



Seagrass macrobenthic biodiversity does not vary in conformity with a leaky-lagoonal confinement gradient

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ABSTRACT

Coastal lagoon ecology often changes on progression from the open, well-flushed mouth region to the depositional zone furthest from the open sea. This is generally considered consequent on increasing 'confinement' and associated features, rather than on the often co-occurring decreasing salinity. The 12 km Rainbow Channel connecting part of Moreton Bay, a microtidal leaky lagoon, to the adjacent Pacific provides a gradient of increasing confinement without any significant salinity change, i.e. a tenfold increase in water residence time for a salinity decrease of <1 . Macrobenthic faunal assemblages characterising intertidal *Zostera* seagrass at strategic points along its length were compared to test whether their nature changed in conformity with confinement models. Results suggest that it does not; faunal abundance, species richness, evenness and composition remaining effectively unchanged along the gradient. Seagrass systems may constitute a special case because they decouple renewal times of the overlying water and local organic enrichment/decomposition; as may leaky lagoons because of their high tidal velocities.

1. Introduction

Moreton Bay (Quandamooka) in southeast Queensland is a large (c. 1500 km²), shallow, subtropical, leaky coastal lagoon (*sensu* Kjerfve, 1986), partially isolated from the Coral Sea region of the Pacific and the prevailing East Australian Current by a chain of four large sand-dune islands: Bribie (Booabee/Yarun), Moreton (Mulgumpin), North Stradbroke (Minjerribah) and South Stradbroke (Curragee/Durungjili) (McPhee, 2017). Most exchange between bay and adjacent ocean occurs through the North Passage between Bribie and Moreton, but some also takes place at other inter-island gaps, particularly through the South Passage between Moreton and North Stradbroke (Fig. 1). Water flow through the latter is directed along the east-west trending Rous Channel and the north-south aligned Rainbow Channel, and is up to 1.5 m s⁻¹ during flood tides although it flushes a very limited area of the bay (Dennison and Abal, 1999). The deep-water Rainbow Channel hugging the northwest coast of North Stradbroke is the more important of the two. It is some 12 km long and extends into the bay to 27°29.3'S (Maritime Safety Queensland, 2014) between Peel Island (Teerk Roo Ra) and the township of Dunwich (Gumpi). Even a small distance beyond its end, however, only just over half the local flushing occurs via the nearby

South Passage, the remainder being through the much larger North Passage some 50 km away, and water residence time increases to 40 days, compared to only 3–5 days at the Rainbow Channel's mouth (Dennison and Abal, 1999) — a residence-time gradient equivalent to that in the Venetian Lagoon (Solidoro et al., 2010).

Below the level of low-water neap tide, the Rainbow Channel supports well-developed seagrass beds on tidal-delta sands, dominated except near and below low-water spring by the dwarf-eelgrass *Zostera* (*Zosterella*) *muelleri capricorni* (Dennison et al., 2003) [= *Nanozostera capricorni* in the revision of the Zosteraceae by Coyer et al., 2013], together with some admixed *Halophila ovalis*. These beds are therefore located along a transitional zone from near oceanic conditions at one end to semi-enclosed, lagoonal ones at the other; part of a general water quality gradient in Moreton Bay, with increasing turbidity and nutrient content on progression away from the Pacific (Maxwell et al., 2014). Six rivers and many smaller creeks drain into the bay, though none into or near the Rainbow Channel and so although there may also be a salinity gradient along it this usually only amounts to some 1 unit at most (Milford and Church, 1977), its water being fully marine except immediately adjacent to the many freshwater springs that are the discharge points from North Stradbroke's > 1 km³ dune groundwater aquifer

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(Leach, 2011; Arnold et al., 2014).

This water-renewal-time gradient approximates those that are the subject of a series of similar conceptual models relating biological conditions in subsidiary semi-enclosed paralic water bodies to their degree of connection to the adjacent sea — the variously-named hypotheses of ‘organic enrichment’ (Pearson and Rosenberg, 1978; Magni et al., 2009), ‘confinement’ (Guélorget and Perthuisot, 1983, 1992), and ‘saprobity’ (Tagliapietra et al., 2012; Foti et al., 2014). Tagliapietra et al. (2012) provide summaries of the three models and show how they are inter-related. In general, the longer the water residence time (i.e. the greater the confinement), the less biodiversity and greater dominance by an increasingly limited number of environmentally-tolerant species are to be expected. These models were originally proposed to explain ecological structuring of coastal lagoons in land-locked European seas (see, e.g., Reizopoulou and Nicolaidou, 2004; Ghezze et al., 2015; Pérez-Ruzafa et al., 2019, 2020), in contrast to hypotheses of control by the often co-occurring gradients in salinity (Guélorget and Perthuisot, 1989), although the two potential forms of control are by no means mutually exclusive (Pérez-Ruzafa et al., 2011; Giangrande and Gravina, 2015).

Confinement processes have been argued to be characteristic only of microtidal situations (Barnes, 1994) [i.e. a tidal range <2 m in the system of Davies (1964), although see Tagliapietra and Ghirardini (2006) for alternative limits]. Tidal rise and fall along the Rainbow Channel are certainly within Davies’s microtidal range, with a mean spring tide of <1.5 m at its mouth and <1.8 m at its end (Maritime Safety Queensland, 2020), and water residence times do increase markedly along its length, as noted above. Tidal fluxes, however, are considerably larger than those characteristically associated with Mediterranean and similar lagoons (Umgiesser et al., 2014; Gravina et al., 2020), although Frénod and co-workers (Frénod and Goubert, 2007; Frénod and Rouseau, 2013) have argued that confinement processes can also explain benthic distribution patterns in paralic systems “even in strong tide regions” (Frénod and Goubert, 2007: 140). On these bases, environmental filtering of eelgrass macrobenthic assemblages (Namba et al., 2020) would be predicted to occur on progression along Rainbow Channel shores consequent on increasing confinement.

Previous studies of confinement gradients (e.g. Tagliapietra et al., 2012; Magni et al., 2022) have investigated effects on the macrobenthos but have not specifically concerned those of seagrass systems, except for

the abundance of different major taxa (Ocampo et al., 2020), or have done so in situations with potentially confounding salinity gradients (Tagliapietra et al., 2016; Magni et al., 2017). Therefore the Rainbow Channel seagrass beds provide an opportunity, in the absence of a salinity gradient, to test for the first time whether biodiversity metrics and assemblage composition of seagrass macrobenthos as a whole vary in conformity with the confinement and, by extension, related models.

2. Methods

2.1. Study area, sample collection and processing

Macrofaunal sampling was conducted over a period of 10 weeks during the 2022 austral spring at four strategic points along and beyond the eastern shore of the Rainbow Channel (Fig. 1): Pulan (27°24′33″S, 153°26′12″E) near its mouth; Capembah (27°28′01″S, 153°25′19″E) in its central region where water residence time begins to increase (Dennison and Abal, 1999); Gumpi (27°29′36″S, 153°25′55″E) at its southern extremity; and Deanbilla (27°30′33″S, 153°24′34″E), some 3 km beyond its end and separated from it by a headland. These are the same general areas as Moreton Bay Seagrass-Watch monitoring sites NS3, NS2, NS1 and NS4, respectively (McKenzie and Yoshida, 2013; WPSQCCS, 2016). Each seagrass site was sampled at some mean low-water level at three replicate stations at least 50 m apart, each station by a series of 20 randomly-placed cores, each core of 0.0054 m² area and 100 mm depth, i.e. a total of 60 replicate samples per site, with each core centred on one seagrass ramet. This relatively shallow core depth was adopted because most seagrass benthic macrofauna is known to be located at or near the sediment surface [e.g. 98% in the top 5 mm in the study by Klumpp and Kwak (2005) at other localities in Queensland]. Such a sampling procedure collects the smaller (<10 mm) and more numerous macrofaunal elements that usually constitute the large majority of shallow-water benthic invertebrate biodiversity, at least insofar as molluscs are representative (Bouchet et al., 2002; Albano et al., 2011), though not the meiofauna nor much scarcer megafauna nor sessile animals attached to the seagrass leaves. Warwick et al. (2006) have shown that different spatial patterning rules may apply to meiofauna and macrofauna (although see Magni et al., 2022), and likewise Davidson et al. (2004) and Leopardas et al. (2014) to sessile and motile species. Temporary

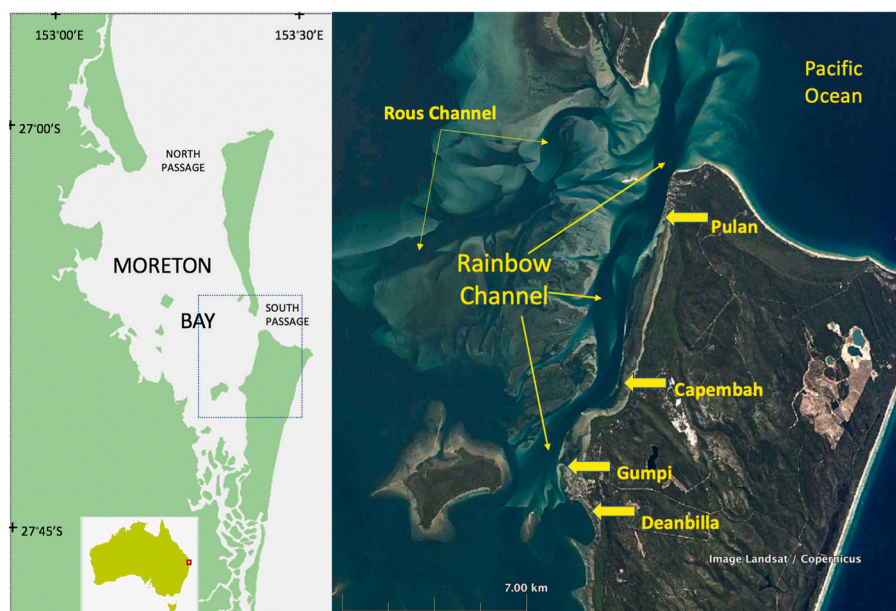


Fig. 1. Location of the Rainbow Channel, Moreton Bay, Queensland, and of the four study sites at critical points along and beyond it (Google Earth Pro satellite image © 2020 Landsat/Copernicus).

members of the benthos, such as the larvae of chironomid midges, were also excluded.

The seagrass fauna along the Rainbow Channel is known to display a long tail of rare species (Barnes, 2014a, 2017b), indicating marked undersampling bias (Coddington et al., 2009). At least one third of the local microgastropods, for example, have abundances $\leq 0.6 \text{ m}^{-2}$ and occupancies $\leq 0.3\%$ (Barnes, 2019b). Since very large numbers of samples would have to be taken simply to record their presence, let alone to determine if they were particularly characteristic of one point along the gradient, the survey was effectively restricted to the major elements of the fauna, not least so as to cause minimum disturbance to a Marine Protected Area, to a habitat type under worldwide threat (Waycott et al., 2009; Turschwell et al., 2021) and to one specifically protected under the Queensland Fisheries Act 1994. This is unlikely to have influenced conclusions, however, since assemblage structure is determined largely by the more numerous component species (Pos et al., 2014; Sgarbi et al., 2020).

Collection and treatment of samples followed the same procedure as earlier studies of macrobenthic assemblages associated with intertidal seagrass beds along the Rainbow Channel (Barnes, 2017a, 2020, etc.). Cores were collected during daylight hours some 90+ minutes before the point of low tide whilst the substratum was still covered by $> 15 \text{ cm}$ of water, and were gently sieved through $710 \mu\text{m}$ mesh on site. Retained material from each core: (i) was placed in a large polythene bag of local channel water within which all seagrass was shaken vigorously to dislodge all but sessile animals and then discarded; (ii) was re-sieved and transported immediately to a local laboratory, and (iii) was there placed in a $30 \times 25 \text{ cm}$ translucent tray over an A3 LED pad in which the living fauna was located by visual examination using 3.5x magnifying spectacles until no further animal could be observed. Animals were identified to species level wherever possible, with all organismal nomenclature being as listed in the World Register of Marine Species (www.marinespecies.org), accessed November 2022, and were then returned to their habitat. Several taxa, however, including polyclads, nemertines and various polychaete and peracaridan groups, although relatively important in Moreton Bay have not yet been investigated systematically in or near southern Queensland. Consequently, positive identification to named species was often not possible. Such animals were treated as morphospecies, an operationally appropriate procedure to detect spatial patterns of biodiversity and differential abundance (Dethier and Schoch, 2006; Albano et al., 2011; Pos et al., 2014). Although this incurs a high probability of failing to distinguish any closely similar species, experience of taxonomic resolution/sufficiency in other soft-sediment macrobenthic studies (e.g. Tataranni et al., 2009; Brind'Amour et al., 2014) indicates that operating at various levels from species up to family produces similar conclusions. The seagrass material from one core in each batch was used to estimate local *Zostera* leaf abundance by means of a 'shoot number x mean length' index.

Historical datasets from a spring 2013 study of macrofaunal patchiness in the seagrass beds and adjacent bare sandflats at each of the three southern Rainbow Channel sites (Capembah, Gumpi and Deanbilla) are also available (Mendeley data, VI, <https://doi.org/10.17632/xtjs527cgr.1> and [10.17632/h6y3bhbr7c.1](https://doi.org/10.17632/h6y3bhbr7c.1)) (see Barnes, 2014a). Each was based on 50 core samples of the same size as above per site (at $2 \times 25\text{-core}$ stations); were collected, sorted, etc. in identical fashion; and these datasets are here re-analysed for comparative purposes over this critical section of the confinement gradient.

At Capembah, Gumpi and Deanbilla, the overall macrobenthic abundances prevailing in the *Zostera* in both 2013 and 2022 [a range of $1886\text{--}2424 \text{ m}^{-2}$] were within those reported from the same time of year over the previous decade [$1635\text{--}3395 \text{ m}^{-2}$ (Barnes and Barnes, 2012; Barnes, 2014a; Barnes and Hamylton, 2019; Barnes, 2020; etc)] and could be considered representative of those sites. No earlier data are available for Pulan.

2.2. Analyses

Numbers of each component zoobenthic morphospecies at each station and site were subjected to similarity analysis, and assemblage metrics were derived and compared, all based on animal abundance. Univariate and multivariate assessments of assemblage similarity, calculation of biodiversity metrics, and statistical analyses were carried out using PAST 4.11 software (Hammer et al., 2001) or Microsoft Excel for Mac 16.67 with the StatPlus:mac Pro 8.0.1 add-on. All station and site datasets analysed were balanced (station replicates 20, site replicates 60; or for the 2013 data, station replicates 25, site replicates 50).

Univariate metrics assessed per unit area for each seagrass station and site were those known to have a major influence on local-scale biodiversity patterns (Blowes et al., 2022); i.e. (i) total macrofaunal numbers, (ii) observed numbers of morphospecies [N_0 , i.e. 'species density'] plus estimated real morphospecies density [Chao1 as modified by Chiu et al. (2014) and abundance-based coverage (ACE) estimates], and (iii) relative evenness or equitability (Pielou's J). In addition these were joined by (iv) the 'effective' or 'equivalent' number of morphospecies (i.e. Hill's N_2), (v) Berger-Parker dominance (D), and (vi) patchiness of faunal abundance [ascertained by spatial point pattern analysis using Lloyd's index of patchiness, I_p] to permit comparison with data from other intertidal seagrass species and localities obtained earlier (Barnes and Hamylton, 2019; Barnes, 2019a, 2020). Comparison of metrics used one-way ANOVA and post hoc Tukey HSD tests, where necessary after transformation of data to achieve homoscedasticity of variances; and potential correlations were assessed as the Spearman's non-parametric coefficient S_p . Relative importance of individual species within the macrofaunal assemblage at each site was assessed by the Index of Numerical Importance (INI) which combines data from both relative abundance and relative occupancy (Barnes, 2014b), and hence downplays the importance of animals such as *Circulus* which are superabundant in the relatively low-density burrows of alpheid or stomatopod shrimps (Goto and Sato, 2021). Differences in rank orders of INI were tested by Friedman non-parametric ANOVA.

Multivariate comparison of macrofaunal assemblage composition used hierarchical clustering analysis of S_{17} Bray-Curtis similarity, one-way ANOSIM and PerMANOVA, IndVal, and ordination by non-metric multidimensional scaling (nMDS) carried out on observed abundances standardised to the same station and site totals to reflect only differential taxonomic composition, all with 9999 permutations. Since significance levels in ANOSIM are very dependent on the number of replicate samples (Clarke and Gorley, 2009), and in a nested ANOSIM there would only be three nested stations per site, as previously (Barnes, 2020) one-way ANOSIM comparisons within and between sites were undertaken using the individual core samples as the replicates.

3. Results

Seagrass was present at the Deanbilla, Gumpi and Capembah sites in the form of extensive and interconnecting beds (at least subtidally). As earlier (Lyons et al., 2011), however, the beds at Pulan at the Channel's mouth were less extensive and were isolated within expanses of intertidal sandflat. Regardless of site, and as is usual in dwarf-eelgrasses growing on channel shores (Park et al., 2021), shoot length was always short (mean length $< 6 \text{ cm}$) but shoot density was high ($350\text{--}1200 \text{ 0.1 m}^{-2}$) (see, e.g., Barnes, 2020; Fig. 2) — unlike well beyond the end of the Channel in the lagoon where even intertidal *Zostera* leaf length was long and ground coverage was 100%. The *Zostera* shoot index along the Channel is displayed in Fig. 2; there was no significant variation across sites (ANOVA $F_{3,8} = 0.4$; $P > 0.7$), no significant linear trend in index value (Spearman $S_p = 0.28$; $P > 0.3$), and no correlation between the per-station value of the shoot index and local macrofaunal density (Spearman $S_p = 0.36$; $P > 0.2$) although there was such with the number of epifaunal microgastropods (Spearman $S_p = 0.69$; $P < 0.02$). There was no correlation between station sampling date over the 10 week study

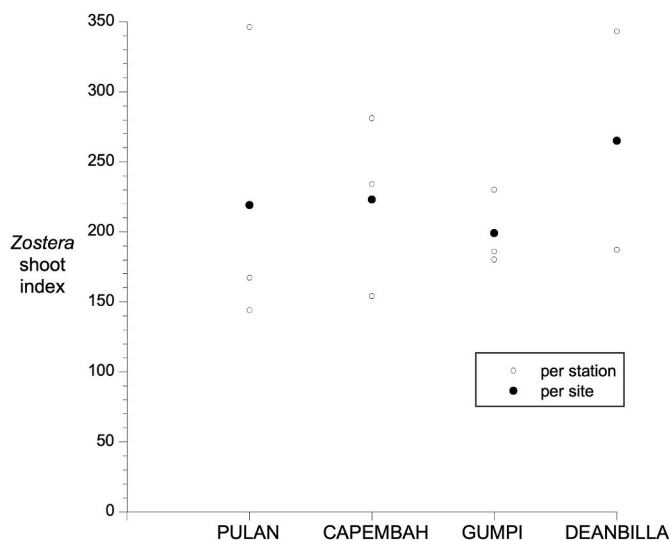


Fig. 2. Values of the *Zostera* shoot index (shoot number x mean length) at sites along the Rainbow Channel in 2022 (replicate measures, open circles; mean values per site, large filled circles).

period and value of shoot index or of any assessed faunal metric (Spearman $P > 0.25$).

Analysis of the 2022 data was based on a total of 2542 individual animals representing 145 morphospecies in the *Zostera*; the four sites each supporting 1582–2293 individuals m^{-2} and 68–88 morphospecies. The 2013 database contained 140 morphospecies and 1839 individuals. The Channel intertidal fauna was dominated by polychaete annelids, malacostracan crustaceans and gastropod molluscs which comprised a constant 90–95% of the assemblage individuals and 77–82% of its morphospecies across the various sites. 31% of the taxa were represented by only a single individual or were present only in a single core sample; these rare species were evenly distributed across the four sites, each supporting 33–41% of singleton/unique taxa. Estimated real overall taxon density was therefore likely to be some 40% higher than that observed.

Per-site and per-station values of the six assessed univariate metrics are shown in Fig. 3. One-way ANOVA of the data disclosed no significant differences in abundance, species density, evenness or any of the other metrics along the Rainbow Channel (all ANOVA $F_{3,8} < 3.3$, $P > 0.08$); neither, with one marginal exception, did the values of any metric significantly increase or decrease along the Channel's confinement gradient (Spearman $P > 0.1$). The exception was a significant increase in numbers of species per station away from the mouth (Spearman $S_p = 0.59$; $P = 0.046$). The same generalities apply to that critical section of the Channel between Capembah and Deanbilla along which confinement increases steeply (Spearman $P > 0.3$; ANOVA $F_{2,6} < 3.2$, $P > 0.1$). Values of abundance were lowest, however, at the three Pulan stations, i. e. the site nearest the Channel's mouth.

Multivariate analyses of assemblage compositional (dis)similarities within and between sites are shown in Table 1. The very low values of all ANOSIM R obtained (i.e. an overall mean of 0.18) generally indicate a large degree of overlap between sites and, within sites, between stations, albeit that such differences as did occur were all significantly above zero ($P < 0.001$). It is also clear that in 2022 there was little difference in the magnitude of within-site and between-site compositional (dis)similarity (ANOVA of within-site and between-site Bray-Curtis values indicating no significant difference between the two, $F_{1,8} = 0.03$, $P > 0.8$); and no difference in the between-site values for adjacent and non-adjacent sites (ANOVA $F_{1,4} = 1.95$, $P > 0.2$). The same statistical result was forthcoming with values of ANOSIM R ($P > 0.6$ and > 0.2 respectively). These generalities also characterised the same seagrass beds ten years earlier (Table 2), except that within-site similarity was then particularly low

across the two Capembah stations; nevertheless there was no difference in within-site and between-site Bray-Curtis similarity then either ($t = 1.94$, $P > 0.1$). At the same time, although within-site and between-site compositional similarities were also generally very high in the adjacent sandflats, in these associated systems values of overall macrofaunal abundance and species density did in contrast appear to respond to the Channel's longitudinal gradient (Table 3); in respect of abundance not least because of decline in numbers of the dominant species, the haustorioid amphipod *Urohaustorius*, from >1500 to $<230 m^{-2}$. Ordination of proportional assemblage compositional data at the twelve 2022 seagrass stations by nMDS is displayed in Fig. 4. This plot shows that although the Capembah and Gumpi sites did segregate separately, each with its own characteristic fauna, two of the Pulan stations and the whole Deanbilla site shared a very similar taxonomic structure notwithstanding that they are at opposite ends of Channel.

The six numerically most-dominant invertebrate taxa in the Rainbow Channel seagrass in 2013 and 2022, together comprising $>50\%$ of the assemblage individuals, are listed in Table 4, together with their relative importances at each site: these INI rank-orders at the different sites were not significantly different (Friedman ANOVA: 2013, $\chi^2 = 0.14$, $df 2$, $P > 0.9$; 2022, $\chi^2 = 1.05$, $df 3$, $P > 0.8$). Most of the more numerous species, and virtually all those that dominated individual local faunas, occurred at all four sites from mouth to channel end (i.e. all but one of those 14 species that occurred at an overall density $>50 m^{-2}$). These thus formed the nucleus of a common pool of species, which in both 2013 and 2022 and at all sites along the Channel were dominated by the tiny (mostly <5 mm) macrophthalmid crab *Enigmaplax*, the <2.5 mm truncatelloid microgastropod *Calopia*, and the <4 mm haustorioid amphipod *Limnoporeia*. Such differences between sites as did occur were then consequent on the relative importance of widespread species such as the apseudoid tanaid *Longiflagrum*, the nassariid gastropod *Tritia* and the polychaetes *Prionospio*, *Goniada*, *Malacoceros* and *Notomastus* whose abundances, although in some cases (*Goniada*, *Malacoceros* and *Prionospio*) distributed non-uniformly along the Channel (ANOVA $F_{3,8} > 0.45$; $P < 0.05$), nevertheless showed no significant relationship with its longitudinal gradient (Spearman $P > 0.1$). [N.B. The occurrence of what appears to be the polyclad *Prosthlostomum amri* at Gumpi and Deanbilla is noteworthy because it is otherwise known only from the type locality, in *Zostera* in Lake Macquarie, a sea-water lagoon 850 km to the south (Rodríguez et al., 2021).]

4. Discussion

Although its overlying water is fully marine, the species characterising the Rainbow Channel seagrass fauna include those regarded as typically 'estuarine' by Hutchings and Murray (1984) and Ponder et al. (2000), and indeed many occur widely in eastern Australian estuaries as far south as Tasmania (Hirst and Kilpatrick, 2007). They are also classically 'paralic' in the terminology of Guélorget and Perthuisot (1983); i. e. comprise the type of assemblage generally exemplifying shallow, sheltered, semi-enclosed, coastal soft-sediment habitats regardless of salinity (Day, 1959; Barnes, 1989).

On the basis of confinement and related models (e.g. Guélorget and Perthuisot, 1992), there is an expectation that the nature of these macrobenthos along the water-renewal-time gradient of the Rainbow Channel should display, albeit maybe with some minor variation (e.g. Magni et al., 2009), a general pattern of decreasing species richness away from the most open-water Pulan site and decreasing evenness of abundance consequent on increasing importance of a few opportunistic species. Instead, there was no statistically-significant variation or correlation with position along the Channel in their overall assemblage abundance, estimated real morphospecies density, evenness or most other assessed metrics, including patchiness, nor in their taxonomic composition except for differential local abundances of some subdominant (mainly polychaete) species. There was, however, a significant change in observed species density along the gradient, but that was a

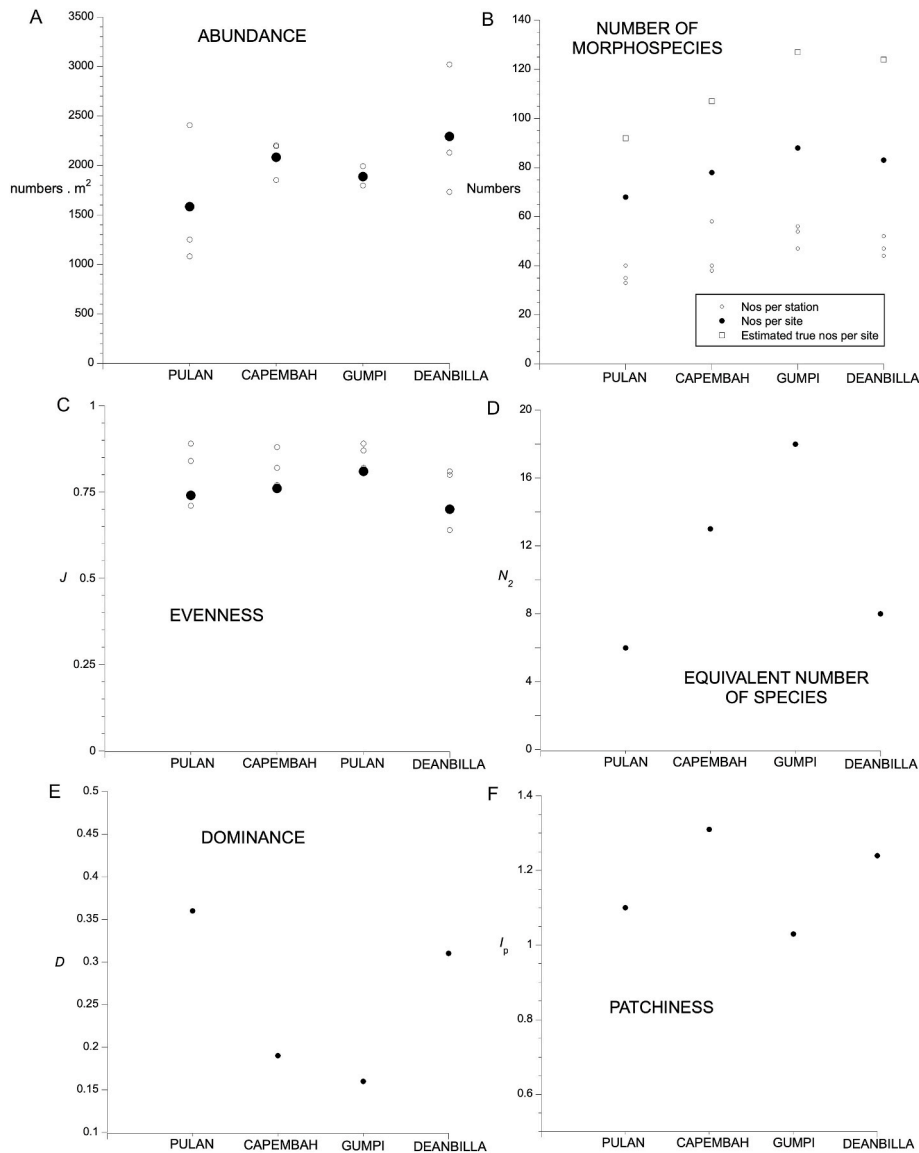


Fig. 3. Variation along the Rainbow Channel in 2022 in per-station (0.11 m^2) and/or in per-site (0.325 m^2) univariate invertebrate biodiversity metrics: (A) total macrofaunal abundance m^{-2} , (B) observed and estimated-real N_0 morphospecies density (average value of Chao1 and ACE estimates), (C) J evenness, (D) N_2 effective or equivalent number of taxa, (E) Berger-Parker dominance (D), and (F) Lloyd's I_p assemblage patchiness. [Mean or overall values per site in filled circles.].

increase in richness not a decrease. Neither were there indications of any expected confinement-related patterns in earlier macrofaunal assemblage data along the stretch between Capembah and Deanbilla (Barnes and Barnes, 2012; Barnes, 2014a) across which most change in water renewal time occurs (Dennison and Abal, 1999). It is often the case (e.g. McCloskey and Unsworth, 2015; Barry et al., 2021) that a significant correlation occurs between overall macrofaunal abundance and the amount of *Zostera* available. Such was not the case in the present study, however, except in respect of the presumed leaf-associated and microphytobenthically-feeding microgastropods.

There are several reasons why such a mismatch with the confinement (or any other) gradient might occur. First, seagrass beds and other structurally complex systems (Hyman et al., 2019) seem generally to support macrofaunal assemblages that display a considerable degree of spatial and temporal stability of abundance and composition, and high levels of resilience (Whanpetch et al., 2010; Gartner et al., 2015). Such relative spatial uniformity and/or temporal constancy characterises, for example, the seagrass macrobenthos within individual Rainbow Channel sites, at Gumpi (Barnes, 2020) and Deanbilla (Barnes and Hamylton, 2019), as well as those of Moreton Bay in general in response to flooding

events (Connolly et al., 2018). Earlier work on variation in macrobenthic seagrass assemblages along a similarly microtidal but there estuarine gradient in South Africa (Barnes, 2022) has indeed suggested that the presence of the vegetation cover permits individual macrobenthic components to occur across longer stretches of the estuary than is the case in adjacent unvegetated sediments, the seagrass assemblage composition manifesting little change over relatively large distances upstream. The 2013 sandflat data from the southern Rainbow Channel sites do not contradict such a notion.

Granted the lack of relationship of seagrass macrofaunal abundance and biodiversity to the marked confinement gradient provided by the Rainbow Channel, it might be tempting to associate this with the lack of a co-occurring salinity gradient, and hence to conclude that generally salinity is a much more potent variable in lagoonal systems than confinement. This may indeed be the case, but matters along the Moreton Bay gradient in question are not so simple, and they are relevant to differences between the various conceptual models proposed in explanation of lagoonal gradients. The present study specifically considered the confinement model because data were available on water residence times along the Rainbow Channel, whereas they were not so in respect of

Table 1

Multivariate comparison of macrobenthic assemblage composition within and between four intertidal seagrass sites along the Rainbow Channel in 2022, based on untransformed abundance data.

	ANOSIM DISSIMILARITY (R)/PerMANOVA (F)	P	BRAY-CURTIS SIMILARITY
Within-site comparisons:			
Pulan	0.29/5.20	<0.0001	0.43
Capembah	0.09/2.07	<0.001	0.55
Gumpi	0.14/2.75	<0.0001	0.55
Deanbilla	0.15/3.07	<0.0001	0.48
Comparisons between adjacent sites:			
Pulan & Capembah	0.29/11.58	<0.0001	0.43
Capembah & Gumpi	0.19/7.62	<0.0001	0.48
Gumpi & Deanbilla	0.18/7.69	<0.0001	0.53
Other between-site comparisons:			
Pulan & Gumpi	0.20/8.23	<0.0001	0.48
Pulan & Deanbilla	0.16/7.18	<0.0001	0.56
Capembah & Deanbilla	0.13/5.76	<0.0001	0.57

Table 2

Variation in seagrass assemblage metrics and compositional similarities across the southern sites of the Rainbow Channel ten years previously (from data of Barnes, 2014a, with Bray-Curtis values taken directly from that paper).

UNIVARIATE BIODIVERSITY METRICS			
	Capembah	Gumpi	Deanbilla
Overall numbers. m ⁻²	2423	2098	2298
Observed N ₀ species density	83	88	76
J evenness	0.74	0.81	0.77
MULTIVARIATE COMPOSITIONAL RELATIONSHIPS WITHIN AND BETWEEN SITES			
	Bray-Curtis similarity	ANOSIM dissimilarity (all P < 0.0001)	
Between sites			
Capembah: Gumpi	0.52	R = 0.17	
Gumpi: Deanbilla	0.61	R = 0.15	
Capembah: Deanbilla	0.62	R = 0.12	
Within sites			
Capembah	0.37	R = 0.56	
Gumpi	0.45	R = 0.28	
Deanbilla	0.56	R = 0.13	

organic matter deposition, burial or metabolism. In most benthic aquatic circumstances, however, rates of input, decomposition and catabolite-removal of organics are related to flushing time of the overlying water mass (Tagliapietra et al., 2012). Hence Tagliapietra et al. (2012) and Foti et al. (2014), borrowing the concept from early freshwater pollution studies (Sládeček, 1965), considered the saprobity hypothesis to encompass and unify both the organic-enrichment and seawater-renewal-time models. Seagrass beds, however, can be considered a special case by virtue of their modification of near-seabed conditions (De Falco et al., 2000; Magni et al., 2008). The vegetation across the sediment/water interface creates its own micro-environment in which local flow rates are reduced (Fonseca et al., 2019), fine particles are trapped, and particulate organic matter is produced, entrapped and buried in the sediments (Miyajima et al., 1998; Cuellar-Martinez et al., 2019). They also render the sediment organic-rich by virtue of their extensive root and rhizome network. Although organic materials may be exported from such meadows by tidal and storm action (Ward et al., 2021), many are known to function as significant stocks of blue carbon (Fourqurean et al., 2012; Duarte, 2017), a role known to be performed by those along the Rainbow Channel (Samper-Villarreal et al., 2018). Therefore, local organic enrichment above and below the sediment and

Table 3

Variation across the southern sites of the Rainbow Channel in 2013 in the macrofaunal assemblages of the bare sandflats located adjacent to the seagrass beds that form the subject of Table 2 (from data of Barnes, 2014a, with Bray-Curtis values taken directly from that paper).

UNIVARIATE BIODIVERSITY METRICS			
	Capembah	Gumpi	Deanbilla
Overall numbers. m ⁻²	1891	1092	648
Observed N ₀ species density	26	22	21
J evenness	0.30	0.61	0.34
MULTIVARIATE COMPOSITIONAL RELATIONSHIPS WITHIN AND BETWEEN SITES			
	Bray-Curtis similarity	ANOSIM dissimilarity (all P < 0.0001)	
Between sites			
Capembah: Gumpi	0.49	R = 0.11	
Gumpi: Deanbilla	0.47	R = 0.13	
Capembah: Deanbilla	0.34	R = 0.16	
Within sites			
Capembah	0.45	R = 0.16	
Gumpi	0.37	R = 0.51	
Deanbilla	0.48	R = 0.11	

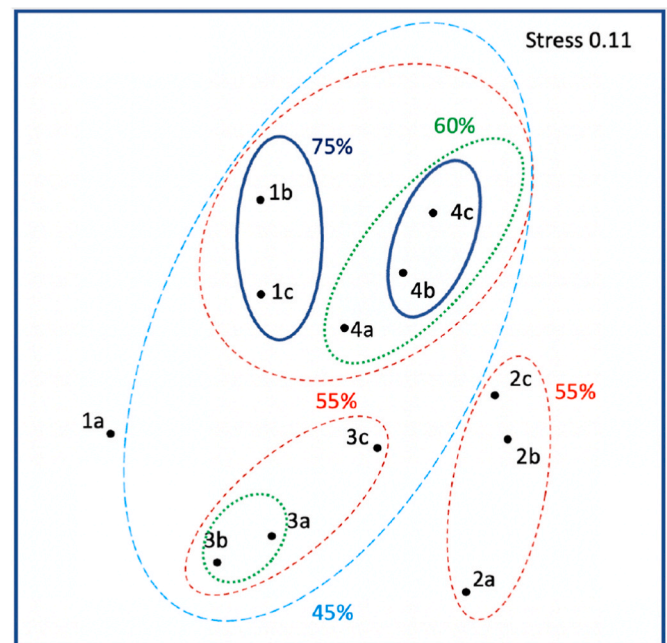


Fig. 4. Variation in proportional taxonomic composition of macrobenthic seagrass assemblages along the Rainbow Channel in 2022: Patterns of Bray-Curtis similarity as indicated by ordination by nMDS. Envelopes enclose stations clustered at the stated levels of similarity. [Sites are numbered from north (oceanic mouth) to south (enclosed lagoon) along the Channel, i.e. 1 = Pulan, 2 = Capembah, 3 = Gumpi, and 4 = Deanbilla; replicate stations at each site are labelled a, b and c.]

renewal times of the overlying water mass are to a considerable degree decoupled in seagrass beds. In addition, the net production and translocation of oxygen by the plants also impacts on the potential anaerobiosis often associated with organic accumulation in the sheltered surface sediments inhabited by the associated fauna of such systems (Borum et al., 2006). Anaerobiosis acts as strong environmental filter, but seagrass can ameliorate the local conditions from the perspective of several benthic species (de los Santos et al., 2020).

A further reason why the seagrass-associated fauna may not obey general confinement models relates to the requirements of the ecosystem-engineering macrophyte itself. Eelgrass distribution in

Table 4

Rank orders of importance of the six overall most numerically-dominant macrobenthic morphospecies in MLW *Zostera* along the Rainbow Channel in 2022 and in 2013, as measured by the Index of Numerical Importance. The species displaying the highest indicator value (IndVal) at each site is asterisked. Note that the top three are the same in each year. [Key to animal taxa: G = gastropod mollusc; M = malacostracan crustacean; P = polychaete annelid. 'Rare' indicates that, although present, the taxon concerned was not amongst the top 20 species at that site.]

MACROFAUNAL TAXON	SITE				OVERALL RANK
	Pulan	Capembah	Gumpi	Deanbilla	
2022					
<i>Enigmaplax littoralis</i> (M)	2	1	1	2	1
<i>Calopia imitata</i> (G)	1	3	5	1*	2
<i>Limnoporeia ? yarrague</i> (M)	4	7	2*	3	3
<i>Prionospio ? tridentata</i> (P)	rare	2*	rare	12	4
<i>Tritia burchardi</i> (G)	6	14	4	7	5
<i>Goniada ?tripartita</i> (P)	3*	rare	8	14	6
2013					
<i>Enigmaplax littoralis</i> (M)		1*	1	1	1
<i>Calopia imitata</i> (G)		2	2	2	2
<i>Limnoporeia ? yarrague</i> (M)		3	3	4	3
<i>Longiflagrum caeruleus</i> (M)		rare	4*	5	4
<i>Leptochelia opteros</i> (M)		4	9	9 =	5
<i>Malacoceros ?divisus</i> (P)		7	rare	3*	6

relation to shelter gradients, and the effects of shelter on its productivity, leaf surface area and other features relevant to the associated macrobenthos, seem to have received little detailed attention, but it is nevertheless clear that *Zostera* species are specifically characteristic of areas sheltered from strong water currents and large waves (Turner and Schwartz, 2006; Gamble et al., 2021) which induce sparse seagrass cover and low plant density and biomass (Schanz and Asmus, 2003). In Port Phillip Bay, Victoria, for example, *Z. muelleri* occurs in sheltered areas with mean wave heights <0.38 m (Hirst et al., 2017). Work on the related *Z. noltei* in the German Wadden Sea (Schanz and Asmus, 2003) suggests that exposure to strong tidal flushing may have been directly reflected in the scarcity of *Z. muelleri*, both in overall area of beds and locally in density, at Pulan. The confinement model, however, is predicated on the fact that water renewal times are shortest (because current velocities are greatest) in the vicinity of lagoonal mouths, and in leaky lagoons such velocities can be large. In the South African Knysna estuarine bay with its large tidal fluxes through the mouth region, for example, areas on the tidal delta sands support only ephemeral and/or patchy beds of *Z. capensis* (Barnes et al., 2023). The same appears to be true of *Z. muelleri* at Pulan (WPSQCCS, 2016; Maxwell et al., 2019). Such temporal and spatial instability of the substratum and seagrass covering are likely to have adverse knock-on effects on the ability of various associated faunal elements to persist, contribute to local species richness and hence constitute the high end of a confinement-related biodiversity gradient.

There may therefore be a limit to the Frénod and Goubert (2007) contention that confinement models also apply to strongly tidal systems, and they may not apply to those with fluxes capable of creating mobile deltaic sediment fans, to leaky lagoons in general, and/or to those with greater than nanotidal ranges (Tagliapietra and Ghirardini, 2006). Nevertheless, even allowing for the particular circumstances of the northern section of the Rainbow Channel mouth by omitting the Pulan

site from analyses, the seagrass macrobenthos of the critical section of the gradient from Capembah to Deanbilla still did not show the type of changes in composition, abundance or biodiversity expected of a confinement-gradient sequence, and hence it is likely that the special nonconformist attributes of seagrass beds extend to all types of semi-enclosed lagoonal situation.

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Author statement

Prof Richard S.K. Barnes was responsible for all aspects of the research and of production of the manuscript and figures.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The morphospecies abundance data on which this paper is based are uploaded to Mendeley Data (doi: 10.17632/3626smzdd8.1).

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