongly denticulated lateral margins known as chomata, a feature typical of this genus that is often found around most of the shell margins, though its expression can be variable and may, in rare cases, be reduced or absent in some individual shells (Sekino & Yamashita 2016; McDougall et al. 2024; Richardson et al. 2025a). Chomata are present in both *O. subtrigona* syntype specimens; however, the extent of the chomata differs markedly between them, being poorly developed and restricted to the hinge area of the upper valve only in the paired specimen (Fig. 1A), but present for half the length of the elongate valve (missing specimen) (Fig. 1B). It is therefore possible that Sowerby's specimens represent two different species. *Ostrea subtrigona* has since been reassigned to *Saccostrea* and currently is recognized as a valid species (*Saccostrea subtrigona*—adopted herein; Huber 2010). However, we note that if the surviving syntype is eventually designated as the lectotype of the species, then its poorly developed chomata likely indicate a position outside of the genus *Saccostrea* (all of which have very well developed chomata).

In the late 1800s it was proposed that *S. subtrigona* and *S. glomerata* (both previously included in the genus *Ostrea*) were the same species, and morphological differences were attributed to whether the oyster grew in intertidal or subtidal environments (Tenison-Woods 1882; Saville-Kent 1891). Some early ecologists vehemently disagreed, and Cox (1883) maintained that these species were different and criticized translocation efforts, stating that, "Our rock oyster has been placed in a similar position to the natural beds of *Ostrea subtrigona* but always with disappointment; when our rock oysters are placed in such a position they will not thrive and fatten, and in fact will not live very long, but will live longer than if the drift oyster is placed in the natural position of the rock oyster". Nevertheless, the interpretation that "bank," "dredge," and "drift" oysters represented a single species gained broad acceptance (Tenison-Woods 1882; Saville-Kent 1891).

Examination of Saville-Kent's (1891) illustrations of intertidal and subtidal *S. glomerata* shells indicates two different species. The subtidal morph was described as "a form very prevalent from deep water or dredge sections, and in which the prolongation and smoothness of the component shells are more conspicuously pronounced than in the typical dredge or drift variety associated in the foregoing diagnosis with the title of '*Ostrea subtrigona*.'" This suggests a second subtidal species in addition to *S. subtrigona*, but Saville-Kent (1891) presumed that this species was also synonymous with *S. glomerata*, proposing that, "the mollusc would grow upwards towards the light, much after the manner of a light starved plant." However, this growth form is atypical of *Saccostrea*, which normally grows broadly attached by the lower valve against a hard substrate (McDougall et al. 2020). Iredale 1939 reported similar specimens on Lindeman Island in north Queensland, but considered them morphologically distinct enough to warrant naming (as "*Saxostrea commercialis dactylena* ecomorph nov") (Fig. 1E). The accepted name for this species is now *Magallana dactylena*, but without molecular data and comparative morphological analyses of live specimens its phylogenetic placement is uncertain. Notably, chomata are absent in the genus *Magallana* (Salvi & Mariottini 2021). Chomata were not noted in Iredale's 1939 descriptions and are absent on all *M. dactylena* specimens observed by us in the Queensland Museum, confirming that this species is taxonomically distinct from the genus *Saccostrea*. However, chomata are present on one subtidal morph at the hinge of the shell depicted in one of Saville Kent's sketches (Fig. 1C). This inconsistency suggests an additional subtidal species which may have been reef-forming, however, there is not enough evidence to taxonomically place this species as several oyster genera display chomata (Salvi et al. 2022). *M. dactylena* also exhibits reef-building capacity through gregarious settlement, as shown in Saville-Kent's (1891) illustrations (Fig. 1D) and Queensland Museum specimens dredged from the mouth of the Brisbane River (1929–1939) (Fig. 1F). Recent collections of (dead) shells and gregarious clusters from tropical Queensland (Fig. 1H–J) support current consensus that *M. dactylena* has a broad distribution along the Queensland

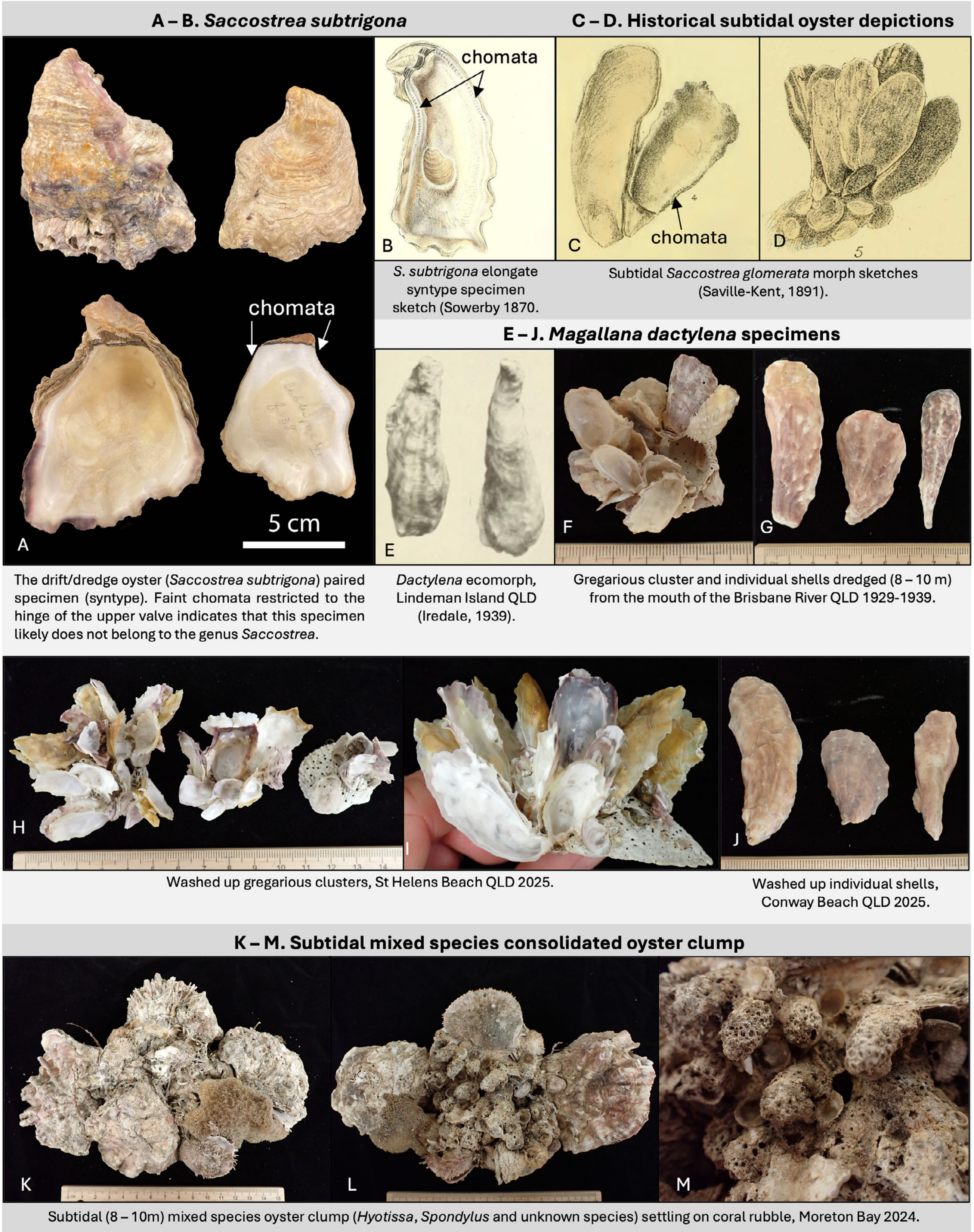

Figure 1. Illustrations and photographs of subtidal reef-building oysters in Queensland, Australia. British Natural History Museum accession number: (A and B) NHMUK_1874.12.11.259; Queensland Museum accession numbers: (F and G) QMMO 79053; (H and I) QMMO 86467; and (J) QMMO 86469.

coast, but has not been recorded in New South Wales (Beechey 2025).

Historical accounts described subtidal reefs as being comprised of mixed oyster assemblages. These assemblages were said to include *M. dactylena* morphs, *S. subtrigona* morphs and an oyster similar to intertidal *S. glomerata* in appearance (Saville-Kent 1891). However, Saville-Kent 1891 noted a considerable size difference between similar looking subtidal and intertidal morphs, stating that subtidally, "the tendency to develop an abnormally massive shell is especially noteworthy, instances occasionally occurring in which the lower valve weighs as much as half a pound." Given this considerable size difference, it is likely that these large oysters represent additional species yet to be documented as reef-building. In 2024, an aggregated clump of large oysters which closely resembles Saville-Kent's descriptions was collected subtidally (8–10 m) in Moreton Bay (Fig. 1K–M). Some of these oysters appear to belong to the genera *Hyotissa* and *Spondylus* while others are unknown; however, they do not appear to belong to the genus *Saccostrea*.

Limited knowledge of subtidal oyster species combined with severe population declines hinders assessment of key ecological traits such as reef-building potential, distribution, and preferred settlement substrates in tropical and subtropical regions. For example, while rock is a common substrate for intertidal oysters, *S. subtrigona* has been observed occurring in beds of unattached individuals, attached to one another by adhesion of the lower valve, or attached within masses of drift material (Tenison-Woods 1882). The mixed species oyster clump collected subtidally from Moreton Bay is attached to coral rubble, while all gregarious clusters of *M. dactylena* specimens are attached to Arcidae shells. These observations suggest that settlement preferences may differ for intertidal versus subtidal species; however, they could also reflect collection bias, as shells attached to consolidated substrates may be less easily washed ashore. Regardless, the disappearance of subtidal reefs may be due to both a collapse in larval supply and substrate availability as well as a decline in environmental conditions, as both live oysters and the substrates they settled on were historically targeted by dredging (Kirby 2004; Ogburn et al. 2007; Diggles 2013). This emerging evidence gives reason to challenge previously held assumptions about the ecology and identity of subtidal reef-building oysters on Australia's east coast.

Future Directions

Improving taxonomic resolution and understanding which species are reef-building will be critical for the conservation of tropical and subtropical subtidal oyster reefs. This requires increased sampling efforts and integrated genetic and morphological analyses, especially for lesser-known rock oysters within genera known to occur subtidally, such as *Ostrea*, *Nanostrea*, *Dendostrea*, *Booneostrea*, *Planostrea*, and *Hyotissa* (Lamprell & Healy 1998; Lam & Morton 2003; Chen et al. 2025). This will help to describe new species and resolve taxonomic ambiguities for taxa with broad geographic ranges where duplicate names exist. Assessing reef-building capacity is more complicated, however, as subtidal reefs may have collapsed and extant species may only exist in fragmented populations (Gillies et al. 2020). "Reef-building" may therefore need to be inferred from experimental recruitment traits and observations of gregarious settlement. Addressing these taxonomic and ecological gaps is essential for developing effective restoration strategies, as methods used in temperate subtidal systems may not suit tropical and subtropical species-specific requirements. Finally, if *S. glomerata* is indeed a predominantly intertidal species capable of naturally recruiting only in very shallow depths, its conservation status warrants reassessment.

Acknowledgments

This research was funded by the National Environmental Science Program, Marine and Coastal Hub. The authors declare no conflicts of interest.

LITERATURE CITED

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, et al. (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61:107–116. https://doi.org/10.1525/bio.2011.61.2.5

Beechey D (2025) The seashells of New South Wales. https://seashellsofnsw.org.au

Chen Y, Li C, Chen M, Wang H, Ma P (2025) Diversity and distribution of oysters from Weizhou Island, China. Journal of Oceanology and Limnology 1–22. https://doi.org/10.1007/s00343-025-5052-x

Cox JC (1883) On the edible oysters found on the Australian and neighbouring coasts. Proceedings of the Linnean Society of New South Wales 7:122–134

Diggles BK (2013) Historical epidemiology indicates water quality decline drives loss of oyster (*Saccostrea glomerata*) reefs in Moreton Bay, Australia. New Zealand Journal of Marine and Freshwater Research 47:561–581. https://doi.org/10.1080/00288330.2013.781511

Diggles BK (2017) Annual pattern of settlement of Sydney rock oyster (*Saccostrea glomerata*) spat in Pumicestone Passage, Moreton Bay. Proceedings of the Royal Society of Queensland 122:17–33. https://doi.org/10.5962/p.357815

Gillies CL, Castine SA, Alleway HK, Crawford C, Fitzsimons JA, Hancock B, Koch P, McAfee D, McLeod IM, Zu Ermgassen PSE (2020) Conservation status of the oyster reef ecosystem of southern and eastern Australia. Global Ecology and Conservation 22:e00988. https://doi.org/10.1016/j.gecco.2020.e00988

Gillies CL, Creighton C, McLeod IM (2015) Shellfish reef habitats: a synopsis to underpin the repair and conservation of Australia's environmentally, socially and economically important bays and estuaries. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Publication, James Cook University, Townsville, Australia

Huber M (2010) Compendium of bivalves: a full-color guide to 3,300 of the world's marine bivalves: a status on bivalvia after 250 years of research. ConchBooks, Hackenheim, Germany

Iredale T (1939) Mollusca. Part I. Scientific reports of the great barrier reef expedition 1928–29. British Museum (Natural History), London. https://doi.org/10.1038/143703a0

Kirby MX (2004) Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. Proceedings of the National Academy of Sciences 101:13096–13099. https://doi.org/10.1073/pnas.0405150101

Lam K, Morton B (2003) Hong Kong's subtidal oysters (Bivalvia: Ostreidae and Gryphaeidae). Pages 311. In: Perspectives on marine environmental change in Hong Kong and Southern China, 1977–2001. Hong Kong University Press, Hong Kong

Lam K, Morton B (2006) Morphological and mitochondrial-DNA analysis of the Indo-West Pacific rock oysters (Ostreidae: *Saccostrea* species). Journal of Molluscan Studies 72:235–245. https://doi.org/10.1093/mollus/eyl002

Lamprell K, Healy J (1998) Bivalves of Australia. Vol 2. Backhuys Publishers, Leiden, The Netherlands

McDougall C, Nenadic N, Healy J (2020) Guide to Queensland's intertidal oyster. Griffith University, Brisbane, Australia

McDougall C, Nenadic N, Richardson M, Healy JM (2024) Molecular identification of intertidal rock oyster species in north-eastern Australia reveals new candidates for aquaculture. Aquaculture 587:740838. https://doi.org/10.1016/j.aquaculture.2024.740838

Ogburn DM, White I, McPhee DP (2007) The disappearance of oyster reefs from eastern Australian estuaries—impact of colonial settlement or mudworm invasion? Coastal Management 35:271–287. https://doi.org/10.1080/08920750601169618

Richardson MA, Nenadic N, Wingfield M, McDougall C (2024) The development of multiplex PCR assays for the rapid identification of multiple *Saccostrea* species, and their practical applications in restoration and aquaculture. BMC Ecology and Evolution 24:67. https://doi.org/10.1186/s12862-024-02250-1

Richardson MA, Zhang Y, Connolly RM, Gillies CL, McDougall C (2022) Some like it hot: the ecology, ecosystem benefits and restoration potential of oyster reefs in tropical waters. Frontiers in Marine Science 9:1–15. https://doi.org/10.3389/fmars.2022.873768

Richardson MA, Buelow C, Connolly RM, Gillies CL, Nenadic N, Porter R, Traurig M, McDougall C (2025a) Characterising tropical oyster reefs: invertebrate-environment associations and a newly documented reef building species. Marine Environmental Research 208:107136. https://doi.org/10.1016/j.marenvres.2025.107136

Richardson MA, Connolly RM, Gillies CL, McDougall C (2025b) Settlement and tidal zonation patterns of closely related oysters within the genus Saccostrea in a subtropical Australian estuary—implications for restoration. Restoration Ecology 33:1–12. https://doi.org/10.1111/rec.70052

Salvi D, Al-Kandari M, Oliver PG, Berrilli E, Garzia M (2022) Cryptic marine diversity in the Northern Arabian Gulf: an integrative approach uncovers a new species of oyster (Bivalvia: Ostreidae), *Ostrea oleomargarita*. Journal of Zoological Systematics and Evolutionary Research 2022:1–19. https://doi.org/10.1155/2022/7058975

Salvi D, Mariottini P (2016) Molecular taxonomy in 2D: a novel ITS2 rRNA sequence-structure approach guides the description of the oysters' subfamily Saccostreinae and the genus *Magallana* (Bivalvia: Ostreidae). Zoological Journal of the Linnean Society 179:263–276. https://doi.org/10.1111/zoj.12455

Salvi D, Mariottini P (2021) Revision shock in Pacific oysters taxonomy: the genus *Magallana* (formerly *Crassostrea* in part) is well-founded and necessary. Zoological Journal of the Linnean Society 192:43–58. https://doi.org/10.1093/zoolinnean/zlaa112

Saville-Kent W (1891) Oysters and oyster fisheries of Queensland. Department of Fisheries, Brisbane, Australia

Sekino M, Yamashita H (2016) Mitochondrial and nuclear DNA analyses of *Saccostrea* oysters in Japan highlight the confused taxonomy of the genus. Journal of Molluscan Studies 82:492–506. https://doi.org/10.1093/mollus/eyw022

Snow M, Fotedar S, Wilson NG, Kirkendale LA (2023) Clarifying the natural distribution of *Saccostrea* (edible rock oyster) species in Western Australia to guide development of a fledgling aquaculture industry. Aquaculture 566: 739202. https://doi.org/10.1016/j.aquaculture.2022.739202

Sowerby BGI (1871) Monograph of the genus *Ostraea*. In: Conchologia iconica, or, illustrations of the shells of molluscous animals. Vol 18. L. Reeve, London, United Kingdom

Tan SK, Wells FE, Tan KS, Lukehurst SS, Morgan M, Fotedar S (2025) Identity of the enigmatic oyster *Saccostrea cucullata* (Bivalvia: Ostreidae). Journal of Molluscan Studies 91:eyaf007. https://doi.org/10.1093/mollus/eyaf007

Tenison-Woods JE (1882) Fish and fisheries of New South Wales. T. Richards, Sydney, Australia

Coordinating Editor: Stephen Murphy

Received: 11 November, 2025; First decision: 30 December, 2025; Revised: 9 February, 2026; Accepted: 6 March, 2026