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The meaning of Benthic Ecological Quality status through a warm temperate South African estuary and in a contained blind-ending marina

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ABSTRACT

Successful management relies on accurate information on local environmental health. A typical macrofaunal assemblage-composition index, the BO2A (Benthic Opportunist Annelids Amphipods) considered to quantify benthic estuarine quality particularly well, was measured throughout the Knysna estuarine system (the one with the highest South African biodiversity and conservation rating, and considered 'largely natural with few modifications'), including in a blind-ending small-boat harbour. All index levels were represented across its intertidal and subtidal areas of bare sediment and seagrass beds, from <0.001 (='high' quality) to 0.240 (='poor' quality). Overall, BO2A did indeed suggest 'good' ecological quality. Nevertheless, only 25% of individual sites displayed 'high' quality; most were rated at the lower levels normally taken to indicate some degree of environmental degradation. The abundance of opportunistic annelids, which averaged 1153 m^{-2} (16% of total macrofaunal numbers), did not vary along its longitudinal axis, and neither did the index. BO2A proved directly related to log $[p/(1-p)]$ where p = proportion of just the opportunistic annelids. As in other equivalent marinas, these annelids also dominated the small-boat harbour, and this showed some evidence of faunal impoverishment relative to adjacent backwaters but its benthos displayed little relationship with the degree of faunal confinement. The record of a spadellid chaetognath from the harbour access channel appears to be the first from Africa. As predicted by the Estuarine Quality Paradox, being based on the questionable assumption that the presence of certain animals considered to be opportunistic indicates unnatural, degraded conditions, macrofaunal composition indices do not contribute unambiguous data to the environmental assessment of brackish-water habitats.

1. Introduction

The Knysna estuarine bay in South Africa's Western Cape is that country's topmost ranked estuary in terms of conservation importance and biodiversity, and it forms part of the Garden Route National Park (Hayes et al., 2022). Knysna is also a sizable town (±75000 inhabitants) and an important domestic and international tourist destination, being ranked in the top 20 best tourism destinations in the world in 2021 (SA Tourism, 2022). There are no reliable statistics on how many annual tourist visits it receives, but one estimate is for this to vary around 500000 (Knysna, 2019). The waterbody is a (probably *the*) major reason for its popularity (Whitfield et al., 2023), and hence it is not surprising that, notwithstanding its high conservation status, amongst other leisure-related facilities, a number of marinas and small-boat harbours have been constructed there. Recently, the benthic invertebrate fauna of the largest of these, the Thesen Islands Residential Marina complex, was investigated by Barnes and Seath (2024), and contrary to general expectation (e.g. Guerra-García et al., 2021), it was found to support rich subtidal macrobenthic assemblages, with considerably more species than any other such marina known to date. One of the main reasons for this healthy state was considered likely to be a design with two opposing entrance/exits to its 25 ha canal system and a through-flow of tidal water between them, passing in one direction at times of high tide and reversing during low tide as a result of the differential rate of rise and fall of water in the two estuarine channels to which it is connected (Schumann, 2004).

Other Knysna marinas, however, have only the standard single entrance/exit, but as yet nothing is known of their benthic invertebrate

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faunas. One such is the small Leisure Isle Boat Club harbour (34°03′40″S, 23°03′18″E) connected to the backwater Steenbok Channel by a 165 m dredged passage, and located only some 1 km from that of the Thesen marina complex (Fig. 1). This harbour has a surface area of ≈0.8 ha and an entrance 34 m wide, and can accommodate up to 250 small (i.e. <6.1 m long) boats with draughts ≤0.6 m. The Steenbok Channel empties into the larger (though still backwater) Ashmead Channel to which one of the two entrance/exits of the larger Thesen marina also connects, the two marinas both being sited in the same system compartment of the Knysna inlet, its outer, well-flushed, fully marine bay (Human et al., 2020). Investigation of this Leisure Isle harbour was carried out with three main aims. First, their very close geographical proximity permitting differences in environment and locally available species pool largely to be eliminated, it was possible to assess the significance of the marked difference in their basic design by using exactly the same procedures and techniques as earlier deployed in the adjacent Thesen system. Accordingly, one hypothesis to be tested was that in contrast to the latter but like other blind-ending marinas throughout the world (Guerra-García et al., 2021), the macrobenthos of the Leisure Isle harbour is impoverished relative to any equivalent site in Thesen and dominated by opportunistic annelids instead of crustaceans. Secondly, although other seemingly equivalent marinas support restricted faunal assemblages in comparison to those outside their entrances, it is not known how rapidly within the confines of such enclosed areas these effects are manifested. The present study therefore sought to examine the extent to which macrobenthic faunal abundance, biodiversity and Ecological Quality Status (EQS) varied in magnitude within the harbour with distance from the single entrance/exit point. Thirdly, the study also raised an important general question of the value of EQS as determined by macrofaunal assemblage indices in an estuarine or lagoonal context. Successful conservation management requires accurate information on health of the environment concerned, but the degree to which this can be assessed via biotic indices is questionable in such habitats, because their use may potentially lead to entirely natural systems being assessed as degraded (Elliott and Quintino, 2007; Dauvin, 2007). Local environmental context is all-important for the establishment of marina management regimes (Guerra-García et al., 2021) and this context for both marinas was provided from recent historical databases by investigation of the relationship between the frequencies of known groups of opportunistic annelids and of disturbance- or pollution-sensitive amphipods in the soft-sediment benthos throughout the inter- and subtidal zone of the surrounding estuarine-bay system as a test for the validity of establishing EQS by use of biotic indices based on macrofaunal assemblage composition (Grall and Glémarec, 1997).

The construction of estuarine marinas is unlikely to reduce over the next few decades (Skarzauskiene et al., 2022), nor are disturbances to estuarine habitats generally, and data such as produced by this study hopefully should inform processes of site location, environmental impact assessment, and the effectiveness of macrofaunal assemblage composition as a management tool not only in marinas but generally in estuaries and similar paralic or transitional wetlands.

2. Methods

Using snorkel, a total of 27 subtidal core samples was taken in a spatially referenced grid across the entire bed of the Leisure Isle Boat Club harbour in the spring of 2024, with individual samples being set 17–20 m apart in four rows ≈20 m apart, together with a further five samples along the entrance/exit channel that connects it to an adjacent backwater creek (Fig. 1). This scheme was adopted to ensure complete coverage of the harbour bed and to facilitate analysis of potential confinement effects. Each core was of 0.0054 m^2 area and 10 cm depth, thus collecting the smaller and most numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity (Albano et al., 2011). Retained material from each core was sieved on site through 710 μm mesh, was then transported to a local laboratory and was there placed in a 30 × 25 cm translucent dish over a LED pad in which the living fauna was located by visual inspection. A total of 32 core samples of those dimensions is the same as those taken from each region of the Thesen marina (Barnes and Seath, 2024) and from adjacent areas of the Ashmead Channel (Barnes and Claassens, 2020; Barnes and Seath, 2024).

Because of taxonomic uncertainty, including amongst numerically-dominant South African animal groups (see e.g. Simon et al., 2022), identification of collected fauna was generally attempted only to morphologically-based operational taxonomic units ('morphospecies'),

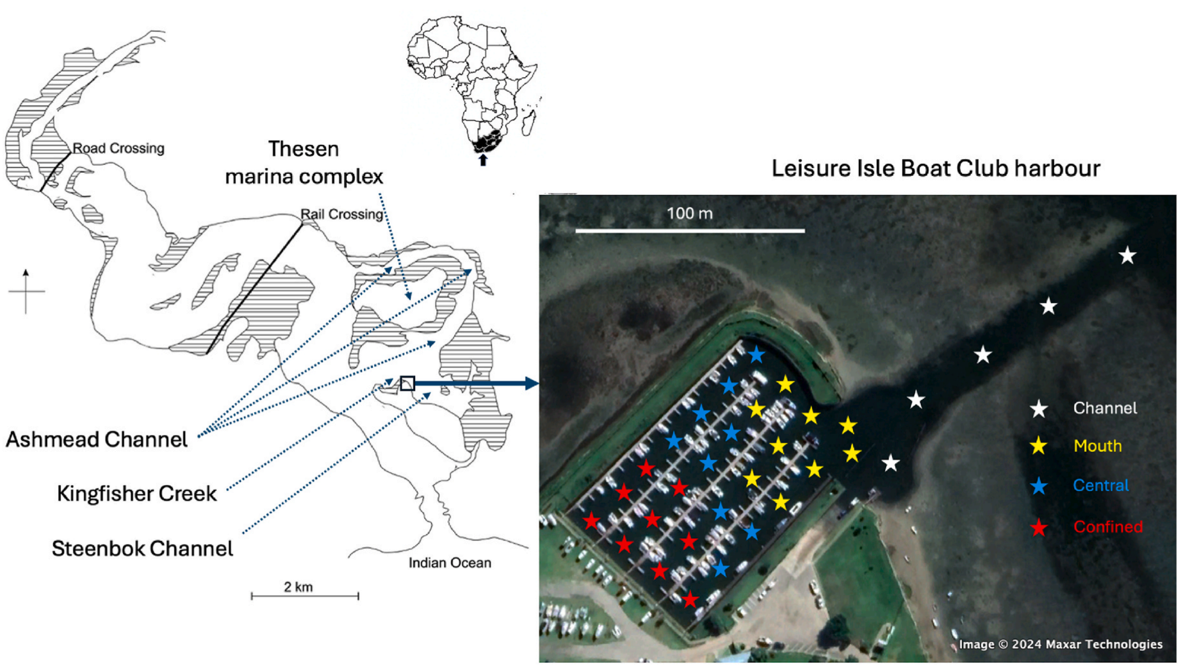

Fig. 1. The Knysna estuarine bay, showing the location of the Leisure Isle Boat Club harbour, and, in it, of the sampled sites in relation to its single entrance/exit (Google Earth image).

an appropriate procedure to detect spatial patterns of numbers of taxa and their differential abundance (Dethier and Schoch, 2006; Gerwing et al., 2020). Wherever possible, however, all animals of particular importance were identified to the lowest taxonomic level currently recognised. Although this incurs a risk of failing to distinguish any closely similar species, experience of taxonomic resolution/sufficiency in equivalent soft-sediment macrobenthic studies (e.g. Tataranni et al., 2009; Kokesh et al., 2022) indicates that operating at various levels from species up to family all produce similar conclusions. Nomenclature below is as given by the World Register of Marine Species (WoRMS, www.marinespecies.org, accessed October 2024).

Number per unit area of each component zoobenthic morphospecies was assessed in relation to their distance from the entrance/exit to the marina, and assemblage data were derived and compared via *PAST* 4.15 software (Hammer et al., 2001) or Microsoft Excel for Mac 16.89 with the StatPlus:mac Pro 8.0.4 add-on, all metrics being based on animal abundance. Univariate assemblage metrics assessed were those that have been argued to have a major influence on local-scale biodiversity patterns (Santini et al., 2017; Blowes et al., 2022): (1) overall faunal abundance; (2) geometric mean morphospecies abundance; (3) relative evenness (=equitability) of individual morphospecies abundances (Pielou's *J*); and (4) observed and (5) estimated likely real numbers of morphospecies per unit area, estimations here being the absolute effective morphospecies density (Gatti et al., 2020), incorporating Hill's H_0, H_1 and H_2 metrics [i.e. in the expression $H_0 + [(H_1^2)/(2^*H_2)]$, where H_0 is the observed taxon density, H_1 is the exponential of their Shannon entropy, and H_2 is the corresponding inverse Simpson concentration]. In addition, (6) taxonomic diversity (*sensu* Clarke and Warwick, 1998) was also assessed.

For variation in quantitative assemblage composition of the marina benthos with distance into the blind-ending harbour, the latter was divided between three notional, equal-sized, confinement regions, each containing nine core samples ('mouth', 'central' and 'confined'; Fig. 1). The faunas in each were compared using ANOVA, hierarchical clustering analysis of Morisita similarity [see Wolda (1981) and Barwell et al. (2015)] carried out on both untransformed and fourth-root transformed taxon abundances by one-way PerMANOVA and SIMPER, both with 9999 permutations. Numbers of animals in each confinement region exceeded 200, well above the number required for robust multivariate comparison (Forcino et al., 2015).

There is no general agreement as to which indices should be used by managers to establish the health of local benthic systems. The Benthic Opportunist Annelids Amphipods (BO2A) index of Dauvin and Ruellet (2009), de-la-Osso-Carretero and Dauvin (2010), Dauvin et al. (2016), etc., is one of the most widely used such indices (Anaisce et al., 2023), and is given by $\log [\{fp/(fa + 1)\} + 1]$ where *fp* and *fa* are the proportions of opportunistic annelids and sensitive amphipods, respectively, in the macrobenthos. It is considered by Dauvin and Ruellet (2009) to be particularly well suited to estuaries. It is also particularly useful in areas where current knowledge of the specific identity and biology of the local fauna is limited, and was therefore most appropriate in the present circumstances. The opportunistic annelids and sensitive amphipods used here for calculation of BO2A are those listed by Dauvin et al. (2016:91): polychaetes by their 'benthic polychaete opportunistic families'; all oligochaetes; and all amphipods except *Jassa*. All compared areas contained considerably more than the Dauvin and Ruellet (2009) and Dauvin (2018) recommended minimum of 20 individuals. The associated EQS categories are those of the European Water Framework Directive (OJEC, 2000), with threshold values for the BO2A index as specified by Dauvin et al. (2016).

Local context was provided by the same opportunistic annelid and sensitive amphipod frequencies at 24 sites scattered throughout the entire Knysna estuarine bay. These were obtained from recent (2011–2024) historical databases of the abundance of non-marina and Thesen Island macrobenthos, i.e. from all of the system's notional ecological and hydrographic system compartments: 'mouth', 'marine bay', 'lagoon', 'estuary', and eastern fringing saltmarsh-enclosed 'backwaters' (Whitfield et al., 2023) (Fig. 2). Hydrographic and sedimentological conditions in these areas are described by Largier et al. (2000) and Reddering and Esterhuysen (1987), respectively. These historical data were originally collected using the same procedures and techniques as applied to the Leisure Isle harbour, and there was no significant relationship between date and opportunistic annelid to amphipod ratio ($P > 0.4$). All calculations were based on a minimum of 32 core samples per site. Local spatial variation in abundance was assessed by Lloyd's I_p index of patchiness, with significance of departures from random dispersal tested by Monte Carlo simulation with 9999 iterations.

3. Results

3.1. The small-boat harbour

Macroecological metrics of the Leisure Isle marina harbour and access channel generally fell within the range of those of other local backwater soft sediments (Table 1). It is clear, however, that the access channel and the associated harbour supported different species assemblages (PerMANOVA $F = 24.5$, $P < 0.0001$; Morisita similarity 0.14), coincident with a change in the substratum from cohesive mud to blancmange-like silt. The five access-channel samples supported 5400 animals per m^2 and an observed number of species of 25 (estimated true number 37), of which the five most numerous species (in descending order) were *Cylindroleberis ?grimaldi*, *Ampelisca spinimana*, *Nassarius kraussianus, Paratylodiplax algoensis* and *Turritella capensis*, which together comprised 62% of total individuals. The 27 samples within the harbour itself supported 4770 animals per m^2 and 30 observed morphospecies (estimated true number 36), with no overlap in the five most numerically dominant animals in the two subsystems, which in the harbour were *Prionospio sexoculata, Capitella capitata, Grandidierella lignorum*, *Hydrobia knysnaensis* and *Orbinia angrapequensis*, together comprising 82% of the total. The harbour fauna also differed from that in the equivalent section of the adjacent Thesen marina adjacent to the Ashmead Channel (PerMANOVA $F = 31.2$, $P < 0.0001$), the smaller Leisure Isle harbour supporting far fewer macrobenthic species than the much larger Thesen marina, although there was no correlation between number of such species and surface area in a series of marinas ranging in size from 1.3 to 8.8 ha along the Portuguese and Spanish south coasts ($R = 0.07$, $P = 0.87$) (calculated from data in Guerra-García et al., 2021). The access channel had a BO2A index value of 0.027, the harbour one of 0.221.

There was no significant variation in per-sample assemblage abundance or species density with distance from the harbour mouth, nor in the density of the overwhelmingly dominant species *Prionospio sexoculata* (Spearman rank $r < 0.19$, $P > 0.3$) (Fig. 3). Nor were there any significant differences between the numbers of individuals or species per core sample in the three confinement zones of the harbour (ANOVA $F_{2,24} < 1.45$, $P > 0.2$) or in their supported species assemblages based on the raw data (PerMANOVA $F = 0.7$–1.6, $P > 0.2$; Morisita similarity >0.97). After fourth-root transformation of the data reduced the importance of the overwhelmingly dominant *Prionospio*, however, a marginally significant difference was apparent between the mouth and confined assemblages ($P = 0.03$). SIMPER identified the mouth region as showing greater numbers of *Hydrobia*, *Orbinia* and *Nassarius*, and the confined region as showing greater numbers of *Grandidierella*, *Prionospio, Capitella* and *Simplisetia*, accounting for 60% of the difference between the two. Nevertheless, at the spatial scale of the hydrographic region, that nearest the entrance/exit supported more species in total than those nearer its blind end (Table 2). The fauna within the harbour was also highly patchy both in terms of numbers of individuals (from 1 to 68 per core sample, Lloyd's $I_p = 1.26$, $P < 0.0001$) and to a lesser extent in numbers of species (1–14 per sample, Lloyd's $I_p = 1.11$, $P = 0.02$).

Only one of the harbour's species has not also commonly been

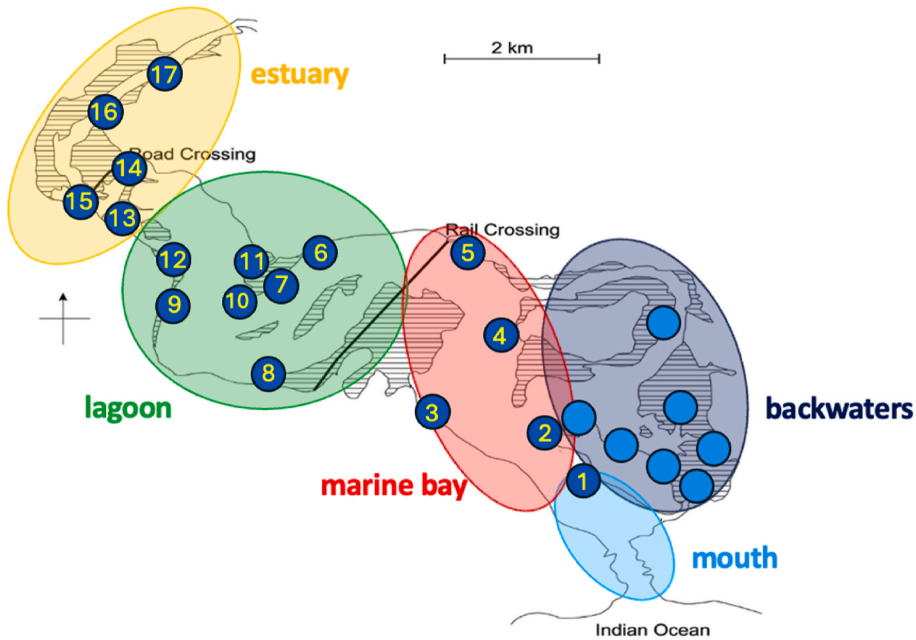

Fig. 2. The various notional hydrographic and ecological compartments of the Knysna estuarine bay (see, e.g. Whitfield et al., 2023), and location of the 17 examined sites along the system's axial channel (numbered sequentially) and the seven sites within the backwater channels and creeks.

Table 1
Macrobenthic biodiversity metrics of the Leisure Isle Boat Club harbour and its access channel in relation to those at other nearby backwater localities (see Fig. 1): observed (obs *N*) and estimated true (est *N*) numbers of morphospecies, total abundance m^{-2} (*A*), geometric mean morphospecies abundance (*G*), evenness (Pielou's *J*), and taxonomic diversity (*D*). Data from 32 core samples in all cases.

obs *N*	est *N*	*A*	*G*	*J*	*D*
Leisure Isle boat harbour and access channel					
40	51	4867	30	0.57	3.17
Thesen residential marina, subtidal low water-velocity zone (from Barnes and Seath, 2024)					
57	71	8905	32	0.67	3.86
Ashmead Channel, subtidal (from Barnes and Seath, 2024)					
63	74	14591	43	0.54	3.46
Kingfisher Creek, intertidal seagrass (from https://doi.org/10.17632/nmwrspd738.1 database)					
39	52	3802	37	0.79	4.17
Kingfisher Creek, intertidal bare sediment (from https://doi.org/10.17632/nmwrspd738.1 database)					
42	52	5214	32	0.65	3.28
Steenbok Channel, intertidal bare sediment (data of Barnes, 2019)					
23	29	3767	28	0.69	3.19

observed in the surrounding inter- or subtidal mudflats, the benthic chaetognath *Spadella.* Its presence in the access channel is particularly noteworthy, because it appears not previously to have been recorded from Africa, let alone Knysna, although otherwise known from scattered records throughout the world (Global Biodiversity Information Facility, accessed October 2024). However, like the minute gastropod *Cornirostra*, also recorded in Africa only from Knysna (Barnes, 2010), this is much more likely to be a reflection of lack of investigation both of the habitat and subhabitats concerned, and of semi-transparent animals <4 mm in size, as well as failure to recognise the organism for what it is. It is most unlikely really only to occur in Knysna.

3.2. The estuary as a whole

A total of 65 datasets from the 24 sites representing the whole estuarine bay were examined, comprising a total of 468000 macrobenthic invertebrates of which 75000 were opportunistic annelids and 15300 were sensitive amphipods. Fig. 4 displays the derived background values of the BO2A index across the soft-sediment benthic systems (intertidal and subtidal, vegetated and bare, main axial channel and backwater creeks) outside of marinas and boat harbours. Areas scoring the higher levels of EQS were located in all five system compartments although 14 out of the 15 achieving the highest level were from seagrass beds (which supported average opportunistic annelid densities of only 350 m^{-2}, and amphipod ones of 300 m^{-2}). Likewise, all compartments except the mouth were also included in the moderate to poor set of EQS scores, with 3 out of the 4 poorest being from intertidal areas of bare sediment. Nevertheless, the compartments nearest the Indian Ocean (mouth and marine-bay) were particularly well represented in the high-quality category and least in the moderate to poor categories. The

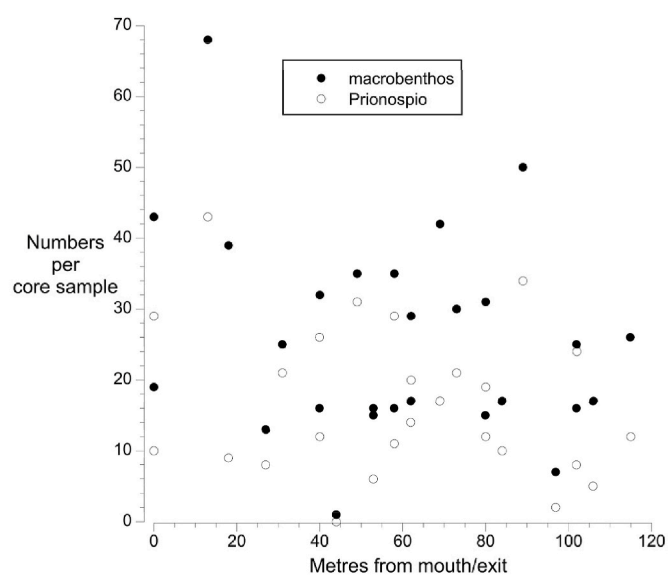

Fig. 3. Variation in macrobenthic abundance per sample and that of the dominant *Prionospio sexoculata* with distance from the single entrance/exit of the Leisure Isle Boat Club harbour.

Table 2
Macrobenthic biodiversity metrics of the three notional hydrological regions within the blind-ending Leisure Isle Boat Club harbour, Knysna (see Fig. 1). (Each region sampled by nine cores, and all regions with *Prionospio* as the numerical dominant.).

Region	Mouth	Central	Confined
Abundance (m^{-2})	5269	4835	4200
Geometric mean numbers (m^{-2})	63	90	74
Evenness (*J*)	0.54	0.48	0.52
Observed species density	27	15	15
Estimated real species density	33	18	19
Taxonomic diversity	2.81	2.19	2.54
BO2A index	0.220	0.239	0.211
2nd most abundant taxon	*Capitella*	*Capitella*	*Grandidierella*
3rd most abundant taxon	*Hydrobia*	*Grandidierella*	*Capitella*

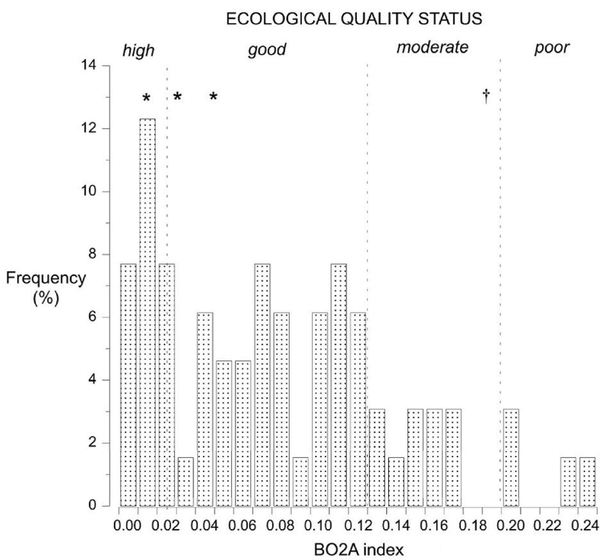

Fig. 4. Range of background values of the BO2A index of Ecological Quality Status across the intertidal and subtidal seagrass and bare sediments of the Knysna estuarine bay. The values for the three water-velocity zones of the Thesen marina are indicated by asterisks and that of the Leisure Isle boat harbour and access channel is indicated by a dagger.

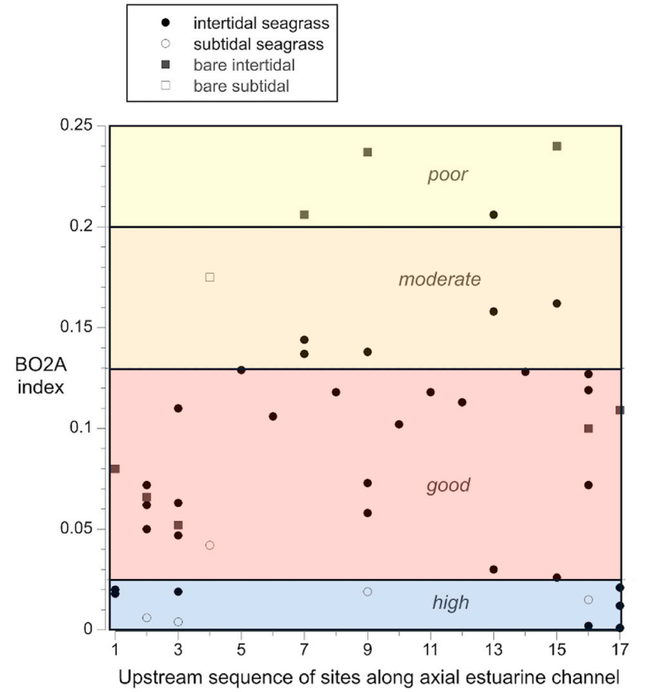

Fig. 5. Values of the BO2A index and associated levels of Ecological Quality along the axial navigation channel of Knysna estuarine bay, i.e. through the upstream gradient of mouth - marine bay - lagoon - estuary compartments with sites as numbered in Fig. 2.

supposed least quality sites on average supported high opportunistic annelid densities (2290 m^{-2}) and low amphipod ones (105 m^{-2}); the four poor-quality sites were also the ones in which the opportunistic annelids comprised the largest proportion of the total fauna (61–74%), in each case because of the high density of a single species, *Prionospio sexoculata* in three sites and *Cirratulus* sp. In the fourth. Overall, the seagrass beds supported mean densities of opportunistic annelids of 913 m^{-2} (SE 113), forming 14% of the macrofaunal numbers (range 0.2–61%), whilst areas of bare sediment supported 1794 m^{-2} (SE 267), equivalent to 21% (range 3–74%) of numbers. Superimposed on Fig. 4 are the BO2A indices of the three water-velocity sections of the Thesen residential marina (from data of Barnes and Seath, 2024), and the overall value for the Leisure Isle boat harbour: all clearly nestle within the range displayed by the estuarine bay as a whole.

Nevertheless, the abundance of opportunistic annelids did not vary along the upstream estuarine axis (R = −0.14, $P = 0.34$), whilst that of the amphipods markedly decreased (R = −0.70, $P \ll 0.00001$). BO2A index values did not vary with position along the longitudinal axis (R = 0.14, P > 0.3), and were especially uniform through the main body of the estuarine bay, where they averaged 0.125, on the border between good and moderate EQS (i.e. sites 4–15 in Fig. 5, R = 0.04, $P = 0.8$). They did, however, indicate particularly high quality (mean BO2A 0.051) in the three sites nearest the ocean and in the two at the head of the estuary (ANOVA $F_{2,44} = 8.5$, $P = 0.0001$), notwithstanding the marked differences in environment between the two ends of the estuarine gradient (e.g. clean compact sand *vs* soft mud, exposed *vs* sheltered conditions, high *vs* at times low salinity, etc.). As would be expected from its nature, overall the value of BO2A correlated both positively with the abundance of the opportunistic annelids (R = 0.76, P $\ll$0.00001) and negatively with that of the amphipods (R = −0.31, $P = 0.01$). Indicated EQS was less in the absence of a seagrass cover, where the abundance of opportunistic annelids was greater (ANOVA $F_{1,63} = 9.8$, $P = 0.003$), and it was likewise less intertidally than subtidally though not quite significantly so (ANOVA $F_{1,63} = 3.8$, $P = 0.056$). It is evident from Fig. 5 that to some extent these factors are responsible for part of the wide range of BO2A values seen within several individual sites. Nevertheless, it is variation within the more numerous intertidal seagrass datasets taken on a number of occasions from individual sites that appears the main cause (although all were taken at the same time of year). BO2A values also differed between the various system compartments (ANOVA $F_{3,61} = 3.1$, P = 0.034) but consequent solely on a significant difference between the lagoon and the mouth/marine-bay region (Fisher LSD $P < 0.004$). The opportunistic annelids in the lagoon comprised the highest proportion of the total macrofauna and the lagoon displayed the poorest BO2A of any compartment, whereas the index value and the proportion of opportunistic annelids were lowest in the mouth/marine-bay compartments.

Values through the estuarine bay of the BO2A index correlated almost perfectly with the much simpler formula of $\log[p/(1\text{-}p)]$, where p is the proportion of opportunistic annelids in the macrobenthos (R = 0.91, $P \ll 0.00001$) (Fig. 6), i.e. without any specific reference to the amphipod component.

Mean densities m^{-2} across the whole Knysna soft-sediment system were: total macrobenthos 7197 (range 1537–35941), opportunistic annelids 1153 (12–3912), and sensitive amphipods 235 (0–964). Abundance of both opportunistic annelids and sensitive amphipods was very

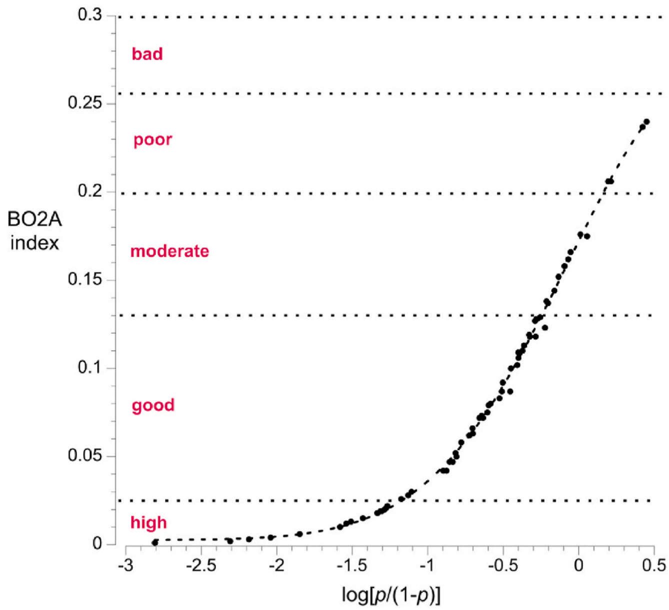

Fig. 6. Relationship between BO2A index (and associated Ecological Quality Status zones) and the logit expression, log [*p*/(1-*p*)], derived solely from data on the opportunistic annelids, in which *p* is their proportion of the local macrobenthic numbers. Curve fit R^2 0.998.

patchily dispersed across each system compartment ($I_p > 1.30$, $P < 0.0001$ in each case). There was no difference between the BO2A values along the main axial estuarine channel (mean 0.09; overall 0.07) and in the saltmarsh-enclosed backwater creeks (mean 0.08; overall 0.05) (ANOVA $F_{1,63} = 0.36$, $P = 0.5$), though there was between seagrass beds (mean 0.07) and bare sediment (mean 0.12) (ANOVA $F_{1,63} = 9.8$, $P = 0.003$). For the estuarine bay as a whole, the overall BO2A index was 0.063 with a mean individual site one of 0.083, indicating good EQS. Nevertheless, only 25% of individual sites had values < 0.025, equating to a pristine state state of health; all others had the higher values normally taken to indicate some degree of 'pollution' (Dauvin and Ruellet, 2009; Dauvin et al., 2016).

4. Discussion

The beds of blind-ending marinas and boat harbours are generally dominated in both number of individuals and number of species by annelids (Callier et al., 2009; Ng et al., 2019; Guerra-García et al., 2021; etc.), especially by the suite of taxa usually labelled the 'opportunistic benthic polychaetes'; mainly members of the families Cirratulidae, Capitellidae, Spionidae, and Dorvilleidae (Dauvin and Ruellet, 2007; Dauvin et al., 2016), together with small tubificine oligochaetes and sometimes with individual members of other polychaete groups. The Leisure Isle harbour is no exception, *Prionospio* comprising 64% of the total faunal individuals, and *Capitella* a further 7%. In this respect it contrasts markedly with the adjacent through-flow Thesen marina in which the dominant species were two amphipods (Barnes and Seath, 2024). Both of these were also present in the Leisure Isle harbour, where *Grandidierella* was locally common, but not nearly as abundantly as in the Thesen system. A blanket of soft silt also characterises the blind-ending harbour, but not its access channel, and this may well be responsible for the large difference between the relatively rich channel fauna and the poorer harbour one. Within the harbour, however, the fauna was evenly if, at a small spatial scale, patchily dispersed and without confinement effects, except very close to the mouth. Differences between the two adjacent marinas would indeed appear largely due to Thesen's unusual tidally-reversing through-flow which has the effect of flushing fine particles out of the system (Schumann, 2004).

The opportunistic worms typifying blind-ending marinas are generally regarded as characterising degraded habitats (Dean, 2008; Sivadas et al., 2010); e.g. those suffering organic and other pollution, and consequently often low in oxygen. In contrast, all but a few amphipod crustaceans are considered to be highly sensitive to environmental disturbance or contamination (Navarro-Barranco et al., 2020), and hence the perceived value of opportunistic-annelid to sensitive-amphipod ratios as indicators of habitat health/degradation (Warwick and Clarke, 1993; de-la-Ossa-Carretero and Dauvin, 2010; Dong et al., 2023). Nevertheless, at least in so far as the Knysna macrobenthos is concerned, the proportions of sensitive amphipods were irrelevant to the assessment of EQS, even though they varied from 0 to 17.7% of the macrobenthos. Calculations including them (i.e. BO2A) or not differentiating them from all the other non-opportunistic-annelid individuals, as in the logit expression in Fig. 6 above, being effectively perfectly correlated.

The observed mean BO2A value within the Knysna estuarine bay as a whole is similar to those of two other equivalent and largely pristine sites: the mouth region of the nearby Keurbooms/Bitou estuary (0.09) and the Eastern Banks region of the Moreton Bay estuarine lagoon in Queensland (0.05) (from data of Barnes, 2023; Barnes et al., 2024). Nutrient pollution does affect some parts of the Knysna system, particularly along the northern arm of the Ashmead Channel and adjacent backwater areas (Human et al., 2020; Claassens et al., 2020). Insofar as is known, however, all the sediments investigated in this study are free of organic (or other) pollution and have average sedimentary organics of only 3–4% (Human et al., 2020), relatively low for an estuary (Brandini et al., 2022) although at the level at which marked affects on species richness are likely to be manifested (Hyland et al., 2005). The estuary is currently assessed as being "largely natural with few modifications" (Hayes et al., 2022), and seagrass beds extend throughout it, a feature generally taken to indicate a healthy estuarine condition (e.g. Orth et al., 2006). Correspondingly, the average BO2A value indicates 'good' EQS, although the opportunistic annelid component comprised a large part (16%) of the fauna. Nevertheless, within the estuarine bay there is effectively as wide a range of BO2A index values as it is possible to obtain (the maximum potential value of the index being 0.3), as well as considerable variation at any given point (see also Magni et al., 2023). One of the human modifications is the Leisure Isle harbour and its access channel (both dredged from the intertidal zone), the latter displaying the low BO2A of 0.027 on the margin between 'high' and 'good' EQS whilst the contiguous mouth region of the harbour showed the widely different value of 0.220, in the middle of the 'poor' class — three-quarters of the possible range in BO2A values apart.

Because of the severe impact of humanity on many estuarine environments, accurate assessment of local ecological health is highly important for their successful management (Gao et al., 2024), and in most cases this has been attempted using data derived from composition of the supported benthic assemblages (Anaisce et al., 2023). Yet the extent to which calculated values of benthic biotic indices actually reflect notions of such quality appears inherently problematic in relatively unpolluted estuaries, not only because of the local variability observed. A major difficulty in semi-enclosed paralic environments relates to the characteristic nature of their benthos (Dauvin, 2007; Elliott and Quintino, 2007). Dauvin and Ruellet (2007, 2009), for example, classify all levels of their BO2A index yielding worse than 'high' EQS as being indicative of some degree of anthropogenic perturbation or direct pollution. However, estuaries and enclosed paralic systems generally are amongst the most productive of habitats (Frankenbach et al., 2020), often supporting abundant submerged and fringing vegetation as well as flourishing microphytobenthos on their tidally-exposed flats (Douglas et al., 2022). Coupled with their high sediment deposition rates (Schubel, 1982), they are consequently naturally very rich in organics (Canuel and Hardison, 2016) and decomposition of these in the sediments can lead to local hypoxic conditions only just below the surface. They are also highly dynamic temporarily, especially when tidal and/or receiving variable freshwater inputs (Schumann et al., 1999; Dauvin and Ruellet, 2009). Benthos that succeed in such naturally sheltered, variable and organic-rich soft sediments are species with short life cycles, rapid turnover and high environmental tolerance, i.e. are those usually labelled 'opportunistic' (Elliott and Quintino, 2007). Hence the opportunistic annelid groups that exploit organically polluted situations are also those characterising natural estuarine habitats throughout the world (Borja et al., 2012; Martins and Barros, 2022), including in South Africa (Day, 1981). This is true of some members of other animal phyla too (e.g. Ates et al., 2014; Abdelsalam and Elnaby, 2024). Basically, such animals may be tolerant of anthropogenically disturbed and polluted habitats but are by no means restricted to them, thus rendering it difficult to distinguish between natural and human-influenced states (Elliott and Quintino, 2007; Le Guen et al., 2019). In effect, the position is equivalent to the relationship of house mice and houseflies to human habitations. It perhaps needs to be stressed that although the index used here was the BO2A, these problem associated with estuaries are not specifically associated with that index, they will apply to all based on data of benthic assemblage composition and the identification of certain species considered characteristic of disturbed or degraded conditions.

In that context, the high level of organic matter in unpolluted estuaries is regarded by Dauvin and Ruellet (2009) as natural 'stress', so that indices such as BO2A can become indices of stress regardless of whether this is anthropogenic in origin, rather than ones of habitat degradation. However, in systems that are already subject to multiple abiotic stressors (Rubinoff and Grosholz, 2022) it might be just as, if not more, appropriate to regard high organic status as an environmental filter through which many estuarine annelids but fewer other taxa pass, rather than as a stressing factor increasing in situ metabolic, reproductive and/or other costs. As Elliott and Quintino (2007) have pointed out, it is essentially those essentially freshwater and marine species that penetrate estuaries only to limited extents that will find brackish-water environments stressful, not the more characteristically estuarine ones. Further, the latter can actually benefit from this situation: for them it can be regarded as a subsidy, not a stress (Constanza et al., 1992). The whole problem of the similarity of estuarine macrobenthos to those characterising some anthropogenically perturbed sites has been considered to constitute an 'Estuarine Quality Paradox' (Dauvin, 2007; Elliott and Quintino, 2007), a situation that consequently has been thought to require subjective local "pragmatism" (Dauvin and Ruellet, 2009) and/or "expert judgement" (Dias et al., 2022) for resolution of the true EQS of any given estuarine area. An alternative approach has been to turn to organisms other than the macrobenthos, e.g. fish (Brind'Amour and Lobry, 2009; Pérez-Domínguez et al., 2012) or meiofauna (Hess et al., 2020; Bouchet et al., 2023). However, these other categories of animal are not necessarily free of the paradox (see below).

For the estuarine system under consideration here, the polychaetes present in the marinas are clearly all well represented in surrounding bay as a whole (Barnes, 2022; Barnes and Claassens, 2020; Barnes and Seath, 2024), averaging some 1153 individuals m^{-2} and with maxima of >3900 individuals m^{-2}. There they can constitute >70% of total faunal individuals (or even more if various orbiniids, paraonids, micro-sabellidans and others are included in the opportunistic category, as various authors have proposed). Indeed no investigated area of benthic sediment in Knysna was without them, and the spionid *Prionospio sexoculata* was the single most abundant intertidal estuarine-bay taxon (Barnes, 2022). The intertidal zone adjacent to the Leisure Isle harbour is also dominated by annelids, all of them widely or occasionally regarded as being opportunistic, the eight taxa *Simplisetia, Prionospio, Paradoneis, Orbinia, Pseudopolydora, Pseudofabriciola, Scoletoma* and a tubificine oligochaete comprising 77% of all faunal individuals. Only the gastropod *Nassarius* was a non-annelid amongst the nine most abundant species (Barnes, 2019, 2022). Frequencies of characteristically estuarine annelids and amphipods at one fifth of the sites investigated indicated levels of moderate to poor EQS, although there are no indications that this reflects any pollution effects in the Knysna estuarine bay at sites sampled. The same situation may extend to estuarine fish. Despite the apparently poor quality of the Leisure Island harbour as assessed by BO2A, for example, its *Codium tenue* beds support the rare and Red-List endangered estuarine seahorse *Hippocampus capensis* (J. Kennedy, pers. com.), and seahorses in general are regarded as being sensitive to environmental degradation (Vincent et al., 2011).

The species in groups IV and V of the Azti Marine Biotic Index (AMBI) of Grall and Glémarec (1997) and Borja et al. (2000) for European estuarine and coastal soft sediments are sometimes taken to indicate 'opportunistic' and 'pollution-indicating' species, respectively (e.g. Rygg and Norling, 2013), and those few species placed in AMBI group V were originally specifically identified as typifying "heavily polluted" systems. Those species, however, are all "deposit feeders, which proliferate in reduced sediments" and several, including *Tubificoides benedii*, *Malacoceros fuliginosus* and *Capitella* spp., in fact also characterise pristine sheltered European mudflats like those in the Scolt Head Island National Nature Reserve in the UK — areas that certainly do not suffer heavy pollution or other anthropogenic effects (Barnes and Ellwood, 2011). This problem of confounding the two situations in Knysna is further evidenced by the dominance of paraonids in the clean sands of the flood-tidal sand delta in the mouth of the estuary. In that pristine and well-flushed region, where *Paradoneis* and *Levinsenia* comprised up to 69% of all animals, some areas would display poor EQS if paraonids were included in the opportunistic-polychaete category as has been argued (e.g. Quintana et al., 2015) (Barnes, in prep.). In marked contrast, the other dominant element in these sands was a species of the pollution-intolerant amphipod *Urothoe* (in ecological group I/II in the AMBI system).

Data derived from macrobenthic assemblage composition have proved useful in the detection of temporal change of EQS at given estuarine points (e.g. Borja et al., 2006; Watson et al., 2018), but considering the large-scale spatial variation shown along the relatively natural Knysna system, they would appear much less useful in indicating local merit at points along an estuarine gradient, as predicted by Elliott and Quintino (2007) and Dauvin (2007). Neither may species diversity wherever species richness and overwhelming dominance by a few species go hand-in-hand, as at Knysna (Barnes, 2021). Such overwhelming dominance by a single species can also affect calculations of EQS (Magni et al., 2023). If some areas of these local relatively undegraded benthic systems are regarded as of poor quality, this may reflect questionable value judgements (Lancaster, 2000), particularly on the relative merits of annelids or their specific low value in providing suitable food for commercially-significant fish, rather than environmental degradation from some previous higher quality state. The BO2A index was proposed specifically to counter such paradox-related difficulties in the lower reaches of estuaries, and Dauvin and Roullet (2009:46) concluded that, perhaps with the addition of further opportunistic species, it could be used "all along the estuarine continuum, from the fresh waters upstream to the marine waters downstream". However, unless local indicator species are discovered that differentiate between the natural temporally-variable and highly-organic state of estuaries and the equivalent opportunist-favouring states induced anthropogenically, the present practical results suggest that use of any benthic biotic indices relying on assemblage composition would indeed appear to be potentially highly misleading. Identifying degrees of anthropogenic perturbation and local ecological wellbeing along estuarine gradients are therefore more likely to be achieved, perhaps not by as broad a panel of interested parties as suggested by Borja et al. (2011), but by direct monitoring of the specific substances of potential concern.

CRediT authorship contribution statement

R.S.K. Barnes: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **J.L. Seath:** Writing – review & editing, Investigation.

Data availability

The data collected or used in this study have been deposited in Mendeley Data and are available at: https://data.mendeley.com/datasets/rr6nt2rpg.5/1.

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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.

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Data availability

Data deposited in Mendeley Data as specified in the article.

References

Abdelsalam, K.M., Elnaby, F.A.A., 2024. Diversity of macro-benthic invertebrates in the Egyptian Nile estuaries. Regional Studies in Marine Science 77, 103689. https://doi.org/10.1016/j.rsma.2024.103689.

Albano, P.G., Sabelli, B., Bouchet, P., 2011. The challenge of small and rare species in marine biodiversity surveys: microgastropod diversity in a complex tropical coastal environment. Biodivers. Conserv. 20, 3233–3237. https://doi.org/10.1007/s10531-011-0117-x.

Anaisce, R., Juen, L., Ligeiro, R., 2023. Scientometrics of the assessment of biotic integrity in estuaries. Ecol. Indicat. 156, 111112. https://doi.org/10.1016/j.ecolind.2023.111112.

Ates, A.S., Katagan, T., Sezgin, M., Acar, S., 2014. The response of *Apseudopsis latreillii* (Milne-Edwards, 1828) (Crustacea, Tanaidacea) to environmental variables in the Dardanelles. Turk. J. Fish. Aquat. Sci. 14, 113–124. https://doi.org/10.4194/1303-2712-v14_1_13.

Barnes, R.S.K., 2010. Spatial variation in abundance and diversity of the smaller surface and near-surface eelgrass-associated intertidal macrobenthos within a warm-temperate estuarine bay in the Garden Route National Park, RSA. Aquat. Conserv. 20, 762–772. https://doi.org/10.1002/aqc.1152.

Barnes, R.S.K., 2019. Context dependency in the effect of *Ulva*-induced loss of seagrass cover on estuarine macrobenthic abundance and biodiversity. Aquat. Conserv. 29, 163–174. https://doi.org/10.1002/aqc.2977.

Barnes, R.S.K., 2021. What does measuring species diversity in estuarine seagrass systems actually assess? Mar. Environ. Res. 172, 105500. https://doi.org/10.1016/j.marenvres.2021.105500.

Barnes, R.S.K., 2022. Biodiversity differentials between seagrass and adjacent bare sediment change along an estuarine gradient. Estuar. Coast Shelf Sci. 274, 107951. https://doi.org/10.1016/j.ecss.2022.107951.

Barnes, R.S.K., 2023. Seagrass macrobenthic biodiversity does not vary in conformity with a leaky-lagoonal confinement gradient. Mar. Environ. Res. 185, 105897. https://doi.org/10.1016/j.marenvres.2023.105897.

Barnes, R.S.K., Claassens, L., 2020. Do beds of subtidal estuarine seagrass constitute a refuge for macrobenthic biodiversity threatened intertidally? Biodivers. Conserv. 29, 3227–3244. https://doi.org/10.1007/s10531-020-02019-0.

Barnes, R.S.K., Ellwood, M.D.F., 2011. Macrobenthic assemblage structure in a cool-temperate intertidal dwarf eelgrass bed in comparison with those from lower latitudes. Biol. J. Linn. Soc. 104, 527–540. https://doi.org/10.1111/j.1095-8312.2011.01738.x.

Barnes, R.S.K., Seath, J.L., 2024. The occurrence of a rich subtidal macrobenthic fauna in through-flow residential marina canals, and the potential of such systems to be managed as biodiversity assets. Ocean Coast Manag. 254, 107191. https://doi.org/10.1016/j.ocecoaman.2024.107191.

Barnes, R.S.K., Seath, J.L., Arendse, C.J., 2024. Differential sampling in the assessment of conservation and biodiversity merit: a comparison of the seagrass macrofauna in three nearby South African estuaries. Biodivers. Conserv. 33, 509–532. https://doi.org/10.1007/s10531-023-02754-0.

Barwell, L.J., Isaac, N.J.B., Kunin, W.E., 2015. Measuring β-diversity with species abundance data. J. Anim. Ecol. 84, 1112–1122. https://doi.org/10.1111/1365-2656.12362.

Blowes, S.A., Daskalova, G.N., Dornelas, M., Engel, T., Gotelli, N.J., Magurran, A.E., Martins, I.S., McGill, B., McGlinn, D.J., Sagouis, A., Shimadzu, H., Supp, S.R., Chase, J.M., 2022. Local biodiversity change reflects interactions among changing abundance, evenness and richness. Ecology 103, e3820. https://doi.org/10.1002/ecy.3820.

Borja, Á., Franco, J., Pérez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Pollut. Bull. 40, 1100–1114. https://doi.org/10.1016/s0025-326x(00)00061-8.

Borja, Á., Muxika, I., Franco, J., 2006. Long-term recovery of soft-bottom benthos following urban and industrial sewage treatment in the Nervión estuary (southern Bay of Biscay). Mar. Ecol. Prog. Ser. 313, 43–55. https://doi.org/10.3354/meps313043.

Borja, Á., Basset, A., Bricker, S., Dauvin, J.-C., Elliott, M., Harrison, T., Marques, J.-C., Weisberg, S.B., West, R., 2012. Classifying ecological quality and integrity of estuaries. In: Wolanski, E., McLusky, D. (Eds.), Treatise on Estuarine and Coastal Science. Academic Press, Waltham, pp. 125–162. https://doi.org/10.1016/b978-0-12-374711-2.001091-1.

Bouchet, V.M.P., Zeppilli, D., Frontalini, F., 2023. The ecological quality status assessment of marine and transitional ecosystems: 17ew methods and perspectives for the future. Water 15, 2864. https://doi.org/10.3390/w15162864.

Brandini, N., Machado, E. de C., Sanders, C.J., Cotovicz, L.C., Bernardes, M.C., Knoppers, B.A., 2022. Organic matter processing through an estuarine system: evidence from stable isotopes (δ^{13}C and δ^{15}N) and molecular (lignin phenols) signatures. Estuar. Coast Shelf Sci. 265, 107707. https://doi.org/10.1016/j.ecss.2021.107707.

Brind'Amour, A., Lobry, J., 2009. Assessment of the ecological status of coastal areas and estuaries in France, using multiple fish-based indicators: a comparative analysis on the Vilaine estuary. Aquat. Living Resour. 22, 559–572. https://doi.org/10.1051/alr/2009052.

Callier, M.D., Fletcher, R.L., Thorp, C.H., Fichet, D., 2009. Macrofaunal community responses to marina-related pollution on the south coast of England and west coast of France. Journal of the Marine Biological Association of the UK 89, 19–29. https://doi.org/10.1017/S002531540800235X.

Canuel, E.A., Hardison, A.K., 2016. Sources, ages, and alteration of organic matter in estuaries. Ann. Rev. Mar. Sci 8, 409–434. https://doi.org/10.1146/annurev-marine-122414-034058.

Claassens, L., Barnes, R.S.K., Wasserman, J., Lamberth, S.J., Miranda, N.A.F., van Niekerk, L., Adams, J.B., 2020. Knysna Estuary health: ecological status, threats and options for the future. Afr. J. Aquat. Sci. 45, 65–82.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Anim. Ecol. 35, 523–531. https://doi.org/10.1046/j.1365-2664.1998.3540523.x.

Dauvin, J.-C., 2007. Paradox of estuarine quality: benthic indicators and indices, consensus or debate for the future. Mar. Pollut. Bull. 55, 271–281. https://doi.org/10.1016/j.marpolbul.2006.08.017.

Dauvin, J.-C., 2018. Twenty years of application of Polychaete/Amphipod ratios to assess diverse human pressures in estuarine and coastal marine environments: a review. Ecol. Indicat. 95, 427–435. https://doi.org/10.1016/j.ecolind.2018.07.049.

Dauvin, J.-C., Ruellet, T., 2007. Polychaete/amphipod ratios revisited. Mar. Pollut. Bull. 55, 215–224. https://doi.org/10.1016/j.marpolbul.2006.08.045.

Dauvin, J.-C., Ruellet, T., 2009. The estuarine quality paradox: is it possible to define an ecological quality status for specific modified and naturally stressed estuarine ecosystems? Mar. Pollut. Bull. 59, 38–47. https://doi.org/10.1016/j.marpolbul.2008.11.008.

Dauvin, J.-C., Andrade, H., de-la-Ossa-Carretero, J.A., Del-Pilar-Ruso, Y., Riera, R., 2016. Polychaete/amphipod ratios: an approach to validating simple benthic indicators. Ecol. Indicat. 63, 89–99. https://doi.org/10.1016/j.ecolind.2015.11.055.

Day, J.H., 1981. The estuarine fauna. In: Day, J.H. (Ed.), Estuarine Ecology with Particular Reference to Southern Africa, 178. Balkema, Rotterdam, p. 147.

de-la-Ossa-Carretero, J.A., Dauvin, J.-C., 2010. A comparison of two biotic indices, AMBI and BOPA/BO2A, for assessing the ecological quality status (EcoQS) of benthic macro-invertebrates. Transitional Waters Bulletin 4, 12–24. https://doi.org/10.1285/i1825229xv4n1p12.

Dean, H.K., 2008. The use of polychaetes (Annelida) as indicator species of marine pollution: a review. Rev. Biol. Trop. 56, 11–38.

Dethier, M.N., Schoch, G.C., 2006. Taxonomic sufficiency in distinguishing natural spatial patterns on an estuarine shoreline. Mar. Ecol. Prog. Ser. 306, 41–49. https://doi.org/10.3354/meps306041.

Dias, H.Q., Sukumaran, S., Mulik, J., Janakiram, P., 2022. Ecological quality status assessment of tropical estuaries with benthic indices using differently derived

reference conditions. Mar. Pollut. Bull. 177, 113457. https://doi.org/10.1016/j.marpolbul.2022.113457.
Dong, J.-Y., Wang, X., Bidegan, G., Sun, X., Bian, X., Zhang, X., 2023. Assessment of the benthic ecological quality status (EcoQs) of Laizhou Bay (China) with an integrated AMBI, M-AMBI, BENTIX, BO2A and feeding evenness index. Ecol. Indicat. 153, 110456. https://doi.org/10.1016/j.ecolind.2023.110456.
Douglas, E.J., Bulmer, R.H., MacDonald, I.T., Lohrer, A.M., 2022. Estuaries as coastal reactors: importance of shallow seafloor habitats for primary productivity and nutrient transformation, and impacts of sea level rise. N. Z. J. Mar. Freshw. Res. 56, 553–569. https://doi.org/10.1080/00288330.2022.2107027.
Elliott, M., Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar. Pollut. Bull. 54, 640–645. https://doi.org/10.1016/j.marpolbul.2007.02.003.
Forcino, F.L., Leighton, L.R., Twerdy, P., Cahill, J.F., 2015. Reexamining sample size requirements for multivariate, abundance-based community research: when resources are limited, the reasearch does not have to be. PLoS One 10, e0128370. https://doi.org/10.1371/journal.pone.0128379.
Frankenbach, S., Ezequiel, J., Plecha, S., Goessling, J.W., Vaz, L., Kühl, M., Dias, J.M., Vaz, N., Serôdio, J., 2020. Synoptic spatio-temporal variability of the photosynthetic productivity of microphytobenthos and phytoplankton in a tidal estuary. Front. Mar. Sci. 7, 170. https://doi.org/10.3389/fmars.2020.00170.
Gao, X., Li, W., Zhang, Y., Song, H., Li, Y., Li, H., 2024. Integrated assessment of ecological quality combining biological and environmental data in the Yellow River estuary. Water 16, 1615. https://doi.org/10.3390/w16111615.
Gatti, R.C., Amoroso, N., Monaco, A., 2020. Estimating and comparing biodiversity with a single universal metric. Ecol. Model. 424, 109020. https://doi.org/10.1016/j.ecolmodel.2020.109020.
Gerwing, T.G., Cox, K., Allen Gerwing, A.M., Campbell, L., Macdonald, T., Dudas, S.E., Juanes, F., 2020. Varying intertidal invertebrate taxonomic resolution does not influence ecological findings. Estuar. Coast Shelf Sci. 232, 106516. https://doi.org/10.1016/j.ecss.2019.106516.
Grall, J., Glémarec, M., 1997. Using biotic indices to estimate macrobenthic community perturbations in the Bay of Brest. Estuar. Coast Shelf Sci. 44 (Suppl. A), 43–53. https://doi.org/10.1016/s0272-7714(97)80006-6.
Guerra-García, J.M., Navarro-Barranco, C., Ros, M., Sedano, F., Espinar, R., Fernández-Romero, A., Martínez-Laiz, G., Cuesta, J.A., Giráldez, I., Morales, E., Florido, M., Moreira, J., 2021. Ecological quality assessement of marinas: an integrative approach combining biological and environmental data. J. Environ. Manag. 286, 112237. https://doi.org/10.1016/j.envman.2021.112237.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1), 9.
Hayes, J.S., Russell, I.A., Arendse, C.J., Smith, M.K.S., Lawrence, C., Roux, D.J., Baard, J. A., 2022. Knysna estuary management plan: situation assessment report. SANParks Report No. 43/2022. https://www.sanparks.org/wp-content/uploads/2024/01/Knysna-Estuary-SAR-2022.pdf.
Hess, S., Alve, E., Andersen, T.J., Joranger, T., 2020. Defining ecological reference conditions in naturally stressed environments - how difficult is it? Mar. Environ. Res. 156, 104885. https://doi.org/10.1016/j.marenvres.2020.104885.
Human, L.R.D., Weitz, R., Allanson, B.R., Adams, J.B., 2020. Nutrient fluxes from sediments pose management challenges for the Knysna Estuary, South Africa. Afr. J. Aquat. Sci. 45, 1–9. https://doi.org/10.2989/16085914.2019.1671787.
Hyland, J., Balthis, L., Karakassis, I., Magni, P., Petrov, A., Shine, J., Vestergaard, O., Warwick, R., 2005. Organic carbon content of sediments as an indicator of stress in the marine benthos. Mar. Ecol. Prog. Ser. 295, 91–103. https://doi.org/10.1093/oso/9780198569015.003.0015.
Knysna, 2019. Knysna Economic Development strategy. Knysna municipality. Available at: https://www.knysna.gov.za/wp-content/uploads/2019/09/Knysna-Draft-EDS-Full-Report.pdf.
Kokesh, B.S., Kidwell, S.M., Tomasovych, A., Walther, S.M., 2022. Detecting strong spatial and temporal variation in macrobenthic composition on an urban shelf using taxonomic surrogates. Mar. Ecol. Prog. Ser. 682, 13–2022. https://doi.org/10.3354/meps13932.
Lancaster, J., 2000. The ridiculous notion of assessing ecological health and identifying the useful concepts underneath. Human and Ecological Risk Assessment 6, 213–222. https://doi.org/10.1080/10807030009380056.
Largier, J.L., Attwood, C., Harcourt-Baldwin, J.-L., 2000. The hydrographic character of Knysna Estuary. Trans. Roy. Soc. S. Afr. 55, 107–122. https://doi.org/10.1080/00359190009520437.
Le Guen, C., Tecchio, S., Dauvin, J.-C., de Roton, G., Lobry, J., Lepage, M., Morin, J., Lassalle, G., Roux, A., Niquil, N., 2019. Assessing the ecological status of an estuarine ecosystem: linking biodiversity and food-web indicators. Estuar. Coast Shelf Sci. 228, 106339. https://doi.org/10.1016/j.ecss.2019.106339.
Magni, P., Vesal, S.E., Giampaoletti, J., Como, S., Gravina, M.F., 2023. Joint use of biological traits, diversity and biotic indices to assess the ecological quality status of a Mediterranean transitional system. Ecol. Indicat. 147, 109939. https://doi.org/10.1016/j.ecolind.2023.109939.
Martins, A.D., Barros, F., 2022. Ecological functions of polychaetes along estuarine gradients. Front. Mar. Sci. 9, 780318. https://doi.org/10.3389/fmars.2022.780318.
Navarro-Barranco, C., Ros, M., de Figueroa, J.M.T., Guerra-García, J.M., 2020. Marine crustaceans as bioindicators: amphipods as case study. In: Lovrich, G., Thiel, M. (Eds.), Fisheries and Aquaculture, vol. 9. Oxford University Press, Oxford, pp. 435–462. https://doi.org/10.1093/oso/9780190865627.003.0017.
Ng, C.S.L., Toh, K.B., Toh, T.C., Ng, J.Y., Cheo, P.R., Tun, K., Chou, L.M., 2019. Distribution of soft bottom macrobenthic communities in tropical marinas of Singapore. Urban Ecosyst. 22, 443–453. https://doi.org/10.1007/s11252-019-0828-4.
OJEC, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities L321, 1–72.
Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K. L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2.
Pérez-Domínguez, R., Maci, S., Courrat, A., Lepage, M., Borja, A., Uriarte, A., Neto, J.M., Cabral, H., Raykov, V.S., Franco, A., Alvarez, M.C., Elliott, M., 2012. Current developments on fish-based indices to assess ecological-quality status of estuaries and lagoons. Ecol. Indicat. 23, 34–45. https://doi.org/10.1016/j.ecolind.2012.03.006.
Quintana, C.O., Bernardino, A.F., de Moreas, P.C., Valdemarsen, T.B., Sumida, P.Y.G., 2015. Effect of coastal upwelling on the structure of macrofaunal communities in SE Brazil. J. Mar. Syst. 143, 120–129. https://doi.org/10.1016/j.marsys.2014.11.003.
Reddering, J.S.V., Esterhuysen, K., 1987. Sediment dispersal in the Knysna Estuary: environmental management considerations. S. Afr. J. Geol. 90, 448–457. https://doi.org/10.10520/AJA10120750-976.
Rubinoff, B.G., Grosholz, E.D., 2022. Biological invasions alter consumer-stress relationships along an estuarine gradient. Ecology 103, e3695. https://doi.org/10.1002/ecy.3695.
Rygg, B., Norling, K., 2013. Norwegian Sensitivity Index (NSI) for Marine Macroinvertebrates, and an Update of Indicator Species Index (ISI). Norwegian Institute for Water Research. Report 6475-2013. ISBN 978-82-577-6210-0.
Santini, L., Belmaker, J., Costello, M.J., Pereira, H.M., Rossberg, A.G., Schipper, A.M., Ceausu, S., Dornelas, M., Hilbers, J.P., Hortal, J., Huijbregts, M.A.J., Nararro, L.M., Shiffers, K.H., Visconti, P., Rondinini, C., 2017. Assessing the suitability of diversity metrics to detect biodiversity change. Biol. Conserv. 213, 341–350. https://doi.org/10.1016/j.biocon.2016.08.024.
Schubel, J.R., 1982. Estuarine sedimentation. In: Beaches and Coastal Geology. Encyclopedia of Earth Sciences. Springer, New York. https://doi.org/10.1007/0-387-30843-1_177.
Schumann, E.H., 2004. Water Flow Structures in the Thesen Islands Marina. Seaways Services, Humewood. Unpublished report to The Thesen Islands Development Company (Pty) Ltd.
Schumann, E.H., Largier, J.L., Slinger, J.H., 1999. Estuarine hydrodynamics. In: Allanson, B.R., Baird, D. (Eds.), Estuaries of South Africa. Cambridge University Press, Cambridge, pp. 27–52. ISBN 0 521 58410 8.
Simon, C.A., Kara, J., Clarke, D.T., Sedick, S., 2022. Revisiting 'A monograph on the polychaeta of southern Africa': establishing taxonomic research priorities in southern Africa. Afr. J. Mar. Sci. 44, 83–100. https://doi.org/10.2989/1814232X.2022.2041094.
Sivadas, S., Ingole, B., Nanajkar, M., 2010. Benthic polychaetes as good indicators of anthropogenic impact. Indian J. Mar. Sci. 39, 201–211.
Skarzauskiene, A., Labanauskaite, D., Timonina-Mickeviciene, A., 2022. Development of marina services in the context of sustainable water and coastal tourism. Knowledge 2, 652–662. https://doi.org/10.3390/knowledge2040037.
Tataranni, M., Maltagliati, F., Floris, A., Castelli, A., Lardicci, C., 2009. Variance estimates and taxonomic resolution: an analysis of macrobenthic spatial patterns at different scales in a western Mediterranean coastal lagoon. Mar. Environ. Res. 67, 219–229. https://doi.org/10.1016/j.marenvres.2009.02.003.
Tourism, S.A., 2022. South Africa is among the leading destinations in the world. https://live.southafrica.net/media/293744/final_opportunities-to-increase-positive-sentiment-for-south-africa-infographicupdated-22-july-1.pdf.
Vincent, A.C.J., Foster, S.J., Koldewey, H.J., 2011. Conservation and management of seahorses and other Syngnathidae. J. Fish. Biol. 78, 1681–1724. https://doi.org/10.1111/j.1095-8649.2011.03003.x.
Warwick, R.M., Clarke, K.R., 1993. Comparing the severity of disturbance. A meta-analysis of marine macrobenthic community data. Mar. Ecol. Prog. Ser. 92, 221–231. https://doi.org/10.3354/meps092221.
Watson, S.C.L., Paterson, D.M., Widdicombe, S., Beaumont, N.J., 2018. Evaluation of estuarine biotic indices to assess macro-benthic structure and functioning following nutrient remediation actions: a case study on the Eden estuary, Scoltland. Regional Studies in Marine Science 24, 379–391.
Whitfield, A.K., Breen, C.M., Read, M. (Eds.), 2023. The Knysna Estuary. Jewel of the Garden Route. Knysna Basin Project, Knysna, 978-0-6397-6866-3.
Wolda, H., 1981. Similarity indices, sample size and diversity. Oecologia 50, 296–302. https://doi.org/10.1007/bf00344966.