Cole *et al. BMC Ecology and Evolution* (2024) 24:114
https://doi.org/10.1186/s12862-024-02296-1

BMC Ecology and Evolution

RESEARCH **Open Access**

Determining the best practice for Sydney rock oyster, *Saccostrea glomerata*, reef restoration and enhanced ecological benefits

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Abstract

Background Shellfish reef restoration is relatively new in Australia, particularly to intertidal estuarine environments. In late 2019/early 2020 the first large-scale shellfish reef restoration project of the Sydney rock oyster, *Saccostrea glomerata* was undertaken in the Myall and Karuah Rivers, Port Stephens, on the mid north coast of New South Wales (NSW), Australia. The present study aimed to determine whether locally sourced clean conspecific oyster shells, and/or locally quarried rocks were better for natural recruitment of natural *S. glomerata* for large-scale oyster reef restoration, and subsequent recruitment of fishes and invertebrates. Over two years, recruitment of *S. glomerata* spat, and associated fishes and invertebrates were assessed on reefs made of: (1) rock, and (2) rock and shell.

Results The mean (±SE) density of oyster spat on rock reefs (Myall River: 1790±48, Karuah River: 1928±68) was significantly greater (Myall River: ANOVA Si: MS $_{2,18}$ = 31080167, F = 96.05, $P < 0.001$, Karuah River: ANOVA Si x Ti: MS $_{18,270}$ = 2965449, F = 5.99, $P < 0.001$) than on rock and shell reefs (Myall River: 840±40, Karuah River: 1505±75). Rock reefs had significantly greater densities (Myall River: ANOVA Si x Ti: MS 18, 270 = 15657, F = 2.71, $P < 0.001$, Karuah River: ANOVA Si x Ti: MS 18, 270 = 20322, F = 5.25, $P < 0.001$) of the most abundant invertebrate, *Bembicium auratum* (Myall River: 85±9, Karuah River: 100±8) than reefs of rock and shell (Myall River: 59±8, Karuah River: 44±5), but there was no significant difference in the diversity and relative abundance of the most abundant species of fish, *Acanthopagrus australis*.

Conclusions This study demonstrates that using locally sourced rock is better for *S. glomerata* recruitment than shells. Although shell might have benefits that were not investigated in the present study, such as elicit greater social licence for oyster reef restoration projects, but as shown here, it may not be beneficial from an ecological perspective. With the global expansion of the range of different native species of reef oysters for restoration, the appropriate material used for reef bases needs to be chosen for a specific species and purpose.

Keywords Estuary, Oyster, Recruitment, Shellfish

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Background

Globally oyster reefs have been either severely degraded or completely lost due to overharvesting, disease, and modification of catchments, but there is an increasing recognition of the necessity to restore the ecological functions provided by native oyster reefs, e.g. habitat for fish and invertebrates, and filtration of coastal waters [1–5]. Oyster reef restoration is relatively new in Australia [1], particularly in intertidal and estuarine environments. There has been a focus on restoring subtidal oyster reefs with native Angasi flat oysters, *Ostrea angasi*, in coastal embayments [6–8]. There is, however, increasing interest in restoring intertidal Sydney rock oyster, *Saccostrea glomerata*, reefs within estuaries [8, 9].

Restoration of oyster reefs generally begins with the placement of hard substrata to serve as a base for oyster attachment and growth [10]. Successful oyster reef restoration relies on the presence of suitable material that encourages the long-term recruitment and growth of oysters [10–13]. Due to the loss of self-sustaining populations of native oysters, many restoration projects also rely on seeding reef bases with oyster spat [7, 12, 13]. Although many projects have used recycled oyster shell with small seed oysters [13], others have relied on natural oyster recruitment onto empty shells called “shell planting” [14]. In both cases, strategic site selection and the presence of suitable substrata are essential [15].

Considerable research has been done to determine the most effective method for increasing recruitment of shellfish by investigating the effectiveness of different substrata for oyster reef restoration [7, 10–12]. Although some studies have shown attraction of oysters to conspecific shell or to artificial substrata such as concrete [16], the results are often place and species specific. Most research has focussed on the eastern oyster, *Crassostrea virginica*, and there are very few records on *S. glomerata*. For example, Hemraj et al. [16] conducted a meta-analysis examining various substrata used for successful restoration across multiple oyster species, and their study found no records on *S. glomerata* with the majority of studies focusing on the eastern oyster, *Crassostrea virginica*. In New South Wales (NSW), Australia, oyster farmers have traditionally placed a range of catching and growing substrata on intertidal mud flats for *S. glomerata*, such as sticks, rocks, and shell [17]. Lee et al. [18] compared recruitment of *S. glomerata* on patches of bare rock, rock with live conspecifics, and rock with shell. They initially found more recruits on shell, but not subsequently due to post-settlement mortality [18]. As pointed out by Howie [19], there is also a growing recognition of the preference for natural substrata over anthropogenic materials in restoration efforts, based on their perceived environmental benefits [20].

Moreover, the goal of many oyster reef restoration projects extends beyond recruitment of oysters, and is to provide ecological and economic benefits, including healthy oyster reef habitats that enhance fish and invertebrate biodiversity [21–23]. For example, a meta-analysis showed that the diverse taxa associated with constructed oyster reefs is different from those associated with natural oyster reefs of *C. virginica* in the Gulf of Mexico [24]. Also in the Gulf of Mexico, a study experimentally compared reefs of different substrata on oyster recruitment, growth, and nekton habitat use, which were found to be similar to natural reefs but different from bare sediment [25]. Previously, it has been shown that reefs in NSW, *S. glomerata* have more species of associated fishes and invertebrates than bare sediment [26–28], but it is unknown whether these species are influenced by the type of substratum.

Restoration of the once widespread oyster reefs of native Sydney rock oyster, *Saccostrea glomerata*, in NSW commenced with a large-scale oyster reef restoration project in Port Stephens, NSW. Prior to the planned expansion of the Port Stephens oyster reefs by 2–3 times in area, it needed to be determined whether locally sourced clean shell (cultch) and/or locally quarried rock was better as a reef base for naturally recruiting intertidal oysters and reef-associated fishes and invertebrates. Specifically, we tested the hypothesis that *S. glomerata* recruitment differed significantly between unconsolidated cultch and locally sourced rock. It was also hypothesised that patterns of recruitment of fishes and invertebrates would differ between rock reefs and those constructed of both rock and shell. The material used for the subsequent expansion of these reefs, and others in NSW, was determined by the outcomes of this study.

Materials and methods

Description of sites

This major oyster reef restoration project was conducted on the mid north coast of New South Wales, Australia at the mouths of the Myall and Karuah Rivers in the Port Stephens estuary, the largest drowned river valley in NSW, which lies within the Port Stephens-Great Lakes Marine Park (Fig. 1). Port Stephens is also one of the highest oyster-producing estuaries for aquaculture in New South Wales [29]. In addition to the high spatfall, the estuary also has many natural oyster reefs, and the area was chosen for the potential success of oyster reef restoration. Intertidal sites for restoration were chosen to be in close proximity to natural reefs of the Sydney Rock Oyster, *Saccostrea glomerata* (Fig. 1), and occurred from −0.20 m to 0.62 m Australian Height Datum (AHD). The elevation of oyster reefs was measured relative to known Permanent Survey Marks (PSMs) from the Survey

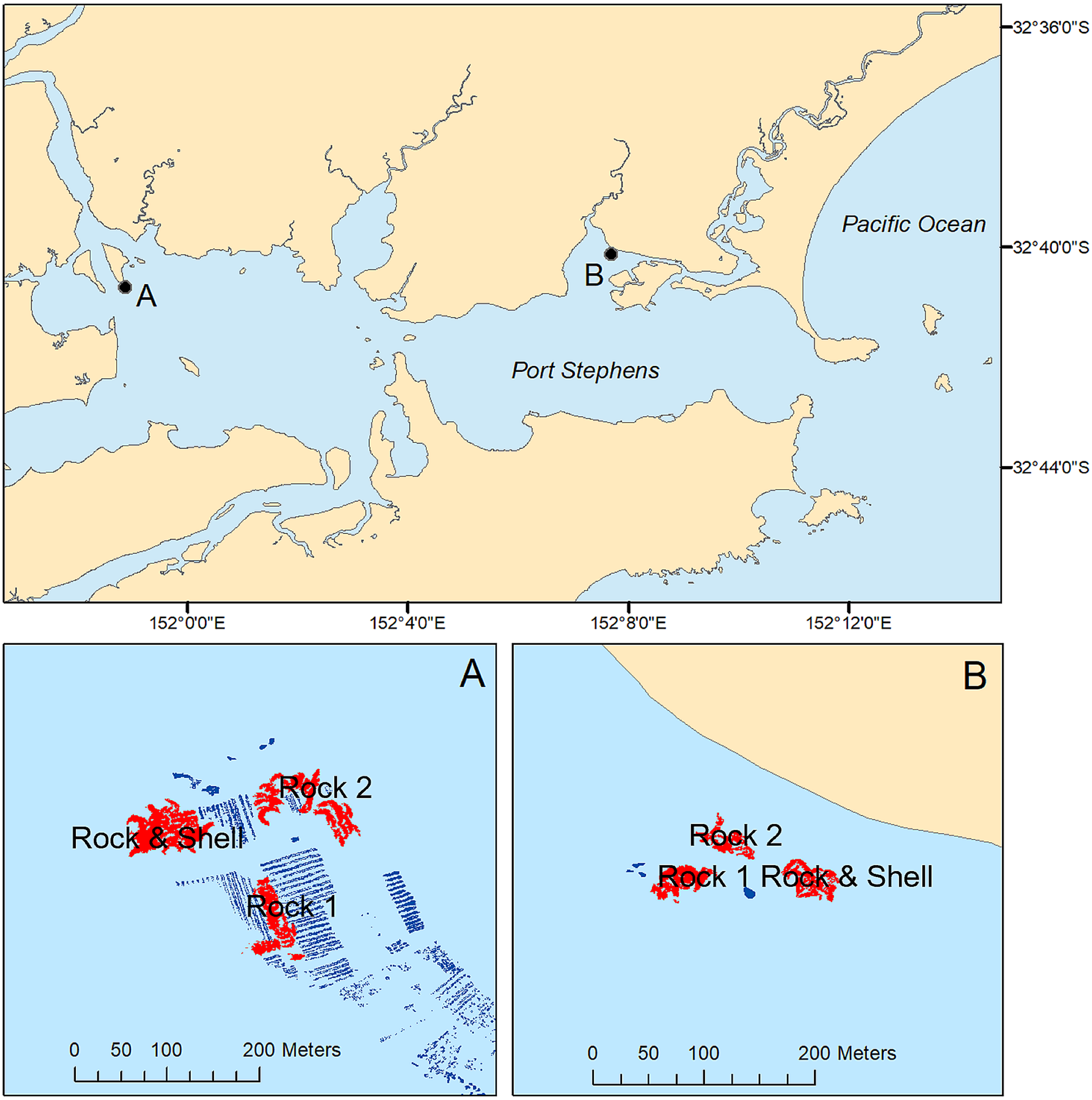

Fig. 1 Port Stephens with rock reefs and rock, and shell reefs, at the (**A**) Karuah River and (**B**) Myall River sites

Control Information Management System (SCIMS) database that contains the coordinates, heights and related attributes for in NSW (SCIMS online - Spatial Services (nsw.gov.au)). The elevation of the reefs was measured relative to the PSMs with a theodolite (Lasertec). The Port Stephens oyster reefs were completely exposed during all low tides and covered by approximately 1–2 m of water during high tides. The water temperature and salinity were measured with a Horiba U-50 Series Multiparameter Water Quality Meter during each sampling event at each site.

Reef construction

Prior to the commencement of the large-scale Port Stephens oyster reef restoration project, a small-scale experiment was done during the peak recruitment period for Sydney rock oysters in Port Stephens (late January 2019), which generally occurs after the peak recruitment of non-native rock oysters, Pacific oysters *Crassostrea gigas* [31]. This study tested the recruitment of oysters in the proposed restoration sites and whether the rock and shell were suitable substrata to be used in the subsequent large-scale restoration works. Within the Myall and

Karuah Rivers, there were two replicate sites with $n=5$ plots (0.5 m x 0.5 m) of locally sourced clean *S. glomerata* shell or locally quarried sandstone rocks, placed on the surface of the sediment at the same tidal height that remnant reefs occur within the estuary. Sandstone is a common type of rock within the Port Stephens estuary which was available at the time of the project.

The first stage of the Port Stephens Oyster Reef Restoration Project was completed in March 2020. The on-ground works consisted of a total of 180 m^3 of locally sourced clean, *S. glomerata* shell sourced from oyster farms within Port Stephens, and the total amount of recycled shell available in Port Stephens over a 14-month period, and 3,300 t of locally quarried igneous (andesite) rock. Andesite is the predominate type of rock in the Port Stephens estuary and was readily available in large volumes from local quarries. Sandstone rocks, which were used for the small-scale study, were not available in large enough volumes. Rocks were approximately $30\times20\times15$ cm in size. In the Myall River and Karuah River sites, there were two reefs of rock, and one reef of rock and shell (Fig. 1). The construction of these multiple and independent reefs (Fig. 1), allowed for experimental comparison of reefs that were constructed of rock (100% rock), and rock and shell (50% rock and 50% shell), hereafter "rock" and "rock and shell" reefs.

In the Myall River site the reefs were 650–750 m^2, and reefs in the Karuah River site were 1500–2500 m^2 in size (Fig. 1). The areas of the reefs were photographed by high resolution aerial imagery (Nearmap) taken during low tide, and mapped using Object-Based Image Analysis (OBIA) techniques (which utilise Trimble eCognition™ to generate the initial polygon boundaries based on segmenting high-resolution ortho-rectified image into smaller image objects based on colour, texture and shape), then exported as ArcGIS shape files [30].

Recruitment of oysters and other invertebrates

The small-scale study tested if there was recruitment of oysters in the proposed restoration sites and whether the rock and shell were suitable substrata to be used in the subsequent large-scale restoration works. At the two replicate sites within the Myall River and Karuah River sites, $n=5$ plots of locally sourced *S. glomerata* shell or locally quarried sandstone rocks, were compared. After twelve months, the newly recruited oyster spat (>1 mm, visible with the naked eye) in the plots were enumerated in situ.

The large-scale on-ground works at the Myall River and Karuah River sites commenced in December 2019 and were completed in March 2020, which matched the peak recruitment of *S. glomerata*. From May 2020 until December 2021, recruitment (defined as the period of post settlement when individuals were detected in the field [32]), of oyster spat and other invertebrates (>1 mm, visible with the naked eye), were enumerated in situ during low tides. At the Myall and the Karuah Rivers, two rock reefs and one rock and shell reef were sampled. At the rock reefs, $n=10$ haphazardly chosen rocks were sampled. At the rock and shell reef, in addition to 10 haphazardly chosen rocks, 5 haphazardly chosen shells surrounding each rock were also sampled. All replicate counts were converted to density per square metre, based on the mean density of rocks and shells determined from $n=10$ replicate 1 m x 1 m quadrats.

Recruitment of fishes

Assemblages of fishes were sampled during high tides in 2020 with baited remote underwater videos (mini-BRUVs [33]). In the Karuah and Myall Rivers, sampling was done at two rock reefs, and a rock and shell reef, all separated by hundreds of metres. Due to the influence of tides, sampling was consistently done during the slack spring high tides in the morning and covered by 1–2 m of water. At each site, GoPro Hero7 cameras attached to weighted frames with a stainless steel 0.5 m arm with a bait bag were deployed, as per the 'mini-BRUV design [27, 33]. Replicate mini-BRUVs at each site (n=3), were placed adjacent to and directly viewing the reefs, and independently deployed so they were at least 20 m apart. Mini-BRUVs (with the field of view set to wide angle, 4K HD resolution and 60 fps to allow for the greatest field of view possible), were baited with crushed pilchards, *Sardinops sagax*. Footage was recorded for 30 minutes which has previously been shown as an effective set time for surveying fish assemblages and key target species in the region [34]. Individuals were identified to the lowest level of classification as possible, which was generally species. The video footage captured was processed with Event Measure version 5.3 (www.seagis.com.au), and MaxN used as a relative estimate of fish abundance being the maximum number of individuals of a species in a single frame [35].

Data analysis

Data were analysed with analysis of variance (ANOVA) with the package GAD [24] in R version 3.5.1 [25]. Prior to analysis, the data were tested for homogeneity of variances, Cochran's C-test, but none of the data required transformation ($P>0.05$) [36]. Sites at the Myall River were analysed separately from the Karuah River, and the experimental design compared the density of oyster spat per m^2, number of species of fishes, and the most abundant fish and invertebrate (maxN of *Acanthopagrus australis*, or density of the gastropod, *Bembicium nanum*), in a two-factor ANOVA with the factor Site (Shell and rock, Rock 1, or Rock 2), and Time as fixed and orthogonal, with $n=10$ (or $n=3$ for BRUVs) replicates for each Time and Site. When sources of variation were significant, Student-Newman-Keuls (SNK) tests were used to compare means and determine the direction of difference.

Results

Recruitment of oysters

The small-scale study comparing rock to shell for recruitment of *S. glomerata* showed a clear difference between substrata. After 12 months, there were no live oysters on the shells at either the Myall River or Karuah River sites. At the Myall River, there were 29.4 ± 5.2 (Mean ± S.E) and 42.6 ± 10.9 (Mean ± S.E) oysters on the rock per m^2. At the Karuah River, the rocks and shells were covered by up to 5 cm of sediment but there were still living oysters on the rock (Site 1: 3.4 ± 1.0, and Site 2: 3.6 ± 0.5 oysters per m^2).

At the larger scale, recruitment of spat was compared among rock reefs and rock and shell reefs. Despite the temperature of the water varying with season (between 14.7 and 22.9 °C), and periods of heavy rain (resulting in large salinity fluctuations: 10.7–34.5), there were clear patterns of the density of oyster spat between the different types of reefs (Fig. 2).

At the Myall River sites there was a significant difference in the density of oyster recruits between the rock and shell reef compared to rock reefs, with more on rock reefs than on the rock and shell reef (Fig. 2a). There was a significant effect of Time (ANOVA Ti: $MS_{9,\,18} = 1213636$, $F = 3.75$, $P < 0.001$), and Site (ANOVA Si: $MS_{2,\,18} = 31080167$, $F = 96.05$, $P < 0.001$). All sites differed, but the shell and rock reef had the fewest recruits and the most were on the rock reefs (SNK: Rock 1 > Rock 2 ($P < 0.01$) > Rock and Shell ($P < 0.001$)).

The pattern in Karuah River sites also showed that there were fewer oyster spat on the shell and rock reef than the rock reefs (Fig. 2b). There was a significant interaction of Site with Time (ANOVA Si x Ti: $MS_{18,\,270} = 2965449$, $F = 5.99$, $P < 0.001$). Specifically, for some times there were significantly fewer recruits on the shell and rock reef than the rock reefs (May 2020 and December 2021 SNK: Rock 1 = Rock 2 > Rock and Shell, $P < 0.001$), and in some months there were differences among all sites (June 2020, September 2020 SNK: Rock 1 > Rock 2 > Rock and Shell, $P < 0.01$). Nevertheless, similar to the Myall River sites, the rock and shell reef consistently over time had the fewest oysters (Fig. 2).

Recruitment of other invertebrates and fishes

In addition to more recruitment of oysters on rocks than shells, there were also more other invertebrates (Appendix A). In the period, December 2020 to December 2021, the gold-mouthed top shell, *B. auratum*, was the most abundant species of invertebrate that recruited to the reefs in the Karuah and Myall Rivers. In the Myall River, recruitment of *B. auratum* was generally six months later than that of *S. glomerata*.

The density of *B. auratum* differed among sites and times in the Myall River (ANOVA Si x Ti: $MS_{18,\,270} = 15657$, $F = 2.71$, $P < 0.001$), and Karuah River (ANOVA Si x Ti: $MS_{18,\,270} = 20322$, $F = 5.25$, $P < 0.001$). There was no consistent pattern among times, but the majority of times had similarly high densities of *B. auratum* (Fig. 2c, d). In the Myall River, at some of the times, the density of *B. auratum* significantly differed among all the reefs (SNK Si(Ti): February, September, December 2021, Rock and Shell < Rock 1 ≤ Rock 2, $P < 0.05$), but notably there were more *B. auratum* on rock reefs than on the rock and shell reef (Fig. 2c). Similarly, in the Karuah River, there were significantly more *B. auratum* on the rock reefs than on the rock and shell reef (SNK Si(Ti): December 2020 - December 2021, Rock and Shell < Rock 1 ≤ Rock 2, $P < 0.05$, Fig. 2d).

The type of reef appeared to make little difference in either fish diversity or composition (Appendix A). For diversity, there was no difference between rock reefs or rock and shell reefs in the Myall River (ANOVA: $MS_{2,12} = 0.7222$, $F = 0.5909$, $P = 0.569$), and the Karuah River (ANOVA: $MS_{2,12} = 0.0556$, $F = 0.0086$, $P = 0.991$). There was no clear difference between rock reefs and the shell and rock reef in terms of the composition of fishes in the Karuah River (PERMANOVA: $MS_{2,12} = 1291.8$, Pseudo-$F = 0.90879$, $P(\text{Perm}) = 0.53$). In the Myall River, there was a significant reef by Time effect, but there was no difference detected between reef types (PERMANOVA: $MS_{2,12} = 4689$, Pseudo-$F = 3.2418$, $P(\text{Perm}) = 0.002$, Pair-wise: Rock and Shell = Rock 1 = Rock 2).

In the Myall River, there was no effect of the type of reef on the number of species of fishes (ANOVA Si: $MS_{2,15} = 1.28$, $F = 0.56$, $P > 0.05$), but there was an effect of Time (ANOVA Ti: $MS_{5,36} = 1.28$, $F = 7.75$, $P < 0.001$). In the Karuah River, there was no effect of the type of reef on the number of species of fishes (ANOVA Si: $MS_{2,15} = 0.57$, $F = 0.16$, $P > 0.05$), or among months (ANOVA Ti: $MS_{5,36} = 3.70$, $F = 0.96$, $P > 0.05$).

The commercially and recreationally important fish, yellowfin bream *Acanthopagrus australis*, was the most abundant species at the restoration sites. In the Myall River, the effect of the reef type on *A. australis* was not consistent among months (ANOVA Si x Ti: $MS_{10,\,36} = 63.44$, $F = 3.99$, $P < 0.001$). Few differences among reefs were detected except in September there were more *A. australis* on the rock and shell reef than the rock reefs (SNK: Reef 1 = Reef 2 < Rock and Shell, $P < 0.05$, Fig. 3a). Similarly, there was no clear effect of the type of reef in the Karuah River (ANOVA Si x Ti: $MS_{10,\,36} = 32.37$, $F = 2.56$, $P < 0.05$, Fig. 3b).

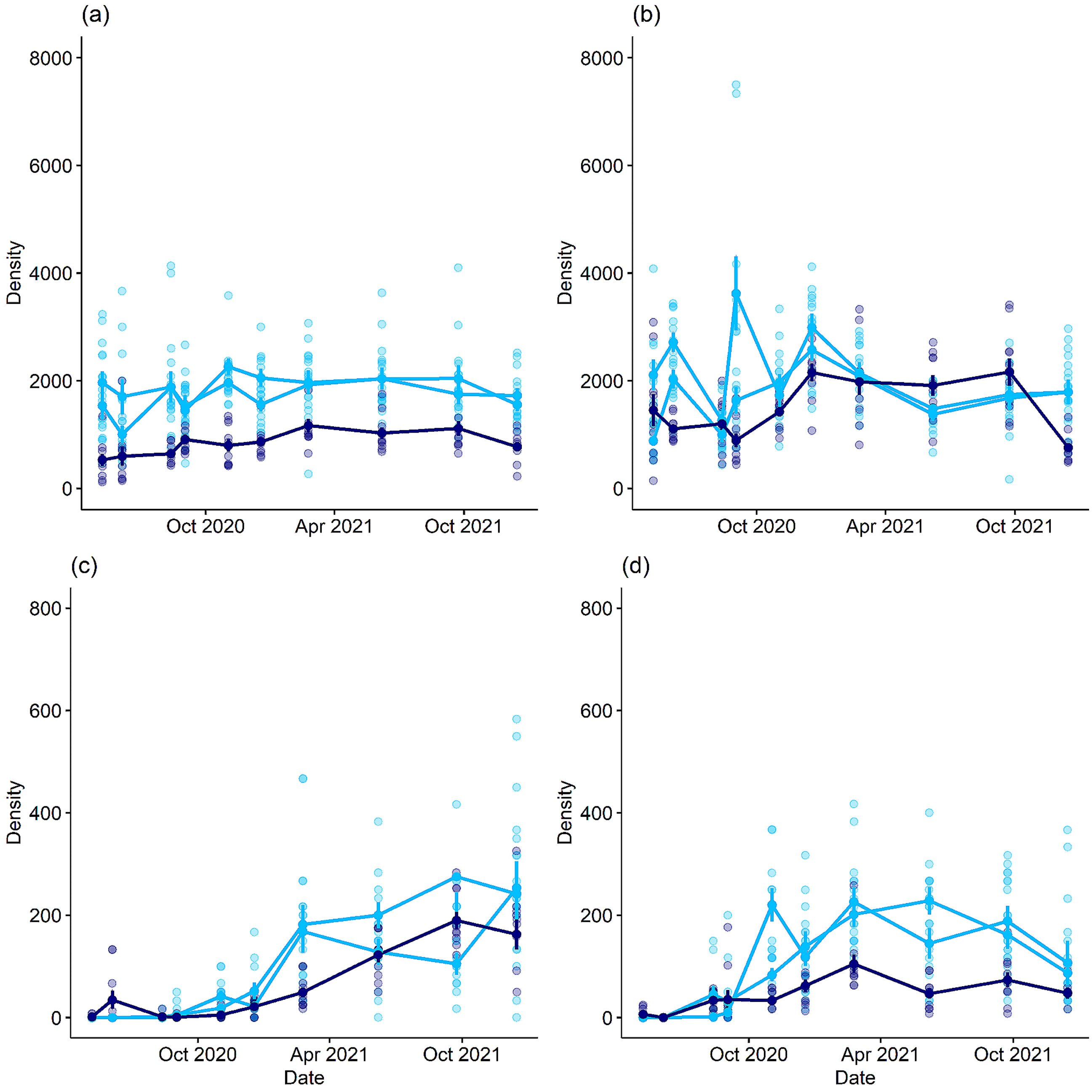

Fig. 2 Mean ± SE density of the Sydney rock oyster Saccostrea glomerata and the gastropod Bembicium auratumon rock reefs (light blue), and the rock and shell reef (dark blue), in Port Stephens. The Sydney rock oyster S.glomerata in the (**a**) Myall River, and (**b**) Karuah River sites. The gastropod B. auratum in the (**c**) Myall River, and (**d**) Karuah River sites

Discussion

It is important to consider the overall ecological benefit when measuring the success of an oyster reef restoration project. Results from the small and large-scale experiments were consistent, recruitment and subsequent survival of *S. glomerata* was significantly greater on sandstone or andesite rock than on shell. There were generally > 10 times more oyster recruits on rock reefs than rock and shell reefs. In addition to greater recruitment of intertidal *S. glomerata* on rock reefs, there were also more other species of invertebrates.

Fewer *S. glomerata* recruited to recycled shell than locally quarried rock. Most importantly, the type of reef base used in a shellfish reef restoration project is highly species specific. In some situations, oyster recruitment of *C. virginica* has been shown to be more successful on conspecific shell [37]. The Australian species *O. angasi* has been shown to recruit in greater numbers on shell than limestone [20], and interestingly, subtidal

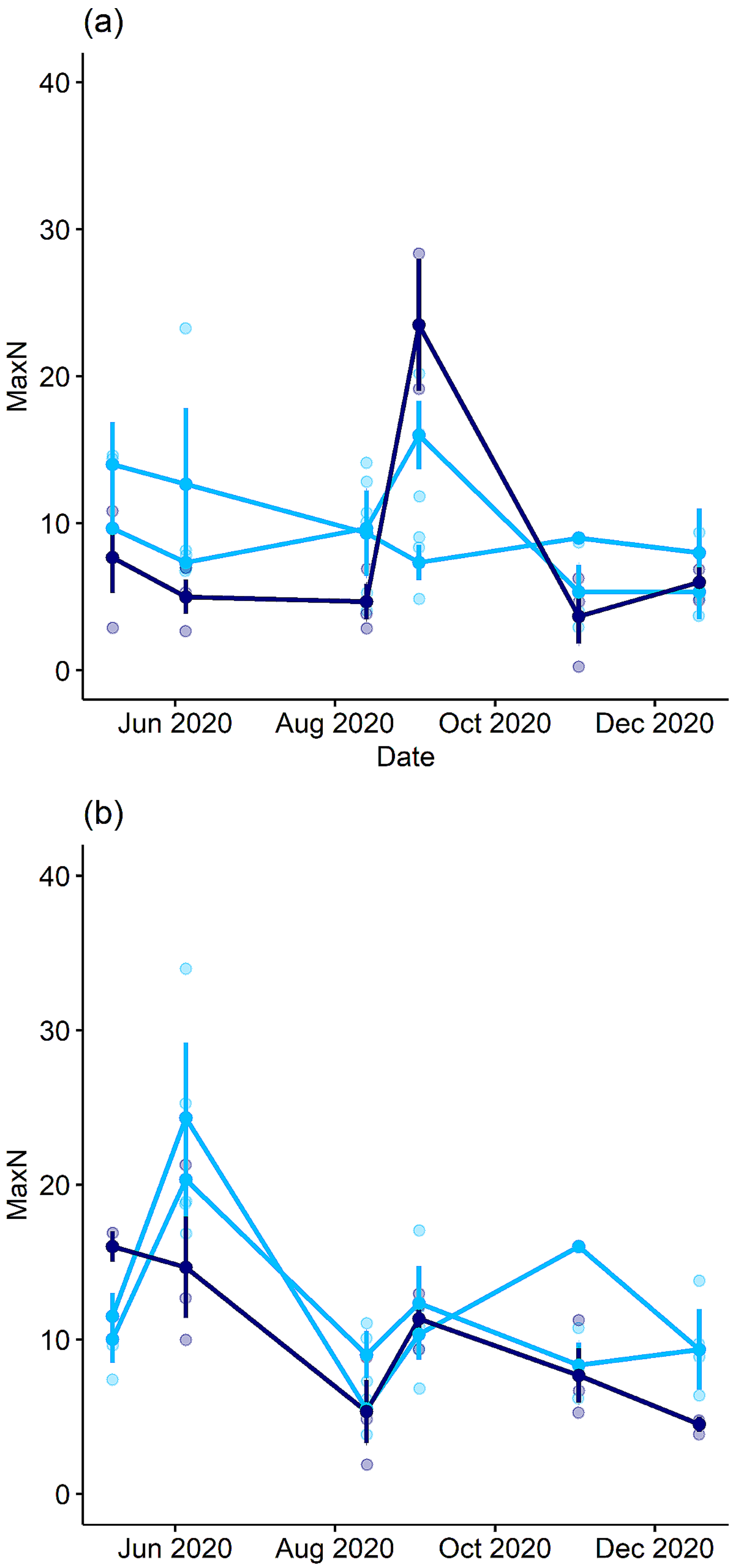

Fig. 3 Mean ± SE MaxN of yellowfin bream Acanthopagrus australis at rock reefs (light blue), and rock and shellreef (dark blue), in the (**a**) Myall River and (**b**) Karuah River sites

settlement of *S. glomerata* was found to be greater on shell than concrete collectors [38]. In a meta-analysis of oyster restoration across all species, mostly *C. virginica*, it was reported that oysters recruit to limestone in similar numbers to oyster shells over alternate substrata (of which shell, limestone, concrete, and granite were most common) [16].

For the rock and shell reefs in Port Stephens, oyster shell was placed on top of the rock base covering half the surface area and some shells fell into the interstitial spaces between rocks. Oyster shells provide increased structural complexity for oyster settlement [4, 16]. It would be expected that rock and shell reefs would also have greater habitat heterogeneity than those without shell due to a higher diversity of structural elements [39]. The rock reefs do, however, provide larger interstitial spaces that can have more habitat for colonisation of oysters [40]. Notably, *S. glomerata* preferentially settle on the underside of surfaces [38], and the rock reefs have more undersides available for recruits. Nevertheless, the overall recruitment of oysters was extremely successful on both rock and shell in Port Stephens. This is promising, as it has been found that oyster reefs (although a different species, *C. virginica*) created from loose shell often failed within the first two years if they did not experience recruitment of oyster spat during that time [41].

While patterns in recruitment of *S. glomerata* were noticeable after two years, further ecological advantages for fish and other invertebrates from restored oyster reefs may not become apparent until several years later [42]. For example, during a three-year study in Xiangshan Bay, China, the comparison of four materials (oyster shell, clam shell, limestone, and clay brick) revealed no differences in the associated macrofauna [11]. Similarly, George et al. [25] found that assemblages of fish and crustaceans did not differ among different substrata (concrete, porcelain, limestone, river rock, and oyster shell) after 4 months. In a meta-analysis of the rate of recovery of restored oyster reefs, it was reported that although there was a rapid increase in biodiversity and abundance of reef-associated species within 2 years, the rate of recovery then decreases and recovery remains 35% below a pre-disturbed state [16]. In the present study, after one year of sampling there was no difference in diversity of fishes on reef bases that were constructed of rock versus the combination of rock and shell. It may take ecological processes such as reduced predation and developed succession to occur on the rock reefs for many years to be detectable [43]. Furthermore, although the present study did not detect a difference in fish diversity between types of reefs, many studies have illustrated species richness increases with increased diversity of structural elements [44].

It is a key consideration to determine the type of material used (e.g. recycled shell, rock, or artificial materials such as concrete blocks), and its spatial arrangement [19], and patch shape and size [45]. Due to constraints on the availability of oyster shell from either aquaculture or shell recycling sources, alternative substrata for the restoration of oyster reefs require investigation [25, 37]. Many studies have investigated the success of using substrata other than those locally available, such as concrete and purpose-built structures. For example, *C. virginica* recruited on shell over artificial substrata, whereas *C. ariakensis* were more abundant on fiberglass than shell [46]. A different study found post-settlement mortality of *C. virginica* on surfclam shell and coal ash reefs exceeded that on oyster shell reefs [47]. In a survey of restoration practitioners in the state of Florida on *C. virginica* oyster reef restoration, responses indicated that many non-plastic materials were used, including rock, cement-infused jute structures, cement reef balls, biodegradable materials (e.g. Biodegradable Ecosystem Engineering Elements made of potato starch), and metal gabions [48]. The purpose-built materials were either more expensive and equally or more difficult to install than previously popular plastic-based materials. Novel methods are also being explored as future materials for restoration in NSW but the present works were required to use natural and locally sourced materials (i.e. occurred naturally within the Port Stephens estuary).

The benefits of oyster reef restoration extend beyond the ecological consequences. Shell recycling provides opportunities for community engagement in oyster reef restoration projects, and provides legitimacy or "social license to operate" these environmental projects [sensu 49, 50]. In Port Stephens, clean *S. glomerata* shell was provided by important stakeholders, i.e. local oyster farmers, who provided support for the project. At a larger scale, the Chesapeake Bay oyster shell recycling program provided 25% of the annual shell required for restoration, and importantly the program engaged and educated the community [51]. Oyster shell recycling facilities might source recycled shell from across many locations, from a variety of sources such as aquaculture facilities, seafood retail outlets and restaurants [52]. Recycled oyster shells can be perceived to carry many biosecurity risks such as exotic organisms [53]. Although recycled shells can be treated, e.g. heat sterilised [54], in many jurisdictions the biosecurity protocols state that recycled shell can only be used if it is sourced from the estuary where the restoration project will take place, or of equal or less risk of the oyster disease QX [55]. The present study has, however, shown that in the case of restoring intertidal *S. glomerata* reefs, efforts to overcome the shortage of recycled oyster shells is not advisable and has proven to be contradictory to success of restoration.

Although numerous studies have indicated that colonisation of oysters on conspecific shell is preferable to other substrata, research focusing on specific species is essential. Managers found this study valuable for developing the second phase of the intertidal *S. glomerata* reef restoration in Port Stephens, doubling the reefs with rock bases alone. These findings illustrate the importance to oyster reef restoration practitioners aiming to get the greatest benefits in terms of reef footprint and ecological benefits relative to restoration costs. The use of shell when constructing reef bases for *S. glomerata* oyster reef restoration should be carefully considered. Shell may have advantages for variables that have not been fully quantified for *S. glomerata* oyster reef restoration, such as social license to operate [50] or shoreline protection [56]. Unlike other species of oysters, recruitment of *S. glomerata* and associated invertebrates (especially gastropods) on reefs with shell were less effective compared to reefs made of locally quarried rock. With the global expansion of oyster reef restoration and the range of different native species of oysters, the substrata used for reef bases need to be chosen to be both species and purpose specific.

Appendix A: List of species sampled at rock reefs, and rock and shell reefs, Port Stephens, Australia

Taxon	Myall River	Karuah River
Mollusca	*Bembicium auratum*	*Bembicium auratum*
	Patelloida mimula	*Patelloida mimula*
Arthropoda	*Australoplax tridentata*	*Australoplax tridentata*
		Ozius truncatus
	Gammaridae	Gammaridae
		Tanaiadacea
	Clunio sp. larvae	*Clunio* sp. larvae
Polychaeta		*Polydora* sp.
Nematoda	Nematoda	
Vertebrata	*Acanthopagrus australis*	*Acanthopagrus australis*
	Afurcagobius tamarensis	
	Ambassis sp.	*Ambassis* sp.
	Aptychotrema rostrata	
	Arenigobius frenatus	*Arenigobius frenatus*
	Bathygobius krefftii	*Bathygobius krefftii*
	Centropogon australis	*Centropogon australis*
	Cryptocentroides gobioides	*Cryptocentroides gobioides*
	Dasyatis fluviorum	*Dasyatis fluviorum*
	Dasyatis kuhlii	*Dasyatis kuhlii*
	Dinolestes lewini	
	Favonigobius exquisitus	
	Gerres subfasciatus	*Gerres subfasciatus*
	Girella elevata	
	Girella tricuspidata	*Girella tricuspidata*
	Gobiidae	Gobiidae
	Hyporhamphus australis	*Hyporhamphus australis*
	Liza argentea	*Liza argentea*
	Microcanthus strigatus	*Microcanthus strigatus*
	Mugil cephalus	*Mugil cephalus*
	Myliobatis australis	*Myliobatis australis*
	Myxus elongatus	
	Omobranchus anolius	*Omobranchus anolius*
	Omobranchus rotundiceps	*Omobranchus rotundiceps*
	Pelates sexlineatus	*Pelates sexlineatus*
	Petroscirtes lupus	*Pomatomus saltatrix*
	Platycephalus fuscus	
	Pseudorhombus sp	*Pseudorhombus* sp.
	Redigobius macrostoma	
	Rhabdosargus sarba	*Rhabdosargus sarba*
	Sillago ciliata	*Sillago maculata*
	Sillago maculata	
	Tetractenos glaber	*Tetractenos glaber*
	Tetractenos hamiltoni	*Tetractenos hamiltoni*
	Torquigener pleurogramma	
	Trygonoptera testacea	*Trygonoptera testacea*
	Trygonorrhina fasciata	*Trygonorrhina fasciata*
	Tylosurus gavialoides	*Tylosurus gavialoides*

Acknowledgements
We acknowledge the Worimi people who are the Traditional Custodians of the Land on which this project was done, and to Elders past and present. The authors are grateful for technical assistance in the field by Isabelle Thiebaud, Ben Kearney, Gwenael Cadiou, and Tristan New, and useful discussions with Charlotte Jenkins and Jillian Keating (DPIRD). Assistance with mapping was provided by Greg West and Alistair Becker (DPIRD).

Author contributions
All authors (VJC, DH, SKD and KR) made substantial contributions to the conception and design of the work. VC analysed the data, and drafted and subsequently revised the work. VC and SKD did the field sampling. DH, SKD and KR also revised the work. All authors agree to be personally accountable for their own contributions and will address any questions related to the accuracy and integrity of their contributions to this work.

Data availability
Data are available from 10.5281/zenodo.12770445.

Declarations

Ethics approval and consent to participate
Use of the baited remote underwater videos were approved under "FISH ACEC-0395 (10/09) Monitoring fish communities using visual and video surveys", by the Fisheries Animal Care and Ethics Committee, as the delegated committee for the Accredited Establishment of the Department of Regional New South Wales, Animal Research Authority.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Funding.
Funding was provided to NSW Department of Primary Industries Fisheries through the Oyster Reef Restoration Project as an initiative of the NSW Marine Estate Management Strategy.

Received: 12 February 2024 / Accepted: 26 July 2024

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