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Spatial and Temporal Changes in the Fish Fauna of a Low-Inflow Estuary following a Mass Mortality Event and Natural and Artificial Bar Breaches

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Abstract: Estuaries that become closed from the ocean through the formation of a sand bar are particularly susceptible to degradation and often experience poor water quality and fish kills. Sampling was conducted seasonally for two years in the deeper waters of the Vasse–Wonnerup (southwestern Australia) after a large fish mortality event to identify the fish species present and determine if richness, abundance, diversity and faunal composition differed among regions and over time. Species richness, abundance and diversity were far greater in the downstream regions than in the upstream regions, reflecting patterns in salinity. Catch rates of two marine estuarine-opportunist mugilids (*Mugil cephalus* and *Aldrichetta forsteri*) and an estuarine-resident sparid (*Acanthopagrus butcheri*), which were the species most affected by the mortality event, were relatively stable. It is suggested that before sampling commenced, mugilids had entered the estuary following an artificial sand bar breach, while the loss of 0+ (new recruits) *A. butcheri* in the mortality event and subsequent recruitment failure prevented stocks from increasing. Temporal shifts in fish composition were driven by less abundant species, which utilized the estuary more opportunistically. Increases in the occurrences and abundances of these species coincided with an open bar and salinities close to those of seawater. The data also show how the estuary responds to differing hydrodynamic phases and artificial breaches.

Keywords: berm; fish kill; intermittently open; ICOLL; mechanical breaching; microtidal; hypoxia; temporarily open/closed; offshore; southwestern Australia

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1. Introduction

Despite temperate estuaries providing valuable ecosystem services, including filtering and detoxification, and the provision of nursery habitat [1–3], they are the most degraded of all marine ecosystems [4]. Much of this degradation has resulted from the colonization and subsequent development of these systems by humans [5,6]. Impacts on estuaries arise from land clearing in the catchment, the loss of fringing habitat and land reclamation, the diversion and abstraction of freshwater, eutrophication, chemical pollution and plastic pollution [7]. These deleterious anthropogenic influences are particularly damaging for microtidal estuaries (tidal range < 2 m), which are less resilient as their lower tidal flushing capacity increases water residence times and reduces turbidity, exacerbating any eutrophication and often causing micro- and macroalgal blooms and hypoxia [8,9].

The situation is particularly dire in microtidal systems located in Mediterranean climates, which are characterized by hot, dry summers and cool, wet winters and thus have highly seasonal rainfall [10]. During periods of rainfall, the subsequent outflow of water from the estuary scours the entrance channel and moves sediment offshore. When freshwater discharge decreases, however, longshore and/or onshore transport of sediment leads to the accumulation of sand that can reach a height sufficient to form a bar, disconnecting the system from the ocean until flows increase and raise the water level sufficiently to breach that bar [11–13]. It is estimated that 3% of estuaries globally and 15% of those on microtidal coastlines are intermittently closed to the ocean [14]. In southwestern Australia, 80% of estuaries are closed to the ocean for part of the year and are subdivided into three categories, i.e., intermittently–open, seasonally–open and normally–closed, depending on the timing and duration of their connectivity to the ocean [5,15].

Disconnection of an estuary from the ocean alters the physicochemical conditions and can impact biota [5,13]. Bar closure increases the residence time of any nutrient contaminants and can lead to increased growth of macro- and microalgae [16] and, following decomposition, hypoxia [17]. Water temperature and salinity are more variable compared to permanently–open estuaries, and stratification can occur [12,18]. Prolonged bar closure can also lead to hypersalinity (salinity > 40), which reduces the range of species able to survive and can cause large mortality events [19–21]. Most fish species present in estuaries, particularly the larger-bodied taxa that reside in deeper waters, are of marine origin and require the estuary mouth to be open to allow the recruitment of juveniles and the immigration of adults and subadults [22,23]. Studies around the world have shown that estuaries with greater connectivity to the ocean contain more fish species [5,24,25].

Artificial breaching of sand bars is often conducted to reduce flooding risk, improve water quality, prevent fish kills, facilitate recruitment/immigration of fishery species and enhance recreational use [26,27]. There is often a historical legacy of breaching, with records of manipulation of estuary bars in the USA [28], Australia [29] and South America [26] dating back to the 1800s. This management option can be common practice, with >50% of the intermittently closed and open lagoons and lakes (ICOLLs) in New South Wales (Australia) having been breached artificially [30]. However, breaching when water levels are lower than those required for a natural breach [18] can result in poor flushing, stratification, hypoxia and fish kills [16,27,31,32], and the inflow of marine water can evapoconcentrate and cause hypersalinity [33]. As such, management protocols are increasingly being developed for regions [34,35] and estuaries [26,36] to determine whether an artificial breach should occur and, if so, how it should be conducted.

As in many temperate regions, southwestern Australian estuaries and their catchments have been substantially modified, with only 1 of the 34 surveyed remaining in “near-pristine” condition, with 7 and 20 being classified as “extensively modified” and “modified”, respectively, and the remaining 6 as “largely unmodified” [37]. Among the most modified is the Vasse–Wonnerup Estuary, which, together with the Moore River Estuary, are the only intermittently open estuaries in the region [38]. The Vasse–Wonnerup Estuary and its catchment have been substantially modified through land clearing and flow diversion [29,39]. Moreover, nutrient input has resulted in the Vasse–Wonnerup becoming “the most grossly enriched major wetland system known in Western Australia” [38,40,41] and suffering from algal blooms, hypoxia and fish kills [29,38]. Fish kills occur regularly, with reports of such events dating back to 1905 [29,42]. Numerous management measures have been used to reduce the frequency and severity of such events, including artificial bar breaches, management of the surge barriers to allow fish to move away from areas of poor water quality, artificial oxygenation, improvements to catchment land use and agricultural practices to reduce eutrophication [29,41,43]. Despite these considerable efforts, a substantial fish kill occurred in the lower reaches of the Vasse Estuary in April 2013 (Austral autumn) [44]. Over 30,000 large-bodied fish died, with postmortem examinations indicating hypoxia was the cause. The mugilids *Mugil cephalus* and *Aldrichetta forsteri* and the sparid *Acanthopagrus butcheri* comprised most of the carcasses. At the time of the fish kill, the sand bar was closed, air temperatures were unseasonably warm, ~30 mm of rain had fallen in the 48 h prior and wind speeds were low [45], all of which would have facilitated the occurrence of stratification-induced hypoxia/anoxia.

Prior to the current study, there was no quantitative data on the fish fauna that resided in the deeper (>2 m) waters of the Vasse–Wonnerup. Seasonal sampling for two years was initiated after the mass mortality event to identify the fish species present and determine if their richness, abundance, diversity and faunal composition differed among the various regions and/or over time. As this study represents the only data on the deeper-water fish fauna of an intermittently open estuary in southwestern Australia, the results were compared to those from permanently–open and seasonally–open estuaries. Finally, as studies from estuaries elsewhere in the world have shown that artificial breaching can lead to a range of detrimental impacts, the results are discussed in the context of breaches.

2. Materials and Methods

2.1. Study Site

The Vasse–Wonnerup is located on the west coast of southwestern Australia, near the town of Busselton, and comprises the Vasse and Wonnerup estuaries, Wonnerup Inlet and the Deadwater (Figure 1). The Vasse and Wonnerup estuaries consist of broad, shallow basins (~1 m deep in winter). Their surface areas change markedly throughout the year due to highly seasonal river flow and evaporation, but the regularly inundated areas cover 3 and 3.5 km, respectively [29,39]. Each estuary has a narrow exit channel at its downstream end that is connected, via a surge barrier, to Wonnerup Inlet [46]. Wonnerup Inlet, which is ~2 km long, up to 100 m wide and covers an area of 0.11 km^2, contains the estuary mouth, i.e., the sand bar that breaches or is artificially breached (see below). The Deadwater is a relatively long (2 km) narrow lagoon (15–100 m wide; 0.14 km^2) that lies parallel to the shore behind coastal dunes (Figure 1). This region receives no freshwater flow from rivers but is connected to Wonnerup Inlet and is tidally influenced when the sand bar is open. Unlike the two estuaries, Wonnerup Inlet and the Deadwater hold permanent water and contain areas > 2 m deep.

The surge barriers were first installed in 1908 to prevent the intrusion of saline water into each estuary during summer and autumn [29]. The current barriers were constructed in 2004, and each contains numerous flap gates that prevent the upstream movement of inflow from tides and/or storm surges but allow water to move downstream when the water level on the upstream side is sufficient to open the flap gates (Figure A1a). To retain water in the estuaries during summer, checkboards (Figure A1b) can be added to increase the effective sill height [29,39]. A propped gate and smaller fish gate (4 m long and 0.4 m wide) can be opened when the tidal height/water level is sufficient to allow water to move in the desired direction. These gates are typically used to increase water levels in the estuaries during summer/autumn to compensate for evaporation, improve water quality and allow fish to escape poor water quality on the upstream side and move into Wonnerup Inlet and/or the ocean [44].

The sand bar is breached multiple times a year [38,47], either naturally when water levels exceed berm height (e.g., following seasonal winter rainfall or an unseasonal storm event) or artificially using a backhoe and/or excavator [12,29]. The bar can remain open for days to months before sand accumulates, disconnecting the system from the ocean (Figure A1c–h). Artificial breaching dates back to the early 1900s, although management of the sand bar has changed over time (see [29] for a review). Such breaches were conducted in summer to improve water quality and prevent fish kills and in winter to expedite the outflow of water and prevent the flooding of urban and agricultural land. Note that as part of the flood management strategy, numerous rivers flowing into the Vasse–Wonnerup were fully diverted and now discharge directly into the ocean, e.g., the Capel River, or partially diverted, e.g., the Vasse and Sabina rivers (90 and 60% of flow diverted, respectively; see [39] for a review).

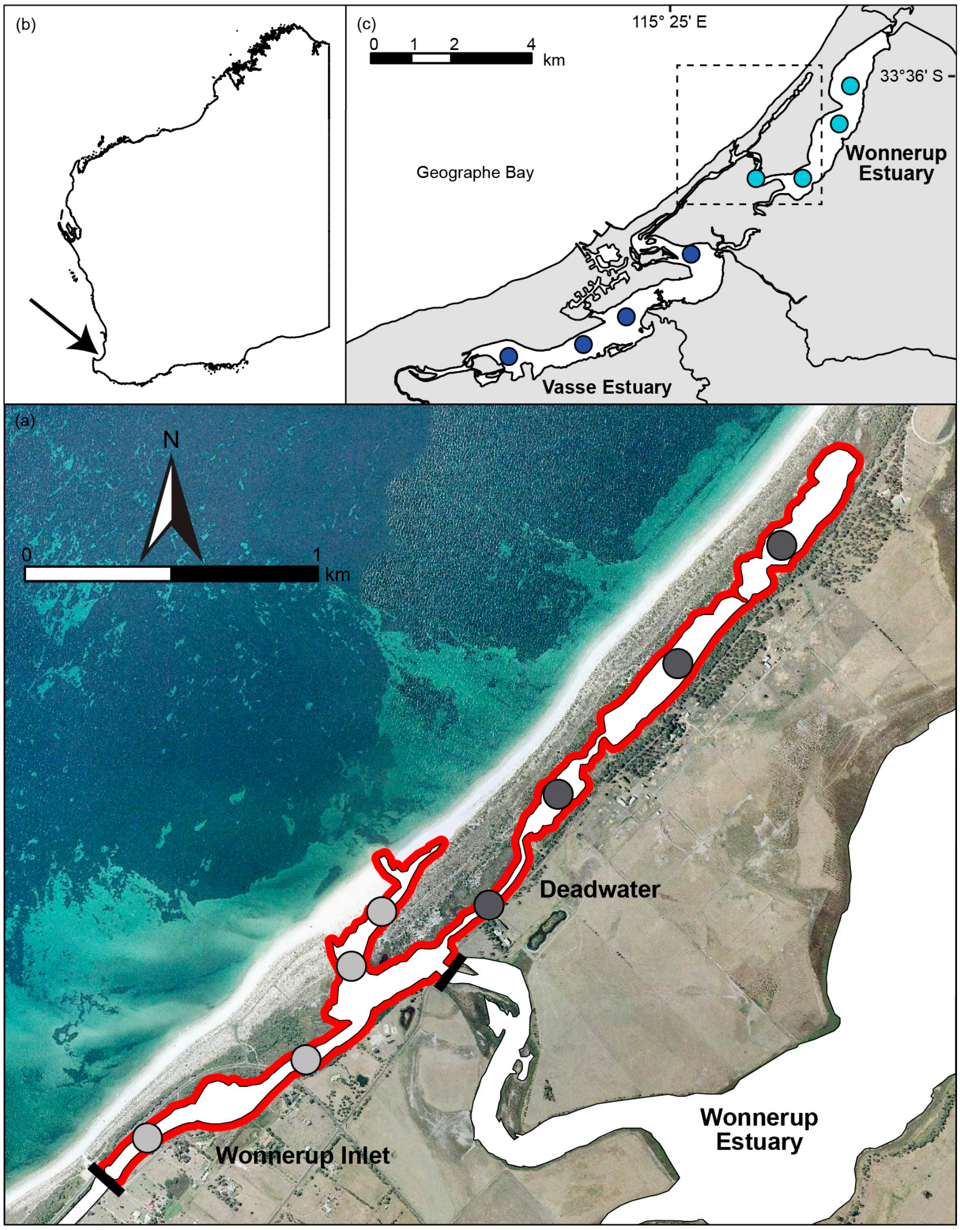

Figure 1. (**a**) Satellite image of the lower reaches (Wonnerup Inlet and the Deadwater) of the Vasse–Wonnerup (red line) and the sites (grey circles) where fish were sampled seasonally between winter 2013 and autumn 2015. Solid bars denote the two surge barriers. Location of (**b**) the Vasse–Wonnerup in Western Australia and (**c**) the lower reaches (dashed box) within the entire estuary and the sites (blue circles) in the Vasse and Wonnerup estuaries sampled in winter and spring 2014.

The Vasse–Wonnerup and the catchments of its rivers experience a Mediterranean climate with hot, dry summers and cool, wet winters [10]. The average annual rainfall between 1961 and 2010 was 752 mm, of which 82% fell between May and September, with the peak occurring in June and July, i.e., 157 and 165 mm, respectively [45]. Peak freshwater flow from rivers occurs slightly later, i.e., from July to September [41]. Pan-evaporation is 1399 and exceeds 150 mm per month between December and March [39].

2.2. Sampling Regime

The fish fauna of the deeper waters (i.e., >2 m deep) at four sites in both downstream regions (i.e., Wonnerup Inlet and the Deadwater) were sampled during the last month of each season over two years between the Austral winter (August) of 2013 and the Austral autumn (May) of 2015 (Figure 1). These regions were sampled as they were the only ones with a water depth > 2 m throughout the year. The regions upstream of the surge barriers (i.e., Vasse and Wonnerup estuaries) often become very shallow and markedly hypersaline (salinity up to 130), and areas may even dry completely during summer [46,48]. Additional sampling was able to be undertaken, however, at four sites in each upstream region in the winter and spring of 2014, the seasons when these areas hold the most water [46].

Sampling was conducted using sunken composite multifilament gill nets that comprised eight 20 m long and 2 m high panels, each with a different stretched mesh size (i.e., 35, 51, 63, 76, 89, 102, 115 or 127 mm). A single net was deployed at each site on each sampling occasion for one hour to minimize impacts on fish. Each fish was identified and measured to the nearest 1 mm in total length before being released. Species were assigned to an estuarine usage functional group sensu Potter et al. [49] and Whitfield et al. [24].

Water temperature (°C), salinity (practical salinity scale) and dissolved oxygen concentration (mgL^{-1}) were recorded at the surface and bottom of the water column at each site on each sampling occasion using a Yellow Springs Instrument 556 water-quality meter (Yellow Springs Instrument, OH, USA). On each day of sampling, the status of the sand bar, i.e., open or closed to the ocean, was noted.

2.3. Statistical Analyses

2.3.1. Downstream Areas of the Estuary

Univariate Analyses

The data for water temperature, salinity and dissolved oxygen were examined visually using a draftsman plot to determine whether any transformation was required to meet the test assumptions of permutational ANOVA (PERMANOVA) [50,51]. As none of the environmental variables required transformation, the data for each variable were used to construct a separate Euclidean distance matrix. Each matrix was subjected to a four-way PERMANOVA test to determine if that variable differed significantly ($p < 0.05$) with year (two levels: 2013/14 and 2014/15), season (four levels: winter, spring, summer and autumn), region (two levels: Wonnerup Inlet and Deadwater) and depth (two levels: surface and bottom). All factors were considered fixed. Emphasis was placed on significant main effects and/or interactions whose mean squares contributed >5% to the total. These terms were further explored using pairwise PERMANOVA and means plots with 95% confidence limits.

The number of species, total catch rate (fish h^{-1}) and Simpson's diversity [52] in each sample were calculated using DIVERSE [53] and combined in a data matrix with the catch rate of each of the three main species known to have been impacted by the April 2013 fish kill event, i.e., *M. cephalus*, *A. forsteri* and *A. butcheri*. The data for each biotic variable were in turn analyzed using the approach described above, with the following differences: (i) the total catch rate and the catch rate of each of the three fish species were square root transformed and (ii) the PERMANOVA design had three variables, i.e., year, season and region.

Multivariate Analyses of Faunal Composition

The catch rate (fish h^{-1}) of each fish species in each sample was dispersion–weighted [54], square–root transformed and then used to construct a Bray–Curtis resemblance matrix. This matrix was subjected to the three-way PERMANOVA design described above and, if required, pairwise PERMANOVA. If a significant main effect or interaction was detected, bootstrapped metric multidimensional scaling (bootstrapped mMDS) and centroid non-metric multidimensional scaling (centroid nMDS) ordination plots were used, respectively, to visualize the trends [55]. The averages of repeated bootstrapped samples (bootstrapped averages) were calculated from the Bray–Curtis resemblance matrix for each significant main effect individually and used to produce an mMDS plot. Plots contained a point representing the group average and the associated 95% bootstrap region. Centroid nMDS plots were constructed from a distance-among-centroids matrix for the significant interaction term from the Bray–Curtis resemblance matrix [56].

To elucidate the species responsible for the spatial and temporal differences in faunal composition, the transformed data were used to construct shade plots and subjected to the similarity percentage (SIMPER) routine [55]. As there was a significant year × season × region interaction (see Results), the catch rate of each fish species in each year, season and region combination was averaged and used to produce a shade plot [57]. The order of the fish species (y-axis) was determined by a hierarchical cluster analysis of their mutual associations across years, seasons and regions using a Bray–Curtis resemblance matrix of the average catch rate of each fish species in each combination. A type III SIMPROF test was then employed at each node of the dendrogram to determine whether the group of fish species being subdivided were significantly different. This test provided an objective method of grouping together fish species whose catch rate over the years, seasons and regions was similar within a group (red lines) but statistically significant between groups [58]. Samples (x-axis) were arranged in sequential order from winter 2013 to spring 2015. Interpretation of the shade plots, which used averaged transformed data, was informed by SIMPER. This routine was conducted on the transformed replicate data and identified species that typified the fish fauna in each a priori group and those responsible for distinguishing between groups.

2.3.2. Entire Estuary in Winter and Spring

The same suite of statistical analyses and visualization techniques was applied to each environmental and biotic variable and the faunal composition data from Wonnerup Inlet, Deadwater and Vasse and Wonnerup estuaries in winter and spring 2014. The only differences were that the PERMANOVA tests excluded year as a factor, season contained two levels (i.e., winter and spring) and region contained four (i.e., Wonnerup Inlet, Deadwater, Vasse Estuary and Wonnerup Estuary). As these analyses utilized fewer samples than those described above, the shade plot of the fish species recorded across the four regions in these two seasons was based on replicated rather than averaged data.

3. Results

3.1. Overall Description of the Fish Fauna

A total of 3960 fish representing 18 species were recorded, of which most species (15) and individuals (2974 fish; 75.1%) were marine (Table 1). Among these, all were marine estuarine opportunists, except for three fish from two species that were marine stragglers. The other three species, which together represented 24.8% of all individuals, were estuarine-resident species (i.e., solely estuarine and estuarine & marine) able to complete their life cycle in the Vasse–Wonnerup. The three most abundant species, i.e., the mugilids *M. cephalus* (33%) and *A. forsteri* (21%) and the sparid *A. butcheri* (18%), together comprised ~72% of all fish recorded (Table 1). Other species that were relatively abundant, i.e., contributed >5% to the total catch, were the gerreid *Gerres subfasciatus* and the terapontids *Amniataba caudavittata* and *Helotes octolineatus*. Wonnerup Inlet yielded more species (18 vs. 14) and fish (i.e., mean catch rate 64.6 vs. 51.5 fish h^{-1}) than the Deadwater. Of the 18 species recorded overall, 14 were found in both regions. In contrast, only two species were recorded in regions upstream of the surge barriers, i.e., *M. cephalus* and *A. forsteri* in the Vasse Estuary and *M. cephalus* in the Wonnerup Estuary (Table 1). It should be noted, however, that fewer samples were obtained from these regions (8 vs. 32). Mean total catch rates were 3 to 4.8 times lower in these upstream regions compared to Wonnerup Inlet and the Deadwater.

Table 1. Mean catch rate (fish h^{-1}; Cr), standard error (SE), percentage contribution (%), rank based on catch rate (R) of each fish species in the deeper waters of the Vasse–Wonnerup overall and in each of the four regions between winter 2013 and autumn 2015. Species ranked by total number of individuals caught (#). The mean total length and length range of each species are also provided. Estuarine usage functional groups (EUFG) are abbreviated as follows: E, solely estuarine; E&M, estuarine & marine; MEO, marine estuarine–opportunist; MS, marine straggler.

		Length (mm)			Overall				Deadwater (DW)				Wonnerup Inlet (WI)				Vasse Estuary (VE)				Wonnerup Estuary (WE)			
Species	**EUFG**	**Mean**	**Range**	**#**	**Cr**	**SE**	**%**	**R**	**Cr**	**SE**	**%**	**R**	**Cr**	**SE**	**%**	**R**	**Cr**	**SE**	**%**	**R**	**Cr**	**SE**	**%**	**R**
Mugil cephalus	MEO	243	110–455	1305	16.31	2.24	32.95	1	14.50	3.11	28.17	1	18.78	3.78	29.06	1	12.88	9.61	95.37	1	17.13	6.59	100.00	1
Aldrichetta forsteri	MEO	268	123–394	834	10.43	1.93	21.06	2	9.31	1.11	18.09	3	16.59	4.42	25.68	2	0.63	0.38	4.63	2				
Acanthopagrus butcheri	E	235	103–433	718	8.98	1.22	18.13	3	12.38	2.28	24.04	2	10.06	1.60	15.57	3								
Gerres subfasciatus	MEO	143	112–220	275	3.44	1.30	6.94	4	0.91	0.34	1.76	8	7.69	3.10	11.90	4								
Amniataba caudavittata	E	188	118–290	266	3.33	0.60	6.72	5	2.97	0.67	5.77	5	5.34	1.24	8.27	5								
Helotes octolineatus	MEO	187	136–265	206	2.58	0.76	5.20	6	5.88	1.75	11.41	4	0.56	0.18	0.87	10								
Rhabdosargus sarba	MEO	157	104–249	132	1.65	0.35	3.33	7	2.47	0.67	4.80	6	1.66	0.51	2.56	6								
Sillago schomburgkii	MEO	255	155–317	104	1.30	0.27	2.63	8	1.66	0.40	3.22	7	1.59	0.54	2.47	7								
Argyrosomus japonicus	MEO	386	234–528	46	0.58	0.16	1.16	9	0.63	0.24	1.21	9	0.81	0.31	1.26	9								
Arripis truttaceus	MEO	202	147–283	31	0.39	0.13	0.78	10	0.16	0.09	0.30	11	0.81	0.30	1.26	9								
Pomatomus saltatrix	MEO	234	173–287	19	0.24	0.08	0.48	11	0.38	0.17	0.73	10	0.22	0.12	0.34	11								
Pseudocaranx wrighti	MEO	162	120–183	7	0.09	0.04	0.18	12	0.09	0.07	0.18	12	0.13	0.07	0.19	13								
Sillago bassensis	MEO	279	255–304	5	0.06	0.06	0.13	13					0.16	0.16	0.24	12								
Elops machnata	MEO	322	270–407	4	0.05	0.02	0.10	14	0.09	0.05	0.18	12	0.03	0.03	0.05	17								
Pseudorhombus jenynsii	MEO	198	172–223	3	0.04	0.02	0.08	15	0.06	0.04	0.12	14	0.03	0.03	0.05	17								
Cnidoglanis macrocephalus	E&M	412	264–560	2	0.03	0.02	0.05	16					0.06	0.04	0.10	14								
Sillago vittata	MS	259	215–303	2	0.03	0.03	0.05	16					0.06	0.06	0.10	14								
Trygonorrhina fasciata	MS	560	560	1	0.01	0.01	0.03	18					0.03	0.03	0.05	17								
Number of species					18				14				18				2				1			
Total catch rate (fish h^{-1})					49.5				51.5				64.6				13.5				17.1			
Number of samples					80				32				32				8				8			

3.2. Downstream Areas of the Estuary

3.2.1. Bar Status and Environmental Conditions

At the commencement of sampling (winter 2013), there was a substantial wide and deep connection from Wonnerup Inlet to the ocean following heavy rainfall in August. The sand bar had reformed by spring 2013 but was breached artificially in December 2013 and remained open to the ocean by the time summer sampling occurred in February 2014. By autumn of that year, the bar was closed. The bar was closed when sampling in winter 2014 commenced; however, the estuary was breached while Wonnerup Inlet was being sampled. Before the breach, salinities in this region were ~22 and 27 at the surface and bottom of the water column, respectively, but declined to 0.8 throughout the water column after the breach due to the outflowing of oligohaline water from upstream of the surge barriers. Although sampling in the Deadwater had been completed prior to the breach, salinities in this part of the estuary remained relatively unchanged, i.e., mean = 20.6 before and 19.6 after. The bar was open for all of October 2014 but closed in early November and remained closed during spring sampling. The bar was open in summer 2015 following an earlier artificial breach, and although it was open during autumn 2015 (having breached two days before sampling), it had been closed for most of the previous month.

Water temperature differed significantly among year, season and region and in all two-way interactions between these main effects (Table A1a). Season was by far the most influential term, representing 81% of the total mean squares, followed by region (7%). Temperature underwent a sinusoidal increase from ~17 °C in winter to 22 and 23 °C in spring and summer, respectively, before declining to ~17 °C in autumn (Figure 2a). Values were slightly greater in the Deadwater than in Wonnerup Inlet, i.e., 20.5 vs. 19.6 °C, respectively (Figure 2b).

Significant differences in salinity were detected among year, season and region and all two- and three-way interactions involving these main effects (Table A1b). There was no evidence of stratification as the depth main effect, and all interactions involving this term were not significant (p = 0.092–0.869). As with temperature, season was the main driver (72% of the total mean squares), followed by year × season (12%) and region (7%). Salinity was lowest in winter (~8), before increasing sequentially through spring (~20) to 36 in summer and then declining slightly to 34 in autumn (Figure 2c). The season × year interaction was caused by salinities in spring 2014 being ~18 less than in spring 2013, whereas in most other seasons, values in both years were similar. Salinities were greater in the Deadwater than in Wonnerup Inlet, i.e., 26.8 vs. 22.9, respectively (Figure 2d).

Dissolved oxygen differed among all main effects, and the year × region interaction was also significant (p = 0.001–0.035). Among these terms, year and region were the most influential. Values in the Deadwater in both years were similar (5.6 and 6.1 mgL^{-1}), but those in Wonnerup Inlet were lower in 2013/14 than in 2014/15 (4.0 vs. 5.6 mgL^{-1}; Figure 2f). Concentrations were similar in winter, spring and summer and increased slightly in autumn (5.0–5.2 vs. 5.9 mgL^{-1}), and were marginally greater at the surface than at the bottom of the water column (5.5 vs. 5.1 mgL^{-1}; Figure 2e,g). Only a single hypoxic measurement (<2 mgL^{-1}) was recorded. This occurred at the site in Wonnerup Inlet closest to the bar in May 2014, with values at the surface and bottom of the water column being 1.62 and 1.39 mgL^{-1} (20.5 and 17% saturation, respectively).

3.2.2. Faunal Richness, Abundance and Diversity

The number of species was influenced only by the year × season and the year × season × region interactions, with these terms representing 37 and 19% of the total mean squares, respectively (Table A2a). The mean values ranged from 4 in winter 2013 to ≥7 between summer 2014 to winter 2015 and summer 2015, with the values being ~5 in the other seasons. The three-way interaction was caused by fewer species being recorded in Wonnerup Inlet (2.5) than the Deadwater (5.5) in winter 2013 (Figure 3a). The total catch rate also varied with year × season, with this being the only significant term in the model (Table A2b).

Trends followed those of the number of species with greater catches recorded between summer 2014 and winter 2015 compared to the other five seasons, i.e., 72–106 vs. 35–48 (Figure 3b). Region was the only factor that influenced Simpson's diversity (Table A2c), with greater values in the Deadwater than Wonnerup Inlet (0.72 vs. 0.63, respectively; Figure 3c). Catch rates of *M. cephalus*, *A. forsteri* and *A. butcheri* were relatively homogenous throughout the two regions and over time (Figure 3d–f), with the only significant difference detected being among years for *A. forsteri* (Table A2d–f). In this case, the mean catch rate in 2013/14 was twice that in 2014/15, i.e., 17.6 vs. 8.3 fish h^{-1}, respectively.

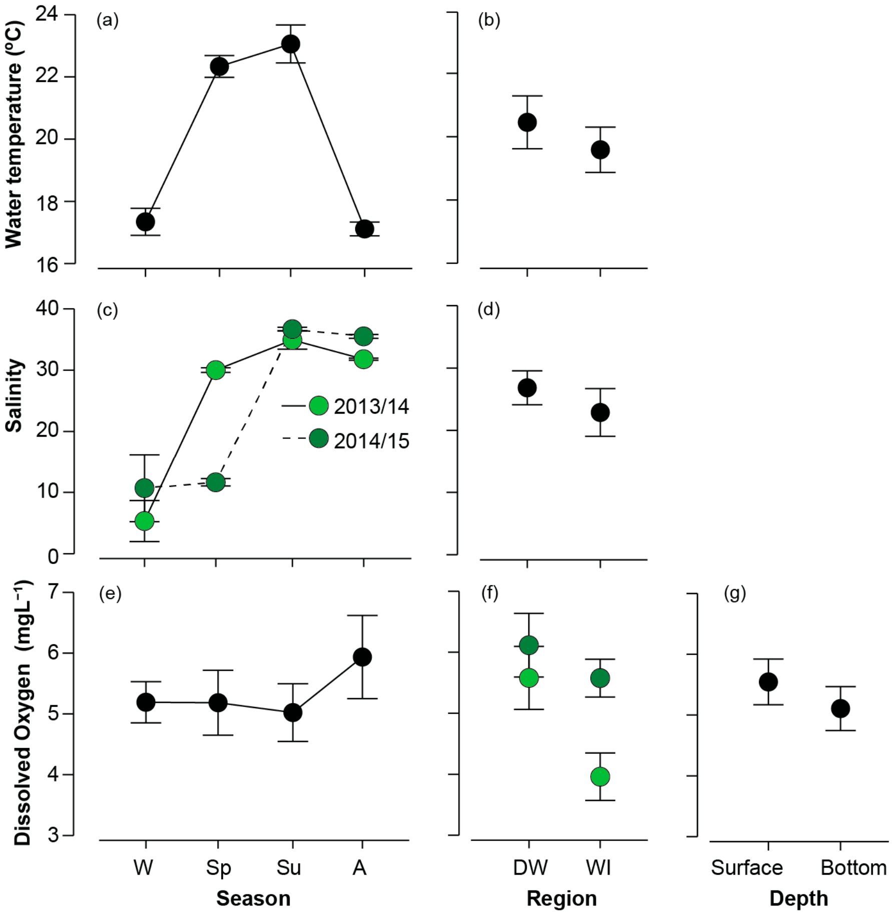

Figure 2. Mean values and 95% confidence limits for (**a**,**b**) water temperature, (**c**,**d**) salinity and (**e**–**g**) dissolved oxygen among seasons, regions and depths in the downstream regions of the Vasse–Wonnerup between winter 2013 and autumn 2015. Plots were selected based on four-way PERMANOVA tests (Table A1). DW = Deadwater; WI = Wonnerup Inlet.

3.2.3. Faunal Composition

Pronounced differences in faunal composition were detected, with year, season and region and the year × season interaction all being significant (Table A2g). The three-way interaction was borderline significant (p = 0.045), as reflected in this term explaining approximately half of the variance of the other significant terms in the model (i.e., 9.4 vs. ~19%). Differences among years are illustrated by the mMDS plot, where the bootstrapped averages and their 95% confidence regions are discrete (Figure 4a). Although the SIMPER routine selected *M. cephalus*, *A. forsteri* and *A. butcheri* as typifying the species in both years, their abundances were greater in 2013/14 than in 2014/15 (Figure 5). In contrast, the abundances of *A. caudavitta* and *R. sarba* increased in 2014/15. Pairwise testing demonstrated that a distinct fish fauna was present in each season (p = 0.001–0.037) except for winter vs. spring (p = 0.079), which is shown by the confidence regions for those seasons overlapping substantially (Figure 4b). The same three key species typified the fauna in all seasons, together with *S. schomburgkii* in spring and summer and *A. caudavitta* in the latter season (Figure 5). Several less abundant species, i.e., *Argyrosomus japonicus* and *Pomatomus saltatrix*, were typically only recorded in summer and autumn. The year × season (Figure 4d) and year × season × region interactions were caused by differences in the seasonal patterns among years and regions. For example, samples in winter 2013 contained fewer species and lower catch rates than in winter 2014, and although the two regions harbored a similar broad suite of species in winter 2014 as in that season in 2013, only three species (*M. cephalus*, *A. forsteri* and *A. butcheri*) were recorded in Wonnerup Inlet, whereas *A. caudavitta*, *S. schomburgkii*, *H. octolineatus* and *G. subfasciatus* were all recorded in the Deadwater. Interannual differences were also detected in summer, with higher catch rates of most species in summer 2014, particularly *H. octolineatus* and *G. subfasciatus*, and *A. japonicus* only being recorded in the summer of 2015. Pairwise testing did not detect a significant difference among years in either spring or autumn, with the points representing these two seasons in each year being situated closer together than those for winter or summer (Figure 4d). Differences between regions (Figure 4c) were due to higher catch rates of *A. butcheri*, *S. schomburgkii*, *H. octolineatus* and *R. sarba* in the Deadwater and *M. cephalus*, *A. forsteri*, *A. caudavitta* and *G. subfasciatus* in Wonnerup Inlet (Figure 5).

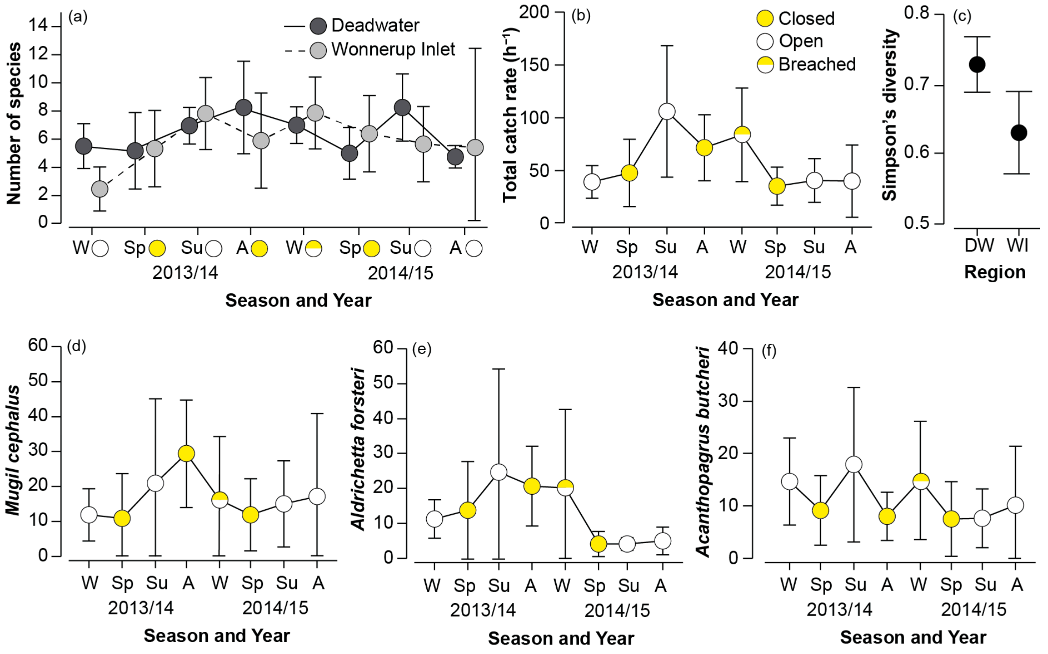

Figure 3. Mean values and 95% confidence limits for (**a**) the number of species among years, seasons and regions; (**b**) total catch rate (fish h^{-1}) among seasons and years; (**c**) Simpson's diversity among regions and catch rate (fish h^{-1}) of (**d**) *Mugil cephalus*, (**e**) *Aldrichetta forsteri* and (**f**) *Acanthopagrus butcheri* in each season and year. Data from the downstream regions of the Vasse–Wonnerup between winter 2013 and autumn 2015. Plots were selected based on three-way PERMANOVA tests (Table A2). The bar status in each season is also provided. DW = Deadwater; WI = Wonnerup Inlet.

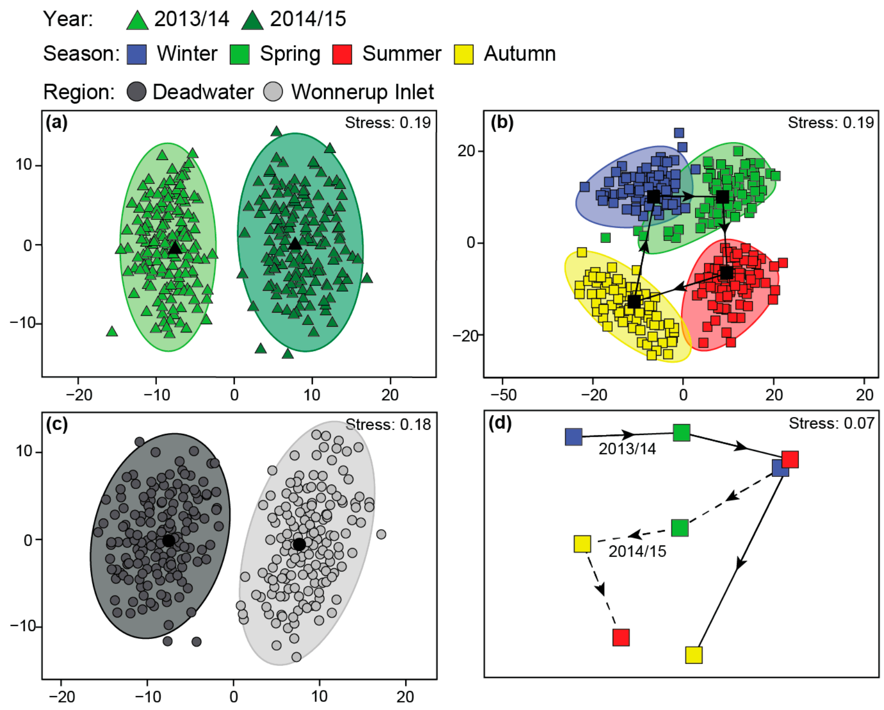

Figure 4. Two-dimensional bootstrapped mMDS ordination plots constructed for each (**a**) year, (**b**) season and (**c**) region using the catch rate of each fish species in the downstream regions of the Vasse–Wonnerup between winter 2013 and autumn 2015. Group averages (larger black symbols) and 95% region estimates are provided. (**d**) Centroid nMDS ordination plot of the season × year interaction. Arrows in (**b**,**d**) denote the direction of seasonal cycling.

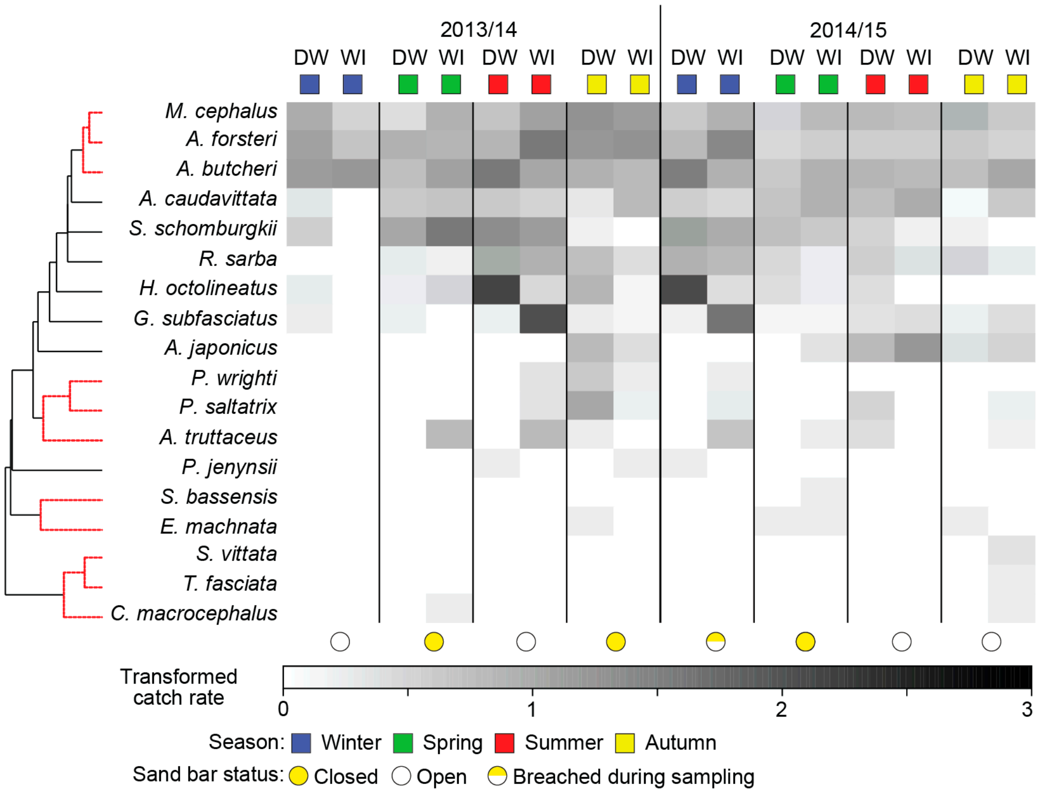

Figure 5. Shade plot of the average dispersion-weighted and square-root transformed catch rate of each fish species in each year, season and downstream region combination. Species are ordered by

hierarchical cluster analysis, with those joined by red lines having a similar spatial and temporal pattern of abundance. The bar status in each season is also provided. Full species names are given in Table 1. DW = Deadwater; WI = Wonnerup Inlet.

3.3. Entire Estuary in Winter and Spring

3.3.1. Environmental Conditions

Water temperature and salinity upstream and downstream of the surge barriers in the winter and spring of 2014 differed with season, region and their interaction (Table A3a,b). For water temperature, season contributed >99% to the total mean squares, with values being cooler in winter than spring (16.9 vs. 22.7 °C; Figure 6a). For salinity, region and season × region were the main drivers, i.e., 74 and 23% of the total mean square, respectively. Salinities in the Deadwater were always the greatest, i.e., 20 in spring and 13 in winter, and the regions upstream of the surge barriers were the freshest (range = 0.8 to 4). The interaction was caused by values in Wonnerup Inlet being variable among seasons, i.e., 0.8 in winter and 11 in spring (Figure 6b). Dissolved oxygen concentrations differed only by region (Table A3c). Pairwise testing identified differences between regions upstream (~5.5 mg L^{-1}) and downstream of the surge barriers (7.6 and 8.2 mg L^{-1}; Figure 6c).

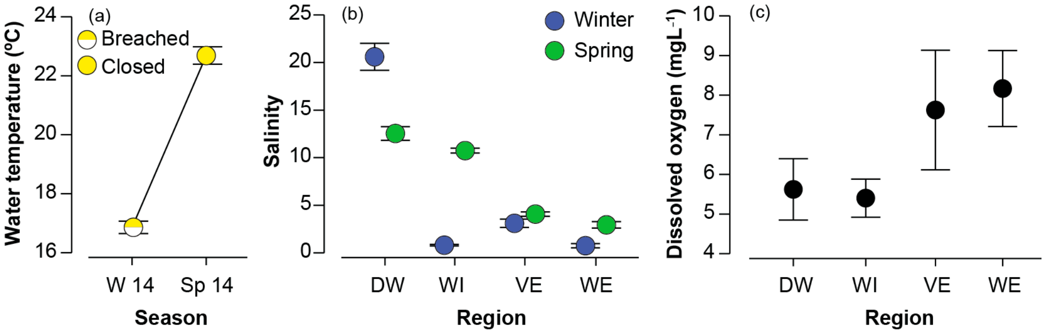

Figure 6. Mean values and 95% confidence limits for (**a**) water temperature among seasons, (**b**) salinity in each region and each season and (**c**) dissolved oxygen among regions. Data from the entire Vasse–Wonnerup in winter and spring 2014. Plots were selected based on three-way PERMANOVA tests (Table A3). The bar status in each season is also provided. DW = Deadwater; WI = Wonnerup Inlet; VE = Vasse Estuary; WE = Wonnerup Estuary.

3.3.2. Faunal Richness, Abundance and Diversity

Both the number of species and catch rates differed significantly among seasons and regions, but the season × region interaction was not significant (Table A4). Region was the most influential term for the number of species (83%), with mean values for the Deadwater (6.0) and Wonnerup Inlet (7.3) being far greater than those in the Vasse and Wonnerup estuaries (<1; Figure 7b). Although variable, more species were caught, on average, in winter than in spring (4.4 vs. 2.9; Figure 7a). Season was the biggest driver of catch rates (58%), with almost three times more fish recorded in winter than in spring (Figure 7c). Larger catches were obtained from the regions downstream than upstream of the surge barriers (Figure 7d). Simpson's diversity only differed among regions (Table A4c), with values in the Deadwater and Wonnerup Inlet being similar (mean = 0.7; Figure 7e) but significantly greater than those in the Vasse and Wonnerup estuaries (0.1 and 0.0, respectively, which also did not differ significantly).

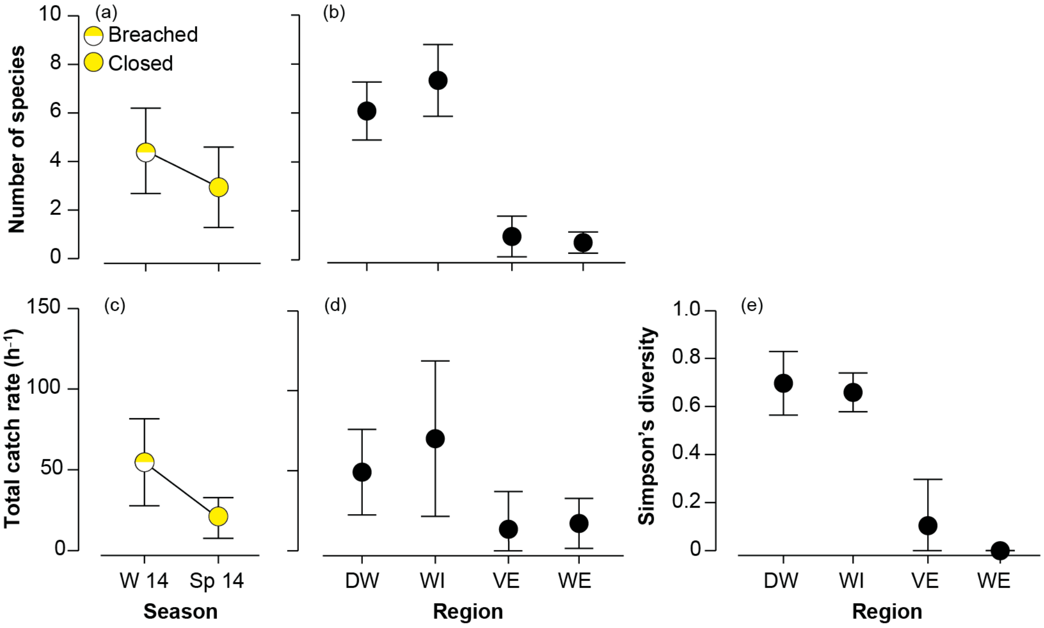

Figure 7. Mean values and 95% confidence limits for the number of species among (**a**) seasons and (**b**) regions, total catch rate (fish h^{-1}) among (**c**) seasons and (**d**) regions and (**e**) Simpson's diversity among regions. Data from the entire Vasse–Wonnerup in winter and spring 2014. Plots were selected based on three-way PERMANOVA tests (Table A4). The bar status in each season is also provided. DW = Deadwater; WI = Wonnerup Inlet; VE = Vasse Estuary; WE = Wonnerup Estuary.

3.3.3. Faunal Composition

The composition of the fish fauna was influenced significantly by season, region and the season × region interaction, with the two main effects explaining a larger proportion of the variance (39%) than their interaction (18%; Table A4d). Pairwise testing among regions showed that, in these seasons, there was no difference between the regions on the same side of the surge barrier (i.e., Deadwater vs. Wonnerup Inlet, p = 0.229; Vasse Estuary vs. Wonnerup Estuary, p = 0.087). This spatial pattern of differences is shown clearly on the mMDS plot, where the bootstrapped averages for the regions downstream of the surge barriers are widely separated from those representing the two upstream regions. There is considerable overlap between those of the Deadwater and Wonnerup Inlet and, to a lesser extent, between those of the Vasse and Wonnerup Inlet (Figure 8b). While there is a clear distinction between the bootstrapped averages for the two seasons (Figure 8a), the centroid nMDS plot shows that there was greater seasonal variability in the regions upstream of the surge barriers (Figure 8c).

A far larger range of species was identified as typifying the fish fauna present in the downstream regions, with species such as *A. forsteri*, *A. butcheri*, *S. schomburgkiii*, *A. caudavitta* and *M. cephalus* being recorded in almost every sample (Figure 9. In contrast to the relatively species-rich fauna downstream of the surge barrier, only the mugilids *A. forsteri* and *M. cephalus* were recorded in the Vasse and Wonnerup estuaries and even then, not in all samples. For example, the former species was present in low abundance in three of the four Vasse Estuary samples in winter but not at all in spring, and although *M. cephalus* was recorded in all samples from both estuaries in winter, this species was only recorded in a single sample in Wonnerup Inlet in spring (Figure 9). Thus, the upstream regions contained a depauperate offshore fish fauna in winter, and by spring, very few fish remained in these waters.

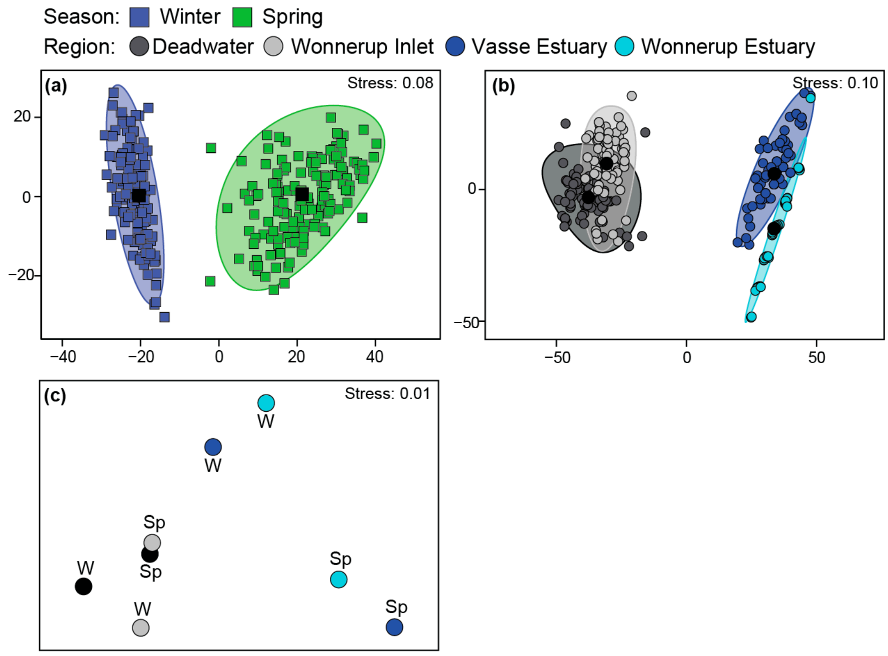

Figure 8. Two-dimensional bootstrapped mMDS ordination plots constructed for each (**a**) season and (**b**) region using the catch rate of each fish species in each region of the Vasse–Wonnerup in winter and spring 2014. Group averages (larger black symbols) and 95% region estimates are provided. (**c**) Centroid nMDS ordination plot of the season × region interaction.

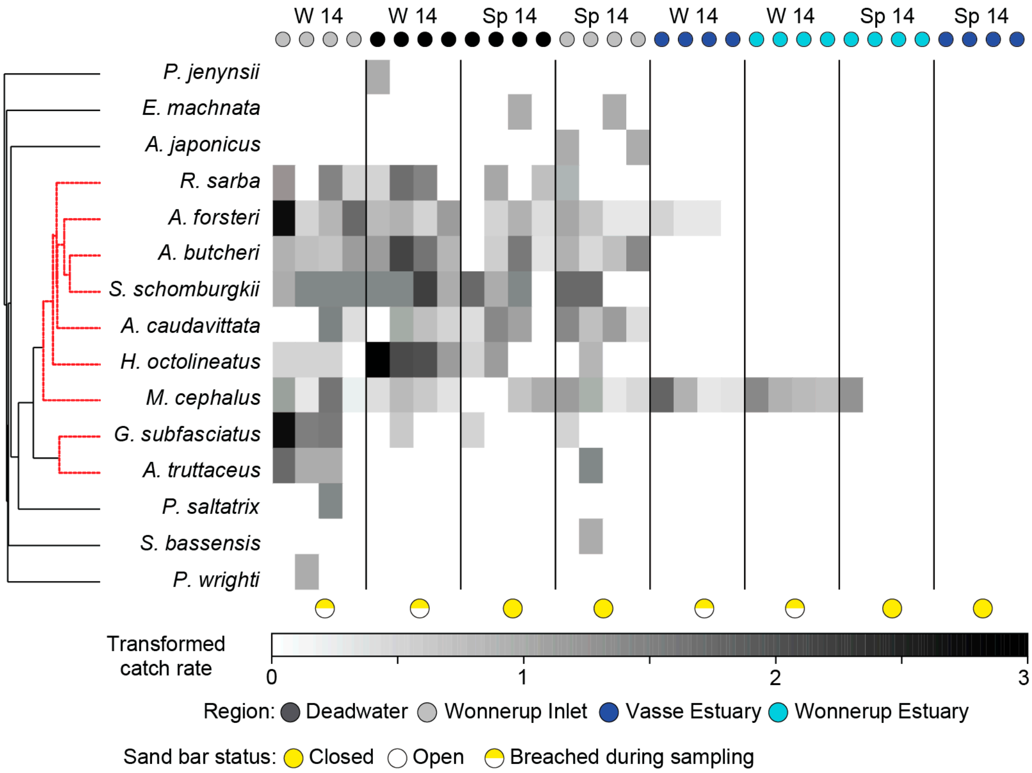

Figure 9. Shade plot of the dispersion-weighted and square-root-transformed catch rate of each fish species in each sample from the entire Vasse–Wonnerup in winter and spring 2014. Species are ordered by hierarchical cluster analysis, with those joined by red lines having a similar spatial and temporal pattern of abundance. The bar status in each season is also provided. Full species names are given in Table 1.

4. Discussion

This study was initiated following a large fish kill in the Vasse–Wonnerup that led to the mortality of >30,000 large-bodied fish, mainly the mugilids *Mugil cephalus* and *Aldrichetta forsteri* and the sparid *Acanthopagrus butcheri*, which reside in the deeper waters [44]. The main aim was to identify the fish species present in the system and determine if richness, abundance, diversity and faunal composition differed among the various regions and over time. As most species recorded spawn in marine waters, and the sand bar breaches multiple times a year allowing movement of fish to and from the ocean, the impacts of such breaches on the fish fauna are also discussed.

4.1. Overall Fauna

A total of 18 fish species were recorded across the two years of seasonal gill netting in the deeper waters of the Vasse–Wonnerup. This is considerably less than those recorded using gill nets in the three permanently–open estuaries on the lower-west coast of Western Australia, i.e., 24 in Swan–Canning [59], 25 and 26 in Peel–Harvey [60,61] and 30 in Leschenault [62]. However, it is greater than in the other intermittently–open estuary in the region, i.e., Moore River, in which 8 species were recorded (Ian Potter, unpublished data) and for the two seasonally–open estuaries, i.e., 12 in Toby Inlet [63] and 4 in Hill Inlet [64]. Thus, there is a consistent reduction in the species richness recorded in estuaries with decreased connectivity to the ocean. This mirrors the pattern recorded between permanently–open, seasonally–open and normally–closed estuaries on the south coast of Western Australia [22]. Such trends are driven by most of the species present in the deeper waters of estuaries spawning in the ocean, and thus their individuals can only immigrate into estuaries if the bar is open. For example, in Toby Inlet, which is located ~20 km south of the Vasse–Wonnerup, only 4 fish species were recorded when the bar was closed, but identical sampling yielded 12 species several months later following an artificial bar breach [63].

Similar to Toby Inlet, but in contrast to seasonally–open estuaries on the south coast of Western Australia, very few marine straggler species were recorded in the Vasse–Wonnerup [22,63]. The nearshore marine environment on the south coast is exposed to greater swell and wave action, which may make the sheltered waters of estuaries attractive to such species for short periods of time [65]. Conversely, both Toby Inlet and the Vasse–Wonnerup are located in Geographe Bay, a sheltered marine embayment that contains extensive seagrass beds and thus provides ample shelter, habitat and food [66].

4.2. Spatial Differences

4.2.1. Downstream Areas of the Estuary

Water temperature, salinity and dissolved oxygen were broadly similar between the two regions, although, on average, slightly lower values were recorded in Wonnerup Inlet. This is due to the seasonal discharge of water from the Vasse and Wonnerup estuaries into the latter region, whereas the Deadwater receives no direct flow [46]. When the bar is breached during times of the year when the estuaries contain high levels of water (i.e., winter), the force generated by that cooler, fresh–oligohaline water opens the flap gates and travels through the surge barriers into Wonnerup Inlet and out to the ocean. Similar hydrodynamics have been recorded in the temporarily open/closed East Kleinemonde Estuary in South Africa [13]. Unlike in some intermittently–open estuaries around the world [16,27,31,32], this flow did not lead to stratification or hypoxia. The lower mean value for dissolved oxygen in Wonnerup Inlet was caused by several low values in May 2014, which coincided with accumulations of seagrass wrack that had washed in through the open sand bar and were decomposing [JRT pers. obs., 29], which may have lowered oxygen concentrations at that time [67].

Overall, 14 of the 18 fish species were found in both downstream regions, with 4 being unique to Wonnerup Inlet. None of these four species were abundant (all <5 individuals), and two of these were the only marine stragglers recorded, which by definition are most likely to occur in the most downstream areas of the estuary [49]. There were no consistent differences in mean species richness or total catch rate between the regions, likely reflecting their small size and close proximity and the fact that the most abundant fish species are highly mobile. For example, acoustically tagged adult *A. butcheri* in the Vasse–Wonnerup and *M. cephalus* in the Sundays Estuary (South Africa) traveled, on average, 2.73 and 3.87 km per day, respectively [44,68].

Differences in faunal composition were due, in part, to higher catch rates of *A. butcheri* and *S. schomburgkii* in the Deadwater and *M. cephalus*, *A. caudavitta* and *G. subfasciatus* in Wonnerup Inlet. Although each of these species was recorded in both regions, their greater abundance in one can be explained by their reproductive biology and diet. For example, *A. butcheri* moves into the Deadwater in winter to spawn [44] as salinities in the Vasse and Wonnerup estuaries are too low at this time of year for their eggs to survive [69]. As *M. cephalus* is a detritivore [70,71], its higher abundance in Wonnerup Inlet likely reflects the accumulation of seagrass wrack in this region. The abundances of *S. schomburgkii*, *A. caudavitta* and *G. subfasciatus* are also likely influenced by the availability of food, with the former species consuming mainly amphipods [72], which are more abundant in the poorly-flushed Deadwater [73]. Conversely, *A. caudavitta* and *G. subfasciatus* primarily feed on polychaetes [74,75], which are more numerous in Wonnerup Inlet [73].

4.2.2. Entire Estuary in Winter and Spring

With the exception of Wonnerup Inlet in winter (see above), salinities were far greater in the two downstream than upstream regions due to the input of freshwater from seasonal rainfall [46]. Although the waters of all regions were normoxic, the higher concentrations of dissolved oxygen in the upstream areas reflect the extensive beds of the seagrasses *Ruppia polycarpa* and *Ruppia megacarpa* [76].

In contrast to the 18 and 14 species recorded in Wonnerup Inlet and the Deadwater, respectively, only the mugilids *M. cephalus* (both estuaries) and *A. forsteri* (Vasse only) were caught in waters above the surge barrier(s). These results align with those of recreational and commercial fishers, who indicated that, aside from the two mugilids, the only other species regularly caught upstream of the surge barriers, albeit in lower abundances, was *A. butcheri* [77]. The absence of *A. butcheri* in the current study is supported by previous acoustic tracking, where none of the 41 tagged fish moved into the Wonnerup Estuary and only 7 entered the Vasse Estuary [44]. Even when they did, they were most often recorded in the Vasse exit channel, which is located immediately on the upstream side of the surge barrier and downstream from the sampling sites. Moreover, *A. butcheri* typically uses these waters during summer [44] rather than in winter and spring, when the netting was conducted, and opportunistic gill netting in the Vasse exit channel has resulted in the capture of this species (JRT, unpublished data).

Although the number of fish species decreases further upstream in estuaries [60,78], the fish faunas of the upper regions of the Vasse–Wonnerup are particularly depauperate. For example, between 5 and 10 species were caught using the methodology and sampling effort in the three rivers of the Peel–Harvey Estuary [61], and 4–12 species were recorded in rivers of estuaries on the south coast of Western Australia [22]. The greater richness of the fauna in the uppermost reaches of the other estuaries reflects their more saline conditions and the fact that most species that are euryhaline have marine affinities [24,49].

4.3. Temporal Differences

There were no clear temporal trends in the catch rate of the marine estuarine-opportunist *M. cephalus* in the eight consecutive seasons after the loss of thousands of individuals during the fish kill. As part of the management response to that event, the bar was artificially breached, and the fish gate in the Vasse surge barrier was opened. This would have provided the opportunity for the remaining individuals to move downstream and leave the estuary and for "new" individuals to immigrate from the ocean, replenishing stocks. In contrast to *M. cephalus,* catch rates of *A. forsteri* were significantly lower during 2014/15 than 2013/14. The reasons for this lower recruitment are unclear and unlikely to be related to conditions in the downstream regions of the estuary, as in the summers of both years, the bar was open and salinities were similar to full-strength seawater. In the absence of subsequent environmental perturbations, it is hypothesized that the abundance of mugilids in the Vasse–Wonnerup likely reflects recruitment strength in the marine environment and their population size in Geographe Bay during a time when the bar of the estuary was open, allowing immigration.

In contrast to the two mugilids, where the size of the populations is dynamic due to immigration from and emigration to the ocean, *A. butcheri* are solely estuarine and complete their life cycle within the Vasse–Wonnerup [44,79]. While the population of *A. butcheri* in deeper waters was unknown before the fish kill, given the thousands that died in that event, the population almost certainly decreased to some extent. The lack of a significant difference in catch rates over the two years of seasonal sampling suggests that populations of this species did not increase after the fish kill. This species is highly fecund, with mean and maximum fecundities of 1.5 and 7 million eggs, respectively [79], and populations have recovered from large perturbations in other estuaries. For example, an estimated 1.3 million *A. butcheri* died in Culham Inlet (south coast of Western Australia) in April 2001 due to extreme hypersalinity (salinity = 82–95), yet individuals were recorded in February 2002 [80,81]. In addition to the mortality of large *A. butcheri* in the Vasse–Wonnerup in the fish kill, seine net sampling indicated that juveniles were recorded in the shallow waters of Wonnerup Inlet and the Deadwater in February 2013 before the fish kill in April but that subsequent recruitment did not occur until November 2014 and even then it was limited [82]. Newly spawned fish would not have reached the size at which they can be caught in gill nets until at least November 2015 (~1 year after birth) and sexual maturity in May 2017 (~2.6 years after birth) [82], i.e., after the completion of sampling. Given this, the lack of an increase in *A. butcheri* in the two years after the fish kill is likely due to the loss of juveniles from the previous spawning period (winter 2012) and recruitment failure in winter 2013.

Fish faunal composition differed significantly among seasons and years; however, the magnitude of those differences was relatively minor. This result mirrors that in three seasonally–open estuaries [22] and reflects the relatively consistent catch rates of the three most abundant species in the Vasse–Wonnerup, which together comprised 75% of all fish caught. The seasonal differences observed were due to shifts in the catch rates of less-abundant species. The faunal community was fairly depauperate in winter 2013, particularly in Wonnerup Inlet, where only the three main species were recorded, likely due to the emigration of species following the breach (see 4.4). Species such as *A. caudavittata* and *R. sarba* increased after winter 2013 and, among the non-dominant species, made relatively large contributions to the fish fauna in the remaining seasons. Although *A. caudavittata* is regarded as a solely estuarine species in south–western Australia [74] individuals of this species have been recorded in Geographe Bay [83]. Thus, some may have recruited into the Vasse–Wonnerup. As this species has a similar spatial distribution within an estuary as *A. butcheri* and consumes the same types of prey [84,85], individuals may have taken advantage of reduced competition following the mass mortality of *A. butcheri*. The same may also be true for the confamilal *R. sarba*. While there is no information on the abundance of *R. sarba* in the deeper waters before the April 2013 fish kill, data from shallow waters showed there was a ratio of *A. butcheri:R. sarba* of 27.1:1.0 in 2012/13 which was 1.8:1.0 in 2017/18 [47,48].

Several other species, most notably *P. saltatrix* and *A. japonicus*, were typically only recorded during summer and autumn following breaches, suggesting they preferred the stable, saline conditions present in Wonnerup Inlet and the Deadwater in these seasons. This assertion is supported by the fact that the former species was recorded in the seasonally open Broke Inlet only during summer and autumn [86].

4.4. Fish Kills and Bar Breaches

The three species reported as representing most of the fish that died in the April 2013 fish kill were the three most abundant species in the deeper waters of the Vasse–Wonnerup. Except for *A. butcheri* and *A. caudavittata*, the 16 other species recorded, representing 75% of all fish recorded, spawn in marine waters and are thus able to recolonize the estuary, provided the bar is open and the cause of the kill is no longer present. This enables, in general, the deeper-water fish fauna to be fairly resilient and recover from mass mortality events. However, despite sampling for almost 2.5 years after the kill, there was no evidence that the population of *A. butcheri* increased, and as the successful recruitment of this species is naturally episodic [87], it may take years to decades for the population to reach pre-fish kill abundances. Moreover, *A. butcheri* is the dominant species in the deeper waters of normally–closed estuaries, thus magnifying the potential impacts of any mass mortality event [22,81].

Based on the timing of the sampling in the current study relative to multiple bar breaches, the data in this study can be used to develop a preliminary model of the impacts of the different hydrodynamic states identified by Whitfield et al. [13] on environmental variables and the deeper-water fish fauna. During the closed phase (Figure A1c,e), species that have immigrated into the estuary become trapped. When a natural breach occurs, oligohaline water passes through the Vasse and Wonnerup surge barriers, lowering salinity in Wonnerup Inlet (and, to a lesser extent, the Deadwater), and scours out an entrance channel (Figure A1f). Sampling in Wonnerup Inlet several hours after the bar breached in winter 2014 (outflow phase) yielded among the highest number of species, presumably as fish were caught attempting to emigrate to the ocean. The duration of this relatively short phase, which is <2 days in the East Kleinemonde Estuary [13], depends on the height of the water level before the breach. Sampling in winter 2013, where only three species were recorded in Wonnerup Inlet, occurred towards the end of this phase, suggesting that all species (and individuals) that wished to leave the estuary had done so. Given the lack of direct discharge into the Deadwater, this region acts as a saline and calmer refuge for those fish wanting to remain within the estuary during periods of high flow. As outflow decreases and sediment starts to infill the entrance channel, the breach is in the tidal phase (Figure A1g). This represents the optimal time for the immigration of marine estuarine opportunists, particularly those that are less euryhaline, as occurred in summer 2014. As sand continues to accumulate, connectivity with the ocean decreases (semi-closed phase; Figure A1h), first at low tide and then more frequently, limiting the opportunity for fish to move into or out of the estuary. Finally, the bar reaches a height where the estuary is fully disconnected from the ocean (closed phase) until breached again by natural or artificial means.

Artificial breaching before the water level is sufficient to naturally break the bar reduces scour and flushing and can lead to stratification, hypoxia and fish [16,27,31,32]. The artificial breaching undertaken in summer in the Vasse–Wonnerup is different from that described above because, at this time of the year, freshwater discharge is low and the downstream regions are disconnected from the Vasse and Wonnerup estuaries by the surge barriers and additional stop boards raise the water level retained on the upstream side. This prevents any mixing of waters with different physicochemical properties and thus the risk of any stratification. In the seasons following such events, there was no evidence of hypoxia or fish mortality, and the richness of the fish community increased. Moreover, tidal exchange ensures water in the downstream region is regularly circulated and not stagnant, mitigating the effect of any localized decomposition of seagrass wrack. Finally, maintaining “sea water” in the downstream regions provides the option to open the prop and fish gates to allow this water to move upstream (Figure A1b). This could be done to improve water quality in the exit channels where fish kills often occur [44], reduce the magnitude of any hypersalinity [36], raise the water level to a level suitable for the feeding activities of migratory birds that visit during summer [88] and/or prevent exposure to and oxidation of the monosulfidic black ooze present in the Vasse exit channel [89].

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Institutional Review Board Statement: The study was conducted in accordance with Murdoch University Animal Ethics Permit #RW2471_12.

Data Availability Statement: The data presented in this study are available on reasonable request from the corresponding author.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Mean squares (MS), the contribution of mean squares to total mean squares (%MS), pseudo-F (*pF*) and significance levels (*p*) from four-way PERMANOVA tests on (a) water temperature, (b) salinity and (c) dissolved oxygen measured at the surface and bottom of the water column in the downstream regions of the Vasse–Wonnerup in each season between winter 2013 and autumn 2015. Terms that are significant ($p < 0.05$) and contribute >5% to the MS are highlighted in bold.

		(a) Water Temperature				**(b) Salinity**			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Year	1	9.83	2.77	19.37	0.001	99.71	1.51	34.62	0.001
Season	**3**	**287.11**	**81.00**	**565.87**	**0.001**	**4764.00**	**72.38**	**1654.30**	**0.001**
Region	**1**	**24.83**	**7.00**	**48.94**	**0.001**	**430.74**	**6.54**	**149.57**	**0.001**
Depth	1	0.02	0.01	0.04	0.830	3.16	0.05	1.10	0.292
Year × season	3	12.93	3.65	25.49	0.001	**810.08**	**12.31**	**281.30**	**0.001**
Year × region	1	9.61	2.71	18.95	0.001	100.75	1.53	34.99	0.001
Year × depth	1	0.06	0.02	0.11	0.759	2.01	0.03	0.70	0.393
Season × region	3	7.03	1.98	13.86	0.001	303.44	4.61	105.37	0.001
Season × depth	3	0.05	0.02	0.11	0.949	3.00	0.05	1.04	0.399
Region × depth	1	0.15	0.04	0.29	0.574	1.59	0.02	0.55	0.459
Year × season × region	3	1.80	0.51	3.55	0.024	54.31	0.83	18.86	0.001
Year × season × depth	3	0.06	0.02	0.13	0.957	2.16	0.03	0.75	0.541
Year × region × depth	1	0.02	0.00	0.03	0.853	2.51	0.04	0.87	0.326
Season × region × depth	3	0.15	0.04	0.29	0.826	0.74	0.01	0.26	0.851
Year × season × region × depth	3	0.28	0.08	0.56	0.656	0.67	0.01	0.23	0.869
Residual	86	0.51	0.14			2.88	0.04		

		(c) Dissolved Oxygen			
Term	**df**	**MS**	**%MS**	***pF***	***p***
Year	**1**	**33.83**	**36.53**	**27.99**	**0.001**
Season	**3**	**5.68**	**6.13**	**4.70**	**0.005**
Region	**1**	**32.04**	**34.60**	**26.52**	**0.001**
Depth	**1**	**6.05**	**6.54**	**5.01**	**0.027**
Year × season	3	1.26	1.37	1.05	0.380
Year × region	**1**	**6.02**	**6.50**	**4.98**	**0.035**
Year × depth	1	0.56	0.60	0.46	0.526
Season × region	3	2.39	2.58	1.98	0.140
Season × depth	3	0.59	0.64	0.49	0.701

Table A1. *Cont.*

Region × depth	1	−0.64	−0.69	0.00	1.000
Year × season × region	3	1.65	1.79	1.37	0.253
Year × season × depth	3	0.30	0.32	0.24	0.854
Year × region × depth	1	0.15	0.16	0.12	0.742
Season × region × depth	3	1.09	1.18	0.90	0.446
Year × season × region × depth	3	0.42	0.45	0.35	0.790
Residual	86	1.21	1.31		

Table A2. Mean squares (MS), the contribution of mean squares to total mean squares (%MS), pseudo-F (*pF*) and significance levels (*p*) from three-way PERMANOVA tests on the (a) number of species, (b) total catch rate and (c) Simpson's diversity. Catch rates of (d) *Mugil cephalus*, (e) *Aldrichetta forsteri*, (f) *Acanthopagrus butcheri* and (g) faunal composition recorded in the downstream regions of the Vasse–Wonnerup in each season between winter 2013 and autumn 2015. Terms that are significant ($p < 0.05$) and contribute >5% to the MS are highlighted in bold.

		(a) Number of Species				**(b) Total Catch Rate**			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Year	1	1.89	3.25	0.56	0.441	17.16	20.82	2.49	0.137
Season	3	9.14	15.69	2.73	0.056	9.83	11.92	1.42	0.236
Region	1	2.64	4.53	0.79	0.388	5.80	7.04	0.84	0.357
Year × season	**3**	**21.56**	**37.01**	**6.44**	**0.004**	**32.44**	**39.35**	**4.70**	**0.002**
Year × region	1	5.64	9.68	1.68	0.220	0.10	0.12	0.01	0.914
Season × region	3	2.97	5.11	0.89	0.470	4.39	5.32	0.64	0.586
Year × season × region	**3**	**11.06**	**18.98**	**3.30**	**0.025**	5.83	7.08	0.85	0.454
Residual	48	3.35	5.75			6.90	8.37		
		(c) Simpson's Diversity				**(d) *Mugil cephalus***			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Year	1	17.16	20.82	2.49	0.137	5.54	16.88	1.06	0.304
Season	3	9.83	11.92	1.42	0.236	5.14	15.67	0.98	0.386
Region	1	5.80	7.04	0.84	0.357	1.94	5.92	0.37	0.549
Year × season	**3**	**32.44**	**39.35**	**4.70**	**0.002**	3.98	12.14	0.76	0.521
Year × region	1	0.10	0.12	0.01	0.914	0.01	0.03	0.00	0.961
Season × region	3	4.39	5.32	0.64	0.586	5.61	17.10	1.07	0.377
Year × season × region	3	5.83	7.08	0.85	0.454	5.33	16.24	1.02	0.366
Residual	48	6.90	8.37			5.25	16.00		
		(e) *Aldrichetta forsteri*				**(f) *Acanthopagrus butcheri***			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Year	**1**	**27.10**	**51.66**	**8.36**	**0.006**	3.192	17.61	1.25	0.259
Season	3	3.02	5.76	0.93	0.420	4.042	22.30	1.59	0.203
Region	1	2.68	5.11	0.83	0.366	0.286	1.58	0.11	0.747
Year × season	3	8.47	16.14	2.61	0.064	2.188	12.07	0.86	0.464
Year × region	1	0.19	0.36	0.06	0.806	0.036	0.20	0.01	0.904
Season × region	3	1.37	2.62	0.42	0.731	3.289	18.14	1.29	0.323
Year × season × region	3	6.38	12.17	1.97	0.143	2.552	14.08	1.00	0.421
Residual	48	3.24	6.18			2.544	14.03		
		(g) Faunal Composition							
Term	**df**	**MS**	**%MS**	***pF***	***p***				
Year	**1**	**4075**	**19.10**	**3.13**	**0.003**				
Season	**3**	**3913**	**18.35**	**3.01**	**0.001**				
Region	**1**	**4062**	**19.05**	**3.12**	**0.002**				
Year × season	**3**	**4266**	**20.00**	**3.28**	**0.001**				
Year × region	1	551	2.58	0.42	0.898				

Table A2. *Cont.*

Season × region	3	1155	5.42	0.89	0.645
Year × season × region	**3**	**2005**	**9.40**	**1.54**	**0.045**
Residual	48	1302	6.10		

Table A3. Mean squares (MS), the contribution of mean squares to total mean squares (%MS), pseudo-F (*pF*) and significance levels (*p*) from three-way PERMANOVA tests on (a) water temperature, (b) salinity and (c) dissolved oxygen measured at the surface and bottom of the water column of the downstream and upstream regions of the Vasse–Wonnerup in winter and spring 2014. Terms that are significant ($p < 0.05$) and contribute >5% to the MS are highlighted in bold.

		(a) Water Temperature				**(b) Salinity**			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Season	**1**	**543.47**	**99.30**	**1227.80**	**0.001**	25.41	2.69	40.65	0.001
Region	3	1.71	0.31	3.86	0.012	**700.89**	**74.20**	**1121.20**	**0.001**
Depth	1	0.00	0.00	0.00	0.960	0.13	0.01	0.20	0.671
Season × region	3	1.65	0.30	3.72	0.012	**217.42**	**23.02**	**347.80**	**0.001**
Season × depth	1	0.00	0.00	0.00	0.986	0.02	0.00	0.03	0.873
Region × depth	3	0.00	0.00	0.00	1.000	0.01	0.00	0.02	0.998
Season × region × depth	3	0.04	0.01	0.08	0.971	0.05	0.01	0.08	0.967
Residual	48	0.44	0.08			0.63	0.07		

		(c) Dissolved Oxygen			
Term	**df**	**MS**	**%MS**	***pF***	***p***
Season	1	0.96	2.24	0.23	0.638
Region	**3**	**30.27**	**70.47**	**7.30**	**0.001**
Depth	1	2.36	5.49	0.57	0.491
Season × region	3	1.54	3.59	0.37	0.785
Season × depth	1	1.80	4.18	0.43	0.524
Region × depth	3	0.74	1.73	0.18	0.923
Season × region × depth	3	1.14	2.66	0.28	0.845
Residual	47	4.15	9.65		

Table A4. Mean squares (MS), the contribution of mean squares to total mean squares (%MS), pseudo-F (*pF*) and significance levels (*p*) from three-way PERMANOVA tests on the (a) number of species, (b) total catch rate, (c) Simpson's diversity and (d) faunal composition recorded in the downstream and upstream regions of the Vasse–Wonnerup in winter and spring 2014. Terms that are significant ($p < 0.05$) and contribute >5% to the MS are highlighted in bold.

		(a) Number of Species				**(b) Catch Rate**			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Season	**1**	**18.00**	**15.82**	**17.63**	**0.001**	**92.41**	**58.34**	**15.20**	**0.001**
Region	**3**	**94.21**	**82.78**	**92.29**	**0.001**	**59.23**	**37.39**	**9.74**	**0.001**
Season × region	3	0.58	0.51	0.57	0.643	0.69	0.44	0.11	0.947
Residual	24	1.02	0.90			6.08	3.84		

		(c) Simpson's Diversity				**(d) Faunal Composition**			
Term	**df**	**MS**	**%MS**	***pF***	***p***	**MS**	**%MS**	***pF***	***p***
Season	1	0.03	3.02	1.61	0.205	**13,373**	**39.68**	**11.22**	**0.001**
Region	**3**	**1.06**	**93.16**	**49.68**	**0.001**	**12,935**	**38.38**	**10.85**	**0.001**
Season × region	3	0.02	1.95	1.04	0.437	**6198**	**18.39**	**5.20**	**0.001**
Residual	24	0.02	1.88			1192	3.54		

Figure A1. Photographs showing (**a**) the downstream side of the Vasse surge barrier during winter when freshwater discharge was sufficient to open the flap gates and (**b**) the stop boards installed on the upstream side of the Wonnerup surge barrier in summer. Drone photographs of the sand bar in Wonnerup Inlet when (**c**) closed and (**d**) open to the ocean. Photographs of the bar in four of the major hydrodynamic phases described by Whitfield et al. [13], i.e., (**e**) closed, (**f**) outflow, (**g**) tidal and (**h**) semi-closed. Note the sediment being scoured away in (**f**) and the pile of sediment deposited from the mechanical breaching in (**g**). Photographs (**a**,**b**,**d**–**h**) were taken by James Tweedley and (**c**) by Kurt Krispyn.

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