ANNUAL PATTERN OF SETTLEMENT OF SYDNEY ROCK OYSTER (*SACCOSTREA GLOMERATA*) SPAT IN PUMICESTONE PASSAGE, MORETON BAY

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Natural spatfall of Sydney rock oysters (*Saccostrea glomerata*) was examined on shell cultch and three dimensional concrete spat collection units placed subtidally and intertidally in Pumicestone Passage, northern Moreton Bay. Spatfall of *S. glomerata* peaked in January and was detected in all months when water temperatures exceeded 24°C, which was consistent with historic data from Ningi Creek. The vast majority (93.77%) of *S. glomerata* spat that settled on concrete spat collection units recruited to internal or inverted surfaces that were shielded from silt. The highest numbers of recruited spat and invertebrates were detected subtidally on cleaned oyster shell cultch, which was on a weight for weight (or volume for volume) basis 10-90 (5-42) times more effective for attracting spat and 28-135 (13-62) times more effective for attracting invertebrates than concrete spat collection units. Monthly pressure cleaning of concrete collectors to remove silt deposits and algal turfs increased *S. glomerata* spatfall on the vertical sides of collection units, particularly on intertidal units, as well as encouraged settlement of other bivalves including *Pinctada albina*, *P. maculata* and *Hyotissa imbricata*, while *Trichomya hirsuta* occasionally settled on marker ropes. Increased mortality rates of *S. glomerata* spat on subtidal collectors during February and March was likely due to predation, however mortalities of older spat settled on both intertidal and subtidal units during the autumn and winter months may have been due to other causes, which may include QX disease, smothering due to blooms of cyanobacteria *Lyngbya* sp., brown algae *Ectocarpus fasciculatus* and/or jellyfish *Catostylus mosaicus*. These results confirm that *S. glomerata* spat can successfully recruit to shell cultch and concrete substrates in subtidal areas of Pumicestone Passage, suggesting that restoration of subtidal shellfish reefs in the area is feasible if appropriate settlement substrates are provided.

Keywords: MPA, oyster, shellfish, restoration, water quality, recruitment

INTRODUCTION

Oysters, mussels and other reef forming shellfish are important ecosystem engineers in estuaries, providing hard subtidal and intertidal reef structure, food and habitat for fishes and invertebrates, as well as services such as filtration of phytoplankton, nutrient uptake and fixation, benthopelagic coupling and shoreline stabilization (Newell 2004; Grabowski & Peterson 2007; Beck et al. 2011; zu Ermgassen et al. 2012, 2016). However, the extent of natural shellfish reefs and beds declined dramatically worldwide throughout the 19th and 20th centuries due to a suite of anthropogenic impacts that adversely affect estuaries and inshore marine ecosystems (Kirby & Miller 2005; Beck et al. 2011).

In Australia, shellfish reefs were formerly abundant in most estuaries along the southern and eastern coastlines prior to European settlement (Gilles et al. 2015a,b), but today they are classified as functionally extinct (Beck et al. 2011) and in many locations their historical presence has been erased from human memory (Alleway & Connell 2015). "Generational amnesia" leading to lack of recognition of lost shellfish reefs represents a significantly shifted baseline for management of estuarine and coastal ecosystems in Australia (Diggles 2013; Alleway & Connell 2015; Gilles et al. 2015a,b), prompting realisation of the urgent need to undertake their restoration (Creighton et al. 2015; Gilles et al. 2015a).

Pumicestone Passage is the largest estuary in northern Moreton Bay in south-east Queensland, Australia (Figure 1). Shellfish resources in Moreton Bay were utilized for thousands of years by indigenous groups (Diggles 2015); however, since European settlement shellfish were exploited for food and Aboriginal shell middens were also raided to make lime to build roads and buildings (Smith 1981; 1985). The Moreton Bay oyster industry mainly utilised Sydney rock oysters (*Saccostrea glomerata*), an important reef forming species which was historically exploited on intertidal banks as well as by dredging subtidal shellfish reefs (Saville-Kent 1891; Smith 1981). Industry production peaked in 1891; however, landings subsequently declined to less than 10% of the peak (Smith 1985) due to damage from dredging, sedimentation and declining water quality brought about by development in the catchment (Diggles 2013). In Pumicestone Passage historical records show abundant subtidal and intertidal shellfish reefs occurred in the mid to late 1800s (Saville-Kent 1891), but today around 96% of zonation suitable for natural *S. glomerata* recruitment (recruitment being defined as successful settlement, survival and growth of planktonic spat into juvenile oysters) has been lost and subtidal shellfish reefs are functionally extinct (Diggles 2013).

In contrast to the prolific recruitment of *S. glomerata* spat in Pumicestone Passage over 120 years ago (Saville-Kent 1891), today successful natural spat recruitment is disrupted below approximately 1.1 metres above low water datum (Diggles 2013). Studies in the late 1970's found natural *S. glomerata* spat recruitment at Ningi Creek in Pumicestone Passage occurred from November to April, peaking in December with spatfall generally heavier in the lower part of the tidal range (Potter 1984). The current lack of successful natural spat recruitment below 1.1 meters above low water datum may therefore be a relatively recent phenomena, thought to be due to lack of suitable settlement surfaces for oyster larvae as constantly resuspended sediments (Morelli et al. 2012) lodge in algal biofilms stimulated by eutrophication (McEwan et al. 1998), interfering with settlement cues and resulting in spatfall failure. In view of the desire of traditional owners and the local community to begin restoration of shellfish reefs in Pumicestone Passage (Diggles 2015), the present study was undertaken to determine if the timing of peak natural *S. glomerata* spatfall in the area has changed since the late 1970's (Potter 1984), and to compare spatfall in intertidal vs subtidal areas, to determine whether natural spatfall could be used for reef restoration in subtidal areas if suitable restoration substrates were provided.

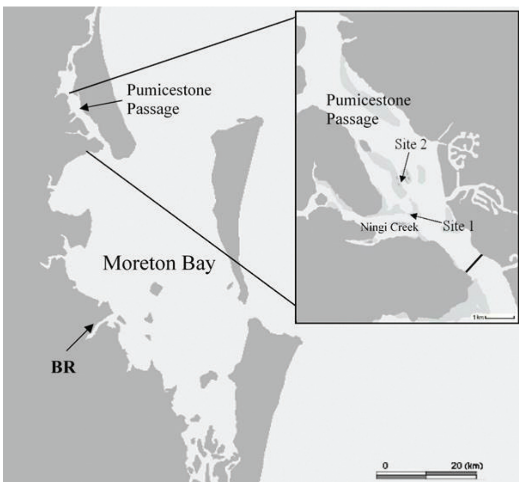

FIG. 1. Map showing location of experimental sites in Pumicestone Passage, northern Moreton Bay. BR = Brisbane River.

METHODS

Natural spatfall of mainly Sydney rock oysters (*Saccostrea glomerata*), but also opportunistic observation of spatfall of several other shellfish species including hairy mussels (*Trichomya hirsuta*), pearl oysters (*Pinctada albina albina*) and saddle shaped oysters (*Hyotissa imbricata*), was examined every month in Pumicestone Passage, northern Moreton Bay for a period of 15 months. Experiments were conducted using artificial three-dimensional concrete spat collection units, concrete oyster reef balls and *Saccostrea glomerata* shells (natural shell cultch) placed on intertidal banks and in subtidal channels at two sites from September 2015 to November 2016.

Site 1 (27°03.504 S, 153°07.349 E) was located on the northern side of the mouth of Ningi Creek (Figure 1). Here the intertidal units were placed approximately 1 metre above low water datum, with subtidal units deployed at around 0.5 metres below low water datum on a mixed sand/mud substratum. Site 2 (27°02.834 S, 153°07.155 E) was located on the western bank of Neds Gutter (Figure 1), where the intertidal units were placed approximately 1 metre above low water datum with subtidal units deployed at around 0.6 metres below low water datum on a natural dead *S. glomerata* shell/mud substrate. Subtidal units deployed at both sites were loosely linked together with 6 mm polypropylene marker rope to facilitate their retrieval.

ARTIFICIAL THREE DIMENSIONAL SPAT SETTLEMENT UNITS

The artificial three-dimensional spat collection units used at both sites were standard concrete Hanson (Besser™) blocks, 13.9 kg in weight, 39 x 19 x 19 cm (LxWxH) in dimension, with 2 internal cavities 14.5 x 19 x 12.5 cm (LxWxH) in dimension (Figure 2). The design of these blocks provided a volume of 14,079 cm^3, a horizontal upper and internal settlement area of 1292 cm^2, a similar area of inverted/internal settlement area, and vertical settlement areas of 1672 cm^2 per unit (Figure 2). Three settlement units were placed subtidally and 3 intertidally at each site (Supplement Figure 1). To provide a measure of monthly spatfall rates, one subtidal unit and one intertidal unit from each site was removed from the water and replaced with a new unit at monthly intervals (replace treatment). One other intertidal and subtidal unit from each site was pressure washed (clean treatment) each month and replaced after counting spatfall prior to washing, while the third remaining intertidal and subtidal unit at each site was monitored for spatfall only (monitor treatment) and otherwise remained undisturbed for the duration of the experiment. Differences in spat recruitment and survival between subtidal and intertidal areas were examined by averaging data for each treatment (monitor, clean, replace) between both sites.

SETTLEMENT ON NATURAL SHELL CULTCH

A polyvinyl chloride (PVC) oyster tray 60 x 40 x 7 cm (LxWxH), containing 100 cleaned and dried *S. glomerata* shells (2.3 kg total weight, 5,000 cm^3 volume) was tied to the top of a single Hanson block (which acted as ballast and elevated shells away from benthic sediment, Sawusdee et al. 2015), and placed subtidally (n = 1) and intertidally (n = 1) at each site (total n = 4 trays) for 30 days every second month (shell cultch treatment, see Supplement Figure 1). At the end of each 30 day period the units were retrieved and the shells were emptied from the trays into a 20 L bucket of seawater to keep them wet until each oyster shell could be visually examined for *S. glomerata* spatfall and the presence of invertebrates or fishes (see section on counting of settled spat, fishes and invertebrates). Data were then averaged between both sites to examine for differences in spatfall between subtidal and intertidal areas.

SETTLEMENT ON OYSTER REEF BALLS

An additional two hollow concrete, conical-shaped oyster reef balls (Reefball Australia Ltd., 35 cm height x 45 cm base diameter with an 18 cm hole through the top) were placed subtidally at each site (Supplement Figure 1). The outer surface of one of the reef balls at each site was pressure washed (clean reef ball treatment) each month after counting spatfall prior to washing, while the second reef ball at each site was monitored for spatfall only (monitor reef ball treatment). After completion of counting and cleaning, each reef ball was returned to its original

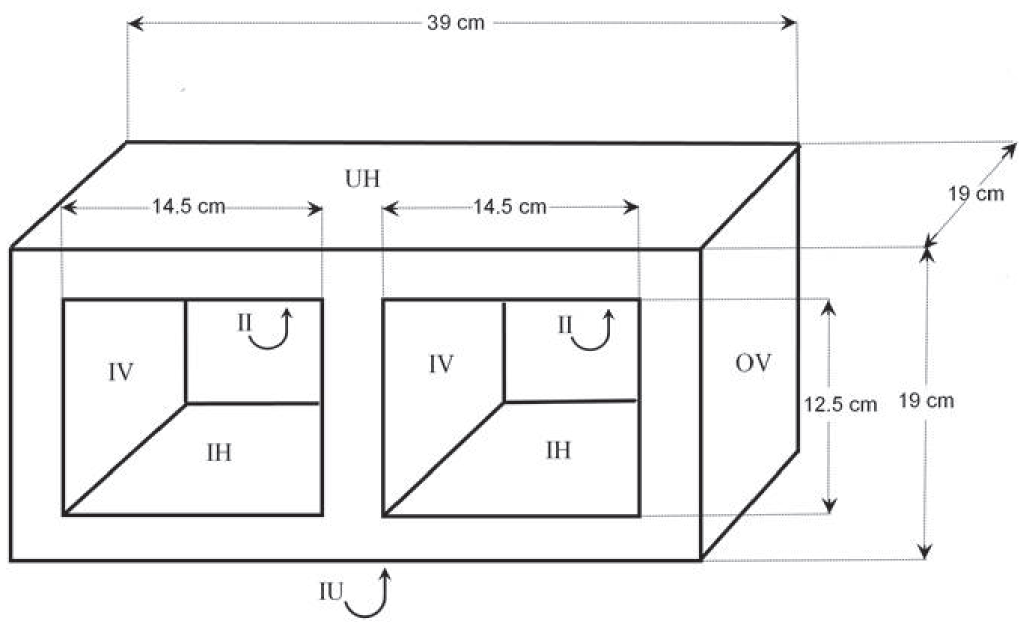

FIG. 2. Dimensions and nomenclature for three-dimensional concrete spat collection units (Besser blocks). UH = upper horizontal surface, IH = internal horizontal surfaces, IV = internal vertical surfaces, OV = outer vertical surfaces, IU = inverted under surface, II = inverted internal surfaces.

subtidal location. Data for each treatment (monitored or cleaned) were then averaged between both sites and compared to examine whether regular cleaning made a difference to spat recruitment and/or survival.

COUNTING OF SETTLED SPAT, FISHES AND INVERTEBRATES

Each month from end of September 2015 to end of November 2016 during low water spring tides, I visually recorded the number of *S. glomerata*, other shellfish spat, fishes and invertebrates recruiting to each three dimensional concrete settlement unit and the oyster reef balls from the previous 30 days' deployment. The relative settlement position of each spat recruiting on the three dimensional settlement units (i.e. upper, vertical, internal and inverted under surfaces) was noted using nomenclature shown in Figure 2. Intertidal units in the monitor treatment were inspected *in-situ*, while subtidal units in the monitor and clean treatments were retrieved onto the intertidal bank during the counting and cleaning process for no more than 30 minutes each month before being replaced subtidally after monitoring was completed. Spatfall and counts of invertebrates on settlement units in the clean treatment were done prior to pressure cleaning. The presence of other associates when they occurred, particularly fishes, was also noted prior to retrieving or inspecting each unit. On 4 occasions (February, April, June and August) an underwater camera (GoPro™) was deployed near the reef units for between 1 to 2 hours to visualise and record behaviour of fishes and invertebrates associating with the units. The pressure cleaning process for units in the clean treatment was undertaken every 30 days using saltwater obtained on-site and pressurised using a gasoline powered self priming high pressure washer (Black Eagle model number AGT-BE80). During cleaning the blasting nozzle was held 30-50 cm from the surface of the settlement units or reef balls being cleaned, so the pressure spray was sufficient to remove sediment and algal overgrowth without removing settled shellfish spat.

Spat and invertebrates which settled on the natural shell cultch were counted by removing the shell cultch from the oyster tray and placing it into a 20 L bucket of seawater taken from the site. The bucket of shells was then taken back to the laboratory where any spat, invertebrates and fish eggs which had settled on each shell were inspected visually, counted and representative taxa identified under a dissecting microscope when necessary. Data were then averaged between both sites to examine for differences in spatfall between subtidal and intertidal areas.

LOSS OF SOME EXPERIMENTAL UNITS

Unauthorised removal and theft of the intertidal natural shell cultch trays at sites 1 and 2 in October and November 2015 lead to subsequent utilisation of a single subtidal natural shell cultch unit at each site, deployed for 30 days every second month from December 2015 to November 2016. Unauthorised removal and theft of two of the subtidal reef balls from site 1 in October 2015 meant that data for subtidal reefballs could be obtained only from site 2 for the remaining 12 months from November 2015 to November 2016.

WATER QUALITY MEASUREMENTS

Basic water quality parameters including temperature, salinity, turbidity and dissolved oxygen were measured each month at both sites. Water temperature (°C) and dissolved oxygen (DO in mg/L and % saturation) were measured using a YSI 85 multimeter with a 30 meter probe cable, salinity (‰) was measured with the YSI 85 multimeter and a calibrated refractive salinometer, while turbidity was measured with a 20 cm diameter secchi disk and a turbidity tube (Westlab Pty Ltd.). The presence of blooms of algae and jellyfish that potentially affected the experimental units was also noted when they occurred.

RESULTS

WATER QUALITY

Basic water quality parameters measured over the duration of the experiment are presented in Supplement Table 1. Water temperature ranged from a high of 27.4°C at site 1 in December 2015 to a low of 15.4°C at site 1 in June 2016. Salinity ranged between 32 and 37.6‰, decreasing from the typical 35-36 ‰ only following occasional heavy rains in the days leading up to sampling in October 2015, April 2016, and June 2016. Dissolved oxygen varied from a low of 4.68 mg/L (75% saturation) at site 1 in November 2015 to a high of 8.5 mg/L (117% saturation) at site 1 in May 2016. Turbidity was variable with secchi depths ranging between 1.3 metres (approximately 12 NTU) and 2.5 meters (<9 NTU) with a trend towards reduced turbidity during the late winter months (Supplement Table 1). This may be due to the fact that turbidity was directly related to rainfall and wind strength due to wave resuspension of sediment over shallow banks during periods where wind exceeded 12-

Table 1. Data on settlement microhabitats utilised by *S. glomerata* spat collected on various surfaces of three dimensional concrete spat collection units (see Figure 1 for nomenclature). The vast majority (93.77%) of spat settled on the inverted and internal surfaces of the spat collection units, while regular pressure cleaning increased the number of spat settling on outer vertical surfaces in intertidal areas. Numbers indicate number of spat settlement observations.

Treatment	**Subtidal**			**Intertidal**		
	Top (UH)	**Sides (OV)**	**Under/internal (IU, II, IV, IH)**	**Top (UH)**	**Sides (OV)**	**Under/internal (IU, II, IV, IH)**
Monitor	0	37	777	0	35	725
Clean	1	11	630	2	197	1750
Replace	1	8	487	0	16	269
Total	2	56	1894	2	248	2744

15 knots (B.K. Diggles, personal observations). Due to the relatively shallow depth of the water at both sites (maximum depth approximately 3 metres over subtidal units at high tide), the water column was well mixed and no differences in water temperature, salinity and DO between the water surface and the bottom were noted.

Two algal blooms of magnitude judged sufficient to cause a smothering risk to the experimental units were observed during the course of the experiment. The first bloom was caused by the toxic cyanobacterium *Lyngbya* sp. (known locally as fireweed) which was noticed in small (15-20 cm) clumps attached to experimental units and marker ropes at both sites in April 2016, increasing in extent by June 2016 then becoming less evident for several months during the *Ectocarpus* bloom (see below) until intensifying into a heavy bloom involving numerous drifts between 30 and 60 cm long by November 2016, at which time the experiment was terminated. The second and more intense bloom was caused by the brown algae *Ectocarpus fasciculatus* (locally known as snotweed) that bloomed into large drifts 1-1.5 metres long that collected on marker ropes and covered spat collection units in August and September 2016 at both sites, but particularly at site 1 where a high risk of smothering of experimental units was noted (Supplement Figure 2). The late winter/early spring *Ectocarpus* bloom coincided with the increase in water temperature from winter lows during a period before turbidity increased due to summer wind and rainfall patterns (Supplement Table 1).

An unusually intense bloom of the blue blubber jellyfish *Catostylus mosaicus* was also observed in October 2016, continuing to increase in intensity into November 2016 to densities estimated to peak around 5-7 individuals/ m^3 in locations near the mouth of Ningi Creek at site 1. These large (20-25 cm bell diameter) jellyfish were observed to lodge against experimental units located in intertidal areas at both sites, representing a smothering hazard. At the end of the experiment in November 2016 the upper horizontal (UH, see Figure 2) surfaces of subtidal experimental units at site 1 became colonised by dense clumps of the brown algae *Padina australis*; however these did not appear to represent a smothering hazard due to the absence of settlement of *S. glomerata* spat on the UH surfaces (see below).

SETTLEMENT ON 3 DIMENSIONAL SPAT SETTLEMENT UNITS

Settlement of *S. glomerata* spat was observed on both intertidal and subtidal spat collection units, but only in months where water temperatures exceeded 24°C (Figure 3). Peak spat settlement was recorded in January 2016 on subtidal units when an average of 108.5 spat/ unit was recorded (Figures 3, 4). More spatfall was recorded on subtidal units during late spring and early summer (Figures 3, 4), but cumulative survival of spat over several months into autumn and winter was highest on intertidal units (Figure 5, Supplement Figures 3, 4), No spionid mudworm infestations were noted on any settled oysters (live or dead) at any time throughout the experiment.

Recruitment and cumulative survival of spat was higher on cleaned spat collection units placed in intertidal areas compared to those that were only monitored (Figure 5, Supplement Figure 4). However, for units placed subtidally, those that were monitored had lower initial spat recruitment, but higher cumulative spat survival compared to units that were pressure cleaned every 30

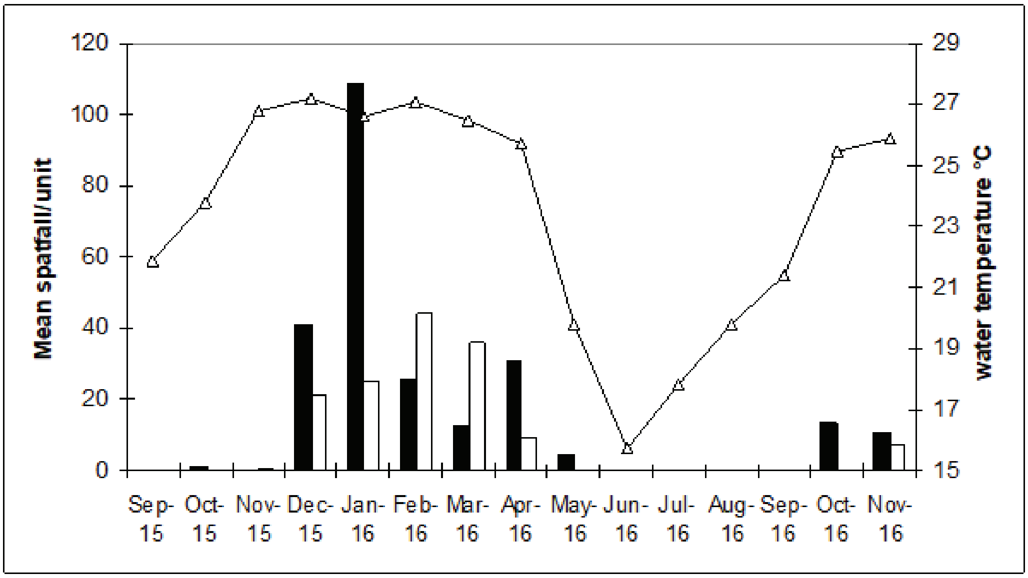

FIG. 3. Mean monthly spatfall recorded from concrete spat settlement units deployed and replaced at monthly intervals at 2 sites in Pumicestone Passage between September 2015 and November 2016 (Replace treatment). Spatfall was recorded on both subtidal (black columns) and intertidal (white columns) units whenever water temperature (-△-) exceeded 24°C. Peak spatfall was on subtidal units in January 2016.

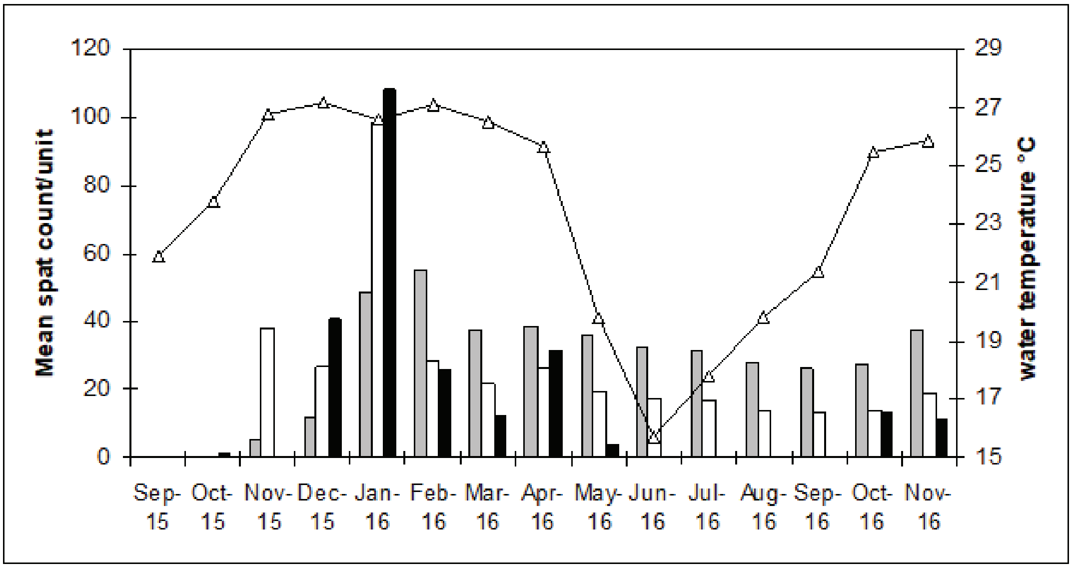

FIG. 4. Cumulative spatfall recorded from concrete spat settlement units deployed subtidally at 2 sites in Pumicestone Passage between September 2015 and November 2016 Units that were monitored only (Monitor treatment, grey columns) had lower spat recruitment, but higher cumulative spat survival compared to units that were pressure cleaned every 30 days (Clean treatment, white columns). Units that were replaced each month (Replace treatment, black columns) show when recruitment occurred. -△- water temperature.

days (Figure 4). When the microhabitats utilised by settled spat were investigated, only 4 out of 4946 spat settlement observations (0.081% of the overall total) were recorded on the upper horizontal surfaces (UH, see Figure 2) of the spat collection units, with all 4 of these being recorded on units that were either pressure cleaned or replaced every 30 days (Table 1). Only 304 spat settlement observations (6.1% of the overall total) were recorded for the outside vertical surfaces of the spat collection units (OV surfaces, see Figure 2), mostly on intertidal units that were subjected to regular pressure cleaning (Table 1). The remaining 4638 spat settlement observations (93.77%) were recorded from the inverted and internal surfaces of the spat collection units including surfaces IU, IH, IV, II (Figure 2).

Monthly pressure cleaning also encouraged settlement of small numbers of other bivalves on the sides of subtidal units including *Pinctada albina* and *P. maculata* (n = 6 observations at site 2 starting from March) and *Hyotissa imbricata* (n = 83 observations starting at site 1 in May and increasing at both sites 1 and particularly site 2 until August), while small numbers of hairy mussel (*Trichomya hirsuta*) spat (n = 39 observations) were observed to settle on marker ropes of subtidal units at site 1 in January.

SETTLEMENT ON OYSTER REEF BALLS

Patterns of spat settlement on the subtidal oyster reef balls at site 2 were similar to those observed on the three dimensional spat collection units, with the vast majority (91.6%) of the 1846 *S. glomerata* spat settlement observations being recorded from the inverted base or inside of the reef balls on surfaces that were protected from silt. The remainder (n = 155, or 8.4%) of *S. glomerata* spat observed settled on the sloped outer sides of the reef balls, mostly on the reef balls that were pressure cleaned every 30 days (n = 96 spat observations) compared to the reef balls that were monitored only (n = 59 spat observations). Again, monthly pressure cleaning encouraged settlement of small numbers of other bivalves on the outside of the reef balls including *Pinctada albina* and *P. maculata* (n = 44 observations, starting from March) and *Hyotissa imbricata* (n = 179 observations, starting from August).

SETTLEMENT ON NATURAL SHELL CULTCH

Unauthorised removal of the intertidal natural shell cultch trays at sites 1 and 2 in October and November 2015, respectively, prevented spatfall comparisons between intertidal vs subtidal shell cultch. However, spatfall data were available from natural shell cultch

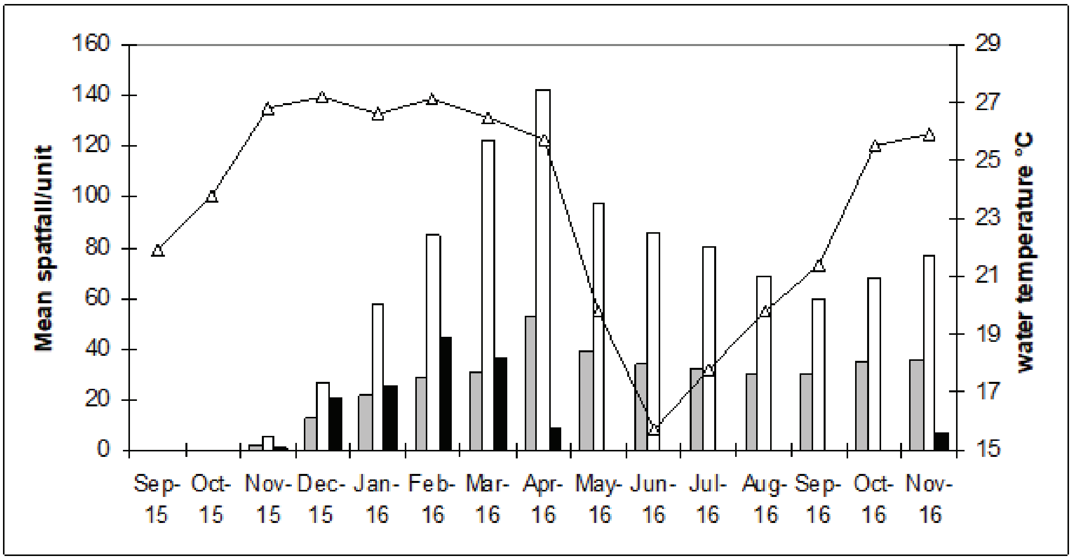

FIG. 5. Cumulative spatfall recorded from concrete spat settlement units deployed intertidally at 2 sites in Pumicestone Passage between September 2015 and November 2016 Units that were monitored only (Monitor treatment, grey columns) had lower spat recruitment, and much lower cumulative spat survival compared to units that were pressure cleaned every 30 days (Clean treatment, white columns). Units that were replaced each month (Replace treatment, black columns) show when recruitment occurred. -△- water temperature.

Table 2. Relative effectiveness of shell cultch vs three dimensional concrete spat collection units on a per weight and per volume basis for attracting settled *S. glomerata* spat at two subtidal sites in Pumicestone Passage. Data from 2.3 kg (5 litres) of oyster shells and 13.9 kg (14.079 litres) of concrete blocks each placed at 2 sites and replaced at 30 day intervals. - = data not available for that month.

Substrate		**Dec 2015**	**Jan 2016**	**Feb 2016**	**Mar 2016**	**Apr 2016**	**May 2016**	**Jun 2016**
Shell cultch	Total spat counted	144	-	768	-	276	-	0
	Spat/kg	31.3	-	166.9	-	60	-	0
	Spat/L	14.4	-	76.8	-	27.6	-	0
Concrete blocks	Total spat counted	82	217	51	25	62	8	0
	Spat/kg	2.95	7.80	1.83	0.9	2.23	0.29	0
	Spat/L	2.91	7.70	1.81	0.89	2.20	0.28	0
Relative effectiveness of shell cultch	per kg	10.6 :1	-	91.2 :1	-	26.9 :1	-	1 : 1
	per L	4.9 :1	-	42.4 :1	-	12.5 :1	-	1 : 1

Table 3. Relative effectiveness of shell cultch vs three dimensional concrete concrete spat collection units on a per weight and per volume basis for attracting invertebrates at two subtidal sites in Pumicestone Passage. Data from 2.3 kg (5 litres) of oyster shells and 13.9 kg (14.079 litres) of concrete blocks each placed at 2 sites and replaced at 30 day intervals. - = data not available for that month.

Substrate	**Subtidal units at 2 sites**	**Dec 2015**	**Jan 2016**	**Feb 2016**	**Mar 2016**	**Apr 2016**	**May 2016**	**Jun 2016**
Shell cultch	Total invertebrates	112	-	280	-	367	-	49
	Invertebrates /kg	24.3	-	60.9	-	79.8	-	10.7
	Invertebrates / L	11.2	-	28	-	36.7	-	4.9
Concrete blocks	Total invertebrates	5	61	60	29	22	10	4
	Invertebrates /kg	0.18	2.19	2.16	1.04	0.79	0.36	0.14
	Invertebrates / L	0.18	2.16	2.13	1.03	0.78	0.35	0.14
Relative effectiveness of shell cultch	per kg	135 :1	-	28.2 :1	-	101 : 1	-	76.4 : 1
	per L	62.2 :1	-	13.2 :1	-	47 : 1	-	35 : 1

placed subtidally every second month at both sites from October 2015 (total = 4.6 kg or 10 litres of shell cultch deployed each month). A total of 1875 spat were collected from oyster shell cultch, the PVC oyster trays and the single Hanson blocks used as ballast. The majority (n = 1207, or 64.4% of all spat) were collected from the natural shell cultch, while 217 spat (11.6%) were collected from the Hanson blocks and 451 spat (24%) settled on the undersides of the PVC oyster tray itself. The vast majority of the spat collected from natural shell cultch were recorded in December 2015 (n = 144, mean 31.3 spat/kg shell or 14.4 spat/L shell), February 2016 (n = 768, mean 166.9 spat/kg shell or 76.8 spat/L shell) and April 2016 (n = 276, mean 60 spat/kg shell or 27.6 spat/L shell) (Table 2). The effectiveness of subtidal shell cultch for attracting spat was a minimum of 10 times and maximum of 91 times more effective than concrete blocks when compared on a weight for weight basis, and around 5 to 42 times more effective when compared volumetrically (Table 2). Similarly, the peak effectiveness of subtidal shell cultch for attracting spat (166.9 spat/kg (76.8 spat/L) in February 2016, Table 2) was over 21 times that of the peak effectiveness recorded from the concrete blocks placed subtidally (mean 108.5 spat/ 13.9 kg block = 7.8 spat/kg (7.7 spat/L) in January 2016, Figure 3). Also notable during December, February and April was the collection of large numbers of crustaceans and other invertebrates of various species (Tables 3, 4) that recruited to shell cultch during these summer and early autumn deployments. Again, the natural shell cultch was far superior for attracting invertebrates, being 28 to 135 times (mean 85 times) more effective than the concrete blocks when considered on a weight for weight basis and 13 to 62 times (mean 39.3 times) more effective on a volume for volume basis (Table 3). Seasonal deposition of adhesive eggs by crested oyster gobies (*Cryptocentroides gobioides*) was also noted on the inside of oyster shells deployed at both sites during October 2015 and October 2016 (Figure 6).

INVERTEBRATES AND FISH

Over 40 species of fish and invertebrates were observed to be directly associated with oyster shells placed in the natural shell cultch trays and/or the three dimensional concrete spat settlement units (Table 4). The fishes most commonly associated with oyster shells inside shell cultch trays included juvenile and adult *C. gobioides* and juvenile (30-50 mm TL) parrotfishes (*Scarus ghobban*), while visual observations when retrieving subtidal units, and GoPro footage revealed at least 12 other species of larger fish to be closely associated with (either inhabiting or swimming adjacent to) the three dimensional spat settlement units or reef balls. The most common species included moses perch (*Lutjanus russelli*), yellowfin bream (*Acanthopagrus australis*), Bengal sergeant (*Abudefduf bengalensis*), tarwhine (*Rhabdosargus sarba*), and silver biddy (*Gerres subfasciatus*) which were visually observed when retrieving subtidal units throughout all months (Table 4). The main types of motile invertebrates observed included crustaceans such as portunid crabs (*Scylla serrata*, *Thalamita crenata*, *Charybdis* sp.), and other crab species from the Families Porcellanidae, Diogenidae and Xanthidae, as well as prawns (Family Penaeidae) and shrimp (Family Palaemoninae) (Table 4). The molluscs observed included several species of bivalves (*Saccostrea glomerata*, *Hyotissa imbricata Trichomya hirsuta*, *Pinctada albina*, *Pinctada maculata*), as well as motile gastropods such as mud whelks, snails, and oyster borers (Table 4). While not specifically noted each month, many species of coralline and encrusting algae, and colonial tunicates (*Symplegma* sp., *Botrylloides* sp.) were also evident on underside surfaces of experimental units placed in subtidal areas, particularly the II (inverted internal) and IV (inverted vertical) surfaces (Figure 2, Supplement Figure 5). No spionid mudworm infestations were noted on any settled oysters (live or dead) from any treatment at any time throughout the entire experiment.

DISCUSSION

It is inferred from study of the intertidal oyster banks in Pumicestone Passage that successful natural spat settlement of *S. glomerata* is currently disrupted below approximately 1.1 metres above low water datum (Diggles 2013). However, the results of the present study confirm that *S. glomerata* spat are still available for settlement below 1.1 metres above low water datum, and indeed spatfall and natural recruitment of *S. glomerata* spat was recorded up to 0.6 metres below the low tide mark in this study, whenever water temperatures exceeded 24°C (Figure 3). When the pattern of recruitment of *S. glomerata* spat onto three dimensional spat settlement units was examined, it was evident that around 94% of successful recruitment occurs on the inverted and internal vertical surfaces of the spat collection units, i.e. surfaces that were protected from silt (Table 1, Supplement Figure 5). It was evident that even when spat settlement units were replaced with new ones every month (replace treatment), rapid accumulation of between 3-8 mm of silt/month onto the upper surfaces of the units prevented successful spatfall onto these surfaces (less than 0.1% of recruitment). Regular (monthly) pressure cleaning of the outer surfaces of three dimensional spat settlement units and reef balls to remove sediment and algal turfs slightly improved spatfall onto the vertical surfaces (Table 1), but not the horizontal surfaces, demonstrating that gravity-induced settlement of silt is less problematic on vertical surfaces where only thin layers of silt can be retained on algal biofilms. These data suggest that failure of successful natural spat settlement of *S. glomerata* in Pumicestone Passage below approximately 1.1 metres above low water datum is due to a lack of availability of suitably clean hard settlement surfaces as constantly resuspended fine sediments (Morelli et al. 2012) blanket virtually all horizontal surfaces and lodge in algal biofilms colonising vertical surfaces, interfering with spat settlement cues (as hypothesized by Diggles 2013).

The period of spat settlement observed in the present study occurred over a slightly longer time period than recorded by Potter (1984), who found recruitment at

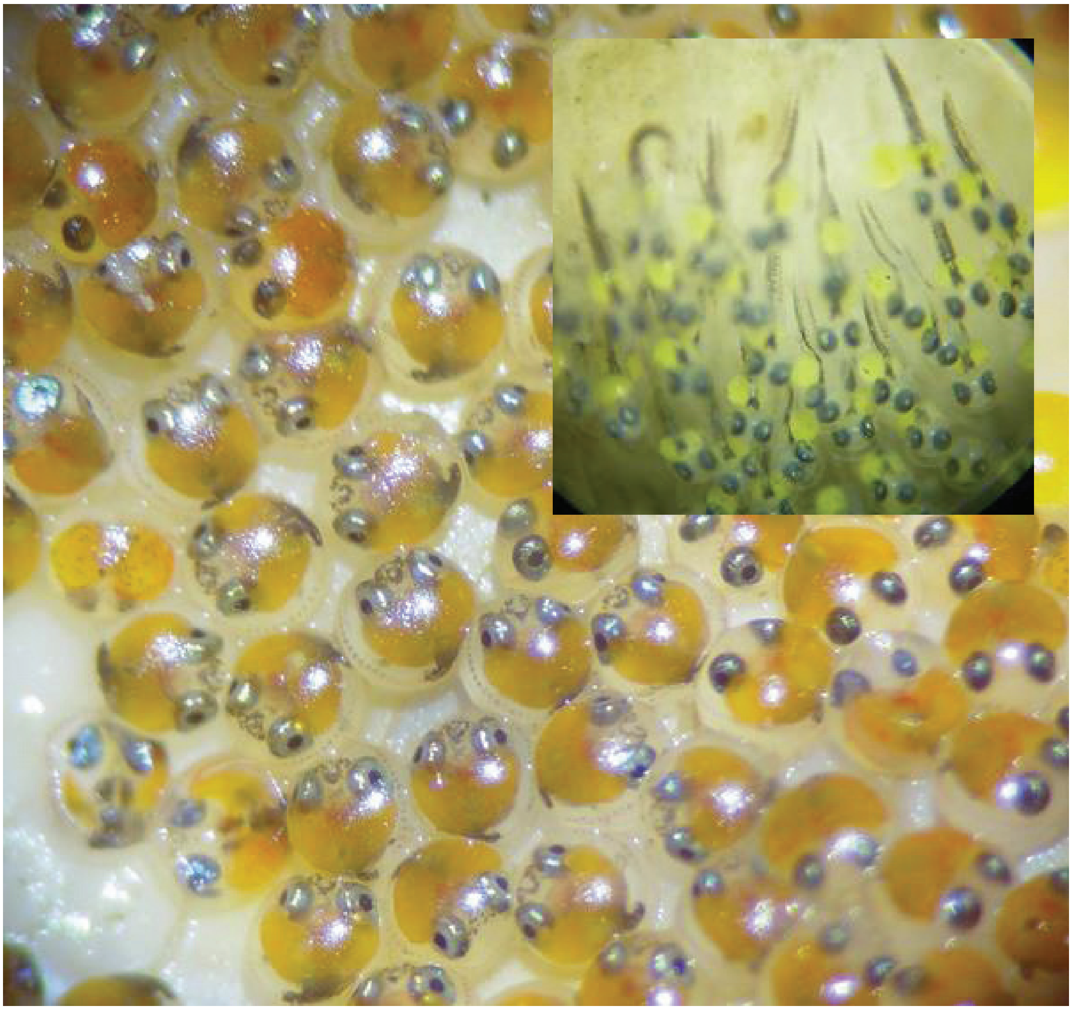

FIG. 6. Many thousands of adhesive eggs and yolk sac larvae (inset) of *Cryptocentroides gobioides* were found deposited on the inner surface of oyster shells deployed subtidally at both sites in October of both 2015 and 2016 (shell cultch treatment).

Table 4. Diversity of fish and invertebrate species observed to be associated with the natural shell cultch trays and three dimensional concrete spat collection units in Pumicestone Passage. Many species of coralline and encrusting algae, and colonial tunicates (*Symplegma* sp., *Botrylloides* sp.) were also evident (see Supplement Figure 5).

Common Name	Scientific Name	Months observed
Fishes		
Crested oyster goby	*Cryptocentroides gobioides*	Jan-Dec, Spawning in Oct
Estuarine stonefish	*Synanceia horrida*	Feb
Bengal sergeant	*Abudefduf bengalensis*	Jan-Dec
Fan bellied leatherjacket	*Monacanthus chinensis*	Aug
Highfin moray eel	*Gymnothorax pseudothyrsoideus*	Apr
Moses perch	*Lutjanus russelli*	Jan-Dec
False scorpionfish	*Centrogenys vaigiensis*	Nov
Silver biddy	*Gerres subfasciatus*	Jan-Dec
Striped cardinalfish	*Ostorhinchus fasciatus*	Apr
Bluebarred parrotfish	*Scarus ghobban*	Feb-Jun
Surgeonfish	*Acanthurus* sp.	Jan-Feb
Snapper	*Pagrus auratus*	May
Tarwhine	*Rhabdosargus sarba*	Jan-Dec
Yellowfin bream	*Acanthopagrus australis*	Jan-Dec
Crustacea		
Mud crab	*Scylla serrata*	Jan-Dec
Mangrove swimming crab	*Thalamita crenata*	Jan-Dec
Swimming crab	*Charybdis* sp.	Jan-Dec
Smooth handed crab	*Pilumnopeus serratifrons*	Dec-May
Porcellanid crab	F. Porcellanidae	Dec-Jun
Blue hermit crab	Clibanarius virescens	Jan-Dec
Xanthid crabs	F. Xanthidae	Jan-Dec
Greasyback prawn	*Metapenaeus bennettae*	Aug
Red handed shrimp	*Palaemon serenus*	Oct-May
Snapping shrimp	*Alpheus* sp.	Jun-Nov
Barnacles	*Balanus variegatus*	Jan-Dec
Unidentified amphipods	O. Amphipoda	Jun-Oct
Unidentified isopods	O. Isopoda	Apr-Dec
Molluscs		
Australian mud whelk	*Velacumantus australis*	Jan-Dec
Chiton	C. Polyplacophora	Jun
Dove snail	*Anachis* sp.	Jan-Dec
Moon snail	*Natica* sp.	Nov-Jan
Oyster borer	*Bedeva paivae*	Jan-Dec
Hairy mussel	*Trichomya hirsuta*	Spatfall Jan
Pale pearl oyster	*Pinctada albina*	Spatfall Mar-Jul
Pearl oyster	*Pinctada maculata*	Spatfall Mar-Jul
Pyramid periwinkle	*Nodilittorina pyramidalis*	Jul
Saddle shaped oyster	*Hyotissa imbricata*	Spatfall May-Sept
Sydney rock oyster	*Saccostrea glomerata*	Spatfall Oct-May
Sea hare	*Aplysia* spp.	Nov
Dendrodoris sp. ?	O. Nudibranchia	Aug-Oct

Ningi Creek in 1978/79 occurred between November and March, peaking in December. In the present study, recruitment was observed between October and May, peaking in January (Figures 3, 5), with the extended period possibly due to increased water temperatures around Ningi Creek in 2015/16 compared to 1978/79. When survival of settled spat was examined over several months n the monitor and clean treatments, it was evident that numbers of *S. glomerata* spat could build up over the summer months in both subtidal and intertidal areas, provided appropriate hard settlement substrates were provided (Figures 4, 5). Regular cleaning of settlement substrates appeared to improve spat settlement rates in intertidal areas, particularly in late summer (Figure 5), but lower survival of spat was observed in subtidal units given this treatment, particularly in February and March (Figure 5). A small number of spat (n = 12) were examined for infection by *Marteilia sydneyi* (causative agent of QX disease) in March 2016 but the parasite was not observed (B.K Diggles, unpublished data). Increased mortality rates of newly settled *S. glomerata* spat on subtidal collectors during February and March was therefore considered likely to be due to predation, as large numbers of fishes and crabs were observed to be closely associated with the subtidal units at that time of year. Reduced survival of newly recruited spat on subtidal units was observed only in the clean treatment (Figure 4, Supplement Figure 4), as a similar reduction in survival was not observed on subtidal units that were monitored only (Figure 4). This may suggest that the process of pressure cleaning the settlement units and removing films of silt and algae made newly settled spat more vulnerable to predation in subtidal areas, indicating that regular cleaning of settlement substrates is not necessary provided sufficient internal and inverted settlement areas are designed into spat settlement units to provide silt-free substrates for spat to attach.

Once recruitment ceased when water temperatures dropped below 24°C in May 2016, a steady rate of mortality continued throughout the autumn and winter months in all treatments, regardless of whether units were subtidal or intertidal (Figures 4, 5, Supplement Figures 3, 4). These mortalities of juvenile *S. glomerata* were apparently not due to infection by mudworm, but may have been due to QX disease, predation, or other causes including smothering due to blooms of cyanobacteria *Lyngbya* sp., brown algae *Ectocarpus fasciculatus* and/or jellyfish *Catostylus mosaicus*. Indeed, smothering by algae drifts (particularly *E. faciculatus*) may have contributed to mortality of juveniles during the cooler winter months when water clarity (and hence sun penetration) was highest, especially after water temperatures began to increase from their winter lows (Supplement Table 1, Supplement Figure 2). Historical studies of the population dynamics of oyster reefs in the United States found that natural mortality of oyster spat in the first year after settlement was around 50% (Winslow 1887). In the present study, survival of spat in the first year varied from a low of 16% for spat held subtidally on cleaned settlement units (Figure 4) to around 58% for spat held intertidally on uncleaned settlement units (Supplement Figure 3). In all treatments, the number of *S. glomerata* recruits began to increase again once water temperatures increased beyond 24°C in October 2016.

At no time during these experiments was there any evidence of infestation of any of the newly recruited *S. glomerata* by spionid mudworms. This provides further evidence to refute theories that introduction of "more virulent exotic species of mudworm" are responsible for loss of subtidal oysters in Australian estuaries (Ogburn et al. 2007). Observations from pre-eminent scientists at the time these losses began (Saville-Kent 1891), together with historical epidemiological evidence combined with modern scientific understanding of settlement cues and taxonomy of spionid polychaetes (Sebesvari et al. 2006; Read 2010; Walker 2011; Diggles 2013), all suggest that mudworm disease, (or, as Saville-Kent (1891) states "the mud disease") is not due to introduction of exotic species , but instead is due to "*the altered conditions of these rivers, brought about mainly through human agency*"(Saville-Kent 1891).

Regular (monthly) pressure cleaning of collectors to remove silt deposits and algal turfs increased *S. glomerata* spatfall on the vertical sides of collection units (particularly on intertidal units), as well as encouraged settlement of other bivalves including *Hyotissa imbricata*, *Pinctada albina*, and *Pinctada maculata*. These data suggest that an absence of clean settlement substrate significantly reduces mollusc biodiversity in Pumicestone Passage, which is consistent with knowledge that siltation and eutrophication result in greatly reduced species diversity in estuarine environments (Newell 2004; Kirby & Miller 2005; Grabowski & Peterson

2007; Beck et al. 2011; zu Ermgassen et al. 2016). Furthermore, these data suggest that loss of natural subtidal *S. glomerata* populations in Pumicestone Passage over the past 100 years is not due to a lack of available spat, but instead is probably due to multigenerational recruitment failure originating from a gradual reduction in availability of suitably clean spat settlement substrates (Diggles 2013).

Despite functional extinction of subtidal *S. glomerata* reef habitat in Pumicestone Passage (Diggles 2013), deployment of clean concrete blocks and shell cultch into subtidal areas resulted in successful recruitment of *S. glomerata* spat. Of these two settlement substrates, the natural shell cultch appeared far superior, attracting 10-90 times more *S. glomerata* spat and 28-135 times more invertebrates than concrete spat collection units on a unit weight basis (Tables 2, 3). When measured volumetrically, shell cultch remained superior to concrete spat collection units for attracting both *S. glomerata* spat (5–42 times more effective) and invertebrates (13–62 times more effective). The high attractiveness of natural shell cultch is likely to be due to its provision of chemical settlement cues (Tamburri et al. 2008, Vasquez et al. 2013), as well as its high surface area and high void volume (Kuykendall et al. 2015) with the shapes of the shells themselves providing a high percentage of nooks, crannies and rugosities including many inverted surfaces shielded from silt. Natural shell cultch is also advantageous for shellfish reef restoration due to its relatively light weight compared to concrete structures, making handling of raw materials easier, while the shells themselves become bound together into extensive reef systems by organic cement naturally secreted by recruited oysters (Burkett et al. 2010). Provided oyster shell cultch can be arranged into 3 dimensional high relief reefs (Schulte et al. 2009; Housego & Rosnam 2016) in hydrodynamically suitable arrangements (Colden et al. 2016), it would appear to be the best suited material for restoration of shellfish reefs in Pumicestone Passage either by itself (Burkett et al. 2010) or in conjunction with appropriate artificial base substrates that elevate and protect oyster shells from siltation (Sawusdee et al. 2015).

The now regular seasonal blooms of toxic and nuisance algae such as fireweed (*Lyngbya* sp.) and snotweed (*Ectocarpus fasciculatus*) together with high intensity of blooms of blue blubber jellyfish (*Catostylus mosaicus*) confirm that a significant reduction in environmental quality has occurred in Pumicestone Passage compared to historic baselines (Dennison and Abal 1999). Some authors have suggested that increased implementation of "no take" sanctuary zones will protect biodiversity and fisheries productivity in Pumicestone Passage and other areas of the Moreton Bay Marine Park (Pillans et al. 2007). However, when the mechanisms affecting this ecosystem are considered, it is clear that it will not spontaneously recover from its current degraded state if the remaining recreational fishing effort in Pumicestone Passage is removed (Diggles 2013). This is because "no take" sanctuary zones do not protect biodiversity whenever habitat and water quality are being degraded (Jones et al. 2004), highlighting an urgent need for active restoration (Creighton et al. 2015; Diggles 2015; Gilles et al. 2015a). The data collected here suggest that the processes driving changes to the Pumicestone Passage and wider Moreton Bay ecosystems appear primarily driven by declining water quality due to sedimentation, eutrophication and other anthropogenic changes derived from catchment development. Hindsight shows that these processes have been occurring for decades over many inshore ecosystems in Queensland (Roff et al. 2013), with the problem being no better articulated than by William Saville-Kent, who in his paper to the Queensland Parliament in 1891 observed:

"*Through the clearance of the land and the establishment of townships and settlements throughout the watersheds of these rivers, the rainfall which in former days fell upon and was more completely absorbed by the primeval forests is now carried quickly away, and emptied by drains and culverts into the watercourses communicating with the rivers. Simultaneously with this augmented discharge of water into the rivers a vastly larger quantity of sediment is brought down, accompanied by a considerable percentage of organic and chemical pollution that had no place in the composition of the water under those conditions in which the oysters originally grew and flourished. This greatly augmented accession of flood water, with its accompaniment of sediment and chemical pollution, cannot exert other than a very deleterious influence upon the riverine oyster fisheries*." (Saville–Kent 1891)

Because this process of degradation has been occurring for several human generations, it is important to recognise that shifting baselines (Pauly 1995; Papworth et al. 2008) already pervade management actions in Moreton Bay. This is demonstrated by review of historical management documents over time, which reveals that ecosystem health measurements[1] currently being made available to the public are not directly comparable to those from previous years (Dennison and Abal 1999). It is therefore very important that management and restoration efforts in Pumicestone Passage and wider Moreton Bay refocus on re-establishing baselines, and developing targets for restoration of water quality (e.g. nutrient and sedimentation reduction), habitat (e.g. regeneration of wetlands, seagrasses and shellfish reefs) and fisheries.

The results presented here confirm that *S. glomerata* spat can successfully recruit to hard subtidal substrates in Pumicestone Passage in the form of either shell cultch (with its high surface area and high attractiveness for conspecific spat and invertebrates) or artificial substrates which appear suitable provided they are designed with sufficient internal and inverted surface area to provide settlement substrates free of siltation. Observations of commercially important fish and invertebrates species associating with the experimental modules in the present study hint at a high likelihood of improved biodiversity and fisheries productivity if these reefs can be restored (Peterson et al. 2003; zu Ermgassen et al. 2016). However, more detailed study is required to properly quantify these biodiversity and fisheries productivity metrics. Nevertheless, these results suggest that restoration of subtidal shellfish reefs in Pumicestone Passage using natural recruitment processes remains feasible, with success most likely if appropriately designed clean settlement substrates (preferably natural shell cultch) are placed into the ecosystem during natural recruitment periods in late spring and throughout the summer months.

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1 http://healthywaterways.org/reportcard#overview/2016/condition

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Editor note. Supplementary material to this paper may be obtained at www.digsfish.com/roysocsupplementary.pdf

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Dr Ben Diggles is a marine biologist (University of Queensland) with over 25 years specialist experience in study of the health of aquatic animals and their environment. In his spare time, Dr Diggles studies the effects of declining water quality on our estuaries, and is active in his local community developing solutions to these problems, like shellfish reef restoration. Ben is also the great, great grandson of Silvester Diggles, who was a founder of the Queensland Philosophical Society (predecessor of the Royal Society of Queensland), and helped establish the Queensland Museum.