The fish faunas of estuaries in the Albany region of south-western Australia

Submitted by

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Cover photograph. Author admiring a school of *Centroberyx lineatus* in Waychinicup Estuary. Photo by Dillon Newman.

Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

Kurt N. Krispyn

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Abstract

Estuaries are amongst the most productive ecosystems and act as important nurseries and habitats for aquatic fauna. Microtidal estuaries (tidal range <2 m) are particularly prone to climate change, the effects of which on fish communities and future predictions on their state under climate change are not well understood, especially for small estuaries (<1 km^2). This study quantitatively determined the fish fauna in the nearshore and offshore waters of eight microtidal estuaries (including six <1 km^2) with varying extents of connectivity to the ocean in the Albany region of south-western Australia. It investigated whether fish faunas were influenced by region, season, "bar status" (*i.e.*, open or closed), and physico-chemical variables. Nearshore waters (<1.5 m) were sampled with four replicate 21.5 m seine nets in each region (lower, basin and upper) in each estuary over four seasons in 2020. Offshore waters (>1.5 m) were sampled using four 160 m composite gill nets set throughout each estuary in the same four seasons. Conductivity and temperature loggers were used to detect any breaches of the sand bar that occurred between sampling occasions. Fish faunas in nearshore and offshore waters were m different among estuaries, and across seasons and regions in shallower waters, although all estuaries were dominated by the same suite of core species. Diversity and faunal composition were highly influenced by salinity and the duration of ocean connectivity. Diversity increased with salinity due to the immigration of marine species up until hypersaline conditions (>50) occurred, however, when salinities exceeded 100 for a protracted period, only a single highly euryhaline estuarine species survived. Permanently-open estuaries, *i.e.,* Oyster Harbour and Waychinicup Estuary, contained the greatest number of species, but lower densities (nearshore) and catch rates (offshore) than those estuaries that open at least once a year, *i.e.*, Torbay, Taylor, Normans and Cheyne inlets and Cordinup River. The normally-closed and extremely hypersaline Beaufort Inlet was depauperate and, after autumn, no fish were recorded in offshore waters with only a single atherinid species occurring in nearshore waters. This study provides baseline information for these data-poor estuaries and identified one system of high conservation significance. It also provides insights on how estuaries and their fish fauna may change due to reduced rainfall and river flow associated with climate change, and become more like Beaufort Inlet.

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Publication list

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CRediT authorship contribution statement

Kurt N. Krispyn: conceptualization, data collection, data curation, formal analysis, methodology, project administration, visualization, roles/writing - original draft. Neil R. Loneragan: conceptualization; funding acquisition, methodology, resources, supervision, writing - review & editing. Alan K. Whitfield: writing - review & editing. James R. Tweedley: conceptualization, data curation, formal analysis; funding acquisition; methodology, project administration, resources, software, supervision, visualization; roles/Writing - original draft.

Chapter 1. Introduction

Estuaries are transitional ecosystems located at the interface between freshwater and coastal marine environments (Boyd et al., 1992; Cooper, 2001; Roy et al., 2001). They are very dynamic systems, with their physio-chemical environment changing over various temporal scales due to tidal cycles and seasonal changes in rainfall and resultant river flow (Potter et al., 2015a; Whitfield and Elliott, 2011). There are an estimated ~54,000 estuaries globally, situated on every continent except Antarctica (McSweeney et al., 2017b). The diversity in their geomorphology and global distribution of estuaries has made finding a universally appropriate definition difficult (McLusky and Elliott, 2007). In this study, the definition of an estuary by Potter et al. (2010) is as follows; "*a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which it receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural seawater and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible*".

Unlike some other definitions *e.g.,* those by Fairbridge (1980); Pritchard (1967) this definition recognizes that estuaries can become disconnected from the marine environment for periods by the formation of a sand bar at their mouth and that all or part of these systems can become hypersaline for periods (salinity > 40; Tweedley et al., 2019b). Estuaries that become disconnected from the ocean (*i.e.,* those that are temporarily-open) comprise ~3% of systems globally, but are far more common on wave-dominated coasts in microtidal regions (tidal range <2 m), where they represent 15% of all estuaries (McSweeney et al., 2017b). Furthermore, 21% of these types of systems are found in Australia (McSweeney et al., 2017a).

Estuaries are amongst the most productive of all aquatic systems, being a sink for organic carbon and nutrients transported by rivers or tidal water movements, supplemented by autochthonous primary production from micro and macroalgae and seagrass (Potter et al., 2015a; Whittaker and Likens, 1975). These characteristics help support a diverse and abundant range of faunal communities including zooplankton, nematodes, benthic macroinvertebrates, fish and marine mammals (Read et al., 2003; Rose et al., 2020; Warwick et al., 2021). Estuaries have high conservation value as they harbor a different suite of species than that found in adjacent freshwater or marine environments (Able, 2005; Hourston et al., 2011; Tweedley et al., 2015; Whitfield, 1999).

Fauna, particularly fish, often utilise estuaries for all or part of their lifecycle as they provide migration routes, nursery habitat and feeding areas (Beck et al., 2001; McLusky and Elliott, 2004). For example, anadromous fishes (*e.g.,* salmonids, anguillids and lampreys) travel through estuaries as they move towards/away from the spawning/feeding grounds (Able, 2005; Bottom et al., 2005; Guelinckx et al., 2006; McDowall, 1988). The productive waters of estuaries facilitate rapid growth and thus the survival of juveniles (Whitfield and Elliott, 2011). Moreover, turbidity from tidal action and/or the structural complexity provided by macroalgae/seagrass reduce predation by piscivorous predators (Blaber and Blaber, 1980; Schelske and Odum, 1961). The high densities of fauna, particularly invertebrates, provide important links between lower trophic levels and resident and migratory birds (Elliott and McLusky, 2002; Greenwell et al., 2021; Trayler et al., 1989).

1.1. Microtidal estuaries

Estuaries can be broadly classified according to their tidal range, separating those that are microtidal (tidal range <2 m) from those that are mesotidal (2-4 m) and macrotidal (>4 m; Davies, 1964). Microtidal systems are found in south-western Australia, the Mediterranean, southern United States of America (USA) and South Africa, with macrotidal systems prevalent in northern Australia, north-western Europe, north-eastern USA and Canada (Whitfield and Elliott, 2011). Tidal range is considered a master variable, influencing the physico-chemical environment and processes, which, in turn, affect the characteristics of the biota (see review by Tweedley et al., 2016b). The large tidal movements in macrotidal estuaries, which can exceed 15 m in height, maintain a permanent connection to the ocean, facilitate efficient flushing and short water residence times (Borja et al., 2006). Combined with the strong scouring of bottom sediments and resultant turbidity, phytoplankton production is limited and phytoplankton blooms are rare in macrotidal systems (Monbet, 1992; Uncles et al., 2002).

In contrast, microtidal estuaries exhibit limited tidal flushing and long residency times, which increase nutrient accumulation and sediment deposition (Brearley, 2005; Defne and Ganju, 2015; Tweedley et al., 2016b). This more limited hydrodynamic movement, combined with greater nutrient retention, facilitates the occurrence of phytoplankton blooms that can, through respiration and/or decomposition, lead to hypoxia and consequently the mass mortality of fish (Becker et al., 2009; Pinckney et al., 2001; Potter et al., 1983). Waters in microtidal estuaries, which have low levels of tidal scour and turbidity, and hence high light penetration, provide suitable environments for the growth of seagrasses such as *Ruppia*, *Halophila* and *Posidonia* (Larkum et al., 2006; Tweedley et al., 2016b).

The microtidal estuaries of south-western Australia and South Africa are of relatively recent origin, having commenced their formation during the Holocene marine transgression up to 8,000 years before present (Hodgkin and Hesp, 1998; Whitfield and Bate, 2007). When formed, these systems were permanently connected to the ocean and tide-dominated. However, a subsequent decline in sea level 3,500 years ago reduced their extent of connectivity with the marine environment (Hodgkin and Hesp, 1998). Currently, relatively few estuaries in south-western Australia remain permanently-open, except for some large systems on the west coast *e.g.,* the Swan-Canning, Peel-Harvey and Leschenault estuaries. Moreover, even in these systems the entrance channels have been modified, artificially constructed and/or are dredged to keep them open for boat traffic and port operations. The vast majority of estuaries in this region and South Africa are only temporarily-open to the ocean for periods and thus have different levels of connectivity (Chuwen et al., 2009a; Hodgkin and Hesp, 1998; Tweedley et al., 2016b).

The status of the bar (open or closed) of temporarily-open estuaries is related to the interaction between wave energy that transports sediment onshore and into the entrance channel, thus establishing a sandbar, and the amount of riverine flow, which exports that material (Haines et al., 2006; Wainwright and Baldock, 2015). At times of low flow (*e.g.,* Mediterranean-climate summers), wave energy dominates sediment transport and bars form (Boyd et al., 1992; Cooper, 2001; Stretch and Parkinson, 2006). The occurrence of a bar breach is influenced by the volume of water in the estuary, the height and width of the bar and the volume of flow, which is determined by the amount of rainfall and catchment size (Behrens et al., 2013; Ranasinghe et al., 1999; Rich and Keller, 2013).

Estuaries can loosely be grouped according to their extent of connectivity with the ocean, into permanently-open estuaries and several types of temporarily-open estuaries, *i.e.,* seasonally-open and normally-closed (Hodgkin and Hesp, 1998). The bars of seasonally-open estuaries are typically breached following heavy winter rainfall and open for several months, whereas those of normally-closed estuaries can remain closed for years at a time and only breach after cyclonic and unprecedented heavy rainfall events (Chuwen et al., 2009a; Hoeksema et al., 2018). Moreover, if the volume of flow that enters an estuary is less than the amount lost to pan evaporation, the estuaries can become hypersaline (Tweedley et al., 2019b). Salinities of over 300 have been recorded in the normally-closed Culham and Hamersley inlets on the south coast of Western Australia

(Hoeksema et al., 2018; Whitfield, 2021) and these represent the highest salinities ever reported for any estuary globally (Tweedley et al., 2019b).

Microtidal estuaries, particularly those in Mediterranean climatic regions, are highly susceptible to climate change which influences permanently-open and temporarily-open estuaries differently (Hallett et al., 2018; Warwick et al., 2018). Since the 1970s, rainfall in south-western Australia has declined by ~15%, which has resulted in a 70% reduction in flow to estuarine catchments (McFarlane et al., 2012; Petrone et al., 2010). In permanently-open estuaries, reduced flow is likely to lead to a greater residence time, water column stratification, and as a consequence, more frequent phytoplankton blooms and hypoxic events. Reduced flows will also lead to greater salinities and the 'marinisation' of estuaries, which allows more marine species to enter and survive in the modified environment, leading increases in species richness and diversity (Hallett et al., 2018; Potter et al., 2016; Valesini et al., 2017).

For temporarily-open estuaries, reduced flow will decrease the extent of connectivity with the ocean causing some seasonally-open estuaries to become normally-closed, reducing opportunities for marine species to immigrate into these estuaries (Hallett et al., 2018). Moreover, increasing salinities, combined with the synergistic effects of higher temperatures, has the potential to push species beyond their physiological tolerances leading to fish kills and reductions in diversity (Hoeksema et al., 2006b; Whitfield, 1999).

1.2. Fish fauna of estuaries

Estuaries around the world have been shown to provide a suite of services for a wide range of fish species, including acting as feeding grounds, nursery areas and as migration routes (Cowley et al., 2022; Whitfield et al., 2022). Individual fish species utilise these different services in various ways and for all or a defined part of their lifecycle. Thus, to facilitate a global understanding of the fish faunas of estuaries, a suite of internationally recognised guilds was developed (Elliott et al., 2007; Whitfield et al., 2022), one of which is the Estuarine Use Functional Group (EUFG; Potter et al., 2015b).

Within in the EUFG, fish found in estuaries are assigned to one of four overarching categories; Marine, Estuarine, Freshwater and Diadromous, each of which has a suite of component guilds (Potter et al., 2015b). Marine species are those that spawn in the ocean, estuarine species comprise those that can complete their life cycle within estuaries, freshwater species are those that spawn in freshwater environments and diadromous species are those that travel between marine and fresh waters to their feeding and spawning grounds (Potter et al., 2015b; Whitfield et al., 2022).

Representatives of these categories and most of their component guilds are found in south-western Australia. The marine category comprises of i) *marine straggler* - species that typically enter estuaries sporadically and in low numbers *e.g., Neoodax balteatus* and ii) *marine estuarine-opportunists* – species which regularly enter estuaries in substantial numbers, particularly as juveniles *e.g., Mugil cephalus* (Elliott et al., 2007; Potter et al., 2015b). Within the estuarine category there are three categories; i) *solely estuarine* – species that complete their lifecycle only in estuaries, *e.g., Acanthopagrus butcheri* and ii) *estuarine & marine* – species complete their entire life-cycle in either marine or estuarine waters *e.g., Favoniogobius lateralis;* and iii) *estuarine & freshwater* – species complete their lifecycle in marine and freshwater environment, respectively *e.g., Pseudogobius olorum* (Potter et al., 2015b). The freshwater category includes i) *freshwater straggler* - species 'accidentally' found in estuaries and whose distribution is usually limited to the low salinity areas *e.g., Galaxias occidentalis* and ii) *freshwater estuarine-opportunist* - species that are usually present in freshwater but can tolerate higher salinities and found in estuarine environments *e.g., Gambusia holbrooki*. Lastly, local representatives in the diadromous category comprise i) *anadromous* - species that migrate from the ocean into rivers to spawn *e.g., Geotria australis* and ii) *semi anadromous* - species whose spawning run from the ocean extends only as far as the upper estuary *e.g., Nematalosa vlaminghi* (Potter et al., 2015b).

Given that fish in some of the above guilds are not resident species in estuaries (*i.e.,* marine, freshwater and diadromous categories), the extent of connectivity with the ocean influences the richness of the fish fauna of the estuaries (Tweedley et al., 2017). Permanently-open estuaries are the most speciose systems as the majority of species in microtidal estuaries spawn in the ocean and require an open connection to enter the estuary (Tweedley et al., 2016b; Whitfield, 2021). Consequently, seasonally-open estuaries contain a smaller suite of species due to the presence of fewer marine species, usually with reduced marine stragglers (Chuwen et al., 2009b; Hoeksema et al., 2009). Normally-closed estuaries can have a depauperate suite of species as they provide the lowest opportunity for recruitment and can become hypersaline resulting in the expiration of less-euryhaline fish species (Tweedley et al., 2016b). For example, in St Lucia (South Africa), the number of fish species recorded declined from 39 at a salinity of 18, to 18 species at a salinity of 80, and only 1 at a salinity of 120 (Whitfield et al., 2006).

The fish faunas of the nearshore (<1.5 m deep), shallow waters of south-western Australian and southern African estuaries are different from those in adjacent offshore (>1.5 m), deeper waters (Bennett, 1989; James et al., 2008; Potter and Hyndes, 1999; Whitfield, 1999). Nearshore waters are dominated by small estuarine species and juveniles of marine species, while the offshore waters contain substantial numbers of larger-bodied estuarine and marine species (e.g. Loneragan et al., 1989; Potter et al., 1993; Young and Potter, 2002). In a study of five estuaries on the south coast of Western Australia, Hoeksema et al. (2009), found that the nearshore waters were dominated by estuarine-residents atherinid and gobiid species, representing between 93.3 and 99.9% of all fish recorded. In the offshore waters, however, the fauna was dominated by marine estuarine-opportunists (*e.g.*, mugillids and arripids) that constituted between 57.3 and 86.1% of the individuals, with estuarine species (only sparids) contributing between 0.4 and 25.4% (Chuwen et al., 2009b).

1.2.1. Spatial patterns in distribution and abundance

Spatial variation in estuarine fish faunas is largely influenced by physical-chemical gradients (typically salinity) and/or the availability of different types of habitats (Potter and Hyndes, 1999; Whitfield, 1999). In south-western Australia, the salinity and temperatures in the lower regions of estuaries closely resemble those of sheltered marine environments for the summer and autumn months. These conditions facilitate colonisation by marine species, the abundance and richness of which declines in an upstream direction (Loneragan et al., 1986; Veale et al., 2014). The distribution of many species are partitioned along the latitudinal axis of the system (Loneragan and Potter, 1990; Loneragan et al., 1986; Valesini et al., 2018). This is particularly true for members of the Atherinidae and Gobiidae, whose spatial partitioning among species has been well documented in the Swan-Canning Estuary (Potter and Hyndes, 1999; Potter et al., 2015b). For example, the dominant atherinid in the lower reaches is the estuarine & marine *Leptatherina presbyteroides*, with the solely estuarine *Atherinosoma elongata* and *Craterocephalus mugiloides* in the middle estuary and the estuarine & freshwater *Leptatherina wallacei* in the upper estuary (Prince and Potter, 1983). Gobies show a similar change in abundant species with distance upstream from the marine & estuarine *Favonigobius lateralis* in the lower estuary to the solely estuarine *Favonigobius punctatus* in the middle reaches and estuarine & freshwater *Pseudogobius olorum* further upstream (Gill and Potter, 1993; Hogan-West et al., 2019). The spatial distribution of individual species may also shift within an estuary in response to changing environmental conditions. For example, the sparid *A. butcheri* is known to shift its abundance during spawning to ensures its eggs are released into an area with the appropriate salinity (Beatty et al., 2018; Sarre and Potter, 1999; Williams et al., 2020).

Within a region, habitats can have a significant influence on fish faunal composition (Bell et al., 1988; Connolly, 1994; Humphries et al., 1992). A range of habitat types can be present in estuaries, including seagrass beds, mudflats, oyster reefs and rocky algal reefs that support different species (Lefcheck et al., 2019; Whitfield et al., 2022; Whitfield, 2017). For example, Humphries et al. (1992) found that atherinids and gobies were more abundant in seagrass beds of *Ruppia megacarpa* than over bare sand in Wilson Inlet (south-western Australia). Furthermore, in a global review on nursery areas and food resources for fishes in estuaries, Whitfield (2017) concluded that seagrass meadows are favoured nursery areas in both estuaries and nearshore environments. While rocky habitats in estuaries are rare and thus have limited available information, a study of coastal fish in the Mediterranean Sea found species to have a preference for one or more of rocky algal reefs, seagrass and bare sand (Guidetti, 2000).

1.2.2. Temporal patterns in distribution and abundance

Temporal changes in estuarine fish faunas have been detected in numerous studies and are typically related to changes in bar state, environmental conditions and/or spawning cycles and subsequent recruitment (Chuwen et al., 2009b; Loneragan and Potter, 1990; Loneragan et al., 1989; Loneragan et al., 1986; Tweedley et al., 2019b). Connectivity with the ocean allows the immigration and emigration of certain species (e.g. Claridge et al., 1986; Hoeksema et al., 2006b; Maes et al., 2005; Young and Potter, 2003). In particular, following spawning, the juveniles of marine estuarine-opportunists, *i.e.,* mugilids, recruit to estuaries in winter and spring in order to use them as nursery areas (Chubb et al., 1981; Thomson, 1955, 1957; Whitfield et al., 2012). As these species do not breed in the estuary, sexually mature individuals leave permanently-open estuaries in winter to spawn, whilst those in seasonally-open estuaries leave after the bar breaches. Immigration of marine straggler species is less temporally-constrained, however, occurs more often during summer and autumn when flow is low and salinities are close to those of full-strength sea-water (Potter and Hyndes, 1999). Immigration or emigration to and from seasonally and normally-closed estuaries is restricted by the timing and duration of bar openings (Bennett, 1989; James et al., 2008; Vorwerk et al., 2003; Young and Potter, 2002). For hypersaline estuaries, temporal changes in the fish fauna have been recorded due to the sequential loss of species as salinities increase beyond the tolerance of different species (Hoeksema et al., 2006b; Tweedley et al., 2019b).

The small-bodied estuarine species of atherinid and gobiid, which dominate the nearshore waters of estuaries in south-western Australia, have a one-year life cycle (Hoeksema et al., 2009). Such species typically spawn in late spring to early autumn to coincide with reduced riverine flow and thus when the environment is more stable (Potter et al., 1986a; Potter et al., 1986b; Prince and Potter, 1983). Thus, the abundances of such species often peak around this time of year (Tweedley et al., 2014a).

1.3. Rationale, aims and thesis components

Although ~50 estuaries are currently recognised in south-western Australia (Brearley, 2005), comprehensive quantitative data on their fish faunas are limited to 18 estuaries. Furthermore, much of this research has focused on larger systems, particularly those close to population centres (*e.g.,* Swan-Canning and Peel-Harvey on the west coast, and the Hardy Inlet/Blackwood River and Wilson Inlet on the south coast). No research has been conducted on small estuaries (*i.e.,* <1 km^2) present on the south coast of Western Australia. Magoro et al. (2020b) found that these types of systems in South Africa function differently from larger estuaries. A number of small estuaries are found around Albany on the south coast of Western Australia. Moreover, the connectivity of these estuaries to the ocean differs and ranges includes two that are permanently-open, five that are seasonally-open and one that is normally-closed.

The overall aim of the study was to provide quantitative data on the physico-chemical environment and characteristics of the nearshore and offshore fish faunas from eight estuaries in the Albany region: *i.e.,* Torbay Inlet, Oyster Harbour, Taylor Inlet, Normans Inlets, Waychinicup Estuary, Cordinup River, Cheyne Inlet and Beaufort Inlet. Particular focus was placed in determining:

i) If salinity, temperature and dissolved oxygen concentration changed between estuaries and among seasons and regions within an estuary and the timing and duration of any breaching of the bar;

ii) If the number of species, abundance, diversity and composition of the fish faunas in nearshore and offshore waters changed between estuaries and among seasons and regions within an estuary and;

iii) If any changes in the composition of the fish fauna were related to those in the physico-chemical variables and bar breaches.

It was hypothesised that i) due to differences in their physical characteristics, each estuary would have a different physico-chemical environment and harbour a unique fish fauna.

ii) Permanently-open estuaries would have the highest number of species and normally-closed estuaries the least and finally that iii) salinity and duration of bar opening will influence the composition of the fish fauna.

By obtaining comprehensive, quantitative data on the fish fauna of these estuaries this study will help inform management and provide a benchmark against which future changes in these estuaries could be measured. Furthermore, elucidating the role of physico-chemical variables and bar breaches in structuring the fauna is vital in predicting the effects of climate change, such as declining rainfall and decreasing river flows, increasing salinities and reduction in the frequency of bar breaches. Thus, the current situation in a normally-closed estuary may foreshadow that to come for seasonally-open systems – they are likely to change to normally-closed estuaries.

Two closely related studies were also completed during my Honours dissertation: i) a meta-analysis and classification of estuaries south-western Australia (see Supplementary material 1) and ii) a study of the effects of extreme hypersalinity on the abundance of Sea Mullet *Mugil cephalus* in Beaufort Inlet (Krispyn et al., 2021).

Prior to commencing this study, ~50 estuaries were recognized across south-western Australia (Brearley, 2005). However, in collating information on these systems and their characteristics for a meta-analysis using virtual globes (*e.g.,* Google Earth), it became apparent that this list was incomplete. Thus, a detailed search of the literature and satellite imagery was employed to identify all estuaries in the region and assign them to an estuary type (*sensu* Hodgkin and Hesp, 1998). Continuous water-quality data from the loggers deployed in the estuaries where fish sampling occurred indicated that the bars of some breached more frequently than previously thought and so these estuaries did not fit into an existing estuary type. Therefore, in addition to identifying all estuaries in the region and collating and measuring their characteristics, a new classification scheme was developed and validated by testing it against existing schemes used in microtidal regions. This research on the new classification scheme is provided in Supplementary Material 1; Literature Review and was carried out to meet the requirements of the literature review for my Honours candidature.

Finally, during the first sampling season (February 2020), salinities in Beaufort Inlet exceeded 100 and a large fish kill was observed. Seasonal sampling for the rest of the year showed a subsequent loss of species with a marine species, which are usually regarded as stenohaline, surviving for a protracted period. A manuscript was produced detailing and explaining this finding that was published in Estuarine, Coastal and Shelf Science (Krispyn et al., 2021). This manuscript is included in Supplementary Material 2: Complementary publication.

Chapter 2. Materials and methods

2.1. Study region

The Albany region, in south-western Australia, borders the Southern Ocean for ~280 km from Wilson Inlet (117°19'48.79"E, 35° 1'19.63"S) in the west to Beaufort Inlet (118°54'5.39"E, 34°28'2.90"S) in the east and contains nine estuaries (Figure. 2.1). The region experiences a Mediterranean climate with hot, dry summers (average maximum 23 ˚C and minimum 15 ˚C in Albany) and cold, wet winters (average maximum 16 °C and minimum 8 °C; Bureau of Meteorology, 2021). Around 80% of the annual rainfall falls between May and October (Hallett et al., 2018; Hodgkin and Hesp, 1998). Air temperatures increase, and rainfall decreases in a gradient from Augusta, in the southwest corner, to the South Australian border (Lester et al., 2014). For example, the long-term median annual rainfall in Albany is ~950 mm compared to ~410 mm in Beaufort (Brearley, 2005).

Tidal heights along the southern coast of Western Australia are microtidal (*i.e.*, <2 m; (Davies, 1964; Tweedley et al., 2016b), and the combination of tides, waves and the Mediterranean climate have large-scale effects on the transport and accumulation of sand and the formation of sand bars at the mouths of estuaries. The Southern Ocean is one of the most energetic wave climates in the world due to a strong global westerly wind belt between the latitudes 30˚ to 60˚ S that generates travelling swells year-round (Bosserelle et al., 2012; Cuttler et al., 2020; Hughes and Heap, 2010). These swells have a long period (>12 s) and are large, particularly in winter, with a mean monthly offshore wave height ranging from 2.9 to 4.5 m throughout the year (Gaudin et al., 2018; Sanderson et al., 2000). Storm waves typically come from southerly directions, and summer sea breezes generate south to southeast wind waves (Hodgkin and Hesp, 1998). Thus, shifting sediment in longshore currents perpetuated by the wave energy and during periods of low riverine flow can create sand barriers (bars) at the mouths of estuaries that can periodically stop the connectivity and exchange with the ocean (Ranasinghe et al., 1999). Sand bars are typically breached during winter following the typical winter rainfall, but can also occur in summer and autumn following atypically high, unseasonal rainfall, often associated with cyclonic activity (Hoeksema et al., 2018).

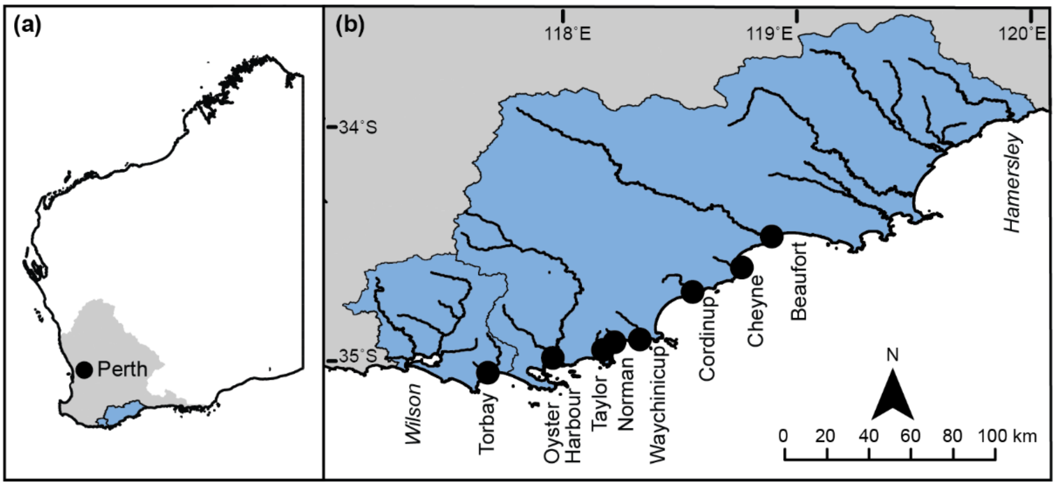

Figure 2.1. Map of (a) Western Australia showing the south-western drainage division (grey shading) and (b) catchments in the Denmark and Albany coasts (blue shading), including those of the eight estuaries sampled (black circles). Wilson and Hamersley's Inlets are shown to illustrate the western and eastern ends of the catchments, respectively.

2.2. Study estuaries

The estuaries sampled in this study, *i.e.*, Torbay Inlet, Oyster Harbour, Taylor Inlet, Normans Inlet, Waychinicup Estuary, Cordinup River, Cheyne Inlet and Beaufort Inlet, are located within 130 km of each other and ~100 km from the City of Albany (Table 2.1, Fig. 2.1). For brevity, each estuary will subsequently be referred to using their first name only *e.g.*,, Torbay for Torbay Inlet. These eight estuaries represent five different categories of south-western Australian estuaries (see classification in Supplementary Material 1 – Literature Review for full details and rationale). In brief, Torbay, Taylor and Normans are all *Annually-open basin* estuaries, *i.e.*, those systems that open to the ocean one or more times per year and have a relatively large circular basin area. Oyster is a *Permanently-open deep* estuary *i.e.*, retains a permanent connection to the ocean through a relatively deep wide entrance channel, and has an average depth of >1.5 m with deep areas, and Waychinicup is a *Morphologically-open* estuary *i.e.*, remains open to the ocean due to the presence of a natural (or anthropogenic) morphological feature. Cheyne and Cordinup are *Annually-open linear* estuaries, which are open to the ocean one or more times per year with a long, sinuous riverine shape. Finally, Beaufort is classified as *Normally-closed*, *i.e.*, the sand bar closes the estuary to the ocean for years at a time and only opens in response to freshwater flow associated with heavy winter rainfall or cyclonic events. Beaufort did not open during this study between February to November 2020.

Among the eight estuaries, Beaufort has the largest catchment, draining an area of 6,576 $km^{2,}$ followed by Oyster (2,983 km^2). The catchments of the other systems are

<300 km^2, with the smallest being those of Taylor and Normans at 10 and 23 km^2, respectively (Table 2.1). In terms of estuary area, Oyster is the largest at 17.67 km^2, followed by Beaufort (6.49 km^2), while all other estuaries are <1 km^2. Mean annual flow into the estuaries from rivers is greatest in Oyster, which receives (97 GL) from the King and Kalgan Rivers, followed by Torbay (75 GL), Beaufort (~10 GL) and Waychinicup (8.0 GL), while annual flows in the other estuaries (Taylor, Normans, Cordinup and Cheyne) are <2 GL. It should be noted, however, that in the two years prior to this study (*i.e.*, 2018 and 2019) and also in 2020, Beaufort, received on average <0.5 GL of flow from the Pallinup River (Supplementary Material 2; Krispyn et al., 2021).

Table 2.1. Location and morphological characteristics of each of the eight estuaries studied.

Estuary	**Torbay**	**Oyster**	**Taylor**	**Normans**	**Waychinicup**	**Cordinup**	**Cheyne**	**Beaufort**
Longitude (E)	117°40'36"	117°56'60"	118° 3'44"	118°12'58"	118°19'49”	118°33'34"	118°45'17"	118°54'5"
Latitude (S)	35° 2'37"	34°59'50"	34°59'52"	34°55'24"	34°53'52"	34°42'4"	34°36'15"	34°28'3"
Estuary type*	Ann.-open basin	Perm.-open deep	Ann.-open basin	Ann.-open basin	Morph.-open	Ann.-open river.	Ann.-open river.	Normally -closed
Domination class.	Wave	Wave	Wave	Wave	Tide	Wave	Wave	Wave
Catchment size (km^2)[2]	287	2983	10	23	242	131	98	6576
Catchment clearing (%)[1]	58.75	81.16	70.00	46.00	41.00	38.00	61.00	84.00
Annual rainfall (mm)[1]	943	949	800	810	760	610	610	410
Mean annual flow (GL)[1]	75	97.2	1.4	1.8	8	1.7	1.8	9.7
Surface area (km^2)*	0.93	17.67	0.47	0.15	0.10	0.11	0.17	6.49
Length (km)*	6.15	15.49	1.93	1.5	1.04	2.18	3.43	13.97
Bar height (m)[1]	1.5	N/A	1	1.5	N/A	2	1.5	3.5
Bar width (m)*	28	N/A	50	31	N/A	88	74	100
Entrance channel width (m)*	83	156	62	45	144	88	65	500
Mean and (maximum) depth (m)*	1.5 (5.0)	5.0 (12.5	2.0 (5.0)	1.0 (2.0)	2.0 (22.0)	2.0 (4.0)	1.0 (2.0)	1.5 (4.0)

* see Supplementary Material 1 – Literature Review, [1] (Brearley, 2005) [2] (Department of Water and Environmental Regulation, 2021).

2.2.1 Torbay Inlet (Annually-open basin)

Torbay is a small (0.93 km^2) estuary with a shallow (average depth ~1 m) round basin and a deeper (<5 m), elongated (1.3 km), narrow (83 m) entrance channel that runs perpendicular to the sea (Figure 2.2a, b). The mouth of the inlet is closed by a sand bar with an average height of 1.5 m and has a width of ~28 m; the bar breaches several times a year naturally and as a management intervention to prevent salt water inundation and maintain soil moisture in the surrounding agricultural lands (Hodgkin and Clarke, 1990). The coarse sediment banks in the lower, basin and parts of the upper regions have a slight inclination into deeper waters. Saltmarsh comprising *Juncus krausii* is present along the shores of the lower and basin regions, where it represents the only “in water” structure. However, the steep banks of the upper region are characterised by fallen trees (*Eucalyptus diversicolor* and *Agonis flexuosa*) and live *Melaleuca cuticularis* (Figure 2.2b). No macroalgae was observed in this estuary (Newman, D., Murdoch University, unpublished data); however, due to high nutrient levels, algal blooms of toxic blue-green algae have been recorded previously (Brearley, 2005), albeit none during the current study.

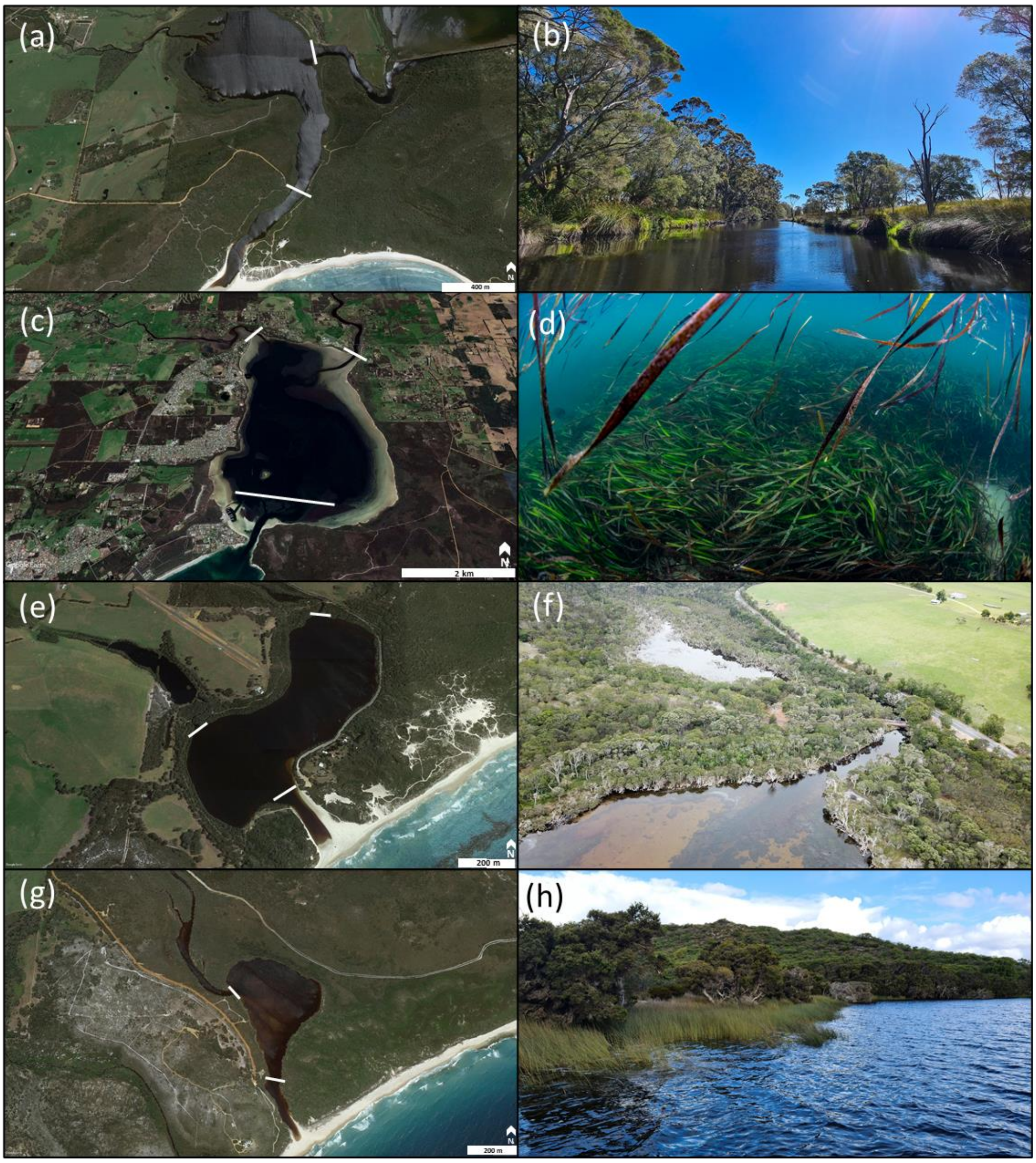

Figure 2.2. Satellite images and photographs showing features of (a, b) Torbay, (c, d) Oyster, (e, f) Taylor and (g, h) Normans. The white lines on the satellite images denote the separation between the lower, middle and upper regions of each estuary (see section 2.3). Images in (a, c, e, g) provided by Google Earth and CNES/Airbus. All other images by Kurt Krispyn.

2.2.2. Oyster Harbour (Permanently-open deep)

Oyster is a large (17.67 km^2) deep round estuary that remains permanently open to the Southern Ocean through a deep (12.5 m) entrance channel that is 156 m wide (Figure 2.2c, d). The estuary is fed by the King and Kalgan rivers which are tidal for 7 and 9 km, respectively (Hodgkin and Clarke, 1990). The rivers are wide (~150 m) and deep with steep banks that are lined with tall *Eucalypts* and dense understory vegetation. The Kalgan River is by far the largest contributor to streamflow into Oyster (Hodgkin and Clarke, 1990). The basin is divided into two deep sections with an average depth of ~5 m but reaches 10 m in some areas. In contrast, some sandbanks in the basin can become exposed on a low spring tide. The banks of the basin are made up of coarse sediment and are shallow for ~100 m to an edge that drops off into the deep sections. Some of the sediment in the basin harbors meadows of the seagrass *Posidonia* spp. (Figure 2.2d), together with some macroalgal species. The current aerial extent of seagrass is, however, only ~20% of that recorded in the past due to catchment clearing from urbanisation and agriculture washing in sediments and nutrients (Brearley, 2005). The basin region of the estuary contains emergent granite boulders, which are covered by oysters. Commercial oyster and mussel farms also operate inside the estuary.

2.2.3. Taylor Inlet (Annually-open basin)

Taylor is a relatively small (0.47 km^2) estuary and comprises a round sunken basin lying between the hard gneiss rock of Mt Taylor and the coastal dunes of Nanarup Beach (Figure 2.2e, f). The entrance channel is short (<250 m), shallow (<1.5m) and narrow (62 m) that opens naturally annually, although due to water quality concerns, fishers and farmers have been known to artificially breach it (Hodgkin and Clarke, 1990). One small creek runs in from the east, and two smaller creeks drain the sandplains from the north. All tributary creeks are narrow (<10 m), shallow (~1 m) and only run for a few hundred metres (Figure 2.2f). They are densely vegetated by inundated *Melaleuca cuticularis* and *Juncus krausii*, which are also present throughout the shores of the basin region. Most of the basin is 2-3 m deep with deeper holes of up to 5 m. The estuary is regarded as eutrophic, with algal blooms. Dense stands of *Ruppia* sp. and charophytes were recorded during sampling in summer, autumn and winter (Newman, D., Murdoch University, unpublished data).

2.2.4. Normans Inlet (Annually-open basin)

Normans is a small (0.15 km^2) estuary that lies in a valley to the west of the granite mountain Mount Manypeaks and high coastal dunes (Figure 2.2g, h). The basin is shallow, reaching ~1 m in depth when the estuary is at its highest; however, after breaching to the ocean, the water level drops to <0.30 m. The short <250 m, narrow 45 m and relatively shallow ~1.5 m deep entrance channel carves through a sandy dune and a small limestone cliff. The bar is ~1.5 m above sea level (Brearley, 2005). The estuary opens at least once per year, however, it remains open for a relatively short period of time as a limestone platform on the shoreline prevents the scouring of a deep channel when the bar is broken (Hodgkin and Clarke, 1990). There are no sandy banks in Normans; it is all thick *Juncus krausii* that is swamped most of the year, providing the only structure in the basin (Figure 2.2h). The upper region is surrounded by dense vegetation, predominantly *M. cuticularis,* and has a short (~1 km) and shallow (~1.5 m) river. Dense stands of *Ruppia* spp. and charophytes are present throughout the basin and river (Newman, D., Murdoch University, unpublished data), and the sediment comprises coarse sandy- mud except for the river with has larger amounts of organic matter and mud.

2.2.5. Waychinicup Estuary (Morphologically-open)

Waychinicup is unique among estuaries in south-western Australia as it resembles a small fjord, that is 0.10 km^2 in surface area (Brearley, 2005). The estuary lies in a gorge carved between two large granite headlands, ensuring the system remains permanently open (Figure 2.3a, b). Most of the shoreline comprises steep granite boulders except for some small patches of sandy beach. The lower region reaches a maximum of 22 m deep, and its depth decreases slowly upstream to 2-3 m into the basin. The vertical shorelines in the lower and parts of the basin region are dominated by marine Phaeophyceae and Rhodophyta macroalgae, while the sandy substratum contains expansive beds of the seagrasses *Posidonia* spp. and *Halophila* spp. (Figure 2.3b), albeit with some sandy substratum interspersed in the beds *i.e.,* "blowouts" (Phillips and Lavery, 1997). The sediment in the lower and basin regions are made up of coarse sand and gravel; however, the upper reaches of the estuary accumulate detritus and organic matter, resulting in finer and muddy sediment and decaying seagrass wrack. The catchment is relatively uncleared as much of it lies within the Waychinicup National Park.

2.2.6. Cordinup River (Annually-open linear)

Cordinup is a small (0.11 km^2) annually-open linear estuary that lies in a depression behind coastal sand dunes (Figure 2.3c, d). The entrance channel is relatively long (~400 m), narrow (88 m) and deep (2-3 m) in comparison to the rest of the estuary. A limestone platform present on the beach influences the position of any breach to the ocean (Hodgkin and Clarke, 1990). The banks of the channel comprise coarse beach sand and are bare of vegetation except for patches of grass. The shoreline of the basin region is bordered by samphire flats, with sparse *J. krausii* and dead *M. cuticularis* and has two spits of alluvial deposits formed from a fluvial delta that become exposed during summer (Figure 2.3b). *Ruppia* sp. and charophytes provide subtidal habitat throughout the basin and upper region. The Cordinup river, which is carved through a narrow valley of granitic rock, is narrow and relatively deep (up to 4 m), with steep banks that are heavily vegetated with *M. cuticularis* and *Eucalyptus marginata* that provides in-water structure. Some of the small catchment has been cleared to establish plantations of *Eucalyptus globulus*.

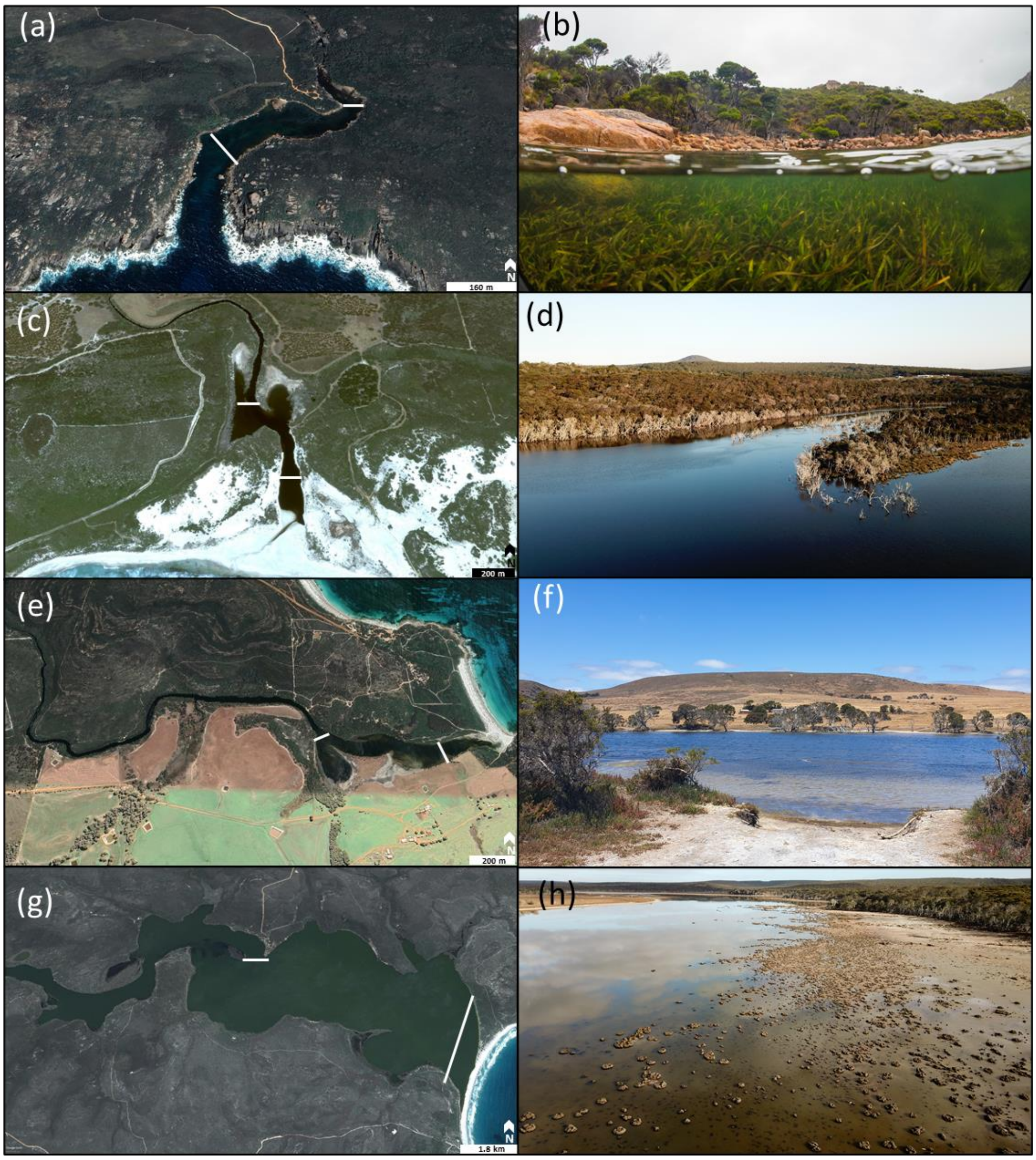

Figure 2.3. Satellite images and photographs show features of (a, b) Waychinicup, (c, d) Cordinup, (e, f) Cheyne and (g, h) Beaufort. The white lines on the satellite images denote the separation between the lower, middle and upper regions of each estuary (see section 2.3). Images in (a, c, e, g) provided by Google Earth and CNES/Airbus.

2.2.7. Cheyne Inlet (Annually-open linear)

Cheyne is a small (0.17 km^2) and narrow estuary of the Eyre River (Figure 2.3e, f). The entrance channel is narrow (65 m), and surrounded by samphire saltmarshes, *M. cuticularis* and *J. krausii,* with the latter species also present along the banks of the riverine reaches (Hodgkin and Clarke, 1990). Most sediment is fine and can be covered in seagrass that has washed in from the ocean. Large amounts of *Ruppia* sp. are present in the estuary together with periodic blooms of filamentous green algae. The estuary was once ~2.5 and 6 m in the basin and bar, respectively (Hodgkin and Clarke, 1990);

however, due to the infilling of sediment, most areas are <1 m deep. This was due, in part, to land clearing in the catchment and along the southern side of the estuary (Figure 2.3e, f).

2.2.8. Beaufort Inlet (Normally-closed)

Beaufort is a relatively large (6.49 km ^{2}) estuary that is normally closed to the ocean by a large sand bar that is 500 m long, 100 m wide and up to 3.5 m high (Figure 2.3g, h). Due to the size of the bar, the estuary opens only every three to five years after, breaching on eight occasions in the 35 years, and the last being in 2017 (Associated publication). The basin is shallow (<2 m) with a volume of 6.5 GL and comprises fine sediments except towards the bar, where they become coarser beach sand (Hodgkin and Clark, 1988). No macrophytes were observed throughout the study (Newman, D., Murdoch University, unpublished data), but mounds of the serpulid polychaete *Ficopomatus enigmaticus* were abundant (K. Krispyn, personal observation). The edges of the basin and upper estuary is surrounded by the spongolite cliffs, low woodlands, samphire flats and mallee shrublands. The estuary is fed by the 250 km long Pallinup River, which is regarded as 'naturally saline', the extent of which has increased since land clearing occurred in the 1950s (Hodgkin and Clark, 1988).

2.3. Sampling regime

Fish faunas in the shallow, nearshore (<1.5 m deep) and deeper, offshore (>1.5 m deep) waters of each of the eight estuaries were sampled in summer (February), autumn (May), winter (July) and spring (November) of 2020. Estuaries was divided into three regions: *i.e.*, lower (entrance channel), basin (middle) and upper (riverine reaches; Figure 2.4). Samples were collected from four sites in each of the three regions, in each of the eight estuaries in four seasons (total n= 384). Note that, as water levels in the estuaries changes markedly depending on the status of the bar and extent of riverine flow, some sites could not be sampled in the same place in all seasons. In this case, a location as close as possible to the original site was sampled. The species accumulation curve for each estuary reached an asymptote well before the maximum number of samples collected was reached (i.e. 48), indicating that the number of samples collected was sufficient (Appendix 2a).

Sampling was conducted using a 21.5 m seine net that consisted of two 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m long cod-end made of 3 mm mesh. The net, which was laid parallel to the shore and then hauled onto the beach, fished to a depth of 1.5 m and swept an area of 116 m^2. When large numbers of fish were caught, a subsample of the catch was retained, euthanised in an ice slurry and frozen (Animal

Ethics Permit RW3212/20). In the laboratory, the total number of individuals of each fish species in each sample was then recorded, and the total length of each individual was measured to the nearest 1 mm, except when a large number of any one species was caught, in which case the lengths of a representative subsample of 50 fish were measured.

Fish in adjacent offshore, deeper waters were sampled using composite sunken gill nets deployed for 1 hour at dusk. Each net comprised eight 20 × 2 m panels with stretched mesh sizes of 35, 51, 63, 76, 89, 102, 115 and 127 mm. Due to the small size of the estuaries and ethical concerns over potentially high catches, only four widely dispersed sites were sampled throughout the estuary, with at least one site in each region (Figure 2.4). Four gill nets were set in each of the eight estuaries for four seasons (total n= 96). Upon retrieving the net, each fish was identified to species, measured (TL in mm) and returned to the water. The species accumulation curve for each estuary reached an asymptote well before the maximum number of gill net samples collected was reached (i.e. 16), indicating that the number of samples collected using this relatively long net was sufficient (Appendix 2b).

Figure 2.4. Satellite images of Normans Inlet showing the location of the nearshore sites in the lower (●), middle (●) and upper (●) regions. Offshore sites (O) and the approximate lengths of the gill nets are (white lines, with white circles) also shown. The extent of regions is denoted by the thick white lines. Image provided by Google Earth and CNES/Airbus.

Salinity, dissolved oxygen concentration (DO, mg L^{-1}) and temperature ($^{\circ}C$) were recorded in the middle of the water column at each nearshore site, on each sampling occasion, using a Yellow Spring Instrument 556 Handheld Multiparameter Instrument (YSI Incorporated, Yellow Springs, Ohio, USA). This instrument was calibrated to a maximum salinity of 70. When salinity exceeded this value, salinities were calculated by diluting a sample of water from the estuary (Hoeksema et al., 2018).

A conductivity and temperature logger (HOBO U24, Onset Computer Corp., Bourne, MA, USA) were deployed in all estuaries, except for Oyster, from February until early November 2020. Each logger was attached to a small concrete mooring and placed at a depth of 1-2 m at the upstream end of the entrance channel, except Waychinicup, where it was placed at the lower end of the upper region. The logger recorded conductivity (maximum = 55 000 uS/cm), which was converted to the Practical Salinity Scale using HOBOware Pro Version 3.7.18, and temperature every hour throughout the study. These data, particularly those for salinity, were used to detect any breaches of the sand bar that may have occurred between sampling occasions. A breach was determined when the salinity and/or temperature changed rapidly, and the bar was deemed to have remained open when cyclical patterns in these variables were recorded. Breaches were also validated using social media and by talking to reliable local residents. A total of 241-256 d of data were recorded in each estuary, except for Torbay (152 d), where epifaunal growth inhibited accurate readings.

Mean monthly rainfall for 1991 – 2020 and the total annual rainfall and mean daily maximum temperature for each month in 2020 were obtained from the Bureau of Meteorology (2021).

2.4. Data analyses

All statistical analyses were performed using the PRIMER v7 multivariate statistics software package (Clarke and Gorley, 2015) with the PERMANOVA+ add-on (Anderson et al., 2008).

2.4.1. Physio-chemical variables

The water temperature, salinity and dissolved oxygen concentration recorded at each nearshore site on each sampling occasion were each used to construct a data matrix. A draftsman plot of the replicate values for each pair of variables was examined to assess whether the values for each variable were heavily skewed and, if so, which type of transformation would ameliorate that effect. This plot demonstrated that none of the physio-chemical variables required any transformation. This data matrix was used to construct three separate Euclidean distance matrices, *i.e.*, one for each physio-chemical variable, which was, in turn, subjected to a three-way Permutational Multivariate Analysis of Variance test (PERMANOVA; Anderson et al., 2008) to determine whether the variable differed with Estuary (eight levels; Torbay, Oyster, Taylor, Normans, Waychinicup, Cordinup, Cheyne and Beaufort), Season (four levels; summer, autumn, winter and spring) and Region (three levels; lower, basin and upper). These tests were primarily aimed at detecting inter-estuarine differences whilst accounting for the potentially confounding effects of Season and Region. In this and all other tests, the null hypothesis of no significant difference among *a priori* groups was rejected if P was <0.05. The percentage contributions made by the mean square for each main effect and interaction term to the total mean squares were calculated to provide an estimate of the relative importance of each term in the model (Crisp et al., 2018). When a significant difference in the main effect was detected, a pairwise PERMANOVA test, together with a plot of the means and associated 95% confidence limits, was used to identify the pairwise combination of *a priori* groups responsible for that difference. Intra-estuarine differences for each physio-chemical variable were assessed for each of the eight estuaries separately using a two-way PERMANOVA (*i.e.*, Season and Region) following the same procedure as that outlined for the three-way PERMANOVAs.

To visualise differences in the physio-chemical environments of the eight estuaries and to incorporate seasonal variability, the values for each variable were averaged for each estuary in each of the four seasons. As the variables are measured in different units, the averaged values were normalised to place all variables on a comparable scale prior to constructing a Euclidian distance matrix. This matrix was subjected to Principal Component Analysis (PCA) to produce an ordination plot with vectors on the plot whose direction and length define the direction in which the values for that variable increase. The length of the vector provides an indication of the strength of correlation or the Pearson's correlation coefficient of the variable to the ordination configuration, respectively (Clarke and Gorley, 2015).

2.4.2. Univariate analyses of fish fauna

The abundance of each species in each replicate nearshore sample was subjected to the DIVERSE routine to calculate the number of species, the number of individuals (density; fish 100 m^2) and Simpson's Index (Somerfield et al., 2008). A draftsman plot indicated that the number of individuals required a $\log_e$ (X+1) transformation but that the number of species and Simpson's Index did not require any transformation. The PERMANOVA testing framework for the three univariate measures of community structure in nearshore waters was identical to that described earlier for the physio-chemical variables (Section 2.4.1), *i.e.*, three- and two-way PERMANOVAs were used to test for inter-and intra-estuarine differences, respectively. A similar approach was used for offshore samples, only that for the offshore, no three-way PERMANOVA was possible as regions were not sampled with replication and the number of individuals was a catch rate (fish h^{-1}). Catch rates in the offshore was square-root transformed before analysis.

2.4.3. Multivariate analyses of fish fauna

The abundance of each species from each replicate nearshore sample was pre-treated using dispersion weighting, which down-weights the effects of those species whose numbers exhibited large differences among samples (Clarke et al., 2006). This was achieved by dividing the counts for each species by its mean index of dispersion (*i.e.,* an average of the variance to mean ratio in replicate samples within an estuary, season and region and ensuring that all species have similar variability structures. These data were then square-root transformed to down-weight the contributions of species with consistently high values in relation to those with consistently low values. This pre-treatment has proven effective when analysing fish communities in estuaries, where the prevalence of juvenile and schooling species are typically high (Clarke et al., 2014b; Veale et al., 2014). These pre-treated fish community data for nearshore waters were used to construct a Bray-Curtis resemblance matrix and subjected to the same PERMANOVA testing framework described above for the univariate measures of community structure (Section 2.4.1).

Broadscale (inter-estuarine) trends in nearshore fish faunal composition were visualised using ordination plots. To this end, the Bray-Curtis resemblance matrix, derived from the transformed replicate data, was subjected to the Bootstrap Averages routine (Clarke and Gorley, 2015) to bootstrap those samples in metric multi-dimensional scaling (mMDS) space. The averages of repeated bootstrap samples (bootstrapped averages) for each group of samples (*e.g.,* those for an estuary) were used to construct mMDS ordination plots. Superimposed on each plot was i) a point representing the group average (*i.e.,* the average of the bootstrapped averages) and ii) the associated, smoothed and marginally bias-corrected 95% bootstrap region, in which 95% of the bootstrapped averages fall. This process was repeated for the main effects of season and region separately.

A shade plot, derived from the dispersion-weighted and square-root transformed data averaged for each estuary, season and region combination, was used to visualise the trends exhibited by the abundances of fish species. This shade plot is a simple representation of the relative density matrix, where a white space for a species demonstrates that a particular species was not collected, while the depth of shading from light grey to black is linearly proportional to the density or catch rate of that species (Clarke et al., 2014b). As not all 86 species were able to be clearly seen on the shade plot, only those species (32) that contributed ≥2% to the total density in a single estuary, season and region combination were included. Species (*y*-axis) are clustered based on their Bray-Curtis similarities and placed in optimum serial order (Clarke et al., 2014a). Region and Season combinations (*x*-axis) were ordered in sequential seasonal order and within in seasonal by the geographic location of the estuary, *i.e.,* west to east.

BEST/Biota and Environment matching routine (BIOENV; Clarke and Ainsworth, 1993; Clarke et al., 2008), subsequently referred to as BEST, was used to determine whether the fish faunal composition in estuaries community was significantly correlated with physio-chemical variables individually and then which subset of these variables produced the 'best' match. Prior to conducting this analysis, the average values for water temperature, salinity, and dissolved oxygen for each season in each estuary were calculated and combined with the number of bar breaks and the number of days the bar was open in that season (*i.e.,* the ~90 days prior). As these latter two variables did not require transformation, the data for all five variables were normalised and subjected to BEST. The null hypothesis of no correlation between the fish fauna and any suite of the five environmental variables was rejected if P was <0.05. The test statistic, rho (ρ), reflects the strength of the correlation between the two data sets, with rho ranging from ~0 (little correlation) to ~1 (near-perfect correlation).

Intra-estuarine trends in fish faunal composition were visualised using bootstrapped mMDS plots for significant main effects and a centroid non-metric multi-dimensional scaling (nMDS) plot if the one-way Season × Region interaction was significant. Centroid nMDS plots were produced using a distance-among-centroids matrix, which creates averages in the 'Bray-Curtis space' from points for the four samples representing the region in each season (Lek et al., 2011). A shade plot of the pre-treated abundance of all species present in the estuary was produced. Species (*y*-axis) are placed in optimum serial order, and the samples (*x*-axis) were reordered to produce a serial seasonal order separately for each region, *i.e.,* summer to spring in the lower, basin and upper regions.

Once again, the approach analysing for the composition of the offshore fish fauna followed that for the nearshore fauna, only without Region as a main effect.

Chapter 3. Results

3.1. Climate

Monthly rainfall at Albany in 2020 generally followed the long-term pattern, with most falling between May and September, however, higher than average falls occurred in May, August and November (Figure 3.1). In particular, a large storm event produced 81 mm of rain on the 4th August 2020 (Bureau of Meteorology, 2021).

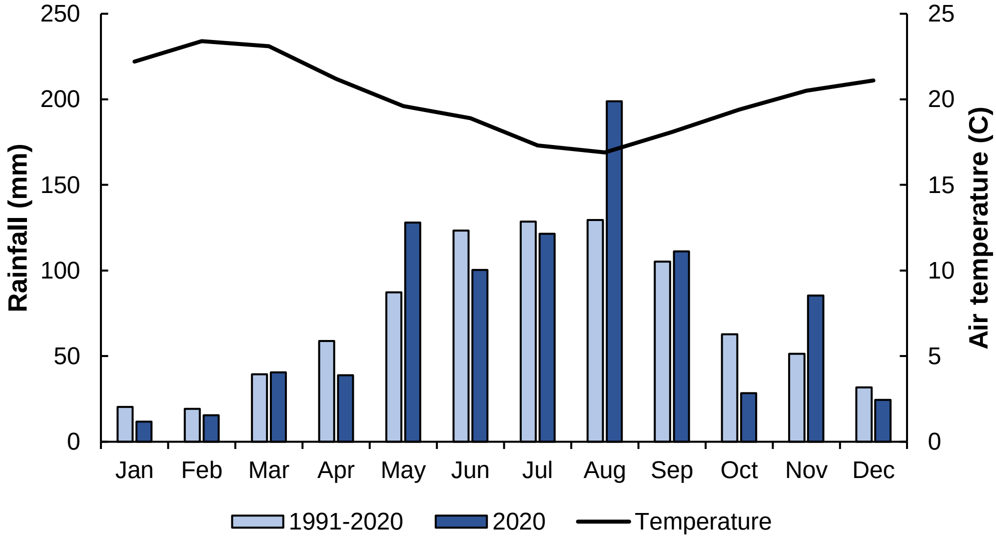

Figure 3.1. Total monthly rainfall (mm) in 2020 (dark blue), mean rainfall between 1991-2020 (light blue) and monthly mean air temperature (^{o}C) at Albany (Site number: 009500), Western Australia. Sampling occurred in February (summer), May (autumn), July (Winter) and November (spring). Data provided by the Bureau of Meteorology (2021).

3.2. Seasonal measurements of water quality

3.2.1. Inter-estuarine differences

Salinity was shown by PERMANOVA to differ among Estuary, Region and Season, and all their interactions were significant except for Season × Region (Table 3.1). Estuary contributed most to the percentage of the total mean squares (93%). Pairwise tests showed that salinities in all estuaries differed significantly (all P <0.003; data not shown). The highest mean values were recorded in Beaufort (96) and Cheyne (43), with the lowest in Normans (4; Figure 3.2a). Salinities in Oyster and Waychinicup were close to those of seawater, with those in Torbay, Taylor and Cordinup ranging between 13 and 20.

Three-way PERMANOVA demonstrated that dissolved oxygen (DO) concentration varied among all main effects and all interactions were significant except for Season × Region and Estuary × Region (Table 3.1). Estuary made the greatest contribution to the total mean squares (46 %) followed closely by Season (42%). Mean DO was similar in all estuaries, ranging from 7.66 – 9.58 mg L^{-1}, except for in Beaufort, where it was lower (5.25 mg L^{-1}; Figure 3.2b). Hypoxic conditions (<2 mg L^{-1}) were never recorded in the nearshore waters of any estuary (data not shown).

Temperature differed significantly with Estuary, Season and all interaction terms, but not with Region (Table 3.1). The Season was the most influential term, accounting for (95% of the total mean squares). Temperatures were greatest in summer (22.35 ^{o} C), coolest in winter (14.24 ^{o} C), with intermediate values in autumn and spring (~17 ^{o} C; data not shown). Values in all estuaries ranged from 16.90 ^{o} C in Normans to 19.12^{o} C in Torbay (Figure 3.2c).

Table 3.1. Mean squares (MS), the percentage contribution of mean squares to the total mean squares (%MS), pseudo-F ratios (pF) and significance levels (*P*) from three-way PERMANOVA tests on the salinity, dissolved oxygen concentration and temperature of eight estuaries sampled across all regions and seasons in 2020. df = degrees of freedom. Significant results (*P* <0.05) and those with a %MS ≥ 10 are shaded in grey.

		Salinity				Dissolved oxygen conc.				Temperature			
Source	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	1,585	3.70	192.9	0.001	65.32	41.53	59.5	0.001	1,156.3	95.29	3,076.0	0.001
Estuary (E)	7	40,048	93.36	4,871.8	0.001	72.71	46.22	66.3	0.001	20.6	1.70	54.8	0.001
Region (R)	2	204	0.48	24.8	0.001	9.25	5.88	8.4	0.001	0.7	0.06	1.9	0.176
S × E	21	980	2.29	119.3	0.001	4.67	2.97	4.3	0.001	28.0	2.30	74.4	0.001
S × R	6	8	0.02	10.0	0.466	0.77	0.49	0.7	0.645	5.3	0.43	14.0	0.001
E × R	14	49	0.11	6.0	0.001	1.48	0.94	1.4	0.187	0.7	0.06	1.9	0.021
S × E × R	42	13	0.03	1.5	0.022	2.00	1.27	1.8	0.003	1.6	0.13	4.3	0.001
Residual	289	8	0.02			1.10	0.70			0.4	0.03		

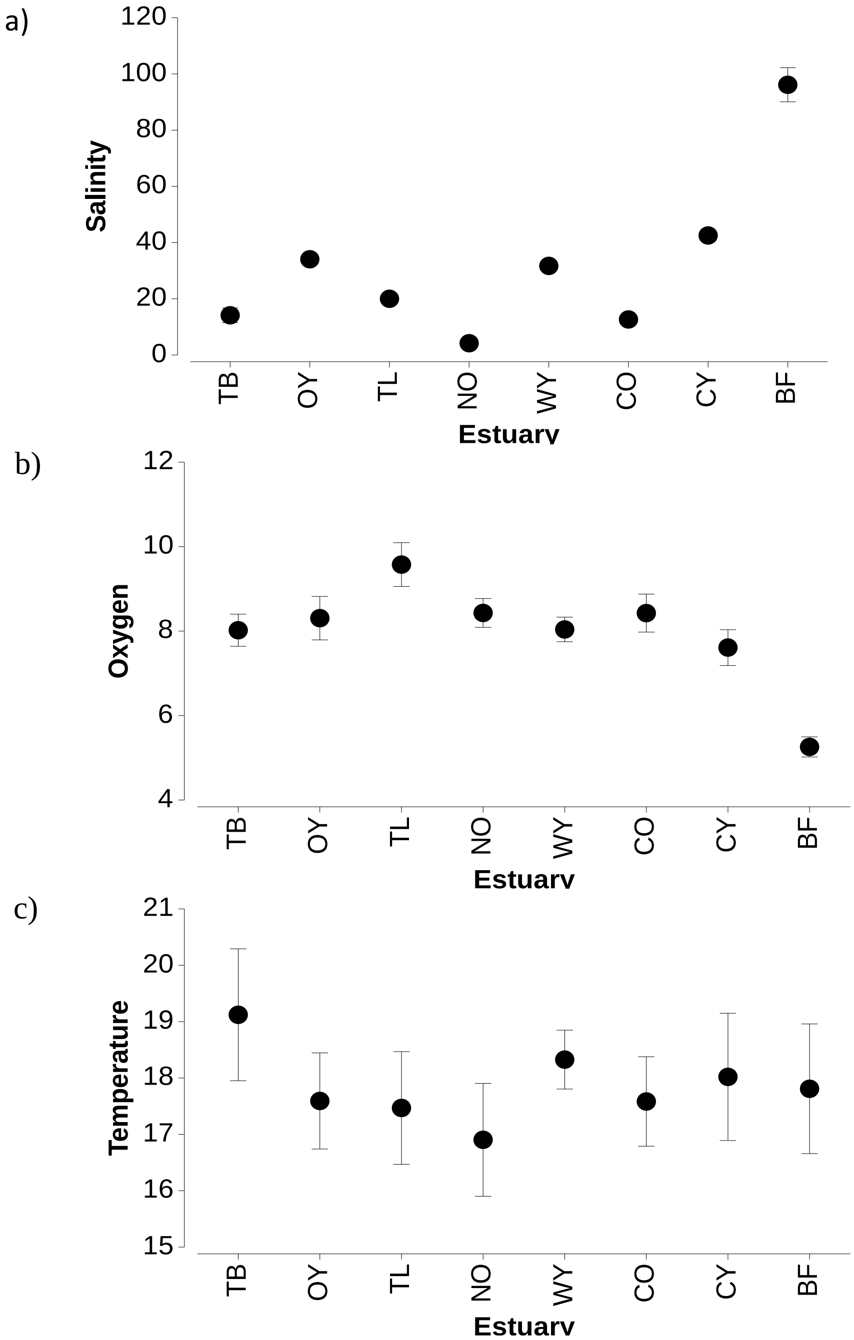

Figure 3.2. Mean and ±95% confidence limits of (a) salinity, (b) dissolved oxygen concentration (mg L^{-1}) and (c) temperature ^{o}C in each of the eight estuaries. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort. Surface and bottom values were essentially the same in offshore waters and therefore are not shown. n = 96 for each estuary.

On the basis of Principal Component Analysis, Beaufort was the most distinct estuary forming a broad group on the left of Axis 1 of the PCA (Figure 3.3). The position of the vectors indicate this was due to the high salinities and low DO recorded in this estuary.

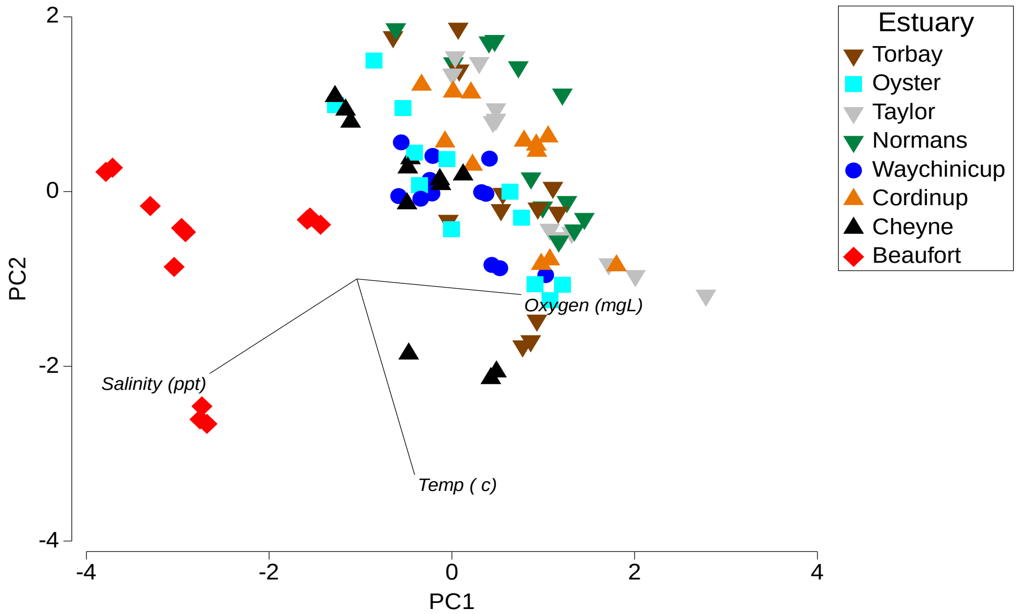

Figure 3.3. Principal coordinates analysis (PCA) of the salinity, temperature and dissolved oxygen data collected each season in eight estuaries of the south coast of Western Australia. Results for the first two axes are shown, which accounted for 87.4% of the variation.

3.2.2. Intra-estuarine differences

For each estuary individually, PERMANOVA tests showed the three variables differed with season, except for salinity in Waychinicup, and this main effect was the most influential (Table 3.2). The season with the highest salinity varied among estuaries, typically being in summer for Torbay, Oyster and Cheyne, in autumn for Cordinup and Beaufort and in spring for Taylor and Normans (Appendix 1). Significantly lower values were recorded in winter in Torbay, Taylor, Normans and most of Oyster and in spring in Cordinup, Cheyne and Beaufort (Appendix 1). Values for DO varied but were never hypoxic, and the seasonal pattern of water temperature in each estuary followed the same seasonal trend described earlier for all estuaries (data not shown).

Looking at regional trends, differences in salinity were only detected in Torbay, Oyster and Waychinicup (Table 3.2). In the case of Torbay, salinities were always highest in the lower region and particularly in autumn (Appendix 1a). Similarly, in Oyster and Waychinicup, salinities in the lower and basin regions, which were around that of full-strength seawater (~35), were greater than in the upper regions, which declined a minimum of 28 and 23, respectively (Appendix 1). Temperatures were generally consistent among regions in most estuaries (Table 3.2).

Table 3.2. Mean squares (MS), the percentage contribution of mean squares to the total mean squares (%MS), pseudo-F ratios (pF) and significance levels (*P*) from two-way PERMANOVA tests on the water quality (*i.e.*, water temperature, salinity and dissolved oxygen concentration) from the eight estuaries sampled across all regions and seasons in 2020. d*f* = degrees of freedom. Significant results are highlighted in bold, and those with a %MS ≥ 10 are shaded in grey.

Torbay		Salinity				Dissolved oxygen				Temperature			
Source	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	983.33	84.89	90.85	0.001	7.4	60.46	6.98	0.001	246.14	98.91	815.16	0.001
Region (R)	2	118.88	10.26	10.98	0.001	0.60	4.92	0.57	0.594	0.25	0.10	0.81	0.468
S × R	6	45.28	3.91	4.18	0.003	3.18	25.96	3.00	0.012	2.17	0.87	7.17	0.001
Residual	36	10.82	0.93			1.06	8.66			0.3	0.12		
Oyster													
Season	3	45.08	39.36	10.03	0.001	23.7	77.56	14.94	0.001	124.13	96.68	417.39	0.001
Region	2	52.63	45.95	11.72	0.001	3.05	10.00	1.93	0.164	0.39	0.3	1.31	0.278
S × R	6	12.34	10.77	2.75	0.010	2.21	7.25	1.40	0.298	3.58	2.79	12.04	0.001
Residual	36	4.49	3.92			1.59	5.19			0.3	0.23		
Taylor													
Season	3	111.52	99.46	1429	0.001	24.09	80.36	13.15	0.001	182.42	99.46	1157.4	0.001
Region	2	0.40	0.36	5.18	0.006	3.11	10.39	1.70	0.221	0.21	0.11	1.32	0.274
S × R	6	0.12	0.11	1.51	0.181	0.94	3.14	0.51	0.800	0.63	0.34	3.98	0.006
Residual	36	0.08	0.07			1.83	6.11			0.16	0.09		
Normans													
Season	3	17.99	93.68	373.49	0.001	4.62	35.74	7.50	0.002	172.15	97.45	266.29	0.001
Region	2	1	5.23	20.84	0.001	4.39	33.98	7.13	0.005	0.94	0.53	1.46	0.266
S × R	6	0.16	0.84	3.36	0.005	3.3	25.51	5.35	0.001	2.92	1.65	4.51	0.001
Residual	36	0.05	0.25			0.62	4.77			0.65	0.37		
Waychinicup													
Season	3	14.39	3.82	0.62	0.676	11.81	77.98	58.35	0.001	44.8	90.95	243.83	0.001
Region	2	331.19	87.86	14.29	0.001	2.32	15.31	11.46	0.002	0.86	1.75	4.71	0.016
S × R	6	8.20	2.18	0.35	0.932	0.81	5.37	4.02	0.002	3.41	6.93	18.57	0.001
Residual	36	23.18	6.15			0.20	1.34			0.18	0.37		
Cordinup													
Season	3	123.99	97.76	140.61	0.001	8.4	58.69	4.35	0.010	109.63	98.36	224.42	0.001
Region	2	0.74	0.58	0.84	0.447	1.42	9.95	0.74	0.486	0.93	0.83	1.90	0.176
S × R	6	1.22	0.96	1.38	0.247	2.56	17.86	1.32	0.279	0.41	0.37	0.84	0.567
Residual	36	0.88	0.70			1.93	13.5			0.49	0.44		
Cheyne													
Season	3	652.12	98.06	255.95	0.001	10.09	57.50	6.99	0.003	225.67	98.80	353.18	0.001
Region	2	6.61	0.99	2.59	0.092	4.56	25.98	3.16	0.041	0.55	0.24	0.87	0.443
S × R	6	3.73	0.56	1.46	0.221	1.46	8.29	1.01	0.412	1.56	0.68	2.44	0.042
Residual	36	2.55	0.38			1.44	8.22			0.64	0.28		
Beaufort													
Season	3	6492.7	98.68	283.79	0.001	7.91	92.21	49.71	0.001	237.31	98.47	782.45	0.001
Region	2	39.72	0.60	1.74	0.187	0.20	2.29	1.24	0.287	1.51	0.63	4.99	0.011
S × R	6	24.54	0.37	1.07	0.404	0.31	3.64	1.96	0.102	1.88	0.78	6.19	0.002
Residual	36	22.88	0.35			0.16	1.85			0.3	0.13		

3.3. Continuous measurements of water quality and bar breaches

The continuous data from the loggers highlights that salinity and/or temperature can change rapidly in between the discrete data collected seasonally (Figure 3.4, Table 3.3). For example, salinity in Torbay increased from 10 to ~16 in <1h in March 2020 and then gradually declined to 10 in late April and then increased suddenly again (Figure 3.4). These sudden changes in salinity and/or temperature provide an indication of when the bar was breached for those estuaries that were closed.

The logger data shows that of those estuaries with a sand bar, the bar was breached on at least two occasions in every estuary except for Beaufort (Table 3.3). On the basis of these data, Torbay was breached on most occasions, with five major changes in salinity recorded between February and mid-July 2020 and reports from news outlets indicate that it was breached two further times in 2020 after the last logger reading. Of the estuaries that become disconnected from the ocean, Torbay and Normans were open the longest at ~53 and 38 days, respectively, followed by Cordinup and Cheyne, ~29 and 25 days, respectively, with Taylor only being open for nine days (Table 3.3).

The number and lengths of bar breaks differed between seasons. Although data were recorded in 2020 prior to the deployment of the loggers in late February, observations from local residents and an examination for satellite imagery from LAND Viewer (2021) did not identify any breaches during summer. Torbay (twice) and Cordinup were the only estuaries to breach in autumn, with both only remaining open for ~10 (20 days in total) and one day, respectively (Table 3.3). Torbay broke on three occasions during winter for around 20 days each time (Figure 3.4). The five annually-open estuaries all breached during the large storm event in early August, remaining open for between 5 (Taylor) and 28 days (Cordinup; Figure 3.4). Torbay, Taylor, Normans and Cheyne all breached again in spring following a second storm event. Torbay was estimated to have remained open for ~80 days, with the other estuaries open for between 4 and 18 days. Torbay was also artificially breached by the Department of Water and Environmental Regulation in November.

Salinity exceeded the maximum limit for conductivity (55 000 uS/cm) able to be recorded in Cheyne (summer) and Beaufort (throughout the study) and epiphytic growths fouled the loggers in Taylor and Cheyne for extended periods, and so complete data sets could not be recorded in these systems. Using the available data, the highest salinities in Torbay (22), Taylor (21) and Cordinup (28) were recorded followed bar breaches or low flow periods in summer (Figure 3.4; Table 3.3). Following the large storm event in early August, all estuaries recorded their lowest salinity, with most declining to <1 for a period (Figure 3.4; Table 3.3).

Table 3.3. Summary of the salinity, temperature and bar dynamics of seven estuaries from using hourly data recorded using a HOBO logger. *unfinished data, CD cannot accurately determine and AL above detection limits of logger. Number of bar breaches are shaded grey with N/A denoting permanently-open systems.

	Torbay Inlet	Oyster Harbour	Taylor Inlet	Normans Inlet
Estuary characteristics				
Logging initiated	19/02/20		26/02/20	01/03/20
Log ended	20/07/20		28/10/20	28/10/20
# days deployed	152		245	241
# functional days deployed	152		47	241
# days of water exchange	53		9	37
Number of bar breaches	7*	N/A	2	2
% of days bar was breached	35	100	4	16
Mean salinity	15.46	N/A	CD	5.99
Minimum salinity	5.69	N/A	CD	0.012
Maximum salinity	22.31	N/A	21.67*	38.86
Mean water temperature	19.23	N/A	18.08	16.014
Maximum water temperature	24.73	N/A	24.68	30.20
Minimum water temperature	13.17	N/A	13.06	6.84

	Waychinicup Estuary	Cordinup River	Cheyne Inlet	Beaufort Inlet
Logging initiated	25/02/20	28/02/20	21/02/20	20/02/20
Log ended	30/10/20	07/11/20	03/11/20	02/11/20
# days deployed	249	253	256	256
# functional days deployed	249	253	106s	173
# days of water exchange	249	29	25	0
Number of bar breaches	N/A	2	2	0
% of days bar was breached	100	11	10	0
Mean salinity	26.45	12.09	CD	CD
Minimum salinity	0.34	0.65	CD	CD
Maximum salinity	31.94	27.54	AL	AL
Mean water temperature	18.41	16.58	16.71	16.65
Maximum water temperature	21.65	24.70	24.84	25.39
Minimum water temperature	10.57	10.25	10.72	10.71

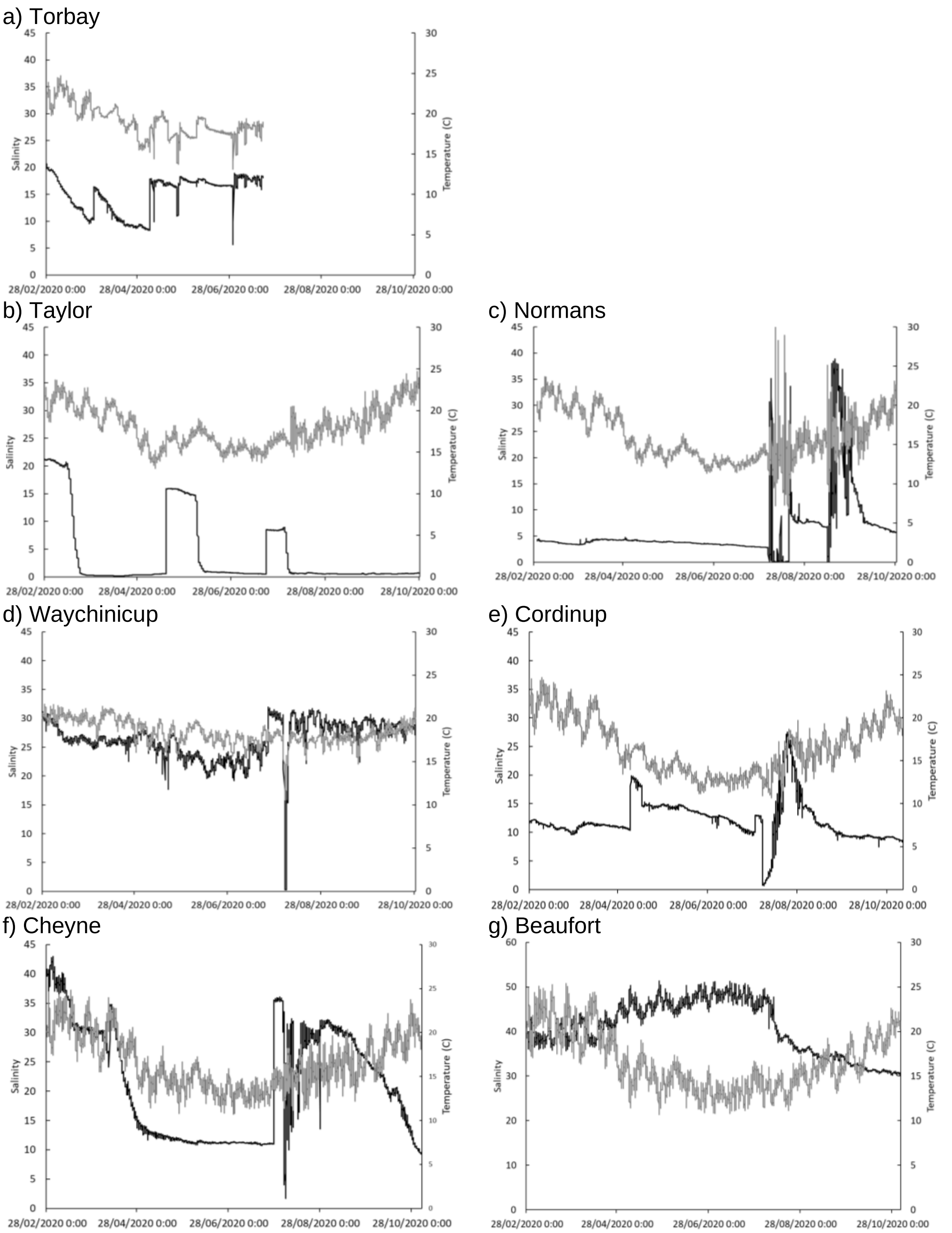

Figure 3.4. Salinity (black line) and temperature (grey line) data recorded hourly using a HOBO U24 logger in seven estuaries between February and November 2020. Note no logger was deployed in Oyster.

3.4. Nearshore fish fauna

This section starts with an overview of the fish fauna found in the nearshore waters of all eight estuaries (Section 3.4.1), followed by an examination of how the characteristics of the fauna, *i.e.,* number of species, total density, Simpson's diversity and composition vary among estuaries accounting for seasons and regions (Section 3.4.2). It finishes with an investigation as to whether these characteristics change seasonally and regionally within each estuary (Section 3.4.3).

3.4.1. Description of the fish fauna

A total of 224,546 fish were caught using seine nets (n = 390) in nearshore waters of the eight estuaries seasonally between February and November 2020, representing 86 species from 39 families and 15 orders (Table 3.4). The species with highest densities across all estuaries were the atherinids *Atherinosoma elongata* (238.9 fish 100 m^{-2}) and *Leptatherina wallacei* (172.5 fish 100 m^{-2}), which occurred in 42 and 53% of all samples, respectively (Table 3.4). These two were present in six estuaries, with *A. elongata* not recorded in Normans and Cordinup and *L. wallacei* not recorded in Cordinup and Beaufort. Less abundant, but frequently caught, were the sparid *Acanthopagrus butcheri* (22.9 fish 100 m^{-2}, 30% occurrence), the gobiids *Pseudogobius olorum* (21.4 fish 100 m^{-2}, 43% occurrence) and *Favonigobius lateralis* (18.0 fish 100 m^{-2}, 35% occurrence) and the atherinid *Leptatherina presbyteroides* (11.4 fish 100 m^{-2}, 13% occurrence). These four species were caught in six or seven of the estuaries, with only the mugilid *Aldrichetta forsteri* recorded in all eight (Table 3.4). Another mugilid *Mugil cephalus*, was caught in six of the eight estuaries albeit at lower densities (1.2 fish 100m^{-2}). No other species had an average density >1 fish 100m^{-2}, a frequency of occurrence >10% or appeared in ≥ 6 estuaries (Table 3.4).

Table 3.4 (Overleaf). Mean density (M; 100 m^{-2}), standard deviation (SD), percentage contribution to the catch (%C); percentage frequency of occurrence (%F), rank by density (R), length range (RL) and mean length (ML) of each fish species recorded in the nearshore waters of the eight estuaries in 2020. Abundant (*i.e.,* those that contributed >5% to the catch) and commonly caught (>8% frequency) species are highlighted in grey. Estuarine Usage Functional Group (EUFG) guilds are: E = solely estuarine; EM = estuarine & marine; FS = freshwater straggler; EF=estuarine & freshwater; FEO = freshwater estuarine-opportunist; MEO = marine estuarine-opportunist; and MS = marine straggler. * denotes that some fish were released.

Species name	Common name	EUFG	All		Torbay Inlet							Oyster Harbour						
			M	%F	M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Atherinosoma elongata	Elongate Hardyhead	E	238.89	42.05	18.86	63.01	6.83	33.33	4	17-79	43	9.18	32.32	6.92	41.67	4	21-81	51
Leptatherina wallacei	Western Hardyhead	EF	172.51	53.33	137.63	233.57	49.87	89.58	1	23-87	49	12.66	54.58	9.54	35.42	3	27-75	53
Acanthopagrus butcheri	Black Bream	E	22.90	29.74	16.76	30.89	6.07	70.83	6	31-320*	97	4.11	15.44	3.10	18.75	9	31-320*	97*
Pseudogobius olorum	Bluespot Goby	EF	21.43	42.82	44.56	125.48	16.15	77.08	2	16-57	30	4.90	35.17	3.70	20.83	6	16-47	33
Favonigobius lateralis	Southern Longfin Goby	EM	18.03	35.13	17.49	44.70	6.34	58.33	5	17-68	37	41.27	86.82	31.10	77.08	2	13-63	32
Leptatherina presbyteroides	Silver Fish	EM	11.44	12.82	0.45	2.54	0.16	4.17	10	49-62	56	42.53	214.20	32.05	29.17	1	30-83	61
Arenigobius bifrenatus	Bridled Goby	E	3.27	7.95	24.68	100.22	8.94	47.92	3	20-103	41							
Aldrichetta forsteri	Yelloweye Mullet	MEO	2.06	8.97	0.47	2.02	0.17	10.42		21-58	46	0.38	2.14	0.28	6.25	13	42-64	50
Mugil cephalus	Sea Mullet	MEO	1.20	5.64	7.58	43.81	2.75	20.83	7	23-350	36	0.05	0.32	0.04	4.17	23	21-30	26
Afurcagobius suppositus	Southwestern Goby	EF	0.78	2.56	6.36	25.23	2.30	20.83	8	15-74	45							
Ostorhinchus rueppellii	Western Gobbleguts	EM	0.61	3.85								4.92	17.53	3.71	31.25	5	18-72	37
Neoodax balteatus	Little Weed Whiting	MS	0.58	5.13								4.69	11.55	3.53	41.67	7	34-96	60
Haletta semifasciata	Blue Weed Whiting	MS	0.51	4.36								4.15	20.73	3.13	35.42	8	56-222	103
Galaxias occidentalis	Western Galaxias	FS	0.28	2.56	0.66	4.79	0.24	4.17	9	35-65	50							
Sillaginodes punctatus	King George Whiting	MEO	0.22	2.31														
Halichoeres brownfieldi	Brownfield's Wrasse	MS	0.20	5.13								0.07	0.35	0.05	6.25	22	26-50	43
Rhabdosargus sarba	Tarwhine	MEO	0.13	0.77														
Dotalabrus aurantiacus	Castelnau's Wrasse	MS	0.12	5.38														
Stigmatopora argus	Spotted Pipefish	MS	0.11	3.59								0.88	2.25	0.66	29.17	10	73-220	178
Kyphosus gladius	Gladius Drummer	MS	0.11	1.03														
Acanthaluteres spilomelanurus	Bridled Leatherjacket	MS	0.10	3.33								0.70	2.05	0.53	22.92	11	24-97	66
Siphonognathus radiatus	Longray Weed Whiting	MS	0.09	3.59								0.43	1.56	0.32	14.58	12	33-115	65
Chromis klunzingeri	Blackhead Puller	MS	0.06	0.77														
Spratelloides robustus	Blue Sprat	MEO	0.05	1.03								0.36	1.93	0.27	6.25	15	37-100	81
Enoplosus armatus	Old Wife	MS	0.05	2.56														
Pelates octolineatus	Western Striped Grunter	MEO	0.04	1.28								0.36	2.18	0.27	10.42	14	19-72	58
Heteroclinus adelaidae	Adelaide Weedfish	MS	0.04	2.56								0.14	0.66	0.11	10.42	18	52-77	67
Gambusia holbrooki	Eastern Gambusia	FEO	0.04	0.77	0.32	2.31	0.12	6.25	11	20-45	27							
Sillago bassensis	Southern School Whiting	MS	0.04	0.51														
Girella zebra	Zebrafish	MS	0.04	1.03														
Arripis georgianus	Australian Herring	MEO	0.03	1.54	0.04	0.29	0.01	2.08	13	74	74	0.09	0.59	0.07	4.17	21	65-69	67
Siphamia cephalotes	Wood's Siphonfish	MS	0.02	0.51								0.18	1.03	0.14	4.17	16	36-44	40
Arripis truttaceus	West. Australian Salmon	MEO	0.02	0.77								0.02	0.14	0.01	2.08	25	44	44
Cnidoglanis macrocephalus	Estuary Cobbler	EM	0.02	2.05														
Gymnapistes marmoratus	Soldier	MEO	0.02	1.79								0.16	0.49	0.12	14.58	17	60-78	69
Posidonichthys hutchinsi	Posidonia Clingfish	MS	0.02	1.54								0.09	0.37	0.07	8.33	20	19-22	20
Achoerodus gouldii	Western Blue Groper	MS	0.02	1.03														
Siphonognathus tanyourus	Longtail Weed Whiting	MS	0.02	1.03														
Helcogramma decurrens	Blackthroat Threefin	MS	0.01	0.77														
Cristiceps australis	South. Crested Weedfish	MS	0.01	1.54	0.02	0.14	0.01	2.08	13			0.09	0.31	0.07	10.42	19	58-138	99
Atherinomorus vaigiensis	Common Hardyhead	MEO	0.01	0.26														
Centroberyx lineatus	Swallowtail	MS	0.01	0.26														
Kyphosus sydneyanus	Silver Drummer	MS	0.01	0.77														
Tilodon sexfasciatus	Moonlighter	MS	0.01	1.03														
Dotalabrus alleni	Little Rainbow Wrasse	MS	0.01	0.26														

Table 3.4. Continued.

Species name	Common name	EUFG	All		Torbay							Oyster						
			M	%F	M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Pseudorhombus jenynsii	Smalltooth Flounder	MEO	0.01	1.03								0.04	0.20	0.03	4.17	24		
Sillago burrus	West. Trumpeter Whiting	MEO	0.01	0.77								0.02	0.14	0.01	2.08	25	97	97
Schuettea woodwardi	Western Pomfred	MS	0.01	0.26														
Microcanthus strigatus	Stripey	MS	0.01	0.26	0.07	0.58	0.03	2.08	12	18-24	20							
Scorpis georgiana	Banded Sweep	MS	0.01	0.26														
Notolabrus parilus	Brownspotted Wrasse	MS	0.01	0.51														
Rhombosolea tapirina	Greenback Flounder	MEO	0.01	0.26														
Acanthaluteres brownii	Spinytail Leatherjacket	MS	0.01	0.26														
Ophthalmolepis lineolatus	Southern Maori Wrasse	MS	0.01	0.77														
Heteroclinus heptaeolus	Ogilby's Weedfish	MS	0.01	0.77														
Callogobius mucosus	Sculptured Goby	MS	0.01	0.51								0.02	0.14	0.01	2.08	25	26	26
Meuschenia freycineti	Sixspine Leatherjacket	MS	0.01	0.77								0.04	0.20	0.03	4.17	24	124-232	178
Hyporhamphus melanochir	Southern Garfish	EM	<0.01	0.26														
Parma victoriae	Scalyfin	MS	<0.01	0.51														
Cheilodactylus rubrolabiatus	Redlip Morwong	MS	<0.01	0.26														
Pictilabrus laticlavius	Senator Wrasse	MS	<0.01	0.51														
Olisthops cyanomelas	Herring Cale	MS	<0.01	0.51														
Monacanthidae sp.	Unknown Leatherjacket	MS	<0.01	0.51								0.04	0.20	0.03	4.17	24	19-25	22
Contusus brevicaudus	Prickly Toadfish	MS	<0.01	0.26														
Trygonoptera mucosa	West. Shovelnose Stingaree	MS	<0.01	0.26								0.02	0.14	0.01	2.08	25	349	349
Engraulis australis	Australian Anchovy	EM	<0.01	0.26								0.02	0.14	0.01	2.08	25	88	88
Urocampus carinirostris	Hairy Pipefish	EM	<0.01	0.26								0.02	0.14	0.01	2.08	25	54	54
Pugnaso curtirostris	Pugnose Pipefish	MS	<0.01	0.26								0.02	0.14	0.01	2.08	25	104	104
Seriola hippos	Samsonfish	MS	<0.01	0.26														
Pseudocaranx georgianus	Silver Trevally	MS	<0.01	0.26														
Parequula melbournensis	Silverbelly	MS	<0.01	0.26														
Upeneichthys vlamingii	Bluespotted Goatfish	MS	<0.01	0.26														
Scorpis aequipinnis	Sea Sweep	MS	<0.01	0.26														
Chironemus maculosus	Silver Spot	MS	<0.01	0.26														
Aplodactylus westralis	Western Seacarp	MS	<0.01	0.26														
Cheilodactylus vestitus	Crested Morwong	MS	<0.01	0.26														
Pictilabrus spp.	Wrasse	MS	<0.01	0.26														
Siphonognathus caninis	Sharpnose Weed Whiting	MS	<0.01	0.26														
Parapercis haackei	Wavy Grubfish	MS	<0.01	0.26								0.02	0.14	0.01	2.08	25	47	47
Ammotretis rostratus	Longsnout Flounder	MEO	<0.01	0.26	0.02	0.14	0.01	2.08	13	106	106							
Ammotretis elongatus	Elongate Flounder	MEO	<0.01	0.26								0.02	0.14	0.01	2.08	25	101	101
Acanthaluteres vittiger	Toothbrush Leatherjacket	MS	<0.01	0.26														
Meuschenia hippocrepis	Horseshoe Leatherjacket	MS	<0.01	0.26														
Meuschenia scaber	Velvet Leatherjacket	MS	<0.01	0.26								0.02	0.14	0.01	2.08	25	135	135
Brachaluteres jacksonianus	South. Pygmy L.jacket	MS	<0.01	0.26														
Meuschenia galii	Bluelined Leatherjacket	MS	<0.01	0.26														
Number of samples			**390**					**48**							**48**			
Number of species			**86**					**16**							**36**			
Density (100m2)			**575.76**					**275.97**							**132.69**			
Number of fish caught			**224,546**					**15,366**							**7,388**			

Table 3.4. Continued.

Species name	Common name	Taylor Inlet							Normans Inlet						
		M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Atherinosoma elongata	Elongate Hardyhead	56.65	150.41	14.06	54.17	2	24-92	43							
Leptatherina wallacei	Western Hardyhead	241.42	448.67	59.92	93.75	1	19-70	40	172.66	289.31	98.43	100.00	1	10-95	44
Acanthopagrus butcheri	Black Bream	12.43	20.05	3.08	75.00	6	26-40*	35*							
Pseudogobius olorum	Bluespot Goby	35.90	93.14	8.91	72.92	4	16-55	29	0.91	3.78	0.52	14.58	3	21-56	36
Favonigobius lateralis	Southern Longfin Goby	13.72	38.68	3.41	64.58	5	19-68	40							
Leptatherina presbyteroides	Silver Fish	37.79	159.91	9.38	41.67	3	22-80	48	0.11	0.86	0.06	2.08	4	49-62	56
Arenigobius bifrenatus	Bridled Goby	0.99	4.16	0.25	10.42	8	27-77	44							
Aldrichetta forsteri	Yelloweye Mullet	3.88	31.18	0.96	2.08	7	30-50	37	1.74	8.14	0.99	8.33	2	30-62	38
Mugil cephalus	Sea Mullet														
Afurcagobius suppositus	Southwestern Goby														
Ostorhinchus rueppellii	Western Gobbleguts														
Neoodax balteatus	Little Weed Whiting														
Haletta semifasciata	Blue Weed Whiting														
Galaxias occidentalis	Western Galaxias														
Sillaginodes punctatus	King George Whiting														
Halichoeres brownfieldi	Brownfield's Wrasse														
Rhabdosargus sarba	Tarwhine														
Dotalabrus aurantiacus	Castelnau's Wrasse														
Stigmatopora argus	Spotted Pipefish														
Kyphosus gladius	Gladius Drummer														
Acanthaluteres spilomelanurus	Bridled Leatherjacket														
Siphonognathus radiatus	Longray Weed Whiting														
Chromis klunzingeri	Blackhead Puller														
Spratelloides robustus	Blue Sprat														
Enoplosus armatus	Old Wife														
Pelates octolineatus	Western Striped Grunter														
Heteroclinus adelaidae	Adelaide Weedfish														
Gambusia holbrooki	Eastern Gambusia														
Sillago bassensis	Southern School Whiting														
Girella zebra	Zebrafish														
Arripis georgianus	Australian Herring	0.07	0.58	0.02	2.08	9	75	75							
Siphamia cephalotes	Wood's Siphonfish														
Arripis truttaceus	Western Australian Salmon														
Cnidoglanis macrocephalus	Estuary Cobbler														
Gymnapistes marmoratus	Soldier														
Posidonichthys hutchinsi	Posidonia Clingfish														
Achoerodus gouldii	Western Blue Groper														
Siphonognathus tanyourus	Longtail Weed Whiting														
Helcogramma decurrens	Blackthroat Threefin														
Cristiceps australis	Southern Crested Weedfish														
Atherinomorus vaigiensis	Common Hardyhead	0.09	0.72	0.02	2.08	9	50-81	66							
Centroberyx lineatus	Swallowtail														
Kyphosus sydneyanus	Silver Drummer														
Tilodon sexfasciatus	Moonlighter														
Dotalabrus alleni	Little Rainbow Wrasse														
Pseudorhombus jenynsii	Smalltooth Flounder														
Sillago burrus	West. Trumpeter Whiting														

Table 3.4. Continued.

Species name	Common name	Taylor Inlet							Normans Inlet						
		M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Schuettea woodwardi	Western Pomfred														
Microcanthus strigatus	Stripey														
Scorpis georgiana	Banded Sweep														
Notolabrus parilus	Brownspotted Wrasse														
Rhombosolea tapirina	Greenback Flounder														
Acanthaluteres brownii	Spinytail Leatherjacket														
Ophthalmolepis lineolatus	Southern Maori Wrasse														
Heteroclinus heptaeolus	Ogilby's Weedfish														
Callogobius mucosus	Sculptured Goby														
Meuschenia freycineti	Sixspine Leatherjacket														
Hyporhamphus melanochir	Southern Garfish														
Parma victoriae	Scalyfin														
Cheilodactylus rubrolabiatus	Redlip Morwong														
Pictilabrus laticlavius	Senator Wrasse														
Olisthops cyanomelas	Herring Cale														
Monacanthidae sp.	Unidentified Leatherjacket														
Contusus brevicaudus	Prickly Toadfish														
Trygonoptera mucosa	Western Shovelnose Stingaree														
Engraulis australis	Australian Anchovy														
Urocampus carinirostris	Hairy Pipefish														
Pugnaso curtirostris	Pugnose Pipefish														
Seriola hippos	Samsonfish														
Pseudocaranx georgianus	Silver Trevally														
Parequula melbournensis	Silverbelly														
Upeneichthys vlamingii	Bluespotted Goatfish														
Scorpis aequipinnis	Sea Sweep														
Chironemus maculosus	Silver Spot														
Aplodactylus westralis	Western Seacarp														
Cheilodactylus vestitus	Crested Morwong														
Pictilabrus spp	Pictilabrus spp														
Siphonognathus caninis	Sharpnose Weed Whiting														
Parapercis haackei	Wavy Grubfish														
Ammotretis rostratus	Longsnout Flounder														
Ammotretis elongatus	Elongate Flounder														
Acanthaluteres vittiger	Toothbrush Leatherjacket														
Meuschenia hippocrepis	Horseshoe Leatherjacket														
Meuschenia scaber	Velvet Leatherjacket														
Brachaluteres jacksonianus	Southern Pygmy Leatherjacket														
Meuschenia galii	Bluelined Leatherjacket														
Number of samples		**48**							**48**						
Number of species		**10**							**4**						
Density (100m2)		**402.93**							**175.42**						
Number of fish caught		**22,435**							**9,971**						

Table 3.4. Continued.

Species name	Common name	Waychinicup Estuary							Cordinup River						
		M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Atherinosoma elongata	Elongate Hardyhead	4.93	25.07	20.49	18.37	2	20-79	38							
Leptatherina wallacei	Western Hardyhead	2.83	11.13	11.76	14.29	3	15-75	37							
Acanthopagrus butcheri	Black Bream	0.02	0.14	0.07	2.04	33			151.92	393.71	53.47	60.42	1	12-57*	21*
Pseudogobius olorum	Bluespot Goby	1.42	8.98	5.88	8.16	4	18-54	36	57.49	147.81	20.24	70.83	3	11-55	28
Favonigobius lateralis	Southern Longfin Goby	1.25	6.43	5.21	18.37	6	12-67	31	72.58	380.46	25.55	62.50	2	12-81	36
Leptatherina presbyteroides	Silver Fish	5.63	25.72	23.39	14.29	1	24-78	50							
Arenigobius bifrenatus	Bridled Goby														
Aldrichetta forsteri	Yelloweye Mullet	1.14	4.40	4.73	18.37	7	26-109	55	0.57	4.62	0.20	2.08	5	77-77*	77*
Mugil cephalus	Sea Mullet	0.11	0.62	0.47	6.12	20	20-31	25							
Afurcagobius suppositus	Southwestern Goby														
Ostorhinchus rueppellii	Western Gobbleguts														
Neoodax balteatus	Little Weed Whiting														
Haletta semifasciata	Blue Weed Whiting														
Galaxias occidentalis	Western Galaxias	0.07	0.43	0.27	3.77	26	18-47	27	1.54	6.74	0.54	12.50	4	27-55	36
Sillaginodes punctatus	King George Whiting	0.05	0.30	0.20	4.08	29	31-102	67							
Halichoeres brownfieldi	Brownfield's Wrasse	1.40	3.50	5.81	34.69	5	28-119	46							
Rhabdosargus sarba	Tarwhine														
Dotalabrus aurantiacus	Castelnau's Wrasse	0.91	2.56	3.79	42.86	8	26-98	44							
Stigmatopora argus	Spotted Pipefish														
Kyphosus gladius	Gladius Drummer	0.78	4.01	3.25	8.16	9	193-193*	193*							
Acanthaluteres spilomelanurus	Bridled Leatherjacket														
Siphonognathus radiatus	Longray Weed Whiting	0.26	0.99	1.08	14.29	13	45-147	93							
Chromis klunzingeri	Blackhead Puller	0.44	2.41	1.83	6.12	10									
Spratelloides robustus	Blue Sprat	0.03	0.27	0.14	2.04	32	39-45	42							
Enoplosus armatus	Old Wife	0.28	0.92	1.15	18.37	11	25-69	36							
Pelates octolineatus	Western Striped Grunter														
Heteroclinus adelaidae	Adelaide Weedfish	0.18	0.79	0.74	10.20	15	27-70	56							
Gambusia holbrooki	Eastern Gambusia														
Sillago bassensis	Southern School Whiting	0.28	1.77	1.15	4.08	12	70-82*	75*							
Girella zebra	Zebrafish	0.26	1.45	1.08	8.16	14									
Arripis georgianus	Australian Herring	0.03	0.27	0.14	2.04	32									
Siphamia cephalotes	Wood's Siphonfish														
Arripis truttaceus	West. Australian Salmon	0.15	1.10	0.61	4.08	16	46-64	58							
Cnidoglanis macrocephalus	Estuary Cobbler	0.15	0.47	0.61	16.33	18									
Gymnapistes marmoratus	Soldier														
Posidonichthys hutchinsi	Posidonia Clingfish	0.05	0.30	0.20	4.08	29	19-20	19							
Achoerodus gouldii	Western Blue Groper	0.13	0.63	0.54	8.16	17	37-40*	39*							
Siphonognathus tanyourus	Longtail Weed Whiting	0.11	0.71	0.47	8.16	19	44-118	72							
Helcogramma decurrens	Blackthroat Threefin	0.10	0.51	0.41	6.12	21	28-37	33							
Cristiceps australis	South. Crested Weedfish														
Atherinomorus vaigiensis	Common Hardyhead														
Centroberyx lineatus	Swallowtail	0.08	0.69	0.34	2.04	24	15-18	16							
Kyphosus sydneyanus	Silver Drummer	0.08	0.45	0.34	6.12	23	108-157*	133*							
Tilodon sexfasciatus	Moonlighter	0.08	0.35	0.34	8.16	22	181-181*	181*							
Dotalabrus alleni	Little Rainbow Wrasse	0.08	0.69	0.34	2.04	24	28-46*	37*							
Pseudorhombus jenynsii	Smalltooth Flounder	0.02	0.14	0.07	2.04	33									
Sillago burrus	West. Trumpeter Whiting	0.05	0.30	0.20	4.08	29	61-67	64							

Table 3.4. Continued.

Species name	Common name	Waychinicup Estuary							Cordinup River						
		M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Schuettea woodwardi	Western Pomfred	0.07	0.55	0.27	2.04	28									
Microcanthus strigatus	Stripey														
Scorpis georgiana	Banded Sweep														
Notolabrus parilus	Brownspotted Wrasse	0.07	0.43	0.27	4.08	25									
Rhombosolea tapirina	Greenback Flounder														
Acanthaluteres brownii	Spinytail Leatherjacket	0.07	0.55	0.27	2.04	27									
Ophthalmolepis lineolatus	Southern Maori Wrasse	0.05	0.23	0.20	6.12	30									
Heteroclinus heptaeolus	Ogilby's Weedfish	0.05	0.23	0.20	6.12	30	35-80	61							
Callogobius mucosus	Sculptured Goby	0.03	0.27	0.14	2.04	32	42-48	45							
Meuschenia freycineti	Sixspine Leatherjacket	0.02	0.14	0.07	2.04	33	43-43	43							
Hyporhamphus melanochir	Southern Garfish	0.03	0.27	0.14	2.04	32	102-124	113							
Parma victoriae	Scalyfin	0.03	0.19	0.14	4.08	31									
Cheilodactylus rubrolabiatus	Redlip Morwong														
Pictilabrus laticlavius	Senator Wrasse	0.03	0.19	0.14	4.08	31	205*	205*							
Olisthops cyanomelas	Herring Cale	0.03	0.19	0.14	4.08	31	27-309	168							
Monacanthidae sp.	Unidentified Leatherjacket														
Contusus brevicaudus	Prickly Toadfish														
Trygonoptera mucosa	Western Shovelnose Stingaree														
Engraulis australis	Australian Anchovy														
Urocampus carinirostris	Hairy Pipefish														
Pugnaso curtirostris	Pugnose Pipefish														
Seriola hippos	Samsonfish	0.02	0.14	0.07	2.04	33	13-13	13							
Pseudocaranx georgianus	Silver Trevally	0.02	0.14	0.07	2.04	33									
Parequula melbournensis	Silverbelly	0.02	0.14	0.07	2.04	33									
Upeneichthys vlamingii	Bluespotted Goatfish	0.02	0.14	0.07	2.04	33									
Scorpis aequipinnis	Sea Sweep	0.02	0.14	0.07	2.04	33	25	25							
Chironemus maculosus	Silver Spot	0.02	0.14	0.07	2.04	33	132	132							
Aplodactylus westralis	Western Seacarp	0.02	0.14	0.07	2.04	33									
Cheilodactylus vestitus	Crested Morwong	0.02	0.14	0.07	2.04	33									
Labrid sp.	Labrid sp.	0.02	0.14	0.07	2.04	33	76	76							
Siphonognathus caninis	Sharpnose Weed Whiting	0.02	0.14	0.07	2.04	33	46	46							
Parapercis haackei	Wavy Grubfish														
Ammotretis rostratus	Longsnout Flounder														
Ammotretis elongatus	Elongate Flounder														
Acanthaluteres vittiger	Toothbrush Leatherjacket	0.02	0.14	0.07	2.04	33	240	240							
Meuschenia hippocrepis	Horseshoe Leatherjacket	0.02	0.14	0.07	2.04	33	100	100							
Meuschenia scaber	Velvet Leatherjacket														
Brachaluteres jacksonianus	Southern Pygmy Leatherjacket	0.02	0.14	0.07	2.04	33	31	31							
Meuschenia galii	Bluelined Leatherjacket	0.02	0.14	0.07	2.04	33									
Number of samples					**48**							**48**			
Number of species					**58**							**5**			
Density (100m2)					**24.06**							**284.11**			
Number of fish caught					**1,479**							**15,819**			

Table 3.4. Continued.

Species name	Common name	Cheyne Inlet							Beaufort Inlet						
		M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Atherinosoma elongata	Elongate Hardyhead	1,546.84	3,891.04	63.72	97.92	1	15-100	43	304.01	1,160.05	99.98	95.83	1	10-287	32
Leptatherina wallacei	Western Hardyhead	830.55	1,864.50	34.21	97.92	2	20-82	39							
Acanthopagrus butcheri	Black Bream	0.81	2.99	0.03	14.58	9									
Pseudogobius olorum	Bluespot Goby	28.79	47.98	1.19	83.33	3	17-64	33							
Favonigobius lateralis	Southern Longfin Goby	0.04	0.20	0.00	4.17	11	24-26	25							
Leptatherina presbyteroides	Silver Fish	5.89	39.87	0.24	12.50	5	35-58	41							
Arenigobius bifrenatus	Bridled Goby	0.90	5.25	0.04	6.25	8	25-114	45							
Aldrichetta forsteri	Yelloweye Mullet	8.37	24.68	0.34	20.83	4	38-74	57	0.04	0.20	0.01	4.17	2		
Mugil cephalus	Sea Mullet	1.96	7.87	0.08	12.50	6	37-70	55	0.02	0.14	0.01	2.08	3		
Afurcagobius suppositus	Southwestern Goby														
Ostorhinchus rueppellii	Western Gobbleguts														
Neoodax balteatus	Little Weed Whiting														
Haletta semifasciata	Blue Weed Whiting														
Galaxias occidentalis	Western Galaxias														
Sillaginodes punctatus	King George Whiting	1.76	5.56	0.07	14.58	7	27-45	34							
Halichoeres brownfieldi	Brownfield's Wrasse														
Rhabdosargus sarba	Tarwhine	1.04	7.02	0.04	6.25	8	25-36	30							
Dotalabrus aurantiacus	Castelnau's Wrasse														
Stigmatopora argus	Spotted Pipefish														
Kyphosus gladius	Gladius Drummer														
Acanthaluteres spilomelanurus	Bridled Leatherjacket	0.14	0.91	0.01	4.17	10	37-46	42							
Siphonognathus radiatus	Longray Weed Whiting														
Chromis klunzingeri	Blackhead Puller														
Spratelloides robustus	Blue Sprat														
Enoplosus armatus	Old Wife	0.07	0.58	0.00	2.08	12	29-33	31							
Pelates octolineatus	Western Striped Grunter														
Heteroclinus adelaidae	Adelaide Weedfish														
Gambusia holbrooki	Eastern Gambusia														
Sillago bassensis	Southern School Whiting														
Girella zebra	Zebrafish														
Arripis georgianus	Australian Herring	0.02	0.14	0.00	2.08	12	90	90							
Siphamia cephalotes	Wood's Siphonfish														
Arripis truttaceus	West. Australian Salmon														
Cnidoglanis macrocephalus	Estuary Cobbler														
Gymnapistes marmoratus	Soldier														
Posidonichthys hutchinsi	Posidonia Clingfish														
Achoerodus gouldii	Western Blue Groper														
Siphonognathus tanyourus	Longtail Weed Whiting														
Helcogramma decurrens	Blackthroat Threefin														
Cristiceps australis	South. Crested Weedfish														
Atherinomorus vaigiensis	Common Hardyhead														
Centroberyx lineatus	Swallowtail														
Kyphosus sydneyanus	Silver Drummer														
Tilodon sexfasciatus	Moonlighter														
Dotalabrus alleni	Little Rainbow Wrasse														
Pseudorhombus jenynsii	Smalltooth Flounder	0.04	0.29	0.00	2.08	12	26-30	28							
Sillago burrus	West. Trumpeter Whiting														

Table 3.4. Continued.

Species name	Common name	Cheyne Inlet							Beaufort Inlet						
		M	SD	%C	%F	R	RL	ML	M	SD	%C	%F	R	RL	ML
Schuettea woodwardi	Western Pomfred														
Microcanthus strigatus	Stripey														
Scorpis georgiana	Banded Sweep	0.07	0.58	0.00	2.08	12	36-41	39							
Notolabrus parilus	Brownspotted Wrasse														
Rhombosolea tapirina	Greenback Flounder	0.07	0.58	0.00	2.08	12	29-37	33							
Acanthaluteres brownii	Spinytail Leatherjacket														
Ophthalmolepis lineolatus	Southern Maori Wrasse														
Heteroclinus heptaeolus	Ogilby's Weedfish														
Callogobius mucosus	Sculptured Goby														
Meuschenia freycineti	Sixspine Leatherjacket														
Hyporhamphus melanochir	Southern Garfish														
Parma victoriae	Scalyfin														
Cheilodactylus rubrolabiatus	Redlip Morwong	0.04	0.29	0.00	2.08	12	66	66							
Pictilabrus laticlavius	Senator Wrasse														
Olisthops cyanomelas	Herring Cale														
Monacanthidae sp.	Unidentified Leatherjacket														
Contusus brevicaudus	Prickly Toadfish	0.04	0.29	0.00	2.08	12	74	74							
Trygonoptera mucosa	Western Shovelnose Stingaree														
Engraulis australis	Australian Anchovy														
Urocampus carinirostris	Hairy Pipefish														
Pugnaso curtirostris	Pugnose Pipefish														
Seriola hippos	Samsonfish														
Pseudocaranx georgianus	Silver Trevally														
Parequula melbournensis	Silverbelly														
Upeneichthys vlamingii	Bluespotted Goatfish														
Scorpis aequipinnis	Sea Sweep														
Chironemus maculosus	Silver Spot														
Aplodactylus westralis	Western Seacarp														
Cheilodactylus vestitus	Crested Morwong														
Pictilabrus spp	Pictilabrus spp														
Siphonognathus caninis	Sharpnose Weed Whiting														
Parapercis haackei	Wavy Grubfish														
Ammotretis rostratus	Longsnout Flounder														
Ammotretis elongatus	Elongate Flounder														
Acanthaluteres vittiger	Toothbrush Leatherjacket														
Meuschenia hippocrepis	Horseshoe Leatherjacket														
Meuschenia scaber	Velvet Leatherjacket														
Brachaluteres jacksonianus	South. Pygmy Leatherjacket														
Meuschenia galii	Bluelined Leatherjacket														
Number of samples		**48**							**48**						
Number of species		**19**							**3**						
Density (100m2)		**2,427.46**							**304.06**						
Number of fish caught		**135,161**							**16,930**						

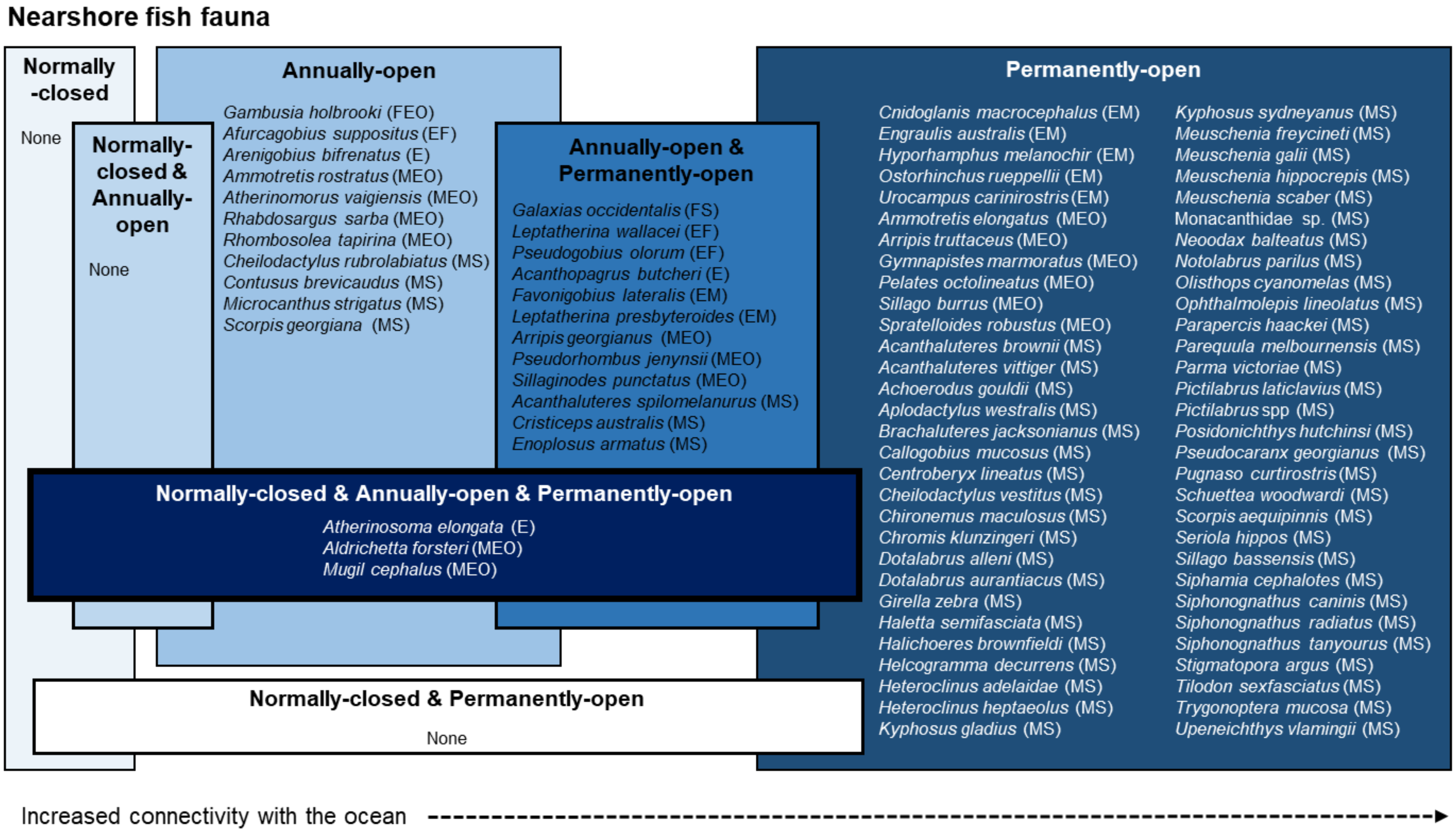

Figure 3.5. Venn diagram of the unique and shared presence of species in the offshore waters of each of the three types of estuary, i.e. permanently-open (Oyster and Waychinicup), annually-open (Torbay, Taylor, Normans, Cordinup and Cheyne) and normally-closed (Beaufort). Estuarine Usage Functional Group (EUFG) guilds are: E = solely estuarine; EM = estuarine & marine; MEO = marine estuarine-opportunist; and MS = marine straggler.

Permanently-open estuaries contained the most number of unique species, i.e. those not found in other broad types of estuary (i.e. 60), followed by annually-open estuaries with 11 unique species, with these two broad types of estuary containing 12 species in common (Figure 3.5). Normally-closed estuaries did not contain any unique species, while only three species were found in all broad types of estuary.

Life history guilds

Of the 86 species recorded across all estuaries, 71 spawn in marine waters, 13 in estuaries and only two in freshwaters (Table 3.5). Although estuarine species comprised 15% of the total number of species caught, they dominated catches representing ~99% of all fish recorded. Conversely, marine species constituted 83% of the species but only ~1% of the fish (Table 3.5). Marine species were represented by 56 marine stragglers and 15 marine estuarine-opportunists and made a low contribution to abundance (0.47 and 0.77%, respectively). The solely estuarine, and estuarine and freshwater guilds were each represented by three species yet contributed 53 and 39%, respectively to the total number of fish (Table 3.5). The species that can complete their entire life-cycle in either marine or estuarine waters (estuarine and marine) comprised seven species and 6% of all fish. A single species from each freshwater guild were recorded albeit in very small numbers (0.01% of all fish caught; Table 3.5).

Marine-spawning species were recorded in every estuary, ranging from only one in Cordinup and Normans to 27 and 49 in the permanently-open Oyster and Waychinicup, respectively (Table 3.5). In the last two estuaries, the majority of these species were marine stragglers (41 and 17, respectively). In terms of abundance, however, marine species contributed little to the overall catch, *i.e.*, 0.02 – 2.97%, except in Waychinicup (32.20%) and Oyster (9.85%). Marine stragglers were not caught in Taylor, Normans, Cordinup and Beaufort. Estuarine-resident species, *i.e.*, all species capable of breeding in estuaries, ranged from one in Beaufort to eight in Waychinicup and Torbay and nine in Oyster and contributed a very significant proportion to the total catch (Table 3.5). For example, they represented >96% of individuals in the six temporally-open estuaries and although their contribution to the total number of fish in the permanently-open systems was lower, they were still 90% and 68% in Oyster and Waychinicup, respectively. Freshwater species were only recorded in Torbay, Waychinicup and Cordinup.

Table 3.5. Number of species (N) and density of individuals (D, fish 100 m^{-2}), together with their percentage contributions (%) recorded in the nearshore waters of the eight estuaries in 2020. Guilds representing >10% in bold and the largest shaded in grey. Estuarine Usage Functional Group (EUFG) guilds are: E = solely estuarine; EF = estuarine & freshwater; EM = estuarine & marine; MEO = marine estuarine-opportunist; and MS = marine straggler; FS = freshwater straggler; FEO = freshwater estuarine-opportunist. Estuarine-residents comprise species in E, EF and EM guilds.

	All		Torbay		Oyster		Taylor		Normans		Waychinicup		Cordinup		Cheyne		Beaufort	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Species																		
E	3	3.49	3	**18.75**	2	5.56	3	**30.00**			2	3.45	1	**20.00**	3	**15.79**	1	**33.33**
EF	3	3.49	3	**18.75**	2	5.56	2	**20.00**	2	**50**	2	3.45	1	**20.00**	2	**10.53**		
EM	7	8.14	2	**12.50**	5	**13.89**	2	**20.00**	1	**25**	4	6.90	1	**20.00**	2	**10.53**		
MEO	15	**17.44**	4	**25.00**	10	**27.78**	3	**30.00**	1	**25**	8	**13.79**	1	**20.00**	7	**36.84**	2	**66.67**
MS	56	**65.12**	2	**12.50**	17	**47.22**					41	**70.69**			5	**26.32**		
FS	1	1.16	1	6.25							1	1.72	1	**20.00**				
FEO	1	1.16	1	6.25														
Total	**86**		**16**		**36**		**10**		**4**		**58**		**5**		**19**		**3**	
	D	%	D	%	D	%	D	%	D	%	D	%	D	%	D	%	D	%
Individuals																		
E	265.06	**53.40**	60.29	**21.85**	13.29	**10.02**	70.06	**17.39**			4.94	**20.55**	151.92	**53.47**	1548.55	**63.79**	304.01	**99.98**
EF	194.72	**39.23**	188.54	**68.32**	17.56	**13.24**	277.32	**68.83**	173.57	**98.95**	4.25	**17.65**	57.49	**20.24**	859.34	**35.40**		
EM	30.11	6.07	17.94	6.50	88.76	**66.89**	51.51	**12.78**	0.11	0.06	7.06	**29.34**	72.58	**25.55**	5.93	0.24		
MEO	3.82	0.77	8.10	2.94	1.49	1.12	4.04	1.00	1.74	0.99	1.58	6.56	0.57	0.20	13.25	0.55	0.05	0.02
MS	2.32	0.47	0.09	0.03	11.58	8.73					6.16	**25.63**			0.36	0.01		
FS	0.28	0.06	0.66	0.24							0.07	0.27	1.54	0.54				
FEO	0.04	0.01	0.32	0.12														
Total	**496.34**		**275.95**		**132.69**		**402.93**		**175.42**		**24.06**		**284.11**		**2427.42**		**304.06**	

3.4.2. Inter-estuarine differences

Number of species, total density and diversity

The total number of species varied greatly among estuaries (Table 3.4). The highest number of species were recorded in Waychinicup (58) and Oyster (36) and the least in Beaufort (3; Table 3.4). Cheyne (19), Torbay (16) and Taylor (10) were more speciose than Cordinup (5) and Normans (4).

The number of species was shown by PERMANVA to differ among estuaries, seasons and regions and that all their interactions were significant (Table 3.6). Estuary was by far the most important term, accounting for over 70% of the total mean squares (Table 3.6). Pairwise PERMANOVA determined that the number of species differed significantly between every pair of estuaries except for Cheyne *vs* Taylor and Waychinicup, Oyster *vs* Torbay, and Taylor *vs* Torbay and Waychinicup (P = 0.115 - 0.230; Figure 3.6a). Torbay, Oyster, Taylor, Waychinicup and Cheyne had the highest mean species richness (4-5), with Cordinup (2) and Normans and Beaufort (~1; Figure 3.6a) being lower. The Season effect, which accounted for 8% of the total mean squares was due to values in spring (3.75) being significantly higher than all other seasons (2.9–3.2; data not shown). On average, slightly more species were found in the lower (3.34) than upper (2.95) regions and the various significant interactions caused by values not being consistent between estuaries, regions and seasons.

Total density also differed significantly among all main effects and their interactions, with Estuary being the most influential term, followed by Season (Table 3.6). Densities of fish differed significantly between all pairwise comparisons except Beaufort *vs* Cordinup, Normans and Oyster, Cordinup *vs* Normans and Oyster, Normans *vs* Oyster and Torbay *vs* Taylor (P = 0.323 - 0.787). Values were highest in Cheyne (2,815 fish 100 m^{-2}), lowest in Waychinicup (30 fish 100 m^{-2}), with intermediate values (154 – 467 fish 100 m^{-2}) in the other size estuaries (Figure 3.6b). Among seasons, the highest mean density was recorded in summer, albeit with considerable variability (Figure 3.6c). The significant interactions were caused by total density not varying consistently between estuaries, regions and seasons. For example, the lowest mean densities for Torbay, Oyster, Waychinicup, Cordinup and Beaufort were recorded in winter, whereas in Taylor and Cheyne they occurred in spring (data not shown).

Significant differences in Simpson's diversity were detected between estuaries and seasons and their interactions, but not among regions and the Season × Region interaction (Table 3.6). Estuary accounted for 80% of total percentage mean squares, followed by the Estuary × Season (6%) and Season (4%). At a pairwise level, Simpson's diversity differed between every comparison, except for Cheyne *vs* Oyster, Torbay and Taylor, and amongst the last three estuaries (P = 0.141 - 0.780). Values were greatest in Waychinicup (0.59) followed by Torbay, Oyster, Taylor and Cheyne (0.44 - 0.48), Cordinup (0.21) and were extremely low in Normans (0.04) and Beaufort (<0.01; Figure 3.6). The Season × Region interaction was caused by Simpson's diversity being highest in Cordinup and Normans in spring but lowest in Torbay and Taylor in this season (data not shown).

Table 3.6. Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS), pseudo-F ratios (pF) and significance levels (*P*) from three-way PERMANOVA tests on univariate measures of diversity and the composition of the nearshore fish fauna in three regions of eight estuaries sampled seasonally in 2020. *df* = degrees of freedom. Significant results are highlighted in bold and those with a %MS ≥ 10 shaded in grey.

		Number of species				Total density			
Term	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	13.06	7.90	7.99	**0.001**	17.85	15.54	11.16	**0.001**
Estuary (E)	7	116.68	70.61	71.35	**0.001**	69.19	60.23	43.24	**0.001**
Region (R)	2	8.26	5.00	5.05	**0.006**	5.16	4.49	3.23	**0.044**
S × E	21	11.43	6.92	6.99	**0.001**	10.64	9.26	6.65	**0.001**
S × R	6	7.05	4.26	4.31	**0.002**	3.9	3.39	2.44	**0.025**
E × R	14	4.29	2.60	2.63	**0.003**	4.06	3.53	2.54	**0.002**
S × E × R	42	2.83	1.71	1.73	**0.004**	2.47	2.15	1.54	**0.016**
Residual	288	1.64	0.99			1.6	1.39		
		Simpson's diversity				**Faunal composition**			
Term	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	0.11	4.19	3.69	**0.016**	11,616	9.33	7.08	**0.001**
Estuary (E)	7	2.13	79.82	70.32	**0.001**	78,947	63.41	48.12	**0.001**
Region (R)	2	0.05	1.93	1.70	0.171	12,319	9.89	7.51	**0.001**
S × E	21	0.15	5.52	4.87	**0.001**	7,163	5.75	4.37	**0.001**
S × R	6	0.05	2.02	1.78	0.107	2,760	2.22	1.68	**0.001**
E × R	14	0.10	3.61	3.18	**0.001**	7,577	6.09	4.62	**0.001**
S × E × R	42	0.05	1.77	1.56	**0.029**	2,486	2.00	1.52	**0.001**
Residual	288	0.03	1.14			1,641	1.32		

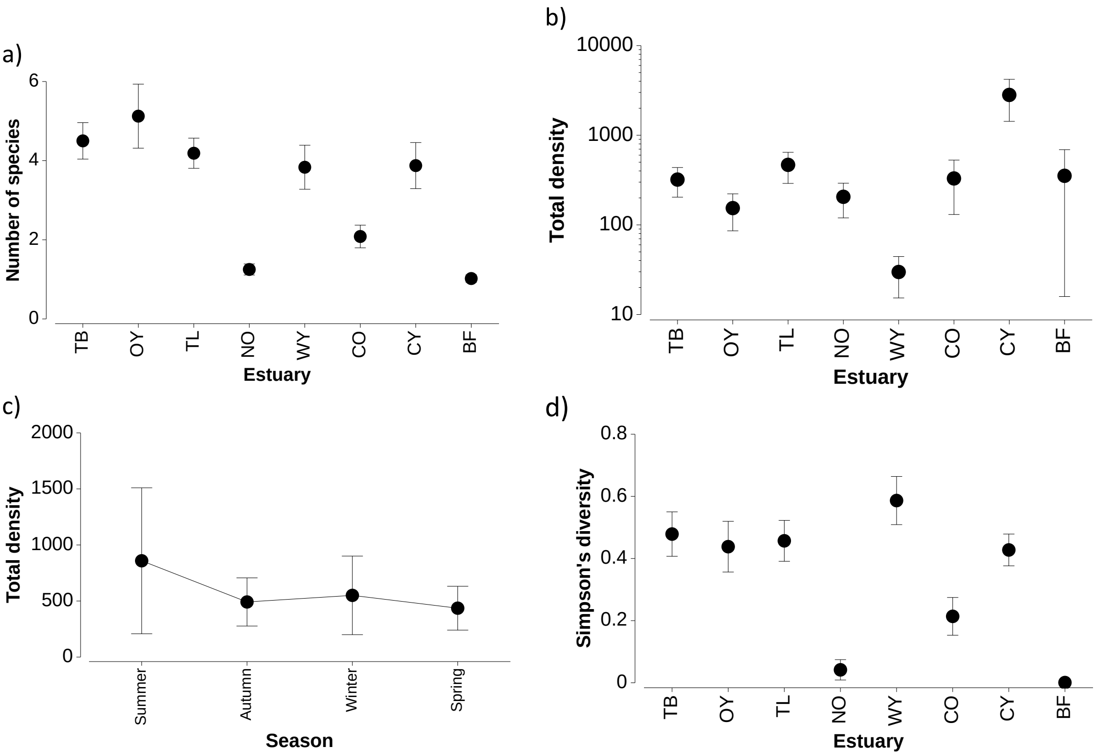

Figure 3.6. Mean and ± 95% confidence limits of (a) number of species (b) total density (fish 100 m^{-2}) and (c) total density density (fish 100 m^{-2}) and (d) Simpsons's diversity among estuaries in each of the four seasons. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

Faunal composition

Nearshore fish composition was found to differ significantly among estuaries, seasons and regions and all of their interaction terms (Table 3.6). Estuary contributed the greatest proportions to the percentage mean squares (63%,) followed by Season and Region (~9% each) and the interaction terms each <5%. On the basis of the far greater influence of the three main effects than interactions, pairwise PERMANOVA analyses were employed to investigate the differences nearshore fish composition among estuaries, regions and seasons. The basis for the two- and three-way interactions are examined in more detail for each estuary separately in Section 3.4.3 below.

Each estuary contained a significantly different fish fauna, with those of Beaufort and Normans being the most distinct (t = 6.57 - 13.53) and those of Taylor *vs* Torbay and Waychinicup *vs* Oyster the most similar (t = 2.15 and 3.84, respectively). This is clearly shown on the bootstrapped mMDS plot, where the bootstrapped averages for seven estuaries form almost entirely discrete groups, with only slight overlap between the points representing Torbay and Taylor (Figure 3.7a).

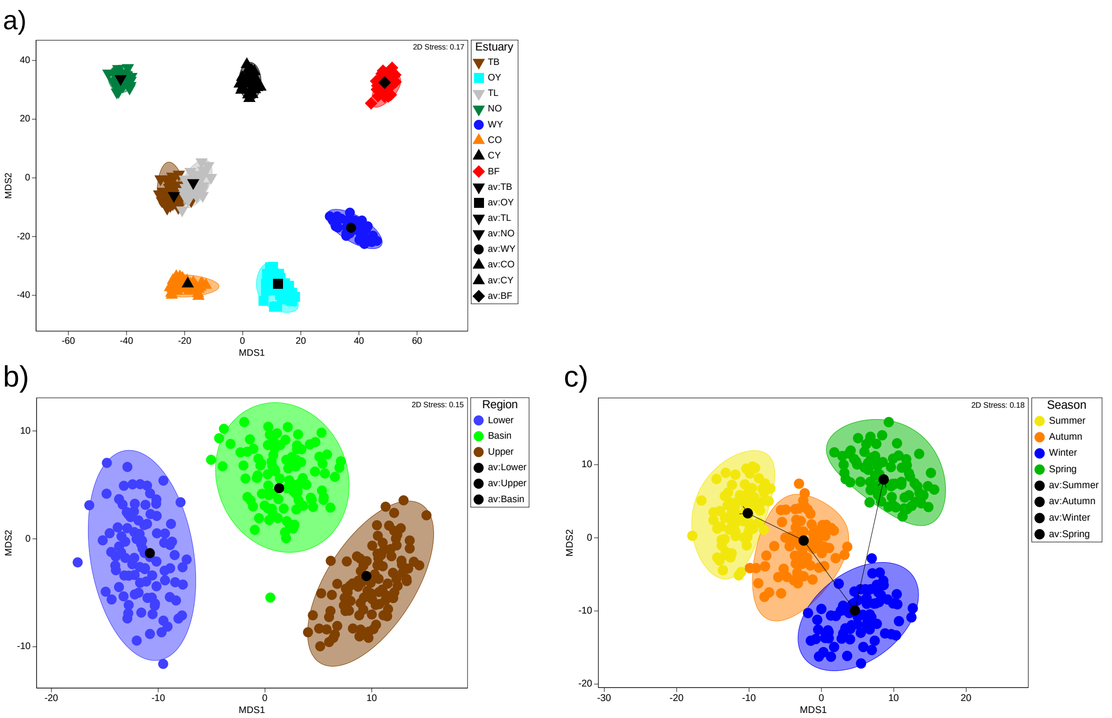

Figure 3.7. Bootstrapped mMDS ordination plots for (a) estuary, (b) region and (c) season, calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

The fish faunas of Beaufort and Normans were distinguished due to their depauperate nature, with generally only a single species, *i.e., A. elongata* and *L. wallacei*, respectively, being caught consistently and in relatively high abundances in either system (Figure 3.8). The next most distinct estuaries were the permanently-open Waychinicup and Oyster, which in addition to a suite of estuarine-resident atherinids and gobiids *e.g., P. olorum, L. wallacei, A. elongata* that were found in almost all systems, contained numerous marine stragglers. For example, the labrids *Halichoeres brownfieldi* and *Dotalabrus aurantiacus* and the enoplosid *Enoplosus armatus* were frequently recorded in Waychinicup, while the same was true for other labrids such as *Haletta semifasciata Neoodax balteatus* and the syngnathid *Stigmatopora argus* in Oyster (Figure 3.8).

Relatively high abundances of *P. olorum*, *L. wallacei* and *A. elongata* were regularly caught in Cheyne, together with the marine estuarine-opportunists *A. fosteri*, *M. cephalus* and *Sillaginodes punctatus* in all regions in spring. While Cordinup contained species commonly found across all systems, no atherinids were recorded, which distinguished this system from the others (Figure 3.8). The fish faunas of Taylor and Torbay differed significantly due to *Galaxias occidentalis, Afurcagobius suppositus*, *M. cephalus* and *Cristicepis australis* only being caught in these systems. However, their similarity was caused by their relatively similar abundances of *P. olorum*, *L. wallacei*, *Arenigobius brifenatus, Acanthopagrus butcheri* and *Favonigobius lateralis* (Figure 3.8).

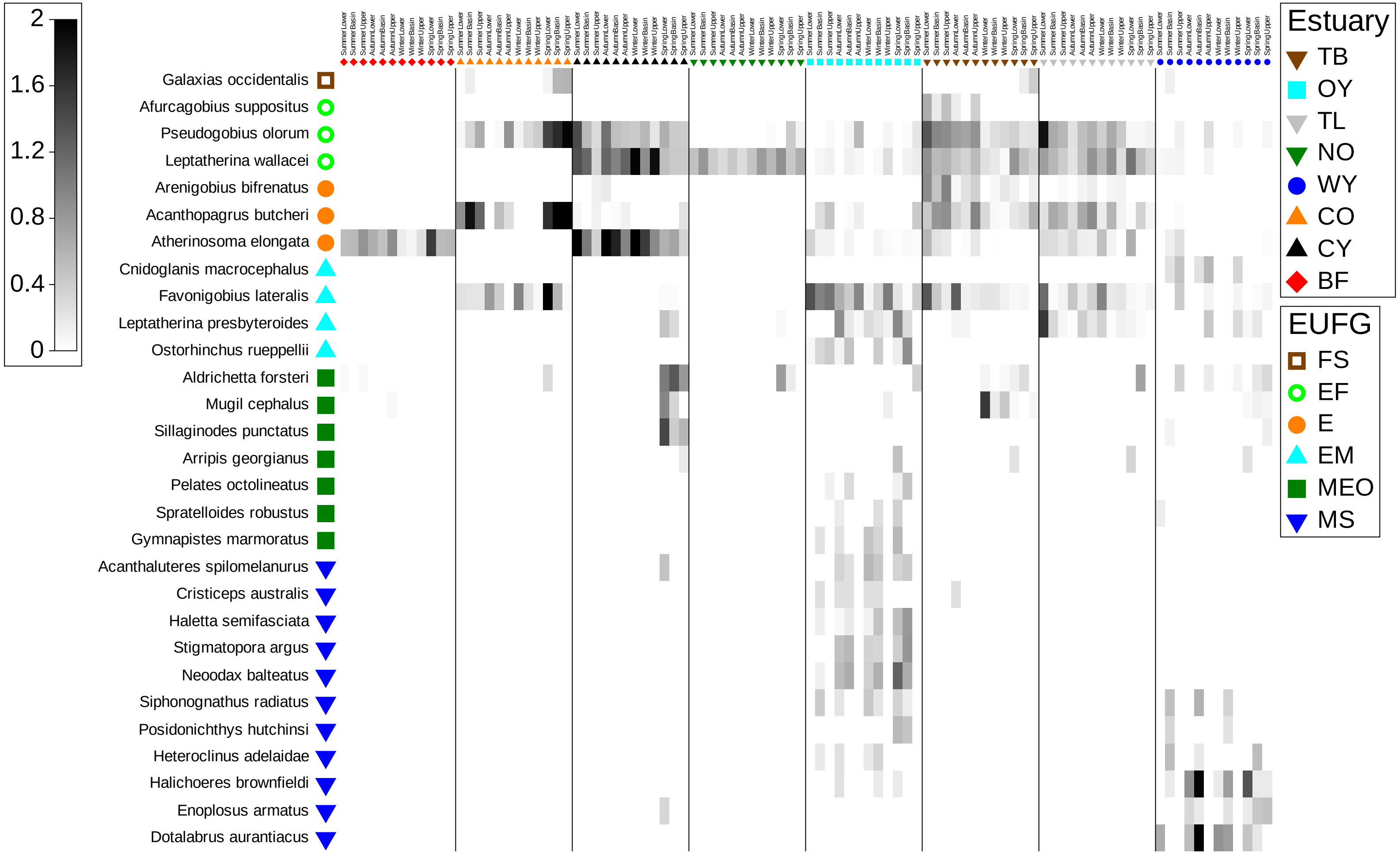

Figure 3.8. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of the fish species found in at least four samples from at least one estuary. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season within an estuary and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

Pairwise PERMANOVA detected significant differences between all regions (all P <0.001). This is illustrated on the mMDS plot (Figure 3.7b), where each region is distinct and there is a progression from the lower region on the left, through the basin to the upper reaches on the right. Typically more species with marine affinities were found in the lower region, *e.g.*, *F. lateralis* and *L. presbyteroides*, the solely estuarine *A. elongata* commonly recorded in the basin regions and those species with freshwater affinities *e.g.*, the estuarine & freshwater *P. olorum* and freshwater straggler *Galaxias occidentalis* in the upstream areas (Figure 3.8).

Overall, a significantly different faunal composition was present in each season (all P <0.001). When the data were visualised using mMDS, the seasons were largely discerte and progressed in an anti-clockwise manner, moving from summer on the left to autumn and winter on the right before moving above to spring in the top right (Figure 3.7c). The seasonal differences were explained by changes in densities of several commonly recorded species and the occurrence of species in spring. Species such as *L. wallacei*, *P. olorum*, *A. elongata* and *F. lateralis* were most abundant during summer and declined in autumn and winter (Figure 3.8). *Acanthopagrus butcheri* and *A. forsteri*, were present in all seasons, but obtained peak densities during spring together with the presence of less frequently caught species *e.g.*, *Arripis georgianus*, *S. punctatus*. Often the densities of the various species were not consistent across all eight estuaries contributing to the significant interactions in the three-way PERMANOVA of faunal composition (Table 3.6).

Relationship between fish composition and environmental variables

The BEST test investigated the relationship between nearshore fish composition and the various environmental variables, firstly individually and then in combination. In isolation, salinity exhibited the strongest correlation (ρ = 0.464), followed by number of days that the bar was open (ρ = 0.335) and dissolved oxygen (ρ= 0.226). The number of bar breaks (ρ= 0.025) and temperature (ρ= -0.077) were not informative. The combination of salinity and number of days the bar was open provided the best correlation (ρ = 0.603, P =0.001). The match between trends in the two data sets is visualised on the nMDS plots, with the points for each estuary determined on the basis of the fish fauna and the vectors reflecting the strength and direction or bubbles the magnitude of the values (Figure 3.9). Estuaries with higher salinities are located towards the top right *i.e.*, Beaufort and lowest to the left *i.e.*, Normans and Cordinup. Furthermore, permanently-open systems (*i.e.*, Oyster and Waychinicup) to the bottom and least days open at the top (*i.e.*, Beaufort).

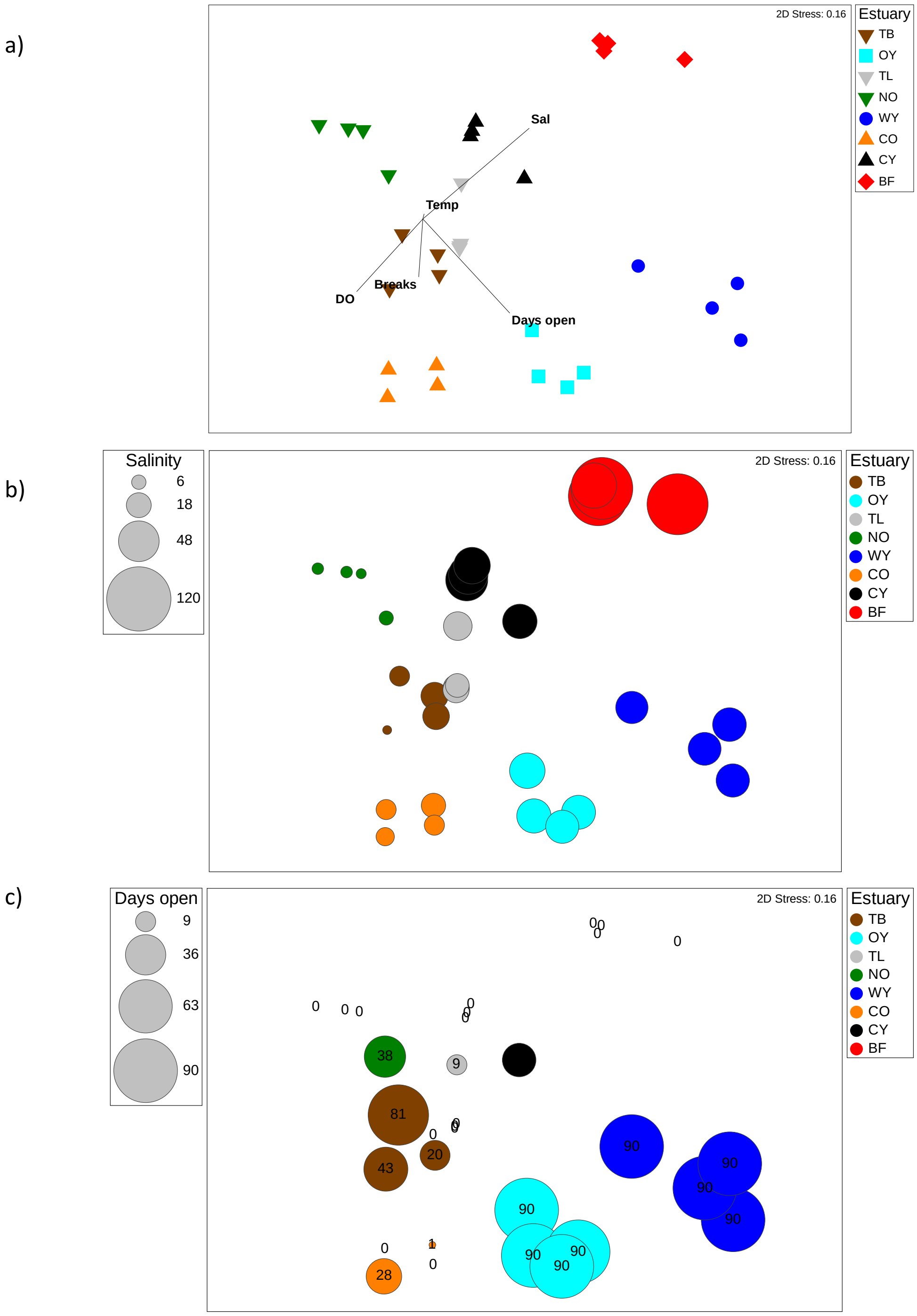

Figure 3.9. nMDS plots of the nearshore fish fauna overlaid with (a) vectors representing the relationship with and environmental variables, with bubbles of proportionate size to show differences in (b) salinity and (c) days open. Note, values added to (c) to highlight those season and estuary combinations where the bar remained closed (*i.e.*, 0 days open). TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

3.4.3. Intra-estuarine differences

Torbay Inlet

A total of 16 species were caught in Torbay, with eight being estuarine resident species which contributed >96% to the total catch (Table 3.5). Two marine stragglers and four marine estuarine-opportunists species were also recorded. The most abundant species were the atherinids *L. wallacei* (49.9%) and *A. elongata* (6.83%), the gobiids *P. olorum* (16.2%), *Arenigobius bifrenatus* (8.94%) and *F. lateralis* (6.34%) and the sparid *A. butcheri* (6.07%; Table 3.4). The most frequently caught species were *L. wallacei* and *P. olorum* that were found in 90 and 77% of all samples, respectively. *Acanthopagrus butcheri* (71%) and *F. lateralis* (58%) were the only other species recorded in more than half the samples.

Number of species, total density and diversity

Number of species differed significantly only among seasons in Torbay (Table 3.7), with pairwise differences detected with summer vs spring and winter and with autumn vs spring (P = 0.001 - 0.042). The mean number of species declined sequentially from 5.8 in summer, to 4.8 in autumn, 4.2 in winter and to a minimum of 3.3 in spring (Figure 3.10a).

Total density differed significantly among seasons and regions (both P <0.032), with season contributing more to the total mean squares (73%) than region (19%; Table 3.7). All seasons differed significantly (all P <0.046), except for autumn *vs* spring, with the greatest difference between summer and winter (t = 7.24, P = 0.001 compared to t <4.03, P = 0.028 – 0.046, for all other significant pairwise seasonal comparisons). Densities were greatest in summer (641 fish 100 m^{-2}), declined sequentially to a low in winter (79 fish 100 m^{-2}), before increasing to spring (280 fish 100 m^{-2}; Figure 3.10b). Mean densities were significantly higher in the lower region (544.5 fish 100 m^{-2}) than basin and upper regions (~210 fish 100 m^{-2}, all P <0.046; Figure 3.10c).

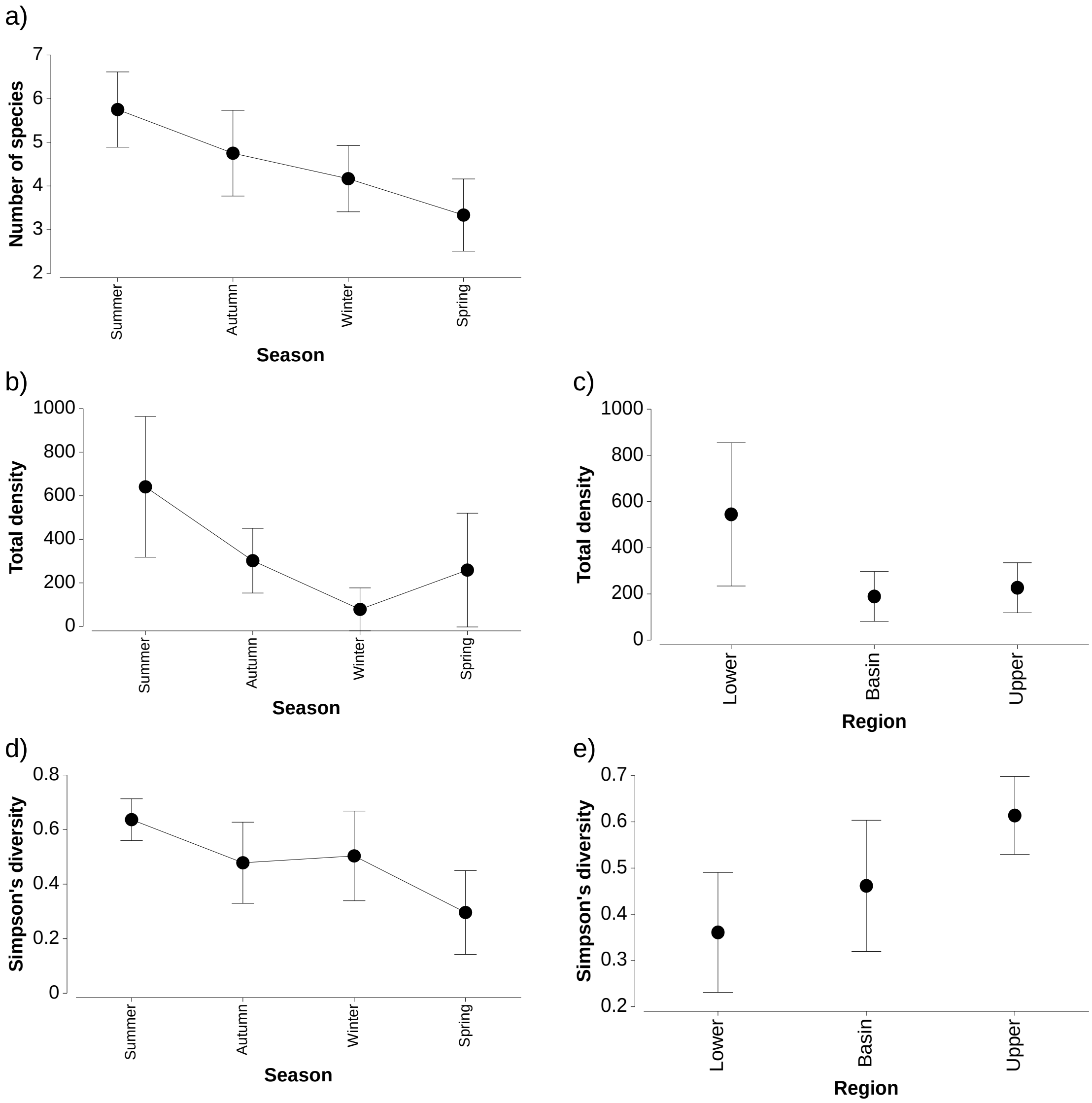

Figure 3.10. Mean and ± 95% confidence limits of (a) number of species (b) total density (fish 100 m^{-2}) and (d) Simpson's diversity among seasons and (c) total density and (e) Simpson's diversity among the regions of Torbay Inlet.

Table 3.7. Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS), pseudo-F ratios (pF) and significance levels (*P*) from two-way PERMANOVA tests on univariate measures of diversity and the composition of the nearshore fish fauna in each of the eight estuaries. *df* = degrees of freedom. Significant results with a %MS ≥ 10% shaded in grey.

		Number of species				Total density				Simpson's diversity				Faunal composition			
Torbay	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	12.39	73.66	6.07	0.007	15.35	73.04	16.11	0.001	0.24	41.06	6.13	0.004	9,525	48.82	5.49	0.001
Region (R)	2	1.75	10.40	0.86	0.441	3.92	18.67	4.12	0.032	0.26	45.25	6.75	0.003	6,069	31.11	3.50	0.001
S × R	6	0.64	3.80	0.31	0.920	0.79	3.76	0.83	0.550	0.04	6.99	1.04	0.426	2,183	11.19	1.26	0.122
Residual	36	2.04	12.14			0.95	4.53			0.04	6.7			1,734	8.89		
Oyster																	
Season (S)	3	17.14	30.64	2.76	0.062	0.91	22.73	0.66	0.596	0.22	35.95	4.53	0.009	6,895	26.81	2.69	0.001
Region (R)	2	26.31	47.03	4.24	0.027	0.14	3.44	0.10	0.896	0.21	33.19	4.18	0.024	13,031	50.67	5.09	0.001
S × R	6	6.28	11.23	1.01	0.444	1.58	39.41	1.15	0.338	0.14	22.92	2.89	0.023	3,228	12.55	1.26	0.098
Residual	36	6.21	11.10			1.38	34.42			0.05	7.93			2,562	9.96		
Taylor																	
Season (S)	3	9.97	77.48	8.59	0.001	1.19	7.74	0.58	0.626	0.25	72.67	6.04	0.002	4,960	30.19	3.29	0.001
Region (R)	2	0.19	1.46	0.16	0.845	8.11	52.69	3.98	0.026	0.04	10.79	0.90	0.420	7,661	46.64	5.08	0.001
S × R	6	1.55	12.04	1.34	0.275	4.05	26.32	1.99	0.097	0.02	4.51	0.37	0.887	2,296	13.98	1.52	0.041
Residual	36	1.16	9.02			2.04	13.25			0.04	12.03			1,508	9.18		
Normans																	
Season (S)	3	2.39	87.76	34.4	0.001	4.39	41.12	2.39	0.091	0.08	65.39	14.78	0.001	4,115	49.85	4.54	0.001
Region (R)	2	0.06	2.30	0.90	0.411	1.97	18.42	1.07	0.377	0.01	10.98	2.48	0.132	1,478	17.9	1.63	0.157
S × R	6	0.20	7.40	2.90	0.007	2.48	23.27	1.35	0.241	0.02	19.2	4.34	0.005	1,756	21.27	1.94	0.024
Residual	36	0.07	2.55			1.83	17.18			0.01	4.42			906	10.97		

Table 3.7. Continued.

		Number of species				Total density				Simpson's diversity				Faunal composition			
Waychinicup	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	5.17	20.47	2.66	0.074	1.50	18.40	1.17	0.305	0.01	2.65	0.14	0.899	6,250	20.44	1.86	0.002
Region (R)	2	5.40	21.38	2.78	0.075	3.37	41.31	2.62	0.113	0.15	47.75	2.55	0.101	16,504	53.98	4.91	0.001
S x R	6	12.73	50.44	6.55	0.001	2.00	24.51	1.55	0.172	0.09	30.89	1.65	0.169	4,459	14.58	1.33	0.025
Residual	36	1.94	7.70			1.29	15.78			0.06	18.71			3,364	11.00		
Cordinup																	
Season (S)	3	8.61	85.99	18.79	0.001	30.32	88.73	23.57	0.001	0.16	59.08	5.14	0.007	14,076	44.72	12.85	0.001
Region (R)	2	0.58	5.83	1.27	0.300	0.23	0.66	0.18	0.856	0.05	18.36	1.60	0.226	13,020	41.36	11.89	0.001
S x R	6	0.36	3.61	0.79	0.575	2.34	6.84	1.82	0.117	0.03	11.06	0.96	0.484	3,286	10.44	3.00	0.001
Residual	36	0.46	4.58			1.29	3.77			0.03	11.50			1,095	3.48		
Cheyne																	
Season (S)	3	37.25	78.67	33.95	0.001	8.54	32.48	8.35	0.001	0.18	72.51	9.91	0.001	8,377	49.70	8.84	0.001
Region (R)	2	4.00	8.45	3.65	0.037	13.44	51.11	13.14	0.001	0.01	4.83	0.66	0.530	5,960	35.36	6.29	0.001
S x R	6	5.00	10.56	4.56	0.003	3.30	12.53	3.22	0.006	0.04	15.35	2.10	0.077	1,570	9.32	1.66	0.014
Residual	36	1.10	2.32			1.02	3.89			0.02	7.32			948	5.62		
Beaufort																	
Season (S)	3	0.19	45.00	1.80	0.161	30.13	74.99	10.05	0.001	<0.001	12.68	0.42	0.692	7,558	65.25	7.48	0.001
Region (R)	2	0.02	5.00	0.20	0.815	2.40	5.99	0.80	0.45	<0.001	48.03	1.58	0.229	1,632	14.09	1.62	0.118
S x R	6	0.10	25.00	1.00	0.441	4.64	11.56	1.55	0.176	<0.001	8.95	0.30	0.886	1,383	11.94	1.37	0.103
Residual	36	0.10	25.00			3.00	7.46			<0.001	30.33			1,010	8.72		

Values for Simpson's index differed among seasons and regions (Table 3.7), with both main effects making a similar contribution to the total mean squares (41% and 45%, respectively). Pairwise comparisons showed that Simpson's diversity differed significantly between summer *vs* autumn and spring and between spring *vs* winter (P = 0.001 - 0.046). Summer had the highest mean diversity (0.64), followed by autumn and winter (~0.49) and lastly spring (0.30; Figure 3.10d). Values were significantly greater in the upper region (0.61) than the lower (0.36) and basin (0.46) regions (P <0.044; Figure 3.10e).

Faunal composition

Fish faunal composition in Torbay differed significantly between season and region but not with the Season × Region interaction (Table 3.7). Season made a greater contribution to the total mean squares (49%) than Region (31%). At a pairwise level, all seasons were distinct (all P <0.008) except for summer *vs* autumn. This is shown on the bootstrapped mMDS plot where there is a clear cyclical pattern among seasons in a clockwise direction but with slight overlap between the 95% confidence regions for summer and autumn samples (Figure 3.11a). Seasonal changes were driven by differences in the abundance of a core suite of estuarine-residents, *i.e.,* *A. butcheri*, *A. elongata*, *L. wallacei*, *P. olorum*, *A. bifrenatus*, *A. suppositus* and *F. lateralis* and the recruitment of several marine species (Figure 3.12). Densities of the estuarine-residents were at their peak in summer and declined to their lowest levels in winter before increasing in spring. The marine stragglers *C. australis* and *Microanthus strigatus* and the marine estuarine-opportunist *Ammotretis rostratus* were recorded in autumn and a large number of *M. cephalus* were caught in winter (Figure 3.12).

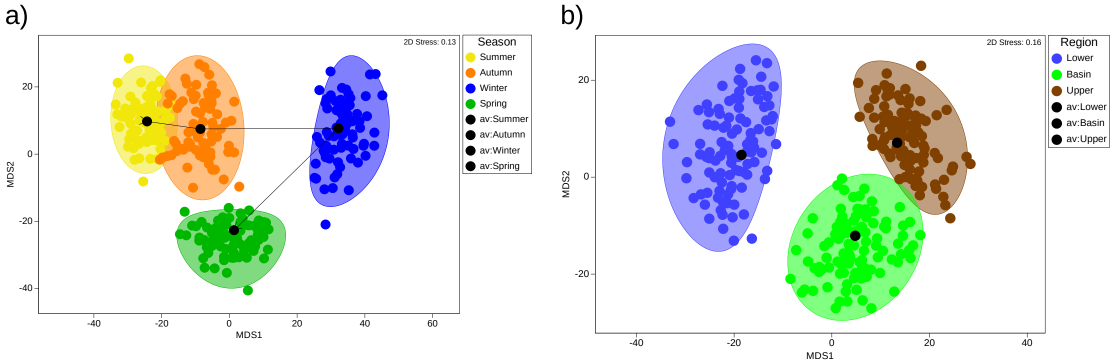

Figure 3.11. Bootstrapped mMDS ordination plots for (a) season and (b) region calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Torbay Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

The faunal composition of each region was also significantly different (all P <0.012), with the lower *vs* upper being the most distinct (t = 2.16 *vs* <1.81 for all other comparisons). Ordination showed a left to right trend along the linear axis of the estuary from the lower region on the left through to the upper region on the right (Figure 3.11b). There is a slight overlap of the 95% confidence regions of the basin and upper areas, indicating the smaller difference in composition between these regions. Marine estuarine-opportunist species *e.g.*, *A. rostratus* and *A. georgianus* and the marine stragglers *C. australis* and *M. strigatus* were only present in the lower region (Figure 3.12). The lower region also contained higher densities of the estuarine-resident species of atherinid and goby, whose densities were lowest in the basin. The absence of *L. presbyteroides* and presence of the freshwater species *G. occidentalis* and *G. holbrooki* distinguished the upper region (Figure 3.12).

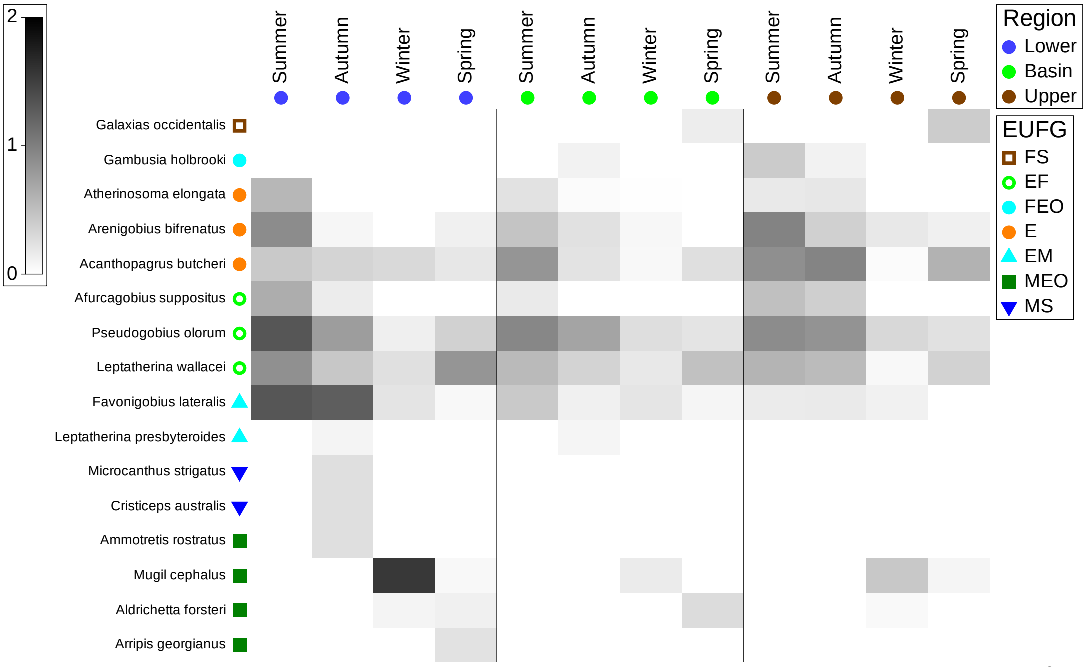

Figure 3.12. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Torbay Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Oyster Harbour

The main guilds of fish found in Oyster were the marine stragglers and marine estuarine-opportunists (17 and 10 species, respectively). However, while fish in these guilds together contributed 75% to the number of species, they only represented 9.9% of all fish in the estuary (Table 3.5). Thus, it was the seven estuarine-resident species (25% of species) that provided 90.2% of all individuals caught. *Leptatherina presbyteroides* and *F. lateralis* were the most abundant, each comprising ~32% of all fish, followed by *A. elongata* (6.9%; Table 3.4). While *F. lateralis* was the most frequently caught fish occurring in 77.1% of samples, the marine stragglers *Neodax balteatus* (41.7%) and *Haletta semifasciata* (35.4%) were also common.

Number of species, total density and diversity

Number of species in Oyster differed significantly only among regions (Table 3.7). Pairwise testing demonstrated values were higher in the basin (6.44) than the upper region (3.38; P = 0.001), with the lower region (5.06) not being significantly different to either adjacent region (P = >0.05, Figure 3.13a). No significant difference was detected between total density and any main effect or interaction term (Table 3.7).

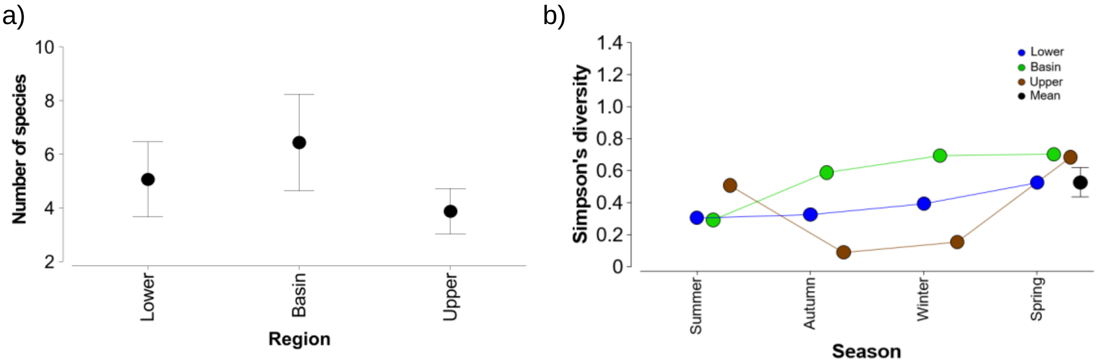

Figure 3.13. Mean and ± 95% confidence limits of (a) number of species among regions and (b) Simpson's diversity among seasons and regions in Oyster Harbour. For clarity black circle represents overall mean and associated ± 95% confidence limits.

PERMANOVA detected differences in Simpson's diversity among seasons and regions and their interaction, with both main effects making a similar contribution to total mean squares (Table 3.7). Seasonal differences were due to spring having a higher diversity (0.64) than all other seasons (0.33 - 0.41; all P <0.012). The only pairwise regional difference was basin *vs* upper (P = 0.010), with values greater in the former than latter region (0.57 and 0.36, respectively). The extent of seasonal change in diversity was greater in the upper region than others explaining the significant Season × Region interaction (Figure 3.13b).

Faunal composition

Significant differences in faunal composition were found with Season and Region, with Region making a substantially greater contribution to the total mean squares (51%) than Season (27%; Table 3.7). Among regions, the upper was distinct from the others (all P = 0.001). This is highlighted on the bootstrapped mMDS ordination plot where the upper region is well separated (Figure 3.14a). Among seasons, most all were distinct (except autumn vs spring; P = 0.047) and their positions on the mMDS plot show some cyclicity (Figure 3.14b).

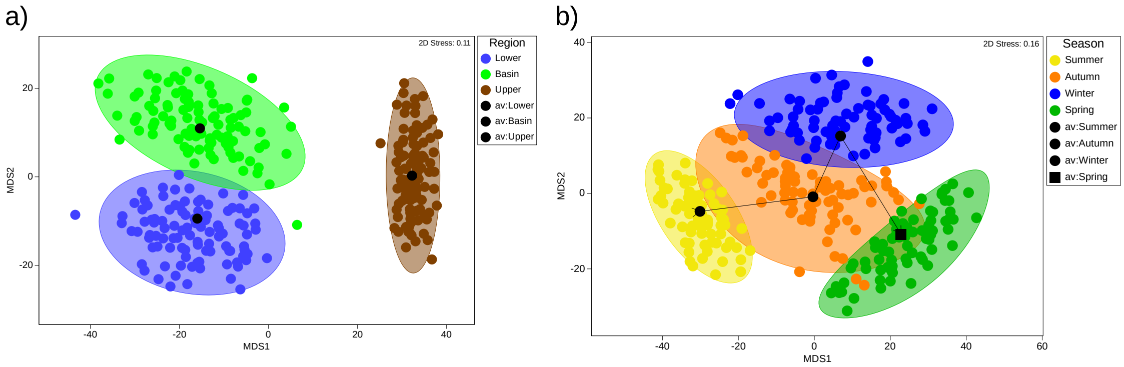

Figure 3.14. Bootstrapped mMDS ordination plots for (a) region and (b) season calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Oyster Harbour. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

The upper region was distinct from the others due it being relatively depauperate and only yielding consistent catches of *F. lateralis* (Figure 3.15). Several estuarine-resident species, *e.g.*, *A. butcheri*, *A. elongata*, *P. olorum* and *L. wallacei* were only found in this region and typically recorded in a single season. In contrast, the lower and basin regions were more speciose and contained a wide suite of marine straggler and marine estuarine-opportunist species, *e.g.*, *S. argus*, *Acanthaluteres spilomelanurus* and *Gymnapistes marmoratus*. Relatively few species were recorded in summer, with *F. lateralis* being the most abundant. Low densities of a range of marine straggler and marine estuarine-opportunist species were present in autumn and winter, with the densities of some increasing in spring, *e.g.*, *N. balteatus*, *G. marmoratus* and *H. semifasciata* (Figure 3.15).

The majority of species recorded were marine straggler species and marine estuarine-opportunists, which except for *A. fosteri*, *M.cephalus* and *Arripis truttaceus*, were only present in the basin and lower regions of the estuary. The interaction is also influenced by species *A. butcheri*, *F. lateralis* and *A. elongata* having higher abundance in summer and decreasing throughout the year (Figure 3.15). Conversely, marine stragglers *i.e.*, *Stigmatopora argus*, *Neodax balteatus* and *Haletta semifasciata* became more abundant throughout the year, with spring having the highest abundance.

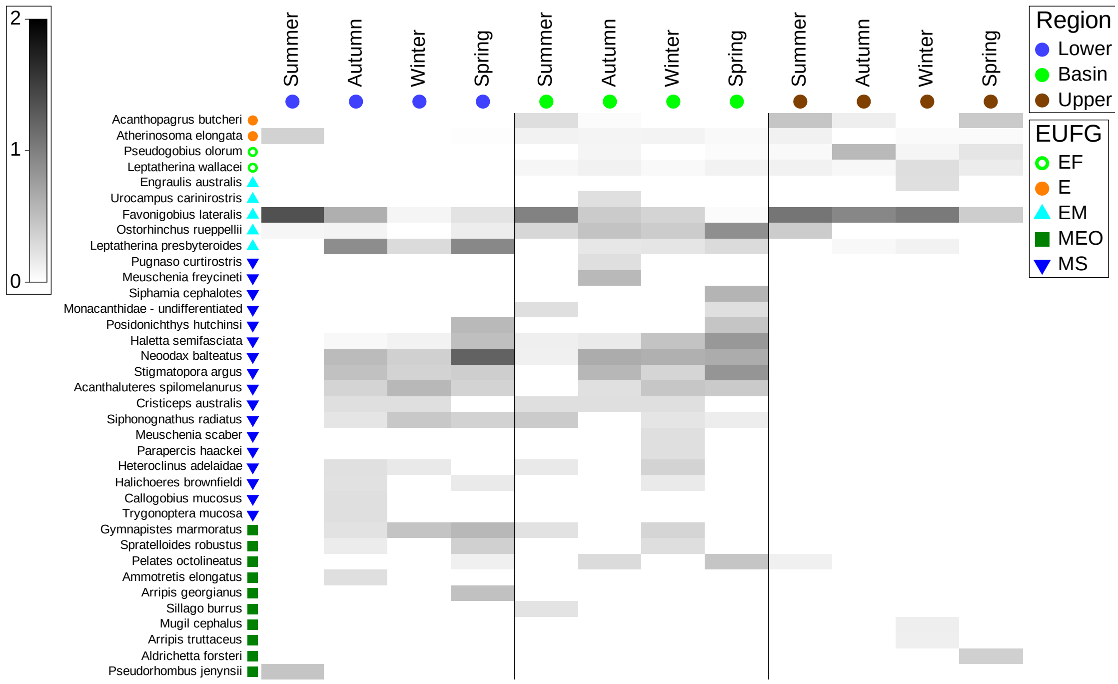

Figure 3.15. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Oyster Harbour. Shading intensity is proportional to density. Samples (x axis) ordered by region and season and species (y axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Taylor Inlet

Most (70%) of the species caught in Taylor were estuarine residents, with these fish contributing 99% to the total catch (Table 3.5). The atherinids *L. wallacei* (59.9%), *A. elongata* (14.1%) and *L. presbyteroides* (9.38%) made the greatest contributions to the fish fauna (Table 3.4). Moreover, these species were common, with *L. wallacei* occurring in 94%, *A. butcheri* in 75%, and *P. olorum*, *F. lateralis* and *A. elongata* in more >50% of samples (Table 3.4).

Number of species, total density and diversity

A significant difference in the number of species was detected only for Season (Table 3.7), with each pairwise comparison being distinct for autumn *vs* both summer and winter (P = 0.001 – 0.046). Values in spring (2.92) were significantly lower than in summer (5.08) and winter and autumn (~4.36).

Total density varied significantly only with Region (Table 3.7), with far greater densities in lower (680 fish 100 m^{-2}) than upper region (256 fish 100m^{-2}), with intermediate and non-significantly different values in the basin (466 fish 100m^{-2}; Figure 3.16b).

PERMANOVA detected a significant difference in Simpson's diversity with Season only (Table 3.7). Values of diversity in spring (0.26) were found to be significantly lower than in summer (0.61), autumn and winter (both ~0.48; *P* = 0.001 – 0.034; Figure 3.15c).

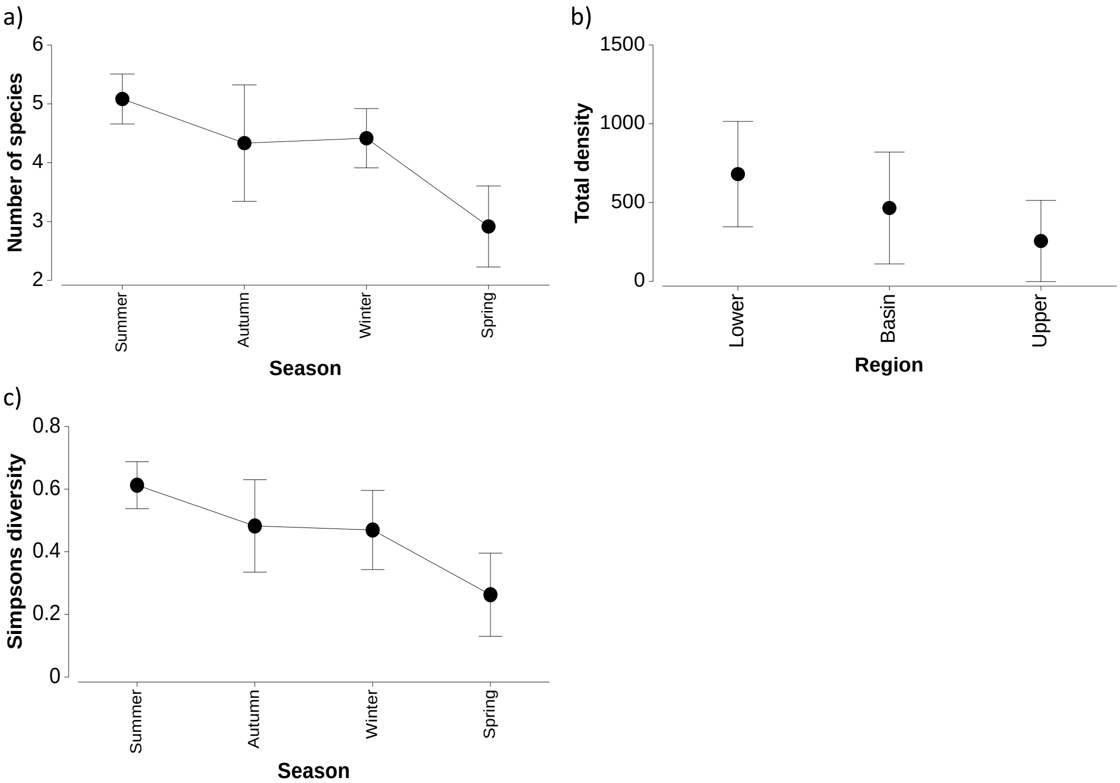

Figure 3.16. Mean and ± 95% confidence limits of (a) number of species and (b) total density (fish 100 m^{-2}) among regions in Taylor Inlet and (c) Simpson's diversity among seasons.

Faunal composition

Fish communities in Taylor differed significantly among seasons, regions and their interaction was also significant (Table 3.7). Region made the greatest contribution to the total mean squares (47%), followed by Season (30%) and lastly the Season × Region interaction (14%). Pairwise PERMANOVA demonstrated that all regions harboured a significantly different fauna (*P* =0.001 – 0.043), with each being largly distinct on the mMDS ordination (Figure 3.17a). Regional differences were driven by the presences of some species only in specific regions and their abundances. For example, *e.g.,* *A. georgianus* was only caught in the lower region and *A. fosteri* and *Atherinomorous vaigensis* only in the basin (Figure 3.18). The abundance of *A. bifrenatus* increased in upstream direction, being absent in the lower, in low densities in the basin and in high densities in the upper region. Conversely, the greatest densities of *A. elongata*, *L. presbyteroides* and *F. lateralis* were found in the lower region (Figure 3.18).

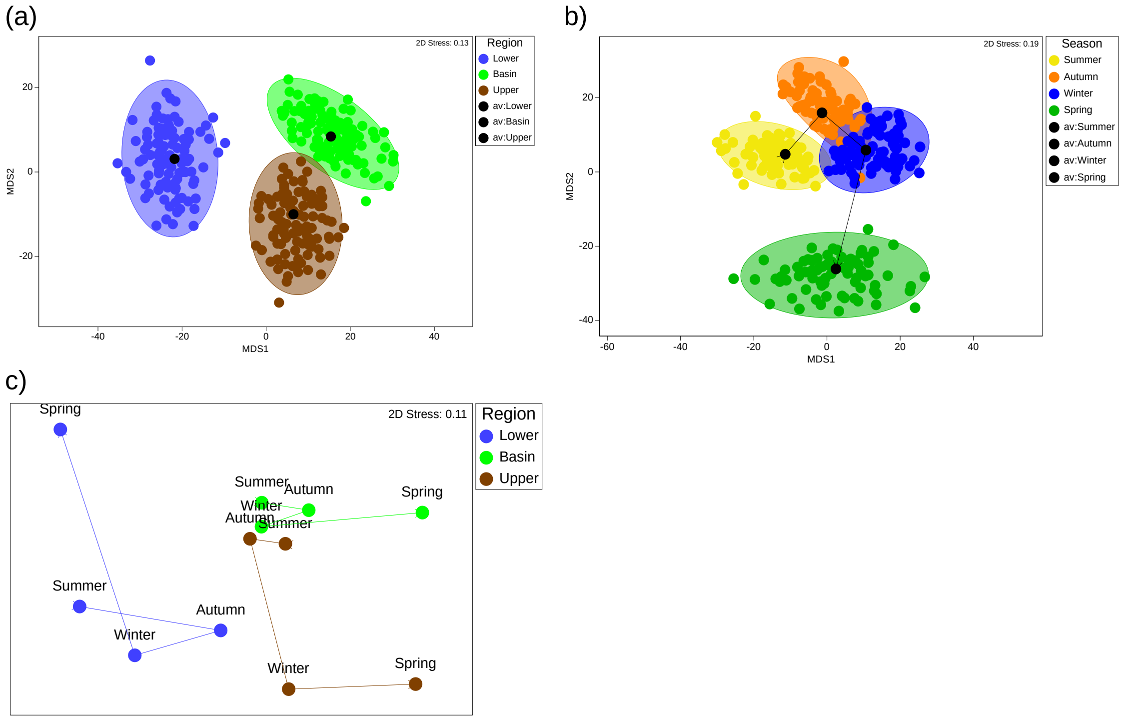

Figure 3.17. Bootstrapped mMDS ordination plots for (a) region and (b) season and (c) centroid nMDS plot, all of which were calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Taylor Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown on (a) and (b).

Among seasons, spring was significantly different to all other seasons (all $P = 0.001$) and the interaction was caused by differences in the seasonal patterns in each region (Figure 3.17b,c). A common suite of species were present in summer, autumn and winter, *e.g.*, *A. butcheri*, *A. elongata*, *L. wallacei*, *F. lateralis*, *P. olorum* but only the first three species were also recorded in spring (Figure 3.18). The densities of these species exhibited bigger seasonal shifts in the lower region than other regions. Finally, the three marine estuarine-opportunist species were present in only a single region in only a single season and so also contributed to the interaction.

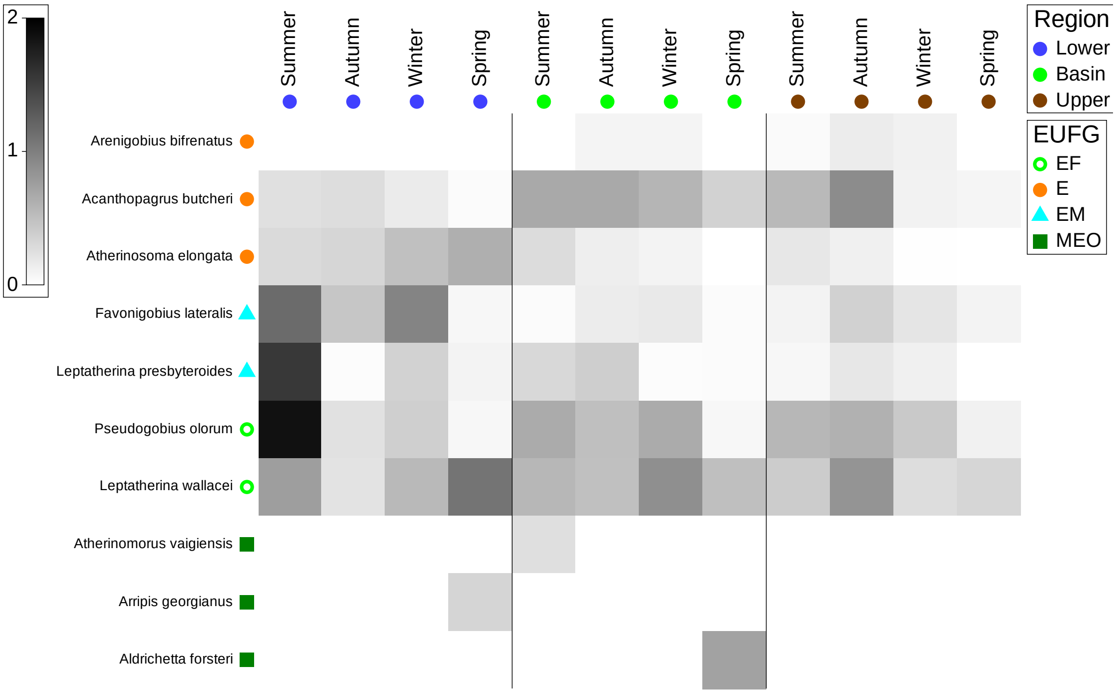

Figure 3.18. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Taylor Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Normans Inlet

Only four species were recorded in Normans, of which three were estuarine residents. The fauna was dominated by *L. wallacei* which represented 98% of all fish and was found in every sample (Table 3.4).

Number of species, total density and diversity

Seasonal effects were the only influence on the number of species in Normans (Table 3.7). Pairwise PERMANOVA showed that, on average, more species were recorded in spring than the other seasons (1.92 vs ~1; all P = 0.001; Figure 3.19a). Total density did not differ significantly with any main effects or their interaction. PERMANOVA detected a significant difference between Simpson's diversity and Season and a significant Season × Region interaction, with the main effect contributing three time more to the total mean squares (Table 3.7). Diversity values were significantly higher in spring (0.17) than in all other seasons (0.00; all P <0.004). The cause of the interaction stems from diversity increasing in the lower and basin regions in spring but not in the upper region (P = 0.024 – 0.038; Figure 3.19b).

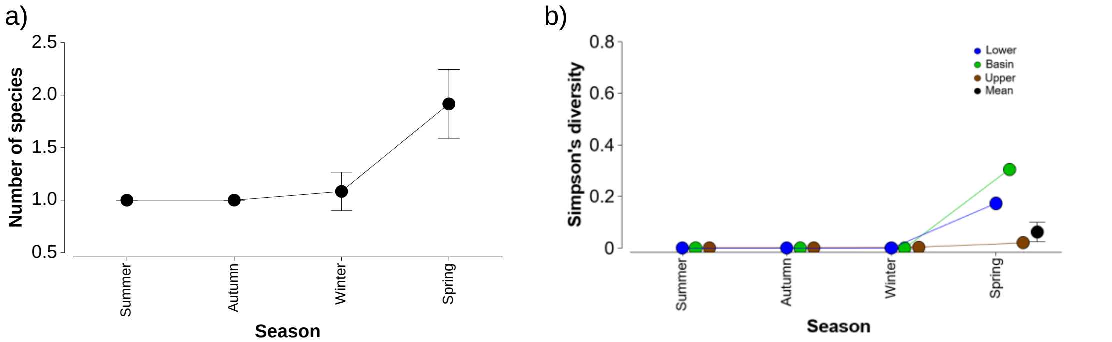

Figure 3.19. Mean and ± 95% confidence limits for (a) number of species and (b) Simpsons Diversity among seasons and regions in Normans Inlet, for clarity black circle represents overall mean and associated ± 95% confidence limits.

Faunal composition

The composition of the fish fauna differed significantly among seasons and the Season × Region interaction was significant, with the Season main effect making the greatest contribution to the total mean squares (Table 3.7). Pairwise testing showed that all seasons were distinct (all *P* <0.042), with the exception of summer *vs* autumn and winter. The biggest difference was between autumn and spring (*t* = 3.28 *vs* 2.09 – 2.28 in the other comparisons). This is shown on the bootstrapped mMDS plot where the points and confidence regions for summer, autumn and winter overlap and that for spring is clearly distinct (Figure 3.20a). The seasonal difference is due to *L. wallacei* being the only species caught in summer, autumn and winter but *P. olorum*, *A. fosteri* and *L. presbyteroides* also being present in spring, albeit in different regions thus accounting for the interaction (Figures 3.20, 3.21).

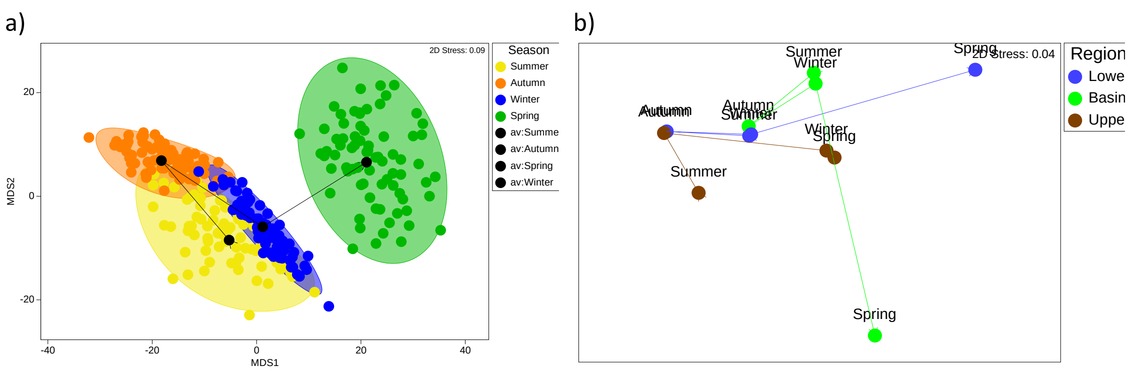

Figure 3.20. Bootstrapped mMDS ordination plots for (a) season and (b) centroid nMDS plot, all of which were calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Normans Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown on (a).

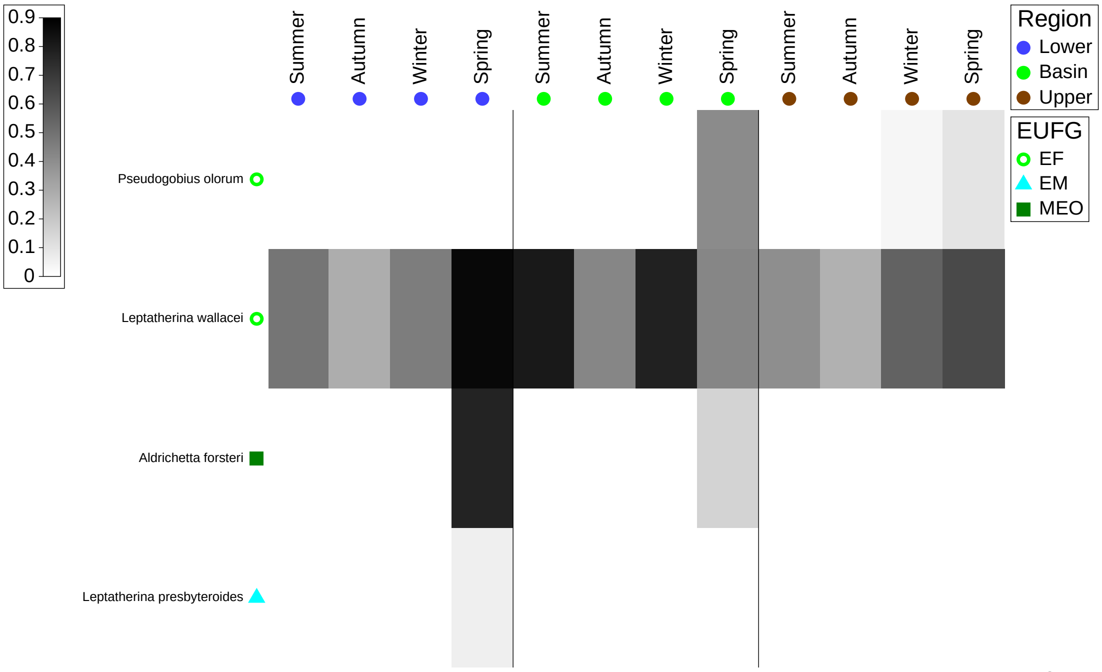

Figure 3.21. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Normans Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Waychinicup Estuary

Most of the species recorded in Waychinicup were marine stragglers (71%), followed by marine estuarine-opportunists (14%; Table 3.5). Fish from these guilds, represented 32% of all fish which is less than the contribution of 68% made by eight estuarine-resident species. Overall, the most abundant species were *L. presbyteroides* (23%), *A. elongata* (20%) and *L. wallacei* (12%), with notable contributions made by *P. olorum* (6%), *H. brownfieldi* (6%) and *F. lateralis* (5%; Table 3.4). *Dotalabrus aurantiacus* was the most common species recorded in 43% of samples, followed by another labrid, *H. brownfieldi* (35%).

Number of species, total density and diversity

Number of species did not differ significantly among seasons or regions, but the Season × Region interaction was significant (Table 3.7). The interaction was due to relatively consistent mean numbers of species being recorded in the basin and upper region (*i.e.*, 2-5), but with more variation in the lower region, *i.e.*, 2 in summer, ~4 in autumn and winter and ~7 in spring (Figure 3.22). Neither total density or Simpson's diversity differed significantly between the main effects and their interaction (Table 3.7).

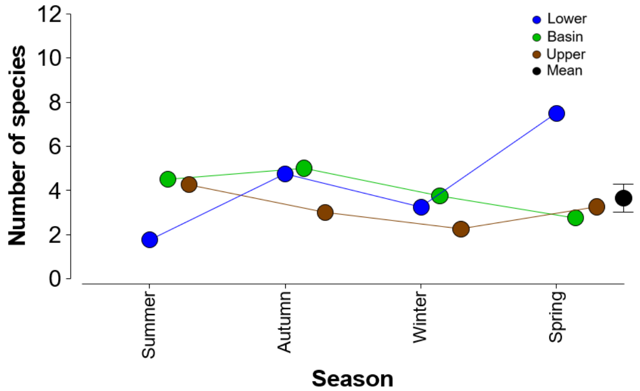

Figure 3.22. Mean number of species among regions and seasons in Waychinicup Estuary. For clarity black circle represents overall mean and associated ± 95% confidence limits.

Faunal composition

The fish community differed between regions and seasons and their interaction was significant (Table 3.7). Region made the greatest contribution to the total mean squares (54%), followed by Season (20%) and the Season × Region interaction (15%). All regions were significantly different (all P <0.003), with each forming a distinct group on the mMDS plot (Figure 3.23a). The lower region was mainly dominated by a broad suite of marine straggler species that were typically only recorded in one season (Figure 3.24). The most abundant and most consistently recorded were *D. aurantiacus*, *A. gouldii*, *H. brownfieldi*, *Enoplosus armatus* and *Tilodon sexfasciatus*. A smaller suite of different marine stragglers was found in the basin region, *e.g.*, *Siphonognathus radiatus*, *Heteroclinus adalaidae* and *Posidonichtys hutchinsi*. The upper region contained mainly estuarine-associated species *i.e.*, the estuarine residents *L. wallacei*, *A. elongata*, *P. olorum*, *F. lateralis*, *L. presbyteroides* and *Cnidoglanis macrocephalus*; and the marine estuarine-opportunists *A fosteri* and *M. cephalus* (Figure 3.24).

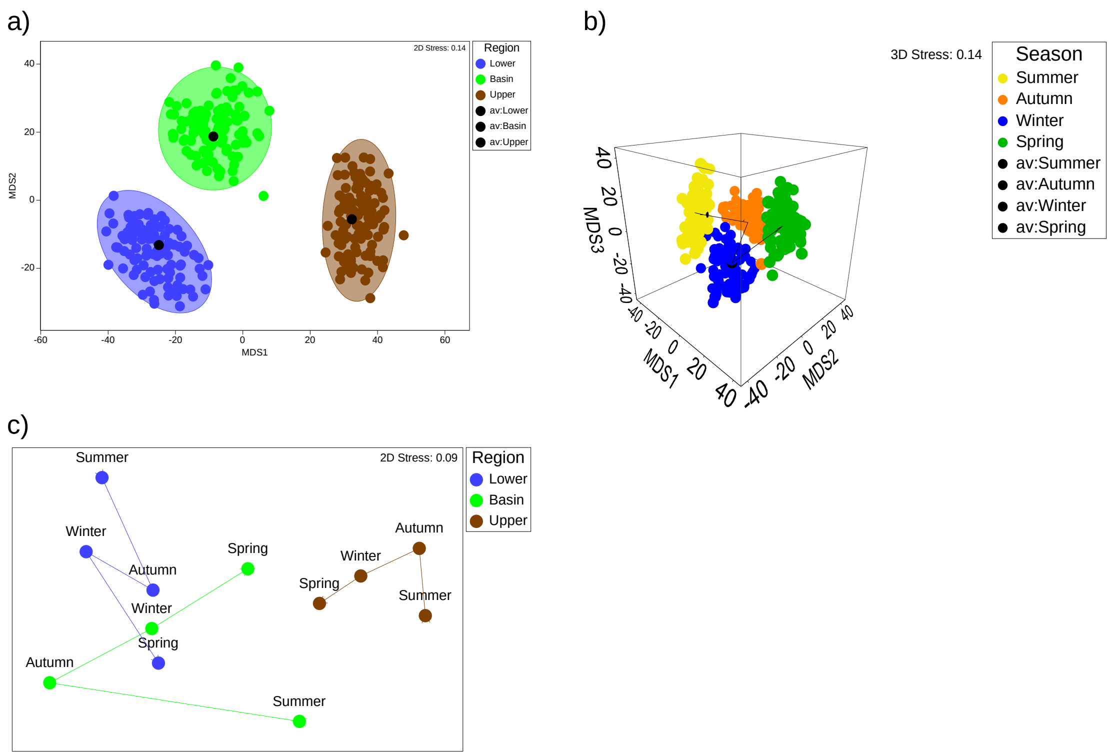

Figure 3.23. Bootstrapped mMDS ordination plots for (a) season and (b) region and (c) centroid nMDS plot, all of which were calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Waychinicup Estuary. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown on (a) and (b).

Pairwise PERMANOVA detected significant seasonal differences between summer *vs* autumn and spring and winter *vs* spring (all *P* <0.048; Figure 3.23b). Looking at the Season × Region interaction, summer *vs* autumn were different in all regions, but the trends were not always consistent, with, in the lower region, differences between summer *vs* spring (*P* = 0.027) and in the basin between autumn *vs* summer and spring (all *P* <0.035). Among regions, the lower *vs* the upper were only different in winter (*P* = 0.030). The complex interaction is illustrated on the centroid nMDS plot, which shows that seasonal patterns were different in each of the three regions, the extent to which were least in the upper region (Figure 3.23c). The relative consistency in the upper estuary was due to the aforementioned suite of six estuarine resident and two marine estuarine-opportunist species being present in most seasons and only shifting in their abundance (Figure 3.24). In the lower and basin regions, however, catches were far more variable with most species being present in one or two seasons.

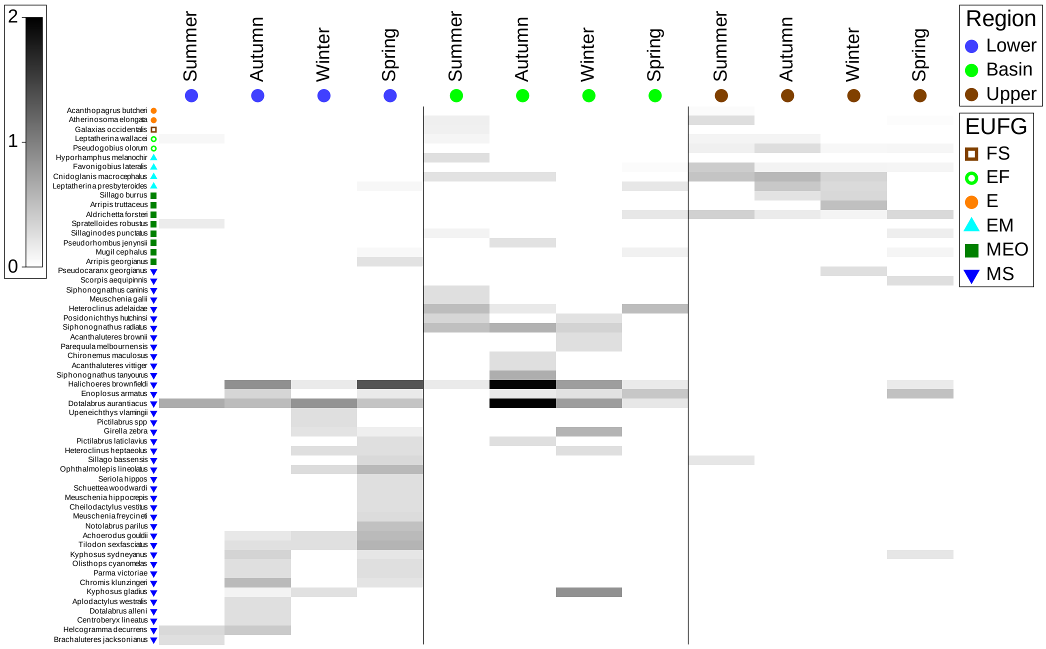

Figure 3.24. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Waychinicup Estuary. Shading intensity is proportional to density. Samples (x axis) ordered by region and season and species (y axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Cordinup River

Five species were caught in the nearshore waters of Cordinup, of which three were estuarine residents, with one marine estuarine-opportunist and one freshwater straggler (Table 3.5). The solely estuarine *A. butcheri* contributed 53% to the number of fish and was present in 60% of the samples (Table 3.4). Notable contributions were also made by *F. lateralis* (26% fish and 63% samples) and *P. olorum* (20% fish and 71% samples; Table 3.4).

Number of species, total density and diversity

Number of species differed significantly only among seasons (Table 3.7), with all pairwise comparisons different (all P <0.041), except for autumn *vs* winter. Mean values were greater in spring (3.25) than summer (2.17) and particularly in autumn and winter (~1.5; Figure 3.25a).

Likewise, total density only differed with Season (Table 3.7), and followed the same seasonal pattern, being greater in spring (1,085 fish 100 m^{-2}) than the other seasons (35 - 162 fish 100 m^{-2}; Figure 3.25b). PERMANOVA detected a significant seasonal trend in

Simpson's diversity (Table 3.7), due to spring having a higher diversity (0.38) than either autumn or winter (both ~0.13; all P <0.009; Figure 3.25c).

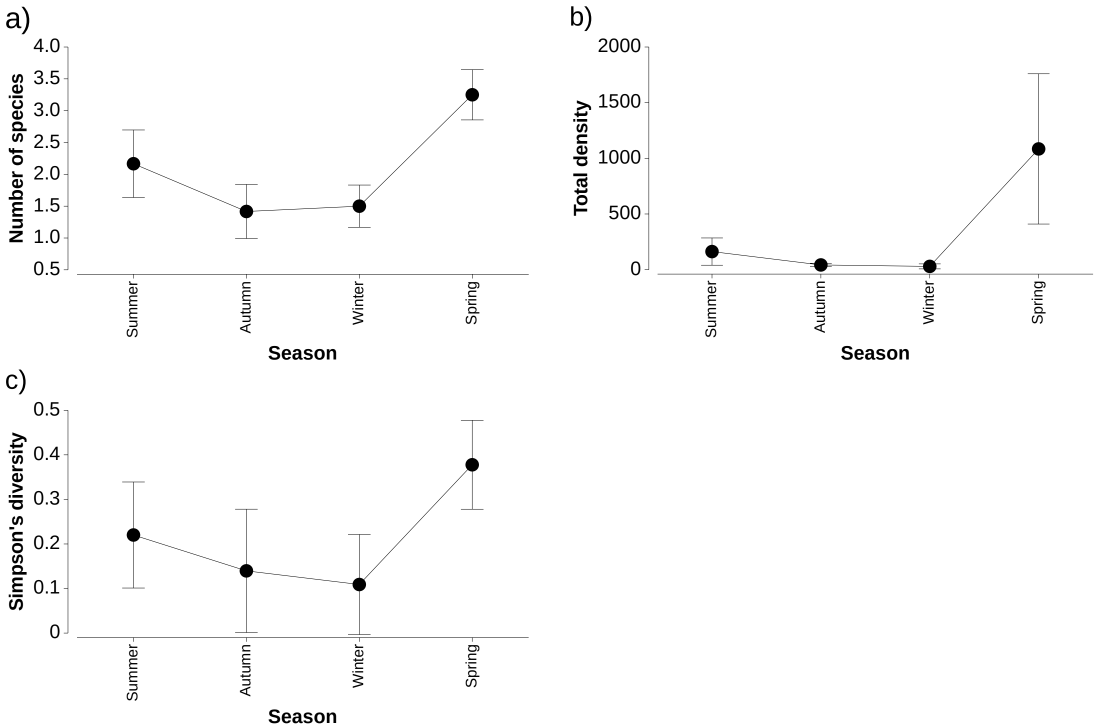

Figure 3.25. Mean and ± 95% confidence limits of (a) number of species (b) total density (fish 100 m^{-2}) and (c) Simpson's diversity among seasons in Cordinup River.

Faunal composition

The composition of the fish communities differed significantly among seasons and regions and their interaction was also significant, with the main effects contributing four times more to the total mean squares than the interaction (Table 3.7). At a pairwise level all seasons and regions were significantly different (all P = 0.001), with each essentially forming a discrete group on the mMDS plots (Figure 3.26a,b). Moreover, seasons show anti-clockwise cycling with regions showing an upstream gradient from the lower to upper. Seasonal and region changes were due to differences in the abundances of *F. lateralis*, *P. olorum* and *A. butcheri* which were typically omnipresent (Figure 3.27). The freshwater straggler *G. occidentalis* was present mainly in spring. The interaction, which was not very influential, was due to slight differences in the cyclical pattern among regions (Figure 3.26c). Such changes were due to species like *A. butcheri* which was abundant in all regions in summer and in most in autumn (not the lower), but were absent winter (Figure 3.27).

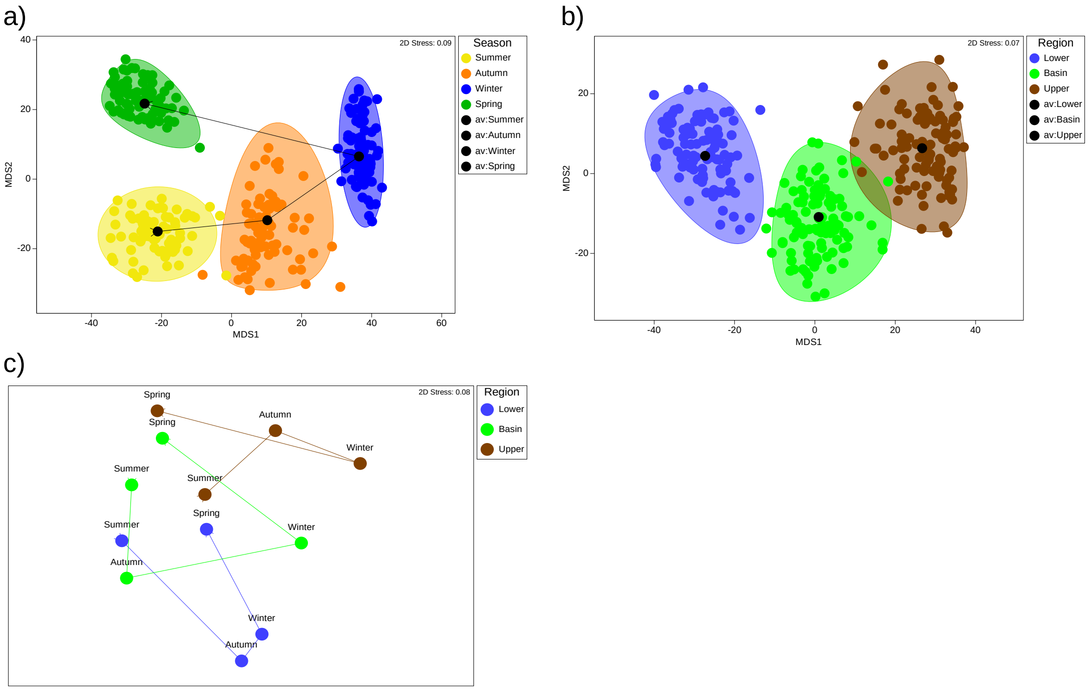

Figure 3.26. Bootstrapped mMDS ordination plots for (a) season and (b) region and (c) centroid nMDS plot, all of which were calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Cordinup River. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown on (a) and (b).

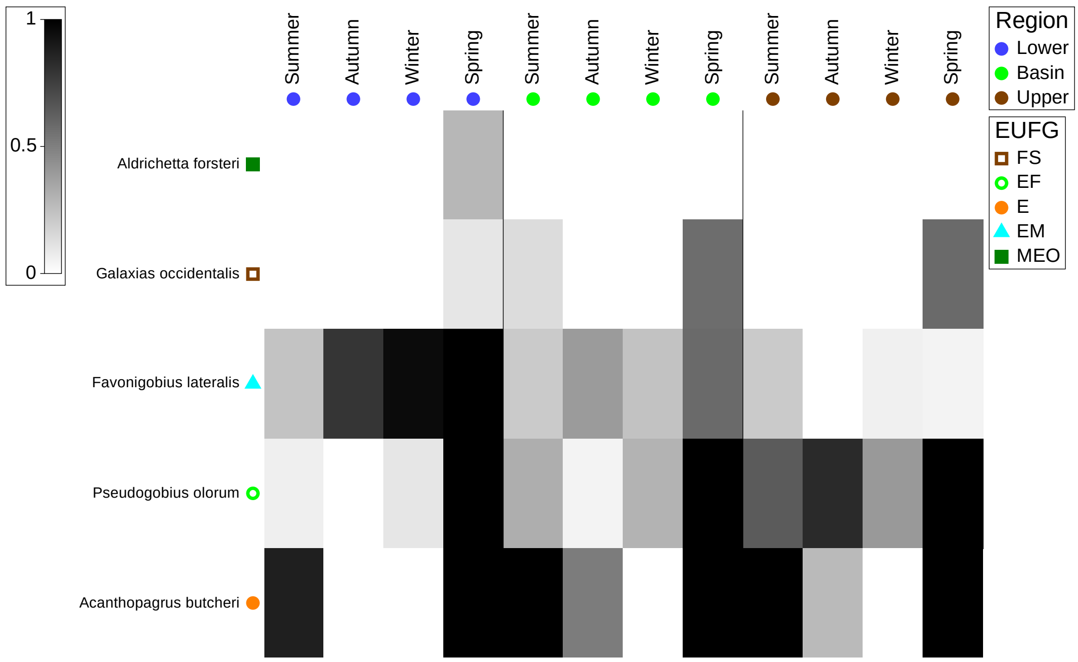

Figure 3.27. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Cordinup River. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Cheyne Inlet

Marine-spawning species represented 63% of all species, however, only contributed 0.56% to all fish caught, with the reverse being true for estuarine residents (*i.e.*, 37% of species and 99% of the catch; Table 3.5). The most numerous species were *A. elongata* and *L. wallacei,* which contributed 64% and 34% to all fish, respectively, and were caught in 98% of samples (Table 3.4). *Pseudogobius olorum* was also frequently recorded.

Number of species, total density and diversity

Number of species differed between seasons and the Season × Region interaction was also significant, with the former term contributing 79% of the total mean squares (Table 3.7). At a pairwise level, more species were caught in spring (6.50) than the other seasons (2.75-3.25; all *P* <0.012: Figure 3.28a). The interaction was caused by all regions having a similar number of species in all seasons except spring (Figure 3.28b).

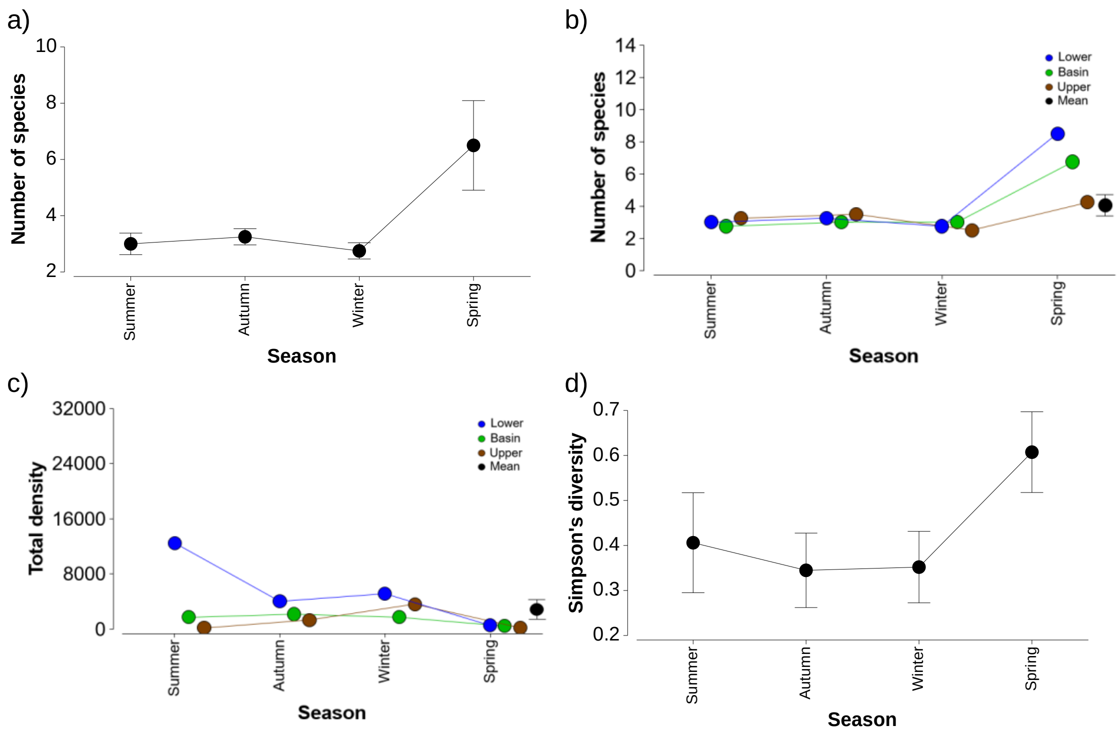

Figure 3.28. Mean and ± 95% confidence limits of number of species among (a) seasons and (b) seasons and regions, (c) total density (fish 100 m^{-2}) among seasons and regions, for clarity black circle represents overall mean and associated ± 95% confidence limits, and (d) Simpson's diversity among seasons in Cheyne Inlet.

PERMANOVA detected a significant difference in total density among seasons, regions and their interaction (Table 3.7). Region had the largest contribution to the percentage mean squares (51%) followed by season (32%) and the interaction (13%). At a pairwise level all regions were significantly different (all P<0.013), decreasing in an upstream direction from 5,555 to 1,541 to, 1,351 fish 100 m^{-2} in the lower, basin and upper region, respectively. The interaction was due mainly to the increased differences between the lower region and the other two regions in summer in comparison to the other seasons (Figure 3.28).

Simpson's diversity differed significantly only among seasons (Table 3.7), with values in spring (0.61) being significantly greater than in every other season (~0.37; all P <0.002; Figure 3.28d).

Faunal composition

The composition of the fish fauna differed significantly with Season and Region and the interaction was also significant (Table 3.7). Season contributed most to the total mean squares (50%), followed by region 35% and lastly their interaction (9%). Among seasons, only that of spring was different from the other three (P <0.002), with regions being well-separated from the others on the mMDS plot (Figure 3.29a). The lack of a difference between summer, autumn and winter was due to them all harbouring similar numbers of *A. elongata*, *L. wallacei* and *P. olorum* (Figure 3.30). Whereas, in spring, there was an influx of marine stragglers and marine estuarine-opportunists, particularly in the lower region (Figure 3.30).

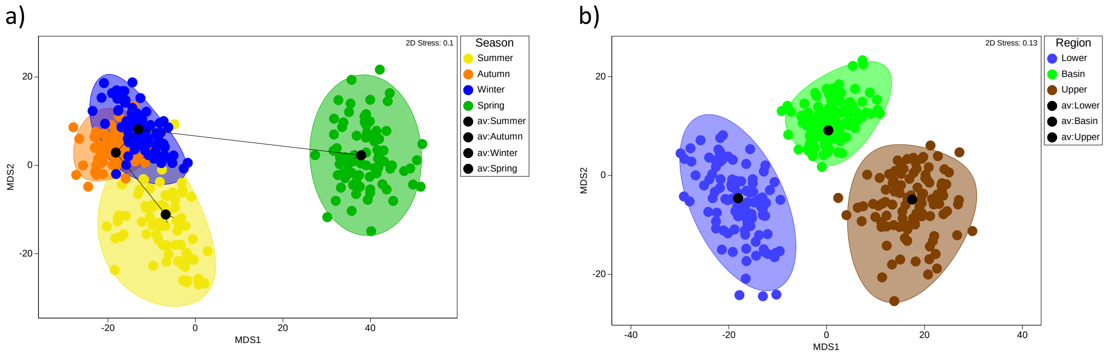

Figure 3.29. Bootstrapped mMDS ordination plots for (a) season and (b) region calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Cheyne Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

Pairwise testing and ordination indicated all regions had a different fish fauna (all P <0.003; Figure 3.29b). The lower region contained marine stragglers species such as *A. spilomelanurus*, *E. armatus*, *Scorpis georgiana*, *Cheulodactylus rubrolabiatus* and

Contusus brevicaudus that were not present in the other regions (Figure 3.30). Differences in the other two regions were due to species like *A. elongata*, *L. wallacei* and *P. olorum* declining in abundance further upstream.

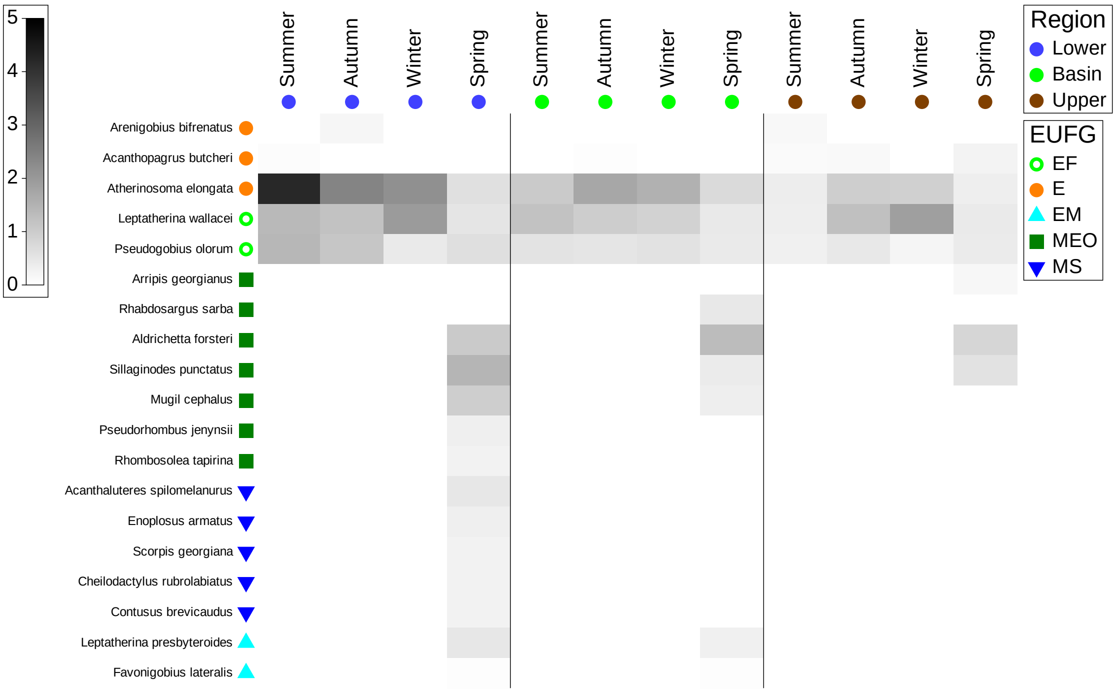

Figure 3.30. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Cheyne Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

Beaufort Inlet

Only three species were caught in the nearshore waters of Beaufort, *A. elongata*, which contributed >99% of all fish and was caught in 96% of samples, and *A. forsteri* and *M. cephalus* (Table 3.4).

Number of species, total density and diversity

Both the number of species and Simpson's diversity index did not differ significantly among regions or seasons and their interaction terms were not significant (Table 3.7). However, total density was found to vary significantly among seasons, with values in winter (20 fish 100 m^{-2}) being significantly lower than in all other seasons (all $P = 0.001$), particularly in spring where a mean of 850 fish 100 m^{-2} was recorded, albeit with considerable variation (Figure 3.31).

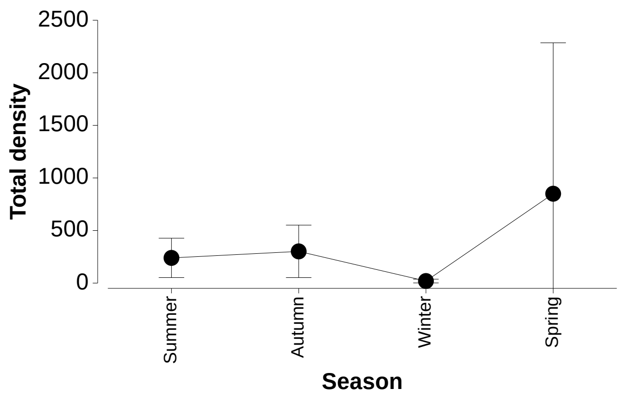

Figure 3.31. Mean and ± 95% confidence limits of total density (fish 100 m^{-2}) among seasons in Beaufort Inlet.

Faunal composition

Seasonal changes in the fish fauna were detected (Table 3.7), due to differences between winter and the other three seasons (all P = 0.001). On the mMDS plot winter remains discrete, while the other seasons are superimposed, reflecting their similarity (Figure 3.32). The differences in composition in winter reflect the lower densities of *A. elongata* recorded then (Figure 3.33).

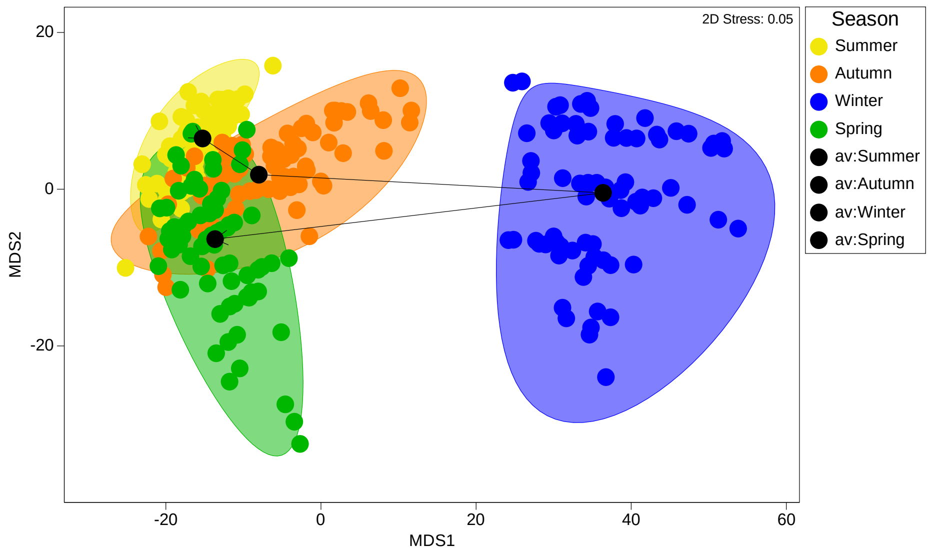

Figure 3.32. Bootstrapped mMDS ordination plots for season calculated from a Bray-Curtis resemblance matrix of the transformed abundance of each nearshore fish species in each sample from Beaufort Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

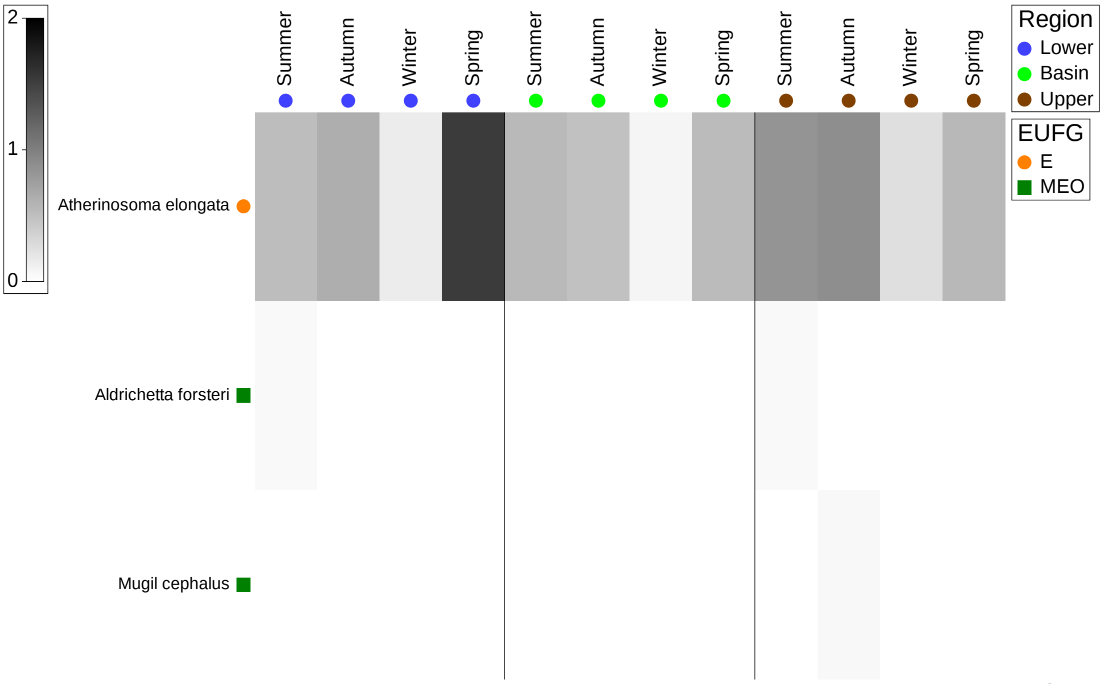

Figure 3.33. Shade plot of the dispersion-weighted and square-root density (fish 100 m^{-2}) of all fish species found in Beaufort Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.5.

3.5. Offshore fish fauna

The presentation of results for offshore waters follows those for the nearshore, except that they do not consider regional variation, as it was not possible to take replicate samples of gill nets in offshore regions.

3.5.1 Description of the fish fauna

A total of 6,860 fish and four cephalopods were caught in gill nets (n = 128) in the offshore waters of eight estuaries seasonally between February and November 2020. The fish represented 44 species and 27 families, and the cephalopods represented three species from three families (Table 3.8). The average catch rate (h^{-1}) across all estuaries was 53.6 fish h^{-1}. The species with the highest catch rates and that were caught most frequently included the mugilids *M. cephalus* (20.4 h^{-1}, in 70% of samples) and *A. forsteri* (7.95 h^{-1}, 55%), and the sparid *A. butcheri* (18.1 h^{-1}, 59%). The two mugilids were the only species caught in all eight estuaries, while *A. butcheri* was recorded in seven (Table 3.8). The arripids *Arripis truttaceus* and *Arripis georgianus* were the next most frequent species (26 % and 23 %, respectively) and at least one species of arripid was caught in all estuaries, except Beaufort. *Sillaginodes punctatus*, *Psuedocaranx georgianus*, *Rhabdosargus sarba*, *Argyrosomus japonicus* and *Enoplosus armatus* were all caught in 10 – 13 % of samples (Table 3.8). *Sillaginodes punctatus* and *R. sarba* were present in four of the systems (Torbay, Oyster, Taylor and Cheyne), *P. georgianus* in three estuaries (Oyster, Waychinicup and Cordinup), *A. japonicus* in two estuaries (Taylor and Oyster) and *E. armatus* only in Waychinicup. Although *Cnidoglanis macrocephalus* had a low overall catch rate and relatively low frequency of occurrence (8.59 %), it was caught in three estuaries (Oyster, Waychinicup and Cheyne). No other species had a mean catch rate >10 h^{-1}, frequency of occurrence >10% or was present in three or more systems (Table 3.8).

Table 3.8. Mean catch rate (M, number of fish h^{-1}), standard deviation (SD), percentage contribution to the overall mean density of the catch (%C), percentage frequency of occurrence in all samples (%F); rank by catch rate (R), length range (LR); and mean length (ML) of each fish species recorded in the offshore waters of eight estuaries in 2020. Abundant species (*i.e.*, contributed >5% to the catch) and in at least four samples (>25% frequency) are highlighted in grey. Estuarine Usage Functional Group (EUFG) guilds are: E = solely estuarine; EM = estuarine & marine; MEO = marine estuarine-opportunist; and MS = marine straggler.

			All		Torbay Inlet							Oyster Harbour						
Species name	**Common name**	**EUFG**	**M**	**%F**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**
Mugil cephalus	Sea Mullet	MEO	20.40	67.97	36.63	31.51	29.51	100.00	2	28-490	265	1.31	3.61	9.50	25.00	4	208-474	364
Acanthopagrus butcheri	Black Bream	E	18.07	59.38	70.94	77.27	57.15	100.00	1	13-420	207	3.81	7.67	27.60	37.50	1	130-393	221
Aldrichetta forsteri	Yelloweye Mullet	MEO	7.95	55.47	12.31	9.65	9.92	93.75	3	150-417	281	0.06	0.25	0.45	6.25		205-205	205
Arripis georgianus	Australian Herring	MEO	1.80	22.66	0.19	0.54	0.15	12.50	7	230-270	247	1.94	3.49	14.03	56.25	3	128-250	215
Pseudocaranx georgianus	Silver Trevally	MS	1.11	11.72								0.38	1.50	2.71	6.25	7	211-278	235
Arripis truttaceus	West. Australian Salmon	MEO	0.92	25.78	2.44	2.66	1.96	68.75	4	130-350	269							
Pelates octolineatus	West. Striped Grunter	MEO	0.47	6.25								3.75	5.42	27.15	50.00	2	125-297	167
Kyphosus gladius	Gladius Drummer	MS	0.38	3.13														
Argyrosomus japonicus	Mulloway	MEO	0.35	10.16								1.25	2.62	9.05	37.50	5	142-632	444
Pempheris multiradiata	Bigscale Bullseye	MS	0.34	4.69														
Sillaginodes punctatus	King George Whiting	MEO	0.32	12.50	0.13	0.50	0.10	6.25	8	280-345	313	0.44	1.03	3.17	25.00	6	291-335	312
Enoplosus armatus	Old Wife	MS	0.21	10.16														
Rhabdosargus sarba	Tarwhine	MEO	0.19	11.72	0.31	0.48	0.25	31.25	6	192-258	229	0.13	0.34	0.90	12.50	9	253-307	280
Cnidoglanis macrocephalus	Estuary Cobbler	EM	0.16	8.59								0.19	0.54	1.36	12.50	8	360-595	449
Centroberyx lineatus	Swallowtail	MS	0.12	4.69														
Sillago schomburgkii	Yellowfin Whiting	MEO	0.12	4.69	0.94	1.61	0.76	37.50	5	230-345	299							
Girella zebra	Zebrafish	MS	0.09	4.69														
Pempheris klunzingeri	Rough Bullseye	MS	0.09	3.91														
Trachurus novaezelandiae	Yellowtail Scad	MS	0.08	3.91								0.19	0.54	1.36	12.50	8	183-210	193
Orectolobus hutchinsi	West. Wobbegong	MS	0.06	4.69														
Sphyraena novaehollandiae	Snook	MS	0.05	3.91								0.06	0.25	0.45	6.25	10	786	786
Kyphosus cornelii	West. Buffalo Bream	MS	0.04	1.56														
Pomatomus saltatrix	Tailor	MEO	0.03	0.78														
Orectolobus halei	Gulf Wobbegong	MS	0.02	1.56														
Hyporhamphus melanochir	Southern Garfish	EM	0.02	2.34														
Ammotretis rostratus	Longsnout Flounder	MEO	0.02	0.78	0.19	0.75	0.15	6.25	7	245-251	249							
Elops machnata	Australian Giant Herring	MEO	0.02	1.56														
Platycephalus laevigatus	Rock Flathead	MS	0.02	1.56								0.06	0.25	0.45	6.25	10	395	395
Tilodon sexfasciatus	Moonlighter	MS	0.02	1.56														
Ammotretis brevipinnis	Shortfin Flounder	MS	0.02	1.56	0.06	0.25	0.05	6.25	9	308	308							
Octopus djinda	Octopus	MS	0.02	1.56								0.06	0.25	0.45	6.25	10	500	500

Table 3.8. Continued.

			All		Torbay Inlet							Oyster Harbour						
Species name	**Common name**	**EUFG**	**M**	**%F**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**
Heterodontus portusjacksoni	Port Jackson Shark	MS	0.01	0.78														
Trygonoptera mucosa	West. Shovelnose Stingaree	MS	0.01	0.78								0.06	0.25	0.45	6.25	10	310	310
Lotella rhacina	Largetooth Beardie	MS	0.01	0.78														
Gymnapistes marmoratus	Soldier	MEO	0.01	0.78								0.06	0.25	0.45	6.25	10	140	140
Leviprora inops	Longhead Flathead	MS	0.01	0.78														
Platycephalus speculator	South. Bluespotted Flathead	EM	0.01	0.78														
Kyphosus sydneyanus	Silver Drummer	MS	0.01	0.78														
Scorpis aequipinnis	Sea Sweep	MS	0.01	0.78														
Scorpis georgiana	Banded Sweep	MS	0.01	0.78														
Cheilodactylus rubrolabiatus	Redlip Morwong	MS	0.01	0.78														
Notolabrus parilus	Brownspotted Wrasse	MS	0.01	0.78														
Clinidae sp.	weedfishes	MS	0.01	0.78														
Acanthaluteres brownii	Spinytail Leatherjacket	MS	0.01	0.78														
Meuschenia freycineti	Sixspine Leatherjacket	MS	0.01	0.78								0.06	0.25	0.45	6.25	10	255	255
Sepia spp.	Cuttlefish	MS	0.01	0.78														
Teuthoidae spp.	Squid	MS	0.01	0.78														
Number of samples			**128**					**16**								**16**		
Number of species			**47**					**10**								**17**		
Total catch rate (h^{-1})			**53.63**					**124.13**								**13.81**		
Number of fish			**6864**					**1986**								**221**		

Table 3.8. Continued.

Species name	Common name	Taylor Inlet M	SD	%C	%F	R	LR	ML	Normans Inlet M	SD	%C	%F	R	LR	ML
Mugil cephalus	Sea Mullet	5.44	8.68	11.66	68.75	2	247-447	349	10.94	11.94	55.03	81.25	1	152-420	322
Acanthopagrus butcheri	Black Bream	32.63	30.73	69.97	100.00	1	95-410	245	1.38	2.68	6.92	25.00	4	257-369	315
Aldrichetta forsteri	Yelloweye Mullet	5.38	8.73	11.53	68.75	3	146-412	327	4.19	4.07	21.07	81.25	2	120-360	252
Arripis georgianus	Australian Herring														
Pseudocaranx georgianus	Silver Trevally														
Arripis truttaceus	West. Australian Salmon	1.31	3.28	2.82	37.50	5	132-540	473	2.75	4.22	13.84	68.75	3	135-362	250
Pelates octolineatus	West. Striped Grunter														
Kyphosus gladius	Gladius Drummer														
Argyrosomus japonicus	Mulloway	1.56	3.16	3.35	43.75	4	545-864	726							
Pempheris multiradiata	Bigscale Bullseye														
Sillaginodes punctatus	King George Whiting	0.19	0.75	0.40	6.25	6	326-335	330							
Enoplosus armatus	Old Wife														
Rhabdosargus sarba	Tarwhine	0.13	0.34	0.27	12.50	7	200-238	219							
Cnidoglanis macrocephalus	Estuary Cobbler														
Centroberyx lineatus	Swallowtail														
Sillago schomburgkii	Yellowfin Whiting														
Girella zebra	Zebrafish														
Pempheris klunzingeri	Rough Bullseye														
Trachurus novaezelandiae	Yellowtail Scad														
Orectolobus hutchinsi	West. Wobbegong														
Sphyraena novaehollandiae	Snook														
Kyphosus cornelii	West. Buffalo Bream														
Pomatomus saltatrix	Tailor														
Orectolobus halei	Gulf Wobbegong														
Hyporhamphus melanochir	Southern Garfish														
Ammotretis rostratus	Longsnout Flounder														
Elops machnata	Australian Giant Herring														
Platycephalus laevigatus	Rock Flathead														
Tilodon sexfasciatus	Moonlighter														
Ammotretis brevipinnis	Shortfin Flounder														
Octopus djinda	Octopus														

Table 3.8. Continued.

Species name	Common name	Taylor Inlet M	SD	%C	%F	R	LR	ML	Normans Inlet M	SD	%C	%F	R	LR	ML
Heterodontus portusjacksoni	Port Jackson Shark														
Trygonoptera mucosa	West. Shovelnose Stingaree														
Lotella rhacina	Largetooth Beardie														
Gymnapistes marmoratus	Soldier														
Leviprora inops	Longhead Flathead														
Platycephalus speculator	Southern Bluespotted Flathead														
Kyphosus sydneyanus	Silver Drummer														
Scorpis aequipinnis	Sea Sweep														
Scorpis georgiana	Banded Sweep								0.06	0.25	0.31	6.25	5	129	129
Cheilodactylus rubrolabiatus	Redlip Morwong														
Notolabrus parilus	Brownspotted Wrasse														
Clinidae - undifferentiated	weedfishes														
Acanthaluteres brownii	Spinytail Leatherjacket														
Meuschenia freycineti	Sixspine Leatherjacket														
Sepia spp.	Cuttlefish														
Teuthoidae spp.	Squid														
Number of samples					**16**							**16**			
Number of species					**7**							**5**			
Total catch rate (h^{-1})					**46.63**							**19.875**			
Number of fish					**746**							**318**			

Table 3.8 Continued.

Species name	Common name	Waychinicup Estuary M	SD	%C	%F	R	LR	ML	Cordinup River M	SD	%C	%F	R	LR	ML
Mugil cephalus	Sea Mullet	0.81	2.32	2.38	18.75	7	270-440	312	38.25	44.63	58.96	100.00	1	34-509	327
Acanthopagrus butcheri	Black Bream								18.88	13.33	29.09	100.00	2	90-387	182
Aldrichetta forsteri	Yelloweye Mullet	0.50	1.55	1.47	12.50	10	175-268	215	6.81	10.22	10.50	68.75	3	150-334	251
Arripis georgianus	Australian Herring	11.13	22.93	32.60	75.00	1	140-342	243	0.06	0.25	0.10	6.25	6	162-162	162
Pseudocaranx georgianus	Silver Trevally	8.44	16.69	24.73	81.25	2	110-451	314	0.06	0.25	0.10	6.25	6	389-389	389
Arripis truttaceus	Western Australian Salmon								0.50	1.51	0.77	18.75	4	215-290	241
Pelates octolineatus	Western Striped Grunter														
Kyphosus gladius	Gladius Drummer	2.75	7.43	8.06	18.75	3	328-532	465	0.31	1.25	0.48	6.25	5	371-448	412
Argyrosomus japonicus	Mulloway														
Pempheris multiradiata	Bigscale Bullseye	2.69	5.41	7.88	37.50	4	109-240	204							
Sillaginodes punctatus	King George Whiting														
Enoplosus armatus	Old Wife	1.69	1.40	4.95	81.25	5	139-250	213							
Rhabdosargus sarba	Tarwhine														
Cnidoglanis macrocephalus	Estuary Cobbler	0.69	1.74	2.01	31.25	9	249-550	335							
Centroberyx lineatus	Swallowtail	0.94	1.65	2.75	37.50	6	215-275	239							
Sillago schomburgkii	Yellowfin Whiting														
Girella zebra	Zebrafish	0.75	1.24	2.20	37.50	8	261-370	331							
Pempheris klunzingeri	Rough Bullseye	0.69	1.25	2.01	31.25	9	116-254	170							
Trachurus novaezelandiae	Yellowtail Scad	0.44	1.26	1.28	18.75	11	210-255	230							
Orectolobus hutchinsi	Western Wobbegong	0.50	0.73	1.47	37.50	10	1100-1500	1319							
Sphyraena novaehollandiae	Snook	0.38	0.81	1.10	25.00	12	615-729	667							
Kyphosus cornelii	Western Buffalo Bream	0.31	1.01	0.92	12.50	13	293-395	341							
Pomatomus saltatrix	Tailor														
Orectolobus halei	Gulf Wobbegong	0.19	0.54	0.55	12.50	14	1000-1500	1300							
Hyporhamphus melanochir	Southern Garfish	0.19	0.40	0.55	18.75	14	215-276	244							
Ammotretis rostratus	Longsnout Flounder														
Elops machnata	Australian Giant Herring	0.13	0.34	0.37	12.50	15	404-496	450							
Platycephalus laevigatus	Rock Flathead														
Tilodon sexfasciatus	Moonlighter	0.13	0.34	0.37	12.50	15	203-283	243							
Ammotretis brevipinnis	Shortfin Flounder														
Octopus djinda	Octopus	0.06	0.25	0.18	6.25	16	1000	1000							

Table 3.8. Continued.

		Waychinicup Estuary							Cordinup River						
Species name	**Common name**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**
Heterodontus portusjacksoni	Port Jackson Shark	0.06	0.25	0.18	6.25	16	963-963	963							
Trygonoptera mucosa	Western Shovelnose Stingaree														
Lotella rhacina	Largetooth Beardie	0.06	0.25	0.18	6.25	16	357	357							
Gymnapistes marmoratus	Soldier														
Leviprora inops	Longhead Flathead	0.06	0.25	0.18	6.25	16	294	294							
Platycephalus speculator	Southern Bluespotted Flathead														
Kyphosus sydneyanus	Silver Drummer	0.06	0.25	0.18	6.25	16	435	435							
Scorpis aequipinnis	Sea Sweep	0.06	0.25	0.18	6.25	16	403	403							
Scorpis georgiana	Banded Sweep														
Cheilodactylus rubrolabiatus	Redlip Morwong	0.06	0.25	0.18	6.25	16	564	564							
Notolabrus parilus	Brownspotted Wrasse	0.06	0.25	0.18	6.25	16	164	164							
Clinidae - undifferentiated	weedfishes	0.06	0.25	0.18	6.25	16	270	270							
Acanthaluteres brownii	Spinytail Leatherjacket	0.06	0.25	0.18	6.25	16	305	305							
Meuschenia freycineti	Sixspine Leatherjacket														
Sepia spp.	Cuttlefish	0.06	0.25	0.18	6.25	16	600	600							
Teuthoidae spp.	Squid	0.06	0.25	0.18	6.25	16	400	400							
Number of samples		**16**							**16**						
Number of species		**31**							**7**						
Total catch rate (h^{-1})		**34.13**							**64.88**						
Number of fish		**546**							**1038**						

Table 3.8 Continued.

		Cheyne Inlet							Beaufort Inlet						
Species name	**Common name**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**	**M**	**SD**	**%C**	**%F**	**R**	**LR**	**ML**
Mugil cephalus	Sea Mullet	60.63	46.09	52.07	100.00	1	30-515	342	9.19	18.12	94.23	50.00	1	270-463	394
Acanthopagrus butcheri	Black Bream	16.69	18.18	14.33	100.00	3	120-413	264	0.25	0.77	3.21	12.50	3	230-320	256
Aldrichetta forsteri	Yelloweye Mullet	34.06	20.30	29.25	100.00	2	180-390	269	0.31	0.87	2.56	12.50	2	225-292	268
Arripis georgianus	Australian Herring	1.13	2.19	0.97	31.25	5	222-345	246							
Pseudocaranx georgianus	Silver Trevally														
Arripis truttaceus	Western Australian Salmon	0.38	1.26	0.32	12.50	7	330-494	430							
Pelates octolineatus	Western Striped Grunter														
Kyphosus gladius	Gladius Drummer														
Argyrosomus japonicus	Mulloway														
Pempheris multiradiata	Bigscale Bullseye														
Sillaginodes punctatus	King George Whiting	1.81	2.74	1.56	62.50	4	245-350	320							
Enoplosus armatus	Old Wife														
Rhabdosargus sarba	Tarwhine	0.94	1.57	0.81	37.50	6	230-340	282							
Cnidoglanis macrocephalus	Estuary Cobbler	0.38	0.81	0.32	25.00	9	270-820	524							
Centroberyx lineatus	Swallowtail														
Sillago schomburgkii	Yellowfin Whiting														
Girella zebra	Zebrafish														
Pempheris klunzingeri	Rough Bullseye														
Trachurus novaezelandiae	Yellowtail Scad														
Orectolobus hutchinsi	Western Wobbegong														
Sphyraena novaehollandiae	Snook														
Kyphosus cornelii	Western Buffalo Bream														
Pomatomus saltatrix	Tailor	0.25	1.00	0.21	6.25	8	155-171	162							
Orectolobus halei	Gulf Wobbegong														
Hyporhamphus melanochir	Southern Garfish														
Ammotretis rostratus	Longsnout Flounder														
Elops machnata	Australian Giant Herring														
Platycephalus laevigatus	Rock Flathead	0.06	0.25	0.05	6.25	10	355	355							
Tilodon sexfasciatus	Moonlighter														
Ammotretis brevipinnis	Shortfin Flounder	0.06	0.25	0.05	6.25	10	240	240							
Octopus djinda	Octopus														

Table 3.8. Continued.

Species name	Common name	Cheyne Inlet M	SD	%C	%F	R	LR	ML	Beaufort Inlet M	SD	%C	%F	R	LR	ML
Heterodontus portusjacksoni	Port Jackson Shark														
Trygonoptera mucosa	Western Shovelnose Stingaree														
Lotella rhacina	Largetooth Beardie														
Gymnapistes marmoratus	Soldier														
Leviprora inops	Longhead Flathead														
Platycephalus speculator	Southern Bluespotted Flathead	0.06	0.25	0.05	6.25	11	365	365							
Kyphosus sydneyanus	Silver Drummer														
Scorpis aequipinnis	Sea Sweep														
Scorpis georgiana	Banded Sweep														
Cheilodactylus rubrolabiatus	Redlip Morwong														
Notolabrus parilus	Brownspotted Wrasse														
Clinidae - undifferentiated	weedfishes														
Acanthaluteres brownii	Spinytail Leatherjacket														
Meuschenia freycineti	Sixspine Leatherjacket														
Sepia spp.	Cuttlefish														
Teuthoidae spp.	Squid														
Number of samples		**16**							**16**						
Number of species		**12**							**3**						
Total catch rate (h^{-1})		**116.44**							**9.75**						
Number of fish		**1863**							**156**						

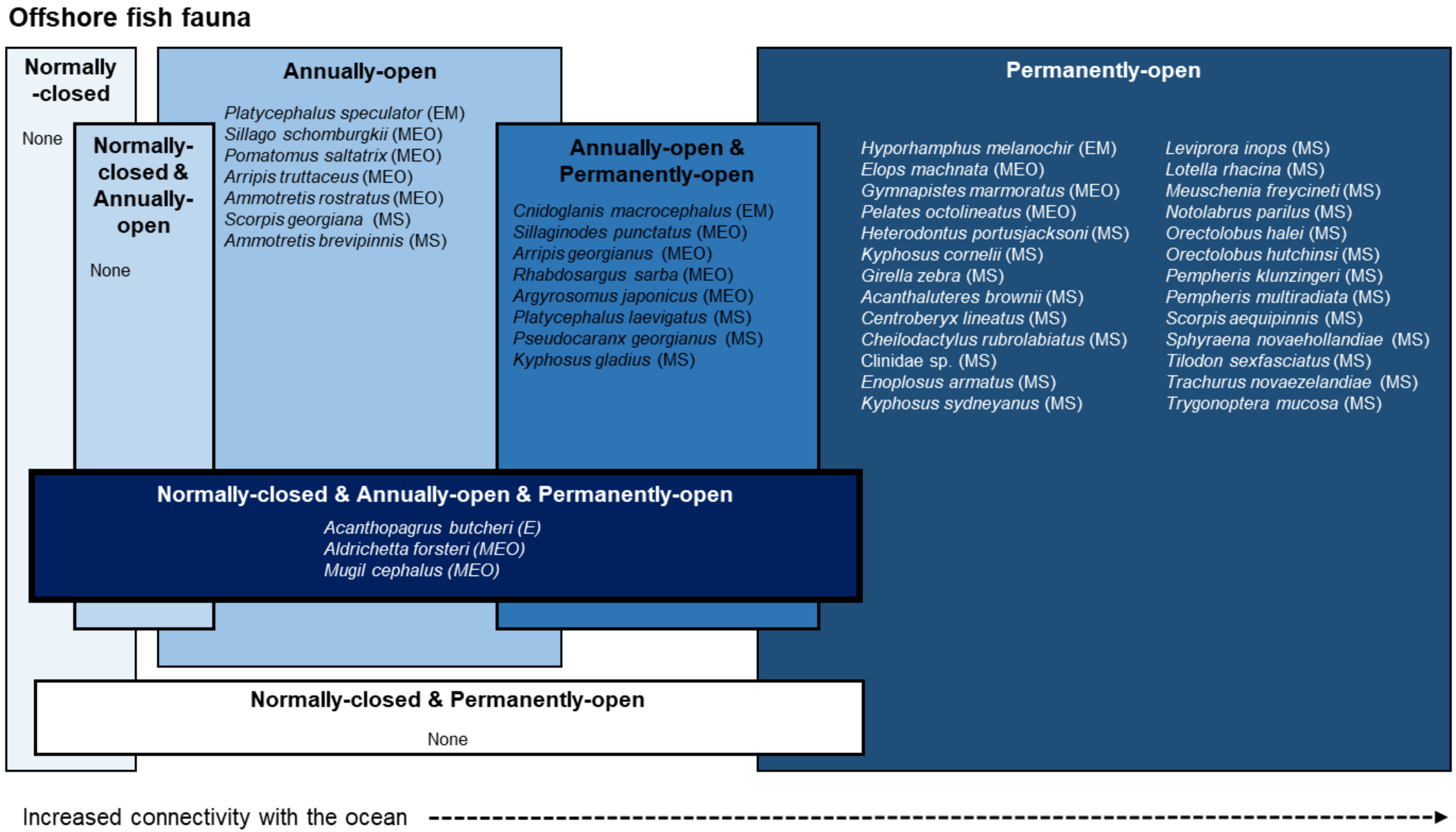

Figure 3.34. Venn diagram of the unique and shared presence of species in the offshore waters of each of the three types of estuary, i.e. permanently-open (Oyster and Waychinicup), annually-open (Torbay, Taylor, Normans, Cordinup and Cheyne) and normally-closed (Beaufort). Estuarine Usage Functional Group (EUFG) guilds are: E = solely estuarine; EM = estuarine & marine; MEO = marine estuarine-opportunist; and MS = marine straggler.

The offshore fish faunas followed a similar pattern to the nearshore fish faunas. Permanently-open estuaries contained the most species found in no other broad type of estuary (i.e., 26), followed by annually-open estuaries with seven species, with these two types having eight species in common (Figure 3.34). Normally-closed estuaries contained no unique species and only three species were found in all types of estuaries.

Life history guilds

A total of 47 fish species from four life history guilds were caught in gill nets in the offshore waters of the eight estuaries (Table 3.9). Marine-spawning species contributed 91% to the total number of species (44). The majority of these were marine stragglers (30, 64% of all species), and overall, contributed only 5% to the total number of individuals. Marine estuarine-opportunists, represented by 13 species made the greatest contribution to the total number of individuals (61%; Table 3.9). Although only one solely estuarine species (*A. butcheri*) was caught, it represented 34% of the total number of individuals and was present in all estuaries except Waychinicup. The estuarine and marine guild was represented by three species, *i.e., C. macrocephalus, Hyporhamphus melanochir* and *Platycephalus speculator*, but this group made the least contribution to the total fish caught in gill nets (0.35%).

3.5.2. Inter-estuarine differences

The total number of species varied greatly between estuaries, with the permanently-open Waychinicup and Oyster having the highest number of species (31 and 17, respectively) and the normally-closed Beaufort the least (3). The number of species recorded in Cheyne, Torbay, Taylor, Cordinup and Normans ranged from five to 12 (Table 3.8).

Table 3.9. Number of species (N) and individuals (D, number of fish h^{-1}), together with their percentage contributions (%) recorded in the offshore waters of the eight estuaries in 2020. Guilds representing >10% in bold and the largest shaded in grey. Estuarine Usage Functional Group (EUFG) guilds are: E = solely estuarine; EM = estuarine & marine; MEO = marine estuarine-opportunist; and MS = marine straggler. Estuarine-residents comprises species in E and EM guilds.

	All		**Torbay**		**Oyster**		**Taylor**		**Normans**		**Waychinicup**		**Cordinup**		**Cheyne**		**Beaufort**	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Species																		
E	1	2.13	1	10.00	1	5.88	1	**14.29**	1	**20.00**			1	14.29	1	8.33	1	**33.33**
EM	3	6.38			1	5.88					2	6.45			2	**16.67**		
MEO	13	**27.66**	8	**80.00**	8	**47.06**	6	**85.71**	3	**60.00**	4	**12.90**	4	**57.14**	7	**58.33**	2	**66.67**
MS	30	**63.83**	1	10.00	7	**41.18**			1	**20.00**	25	**80.65**	2	**28.57**	2	**16.67**		
Total	**47**		**10**		**17**		**7**		**5**		**31**		**7**		**12**		**3**	

Individuals	**D**	**%**	**D**	**%**	**D**	**%**	**D**	**%**	**D**	**%**	**D**	**%**	**D**	**%**	**D**	**%**	**D**	**%**
E	18.07	**33.70**	70.94	**57.15**	3.81	**27.60**	32.63	**69.97**	1.38	7.12			18.88	**29.09**	16.69	**14.33**	0.25	2.56
EM	0.19	0.35			0.19	1.36					0.88	2.57			0.44	0.38		
MEO	32.60	**60.80**	53.13	**42.80**	8.94	**64.71**	14.00	**30.03**	17.88	**92.56**	12.56	**36.88**	45.63	**70.33**	99.19	**85.19**	9.50	**97.44**
MS	2.77	5.16	0.06	0.05	0.88	6.33			0.06	0.32	20.63	**60.55**	0.38	0.58	0.13	0.11		
Total	**53.63**		**124.13**		**13.81**		**46.63**		**19.31**		**34.06**		**64.88**		**116.44**		**9.75**	

Number of species, total density and diversity

The number of species was found to differ significantly among estuaries and seasons, with the one-way interaction also significant (Table 3.10). The Estuary main effect was the most important factor, accounting for over 80% of the total mean squares. The mean number of species differed significantly for most pairs of estuaries (P = 0.001 – 0.048), with those for Oyster *vs* Cordinup, Normans and Taylor, Cordinup *vs* Normans and Cheyne *vs* Torbay not differing (P = 0.001 – 0.048). Waychinicup had the highest mean number of species (6.8), followed by Torbay and Cheyne (~4.8) and Oyster, Taylor, Normans and Cordinup (~3.0; Figure 3.35a). A very small number of species were recorded in Beaufort (0.75). The relatively uninfluential seasonal effect (10 %MS) was due to values in spring (3.25) being significantly lower than those summer (4.13) and autumn (4.00), with the values in winter (3.31) significantly lower than those in autumn (all P <0.025; Figure 3.35b). The Estuary × Season interaction only accounted for 7% of the total variation and was caused by minor variations in the seasonal trends among estuaries. For example, number of species was greatest in Waychinicup in autumn and lowest in summer, while in Beaufort the greatest values were recorded in summer and the lowest in winter and spring.

Total catch rate differed significantly among both main effects and their interaction, with Estuary contributing most to the total mean squares (71%; Table 3.10). Pairwise testing among estuaries showed that values differed between all comparisons (all P <0.047), except Taylor *vs* Cordinup and Waychinicup, Cheyne *vs* Torbay and Normans *vs* Oyster (Figure 3.35c). The highest catch rates were in Cheyne and Torbay (~120 fish h^{-1}), followed by Taylor, Waychinicup and Cordinup (34 – 65 fish h^{-1}), Oyster and Normans (~17) and finally Beaufort (10 fish h^{-1}; Figure 3.35c). The seasonal variation in total catch rate was due to values in summer and autumn, being significantly greater than those in winter and spring (all P <0.002; Figure 3.35d). Total catch rates were, however, not always consistent in each estuary, with high catches in Cheyne occurring in winter being partially responsible for the interaction (see Section 3.4.3; Figure 3.51).

Values of Simpson's index differed significantly only among estuaries (Table 3.10), due mainly to the values in Beaufort (0.02) being markedly lower than for all other estuaries (0.40 - 0.62; Figure 3.35e).

Table 3.10. Mean squares (MS), the percentage contribution of mean squares to the total mean squares (%MS), pseudo-F ratios (pF) and significance levels (*P*) from two-way PERMANOVA tests on univariate measures of diversity and faunal composition of the offshore fish fauna of eight estuaries sampled seasonally in 2020. *df* = degrees of freedom. Significant results are highlighted in bold and those with a %MS ≥ 10 shaded in grey.

		Number of species				Total catch rate			
Term	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season (S)	3	6.61	10.20	3.76	0.012	2.51	19.88	10.69	0.001
Estuary (E)	**7**	**51.89**	**80.02**	**29.48**	**0.001**	**8.92**	**70.76**	**38.06**	**0.001**
S × E	21	4.58	7.06	2.60	0.001	0.95	7.51	4.04	0.001
Residual	96	1.76	2.71			0.23	1.86		
		Simpson's diversity				**Faunal composition**			
Term	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season	3	0.01	1.90	0.32	0.795	4.71	14.16	2.96	0.001
Estuary	**7**	**0.56**	**83.32**	**14.03**	**0.001**	**24.75**	**74.45**	**15.59**	**0.001**
S × E	21	0.06	8.85	1.49	0.088	2.2	6.62	1.39	0.001
Residual	96	0.04	5.94			1.59	4.78		

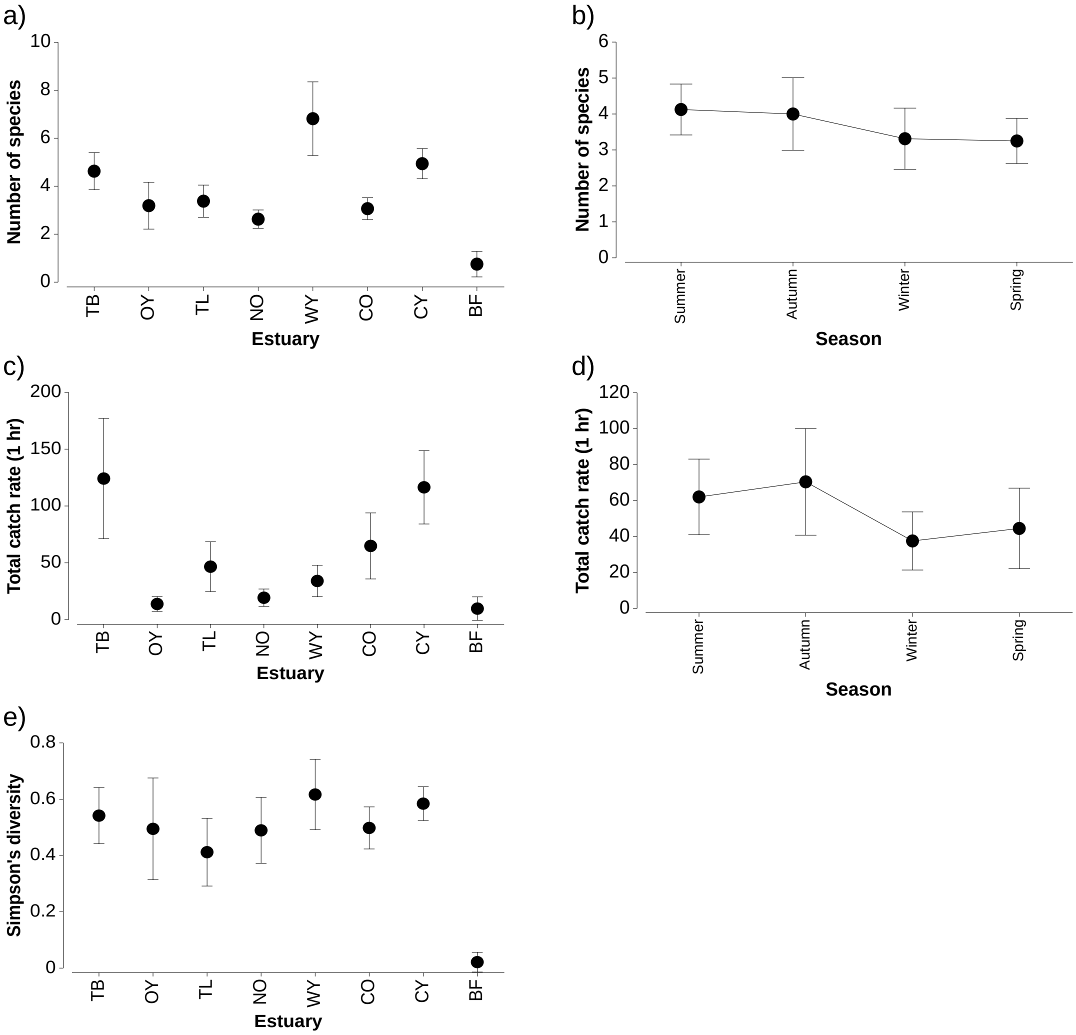

Figure 3.35. Mean and ± 95% confidence limits of number of species among (a) estuaries and (b) seasons, total catch rate (h^{-1}) among (c) estuaries and (d) seasons and (e) Simpsons's diversity among estuaries. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

Faunal composition

Although the composition of the offshore fish fauna differed significantly among estuaries, seasons, and the Estuary × Season interaction was also significant, the Estuary main effect constituted by far the greatest proportion of the total mean squares (77%; Table 3.10). Pairwise testing and ordination showed that the fish fauna of each estuary was unique (all P <0.002; Figure 3.36a). Among the estuaries, Waychinicup and Cheyne, top left and top right of the ordination, were the most distinct being clearly separated from the other estuaries that are broadly grouped in the lower half. Waychinicup contained a wide range of marine stragglers such as *E. armatus*, *Girella zebra*, *Pempheris klungzingeri* and *multiradiata* and *Centroberyx lineatus* that were not caught in the other estuaries (Figure 3.37). Furthermore, *A. butcheri,* which was a key component in most estuaries was not caught. Several marine stragglers were also recorded in Oyster, together with a broad selection of marine estuarine-opportunists, including *Argyrosomus japonicus* and *Pelates octolineatus* that were not caught in many of the other estuaries. Catch rates of the mugilids, *M. cephalus* and *A. forsteri,* which were recorded in all estuaries were lowest in Oyster. Beaufort was also fairly distinct, due to the depauperate nature of its fish fauna. The remaining five estuaries, namely Cordinup, Cheyne, Normans, Torbay and Taylor, were differentiated from each other by their varying catch rates of *M. cephalus*, *A. forsteri* and *A. butcheri* and the occurrence of species such as *Rhabdosargus sarba, S. punctatus* and *Cnidoglanis macrocephalus* in one or more estuaries (Figure 3.37).

The relatively small seasonal changes were caused by each combinations of seasons being different (all P <0.019) except summer *vs* autumn, which exhibited considerable overlap on the mMDS plot (Figure 3.36b). The largest seasonal separation on the mMDS plot was between spring on the top right, and all other seasons, which had a similar faunal composition (Figure 3.36b). Seasonal trends are related the lowest catch rate of some key species *e.g., A. forsteri* and *M. cephalus* across all estuaries and marine stragglers in Waychinicup in spring, and to some species recruiting or becoming absent in different seasons, thus also helping to explain Estuary × Season interaction. For example, *A. butcheri* was only present in Beaufort in summer and Normans in spring (Figure 3.37).

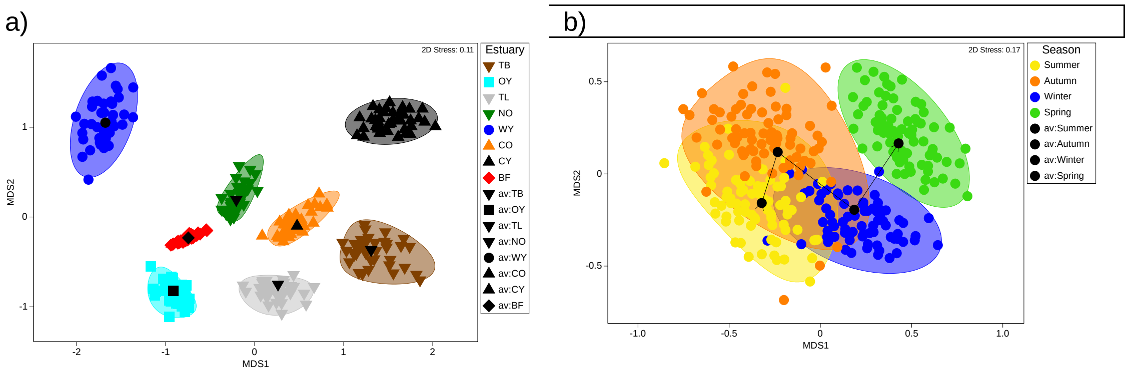

Figure 3.36. Bootstrapped mMDS ordination plots for (a) estuary and (b) season, calculated from a Bray-Curtis resemblance matrix of the transformed catch rate of each offshore fish species in each sample. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

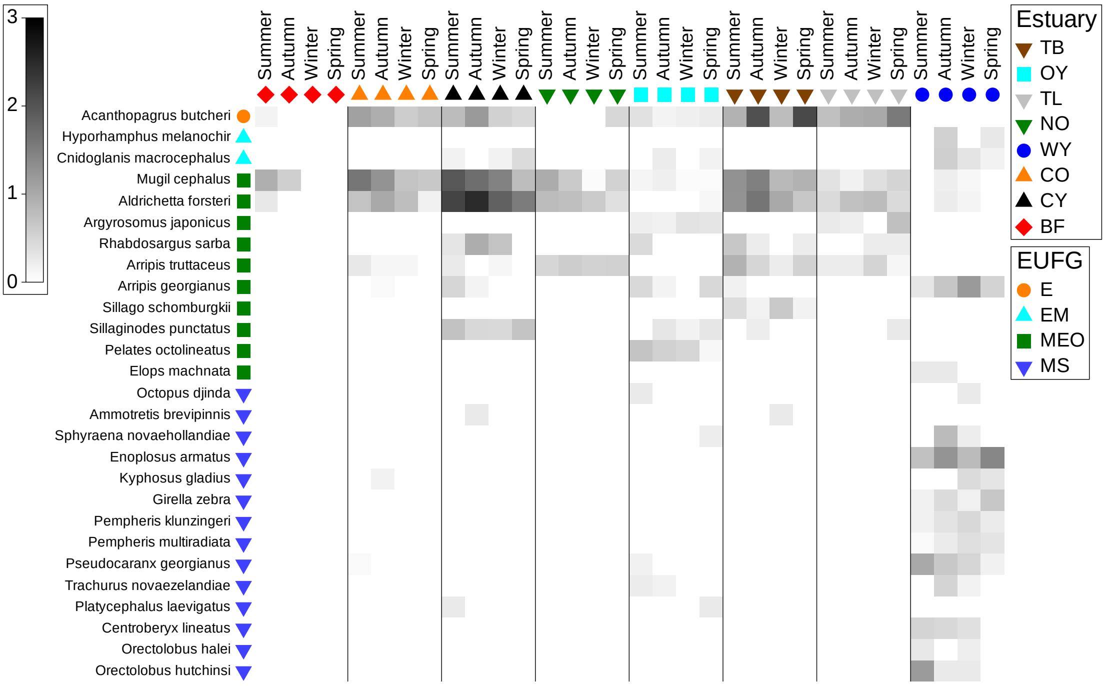

Figure 3.37. Shade plot of the dispersion-weighted and square-rooted catch rate (h^{-1}) of the fish species found in at least two samples from at least one estuary. Shading intensity is proportional to catch rate. Samples (*x* axis) ordered by season within an estuary and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9. TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

Relationships between fish composition and environmental variables

The relationships between each environmental variable individually and the fish fauna was examined by subjecting data averaged for each season in each estuary to BEST. This analysis determined that the number of days that the bar was open had the strongest correlation (ρ = 0.402), followed by salinity (ρ = 0.355), dissolved oxygen (ρ = 0.159), temperature (ρ = -0.095) and the number of bar breaks (ρ = -0.024). However, the suite of variables that best matched the fauna were a combination of the number of days open and salinity (ρ = 0.518; P = 0.001). The significant correlation was due to those estuaries with the most distinct fauna, *i.e.*, Waychinicup and Oyster and two seasons in Beaufort having the most and least extent of connectivity, respectively (Figure 3.38). Salinity helped to distinguish the remaining five estuaries, with values in Normans (lowest), Cordinup (intermediate) and Cheyne (highest in this cluster) in a linear trend in increasing salinity from right to left.

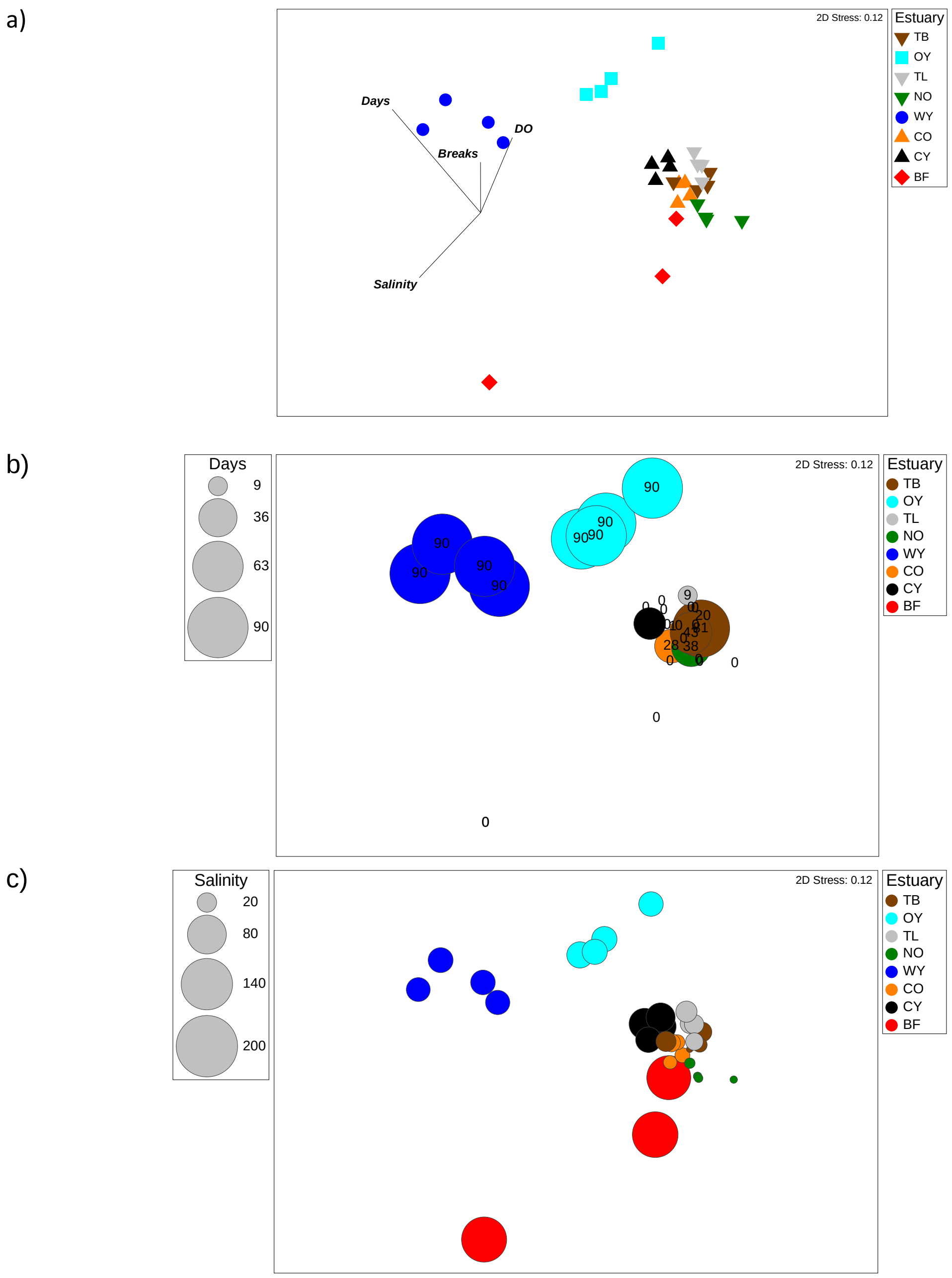

Figure 3.38. nMDS plots of the offshore fish fauna overlaid with (a) vectors representing the relationship of and environmental variables bubble of proportionate size to show differences in (b) days open and (c) salinity. Note, values added to (b) to highlight those season and estuary combinations where the bar remained closed (*i.e.*, 0 days open). TB = Torbay; OY = Oyster; TL = Taylor; NO = Normans; WY = Waychinicup; CO = Cordinup; CY = Cheyne; BF = Beaufort.

3.5.3 Intra-estuarine differences

Torbay Inlet

A total of ten species were caught in Torbay, with eight being marine estuarine-opportunists that contributed 43% of the total catch, due mainly to *M. cephalus* (Table 3.9). The remaining 57% of the catch comprised the solely estuarine species *A. butcheri*. Both *A. butcheri* and *M. cephalus* were caught in every sample, followed by *A. forsteri* (94%) and *A. truttaceus* (69%; Table 3.8).

Neither the number of species nor total catch rates differed significantly among seasons (Table 3.11). The mean number of species ranged from 3.8 in spring to 5.6 in summer and catch rates from <80 fish h^{-1} in winter to >155 fish h^{-1} in autumn (data not shown). A significant difference was detected, however, for Simpson's index (Table 3.11), with the only significant pairwise differences occurring between spring (0.31) and winter (0.66; *P*= 0.035; Figure 3.39).

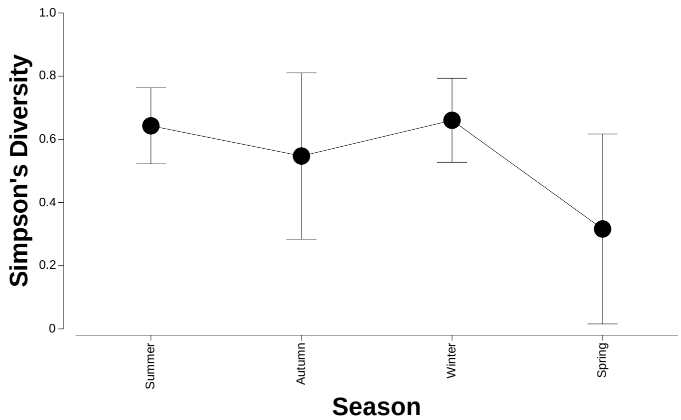

Figure 3.39. Mean and ± 95% confidence limits of Simpson's diversity among seasons in Torbay Inlet.

Table 3.11. Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS), pseudo-F ratios (pF) and significance levels (*P*) from one-way PERMANOVA tests on univariate measures of diversity and the composition of the offshore fish fauna in each of the eight estuaries with season. *df* = degrees of freedom. Significant results with a %MS ≥ 10% shaded in grey.

Torbay		**Number of Species**				**Total catch rate**				**Simpson's diversity**				**Faunal composition**			
Source	**df**	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***	**MS**	**%MS**	**pF**	***P***
Season	3	2.92	60.34	1.52	0.296	1.08	73.05	2.7103	0.088	0.10	84.1	5.29	0.016	4.21	69.57	2.29	0.032
Residual	12	1.92	39.66			0.4	26.95			0.02	15.9			1.84	30.43		
Oyster																	
Season	3	5.73	67.4	2.07	0.177	0.17	30.4	0.44	0.780	0.03	24.39	0.32	0.754	1.3	46.51	0.87	0.665
Residual	12	2.77	32.6			0.4	69.6			0.11	75.61			1.5	53.49		
Taylor																	
Season	3	1.75	53.16	1.14	0.413	0.46	60.79	1.55	0.255	0.03	35.13	0.54	0.635	1.32	51.33	1.05	0.384
Residual	12	1.54	46.84			0.3	39.21			0.06	64.87			1.25	48.67		
Normans																	
Season	3	0.75	62.07	1.64	0.365	0.55	84.9	5.62	0.025	0.09	71.66	2.53	0.114	1.03	62.64	1.68	0.088
Residual	12	0.46	37.93			0.1	15.1			0.04	28.34			0.61	37.36		
Waychinicup																	
Season	3	21.06	80.49	4.13	0.037	0.22	52.48	1.1	0.392	0.09	64.46	1.81	0.170	6.05	58.06	1.38	0.028
Residual	12	5.10	19.51			0.2	47.52			0.05	35.54			4.37	41.94		
Cordinup																	
Season	3	0.73	50.00	1.00	0.488	1.07	82.21	4.62	0.033	0.03	62.64	1.68	0.225	1.65	60.42	1.53	0.178
Residual	12	0.73	50.00			0.23	17.79			0.02	37.36			1.08	39.58		
Cheyne																	
Season	3	2.06	62.66	1.68	0.253	0.87	91.92	11.38	0.002	0.02	55.87	1.27	0.328	3.62	65.57	1.90	0.017
Residual	12	1.23	37.34			0.08	8.08			0.01	44.13			1.90	34.43		
Beaufort																	
Season	3	3.67	91.67	11.00	0.001	4.71	96.26	25.71	0.001	0.01	66.51	1.99	0.216	0.94	86.6	6.46	0.010
Residual	12	0.33	8.33			0.18	3.74			0.00	33.49			0.15	13.4		

The overall shift in composition among seasons (Table 3.11), was due to a pairwise difference between summer and spring (P = 0.031). This is shown on the bootstrapped mMDS plot with all seasons except for spring, which is being the most distinct on the right and separate from summer towards the left (Figure 3.40). Catch rates of *M. cephalus*, *A. forsteri*, *R. sarba* and *Sillago schomburgkii* were lower in spring than in all other seasons, while the reverse was true for *A. butcheri* (Figure 3.41).

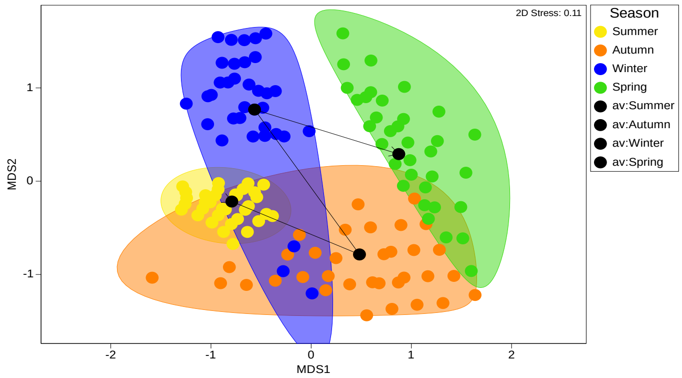

Figure 3.40. Bootstrapped mMDS ordination plots for season calculated from a Bray-Curtis resemblance matrix of the transformed catch rate of each offshore fish species in each sample from Torbay Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

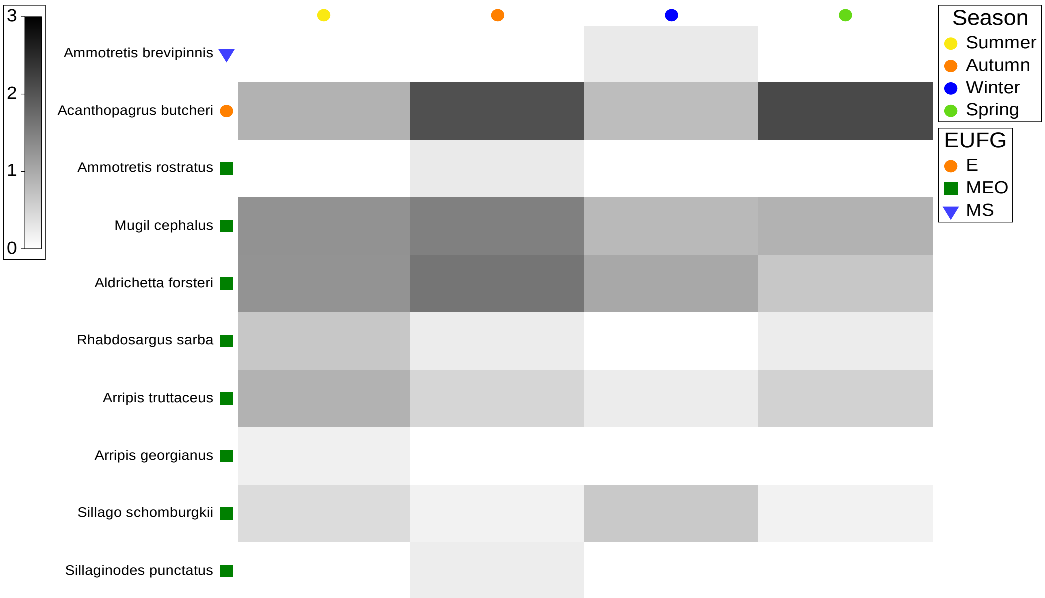

Figure 3.41. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Torbay Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Oyster Harbour

Of the 17 species found in Oyster, 88% are marine spawning species (Table 3.9). Marine estuarine-opportunists represented 47% of species and 65% to the total catch and although marine stragglers were the second most speciose guild (41%), they made a small contribution to the catch rate (6.33%, Table 3.9). The single solely estuarine species, *A. butcheri*, had the second highest catch rate (28%), followed by the marine estuarine-opportunists *P. octolineatus* (27%) and *A. georgianus* (14%). *Pelates octolineatus* was caught in half of the samples, and *A. butcheri* and *A. japonicus* appeared in 38% of samples each (Table 3.8). *Rhabdosargus sarba* and *S. punctatus* (both 25%) were the only other species to be recorded in more than a quarter of samples.

A suite of PERMANOVA tests found no seasonal differences in any of the three univariate measures of diversity (Table 3.11). Although the mean number of species increased from a minimum of 1.8 in winter, through autumn (2.8) and spring (3.8) to a maximum in summer (4.5), there was substantial variation (data not shown).

Similarly, there was no significant difference in fish communities among seasons (Table 3.11), due to the similar catch rates of four dominant species, *i.e.*, *A. butcheri*, *M. cephalus*, *A. japonicus* and *P. octolineatus*, in each season (Figure 3.42).

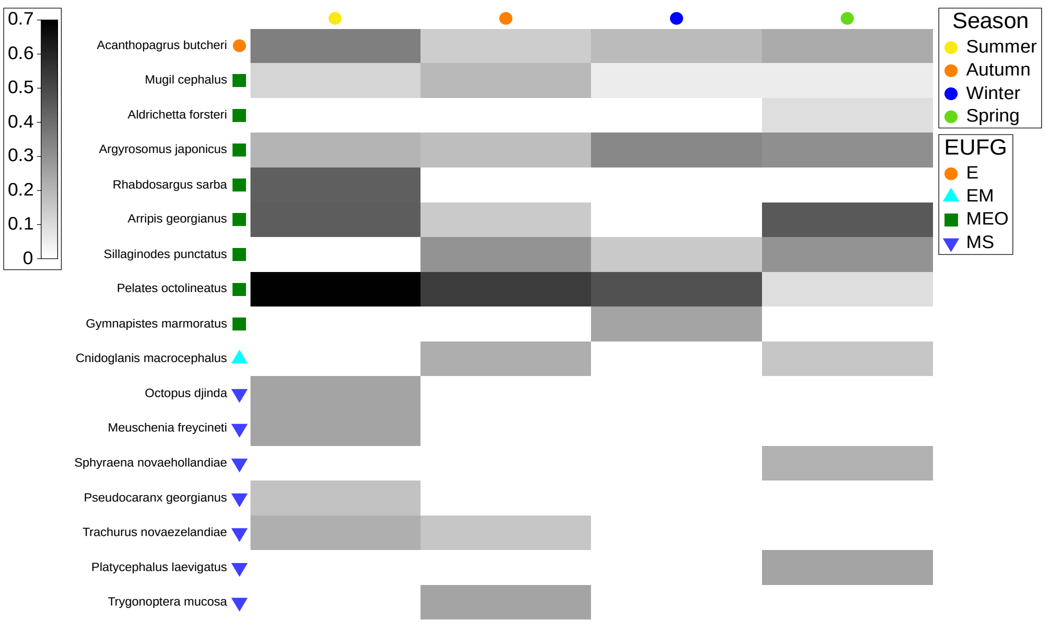

Figure 3.42. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Oyster Harbour. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Taylor Inlet

Six of the seven species (86%) recorded in Taylor were marine estuarine-opportunists and represented 30% of the total catch rate, with *A. butcheri* represented the remaining 70% and was caught in every sample (Tables 3.8,3.9). The mugilids *M. cephalus* and *A. forsteri* made the next highest contribution to catch rate (~12%, each) and were present in 69% of samples. No other species contributed >10% to the total catch rate, but *A. japonicus* and *A. truttaceus* were commonly caught (44 and 38% of samples, respectively; Table 3.10).

There were no significant seasonal differences in number of species (range = 2.75 – 4.25), total catch rate (range = 28 – 79 h^{-1}) or Simpson's diversity (range = 0.34 – 0.64; Table 3.11). Consistent catch rates of *A. butcheri*, *M. cephalus*, *A. forsteri*, *A. japonicus*, and *A. truttaceus*, which were the most abundant species, was responsible for the lack of a significant difference in faunal composition among seasons (Table 3.11; Figure 3.43).

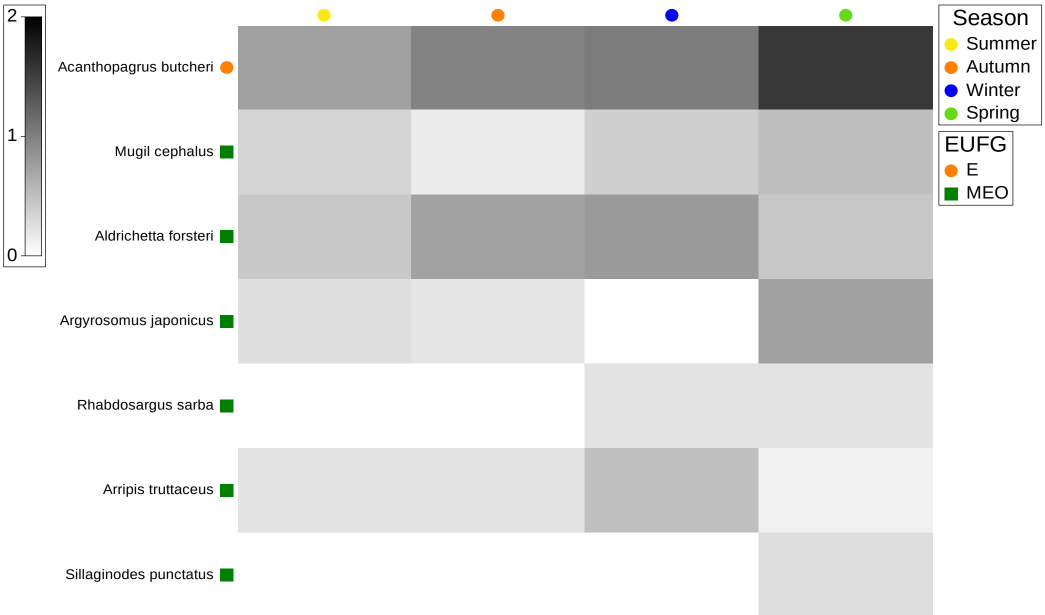

Figure 3.43. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Taylor Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Normans Inlet

Five species were caught in Normans, mainly constituting marine estuarine-opportunist species (60%), which represented 93% of the total catch rate (Table 3.9). The most frequently caught species were *M. cephalus* and *A. forsteri* (81%), with the former species being more abundant than the latter (55 *vs* 21% of the total catch; Table 3.8). *Arripis truttaceus* was caught in 69% of samples and represented 14% of all fish.

Values for the number of species and Simpson's diversity remained similar among seasons, but there was a shift in total catch rate (Table 3.11). Catches in winter (5 fish h^{-1}) were significantly lower than those in both summer and spring (19 – 32 fish h^{-1}; P <0.026; Figure 3.44).

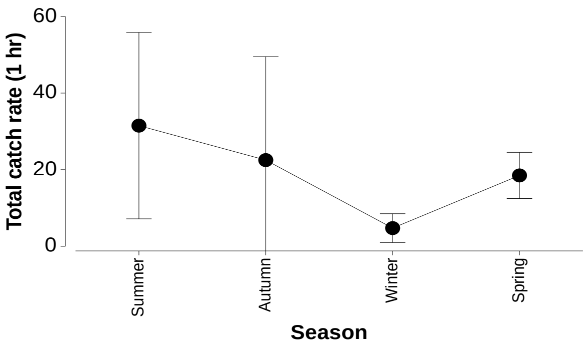

Figure 3.44. Mean and ± 95% confidence limits of total catch rate (h^{-1}) among seasons in Normans Inlet.

Likewise, faunal composition did not differ significantly among seasons (Table 3.11) due to *A. truttaceus*, *A. forsteri* and *M. cephalus* dominating the fauna and having similar catch rates in most seasons (Figure 3.45). *Acanthopagrus butcheri* and *Scorpis georgiana* were both recorded in a single season, but not in sufficient abundances to influence the fauna.

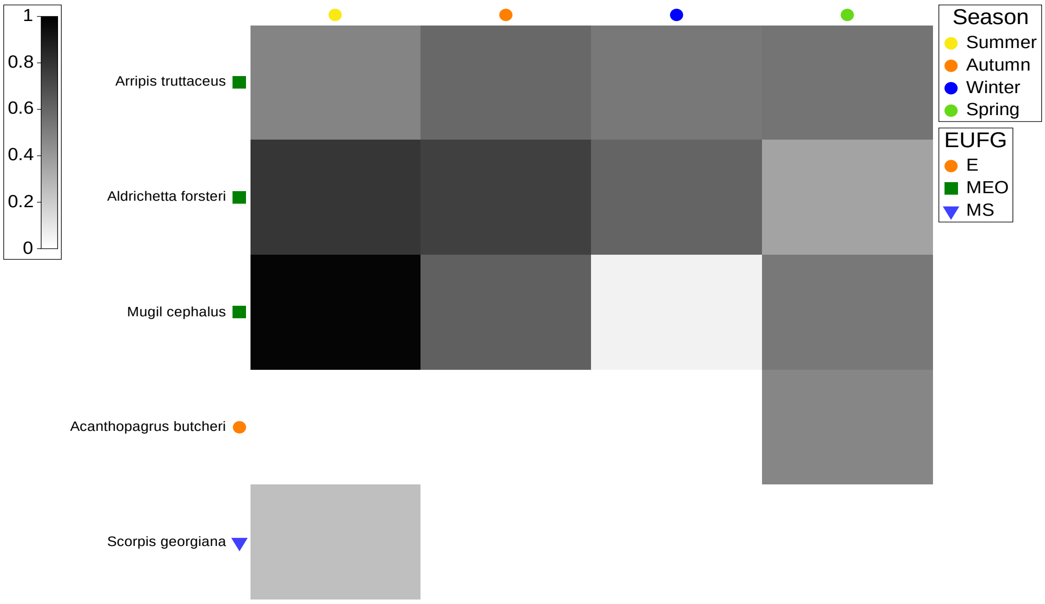

Figure 3.45. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Normans Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Waychinicup Estuary

Twenty-five of the 31 species (81%) caught in Waychinicup were marine stragglers, with these fish contributing 61% to the total catch (Table 3.9). Marine estuarine-opportunists made the next highest contribution to both number of species (13%) and catch rates (37%). Among individual species, *A. georgianus* was the most abundant (33%) and recorded in 75% of samples (Table 3.8). Only *P. georgianus* and *E. armatus* were caught more frequently (81%, each), even though the latter species only comprised 5% of all fish caught. Despite being 'stragglers' *Pempheris multradiata*, *Centroberyx lineatus*, *Girella zebra* and the elasmobranch *Orectolobus hutchinsi* were each present in 38% of samples.

The number of species differed significantly among seasons (Table 3.11), with significantly greater values in autumn (9.50) and winter (7.75) than in summer and spring (4.25 and 5.75, respectively; Figure 3.46). In contrast, neither the mean total catch rate nor Simpson's diversity differed seasonally (Table 3.11). The overall mean catch rate was 34 fish $h^{-1,}$ and the mean Simpson's diversity was 0.61.

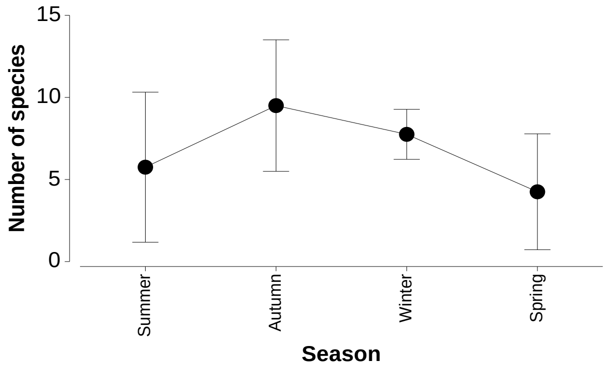

Figure 3.46. Mean and ± 95% confidence limits of number of species among seasons in Waychinicup Estuary.

The composition of the fish fauna in Waychinicup differed significantly among seasons (Table 3.11), with that in summer differing from all other seasons (P = 0.026 – 0.028). This season has the most discrete distribution on the mMDS plot (Figure 3.47).

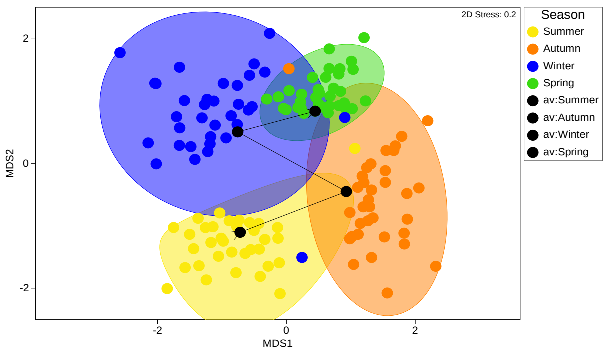

Figure 3.47. Bootstrapped mMDS ordination plots for season calculated from a Bray-Curtis resemblance matrix of the transformed catch rate of each offshore fish species in each sample from Waychinicup Estuary. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

Overall, the fauna in summer was more depauperate than in the other three seasons, with several species not caught such as *C. macrocephalus*, *M. cephalus* and *A. forsteri*, but with two species, *i.e.*, *Kyphosus cornelli*, *Levipora inops* only recorded in summer (Figure 3.48). The similarity in the autumn, winter and spring is due to the relatively high catch rates of *E. armatus*, *G. zebra*, *P. klungzingeri*, *P. multiradiata*, *P. georgianus* and *A. georgianus.*

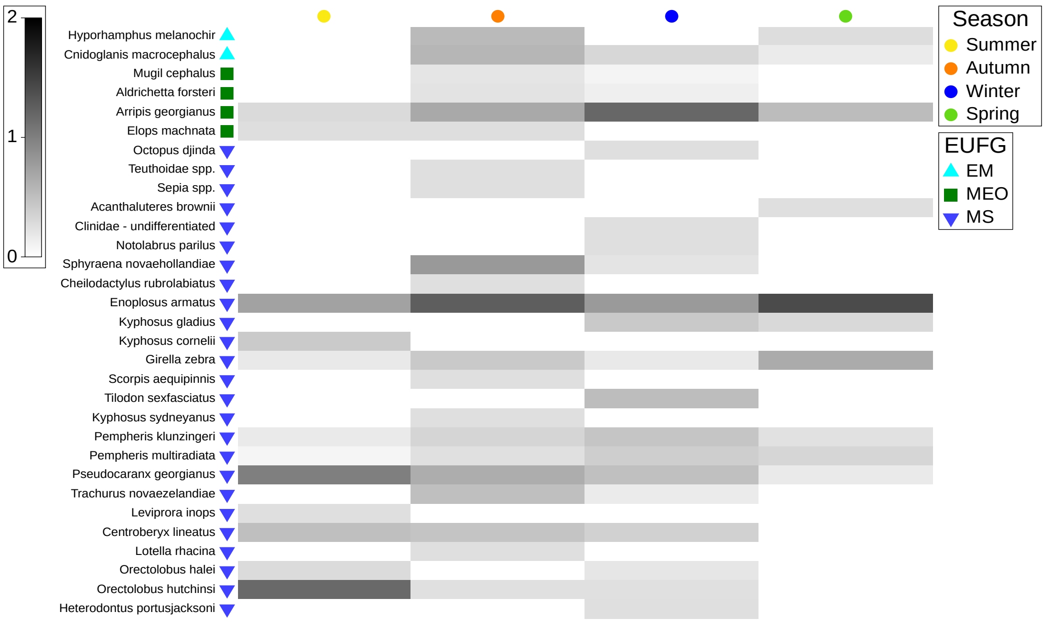

Figure 3.48. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Waychinicup Estuary. Shading intensity is proportional to density. Samples (x axis) ordered by region and season and species (y axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Cordinup River

Marine-spawning species represented 86% of the species recorded in Cordinup, with marine estuarine-opportunist species contributing 70% and marine stragglers 0.57% to the total catch rate (Table 3.9). *Mugil cephalus* was the most abundant species (59% of all fish) and was caught in every sample (Table 3.8). *Acanthopagrus butcheri* and *A. forsteri* represented 29% and 11% of the individuals recorded and were recorded in 100% and 69% of the samples, respectively (Table 3.8).

Both number of species (range = 2.5 – 3.5) and Simpson's diversity (range = 0.42 – 0.58) did not differ significantly among seasons (Table 3.11). There was, however, a difference in total catch rate, with pairwise comparisons showing catches were greater in summer (109 fish h^{-1}) than spring (25 fish h^{-1}; P = 0.031; Figure 3.49).

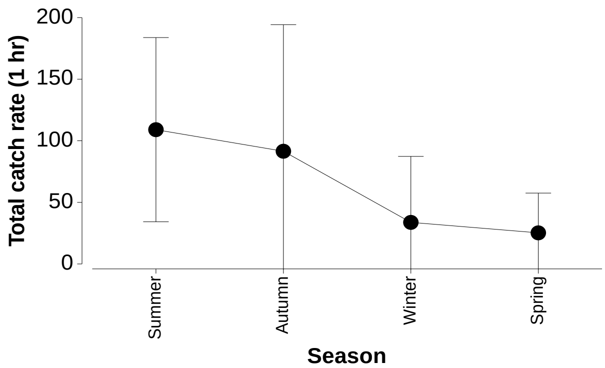

Figure 3.49. Mean and ± 95% confidence limits of total catch rate (h^{-1}) among seasons in Cordinup River.

The composition of the fish fauna in Cordinup remained relatively consistent (Table 3.11). This is due to the similar catch rates of the three most abundant species, *i.e., A. butcheri*, *M. cephalus* and *A. forsteri* across all seasons (Figure 3.50). Several species were caught in only one season *e.g.*, *K. gladius*, *A. georgianus* and *P. georgianus* but only in very small numbers.

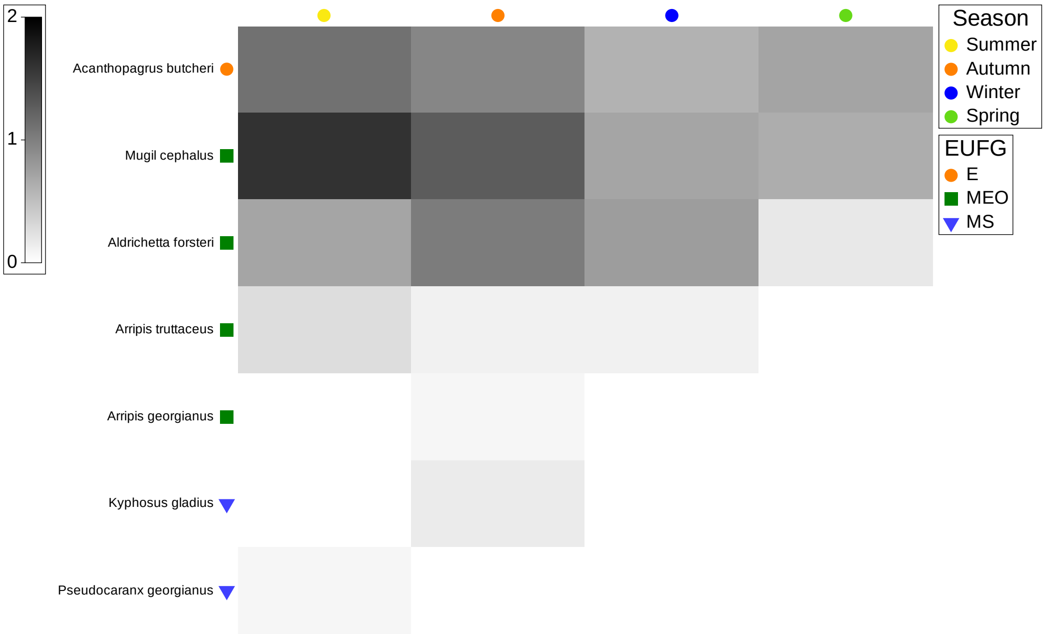

Figure 3.50. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Cordinup River. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Cheyne Inlet

This estuary was dominated by marine estuarine-opportunists, that combined represented 58% of all species and 85% of all fish (Table 3.9). *Mugil cephalus, A. forsteri and A. butcheri* were present in all samples, however made very different contributions to the total catch rates, *i.e.*, 52, 29 and 15%, respectively (Table 3.8). Although *S. punctatus*, *R. sarba*, *A. georgianus* and *C. macrocephalus* were not abundant, each was recorded in between 25 and 63% of samples.

The only seasonal difference in the univariate measures of diversity was with total catch rate (Table 3.11). Catches in spring (47 fish h^{-1}) was significantly lower (all P <0.026) than in all the other seasons (range = 94 – 164 fish h^{-1}; Figure 3.51).

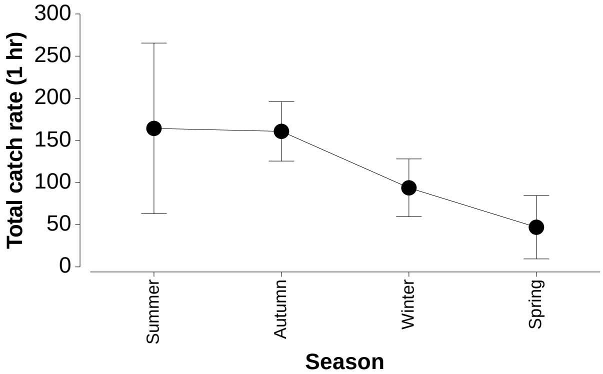

Figure 3.51. Mean and ± 95% confidence limits of total catch rate (h^{-1}) among seasons in Cheyne Inlet.

The composition of the fish fauna in Cheyne differed among seasons (Table 3.11), with the only significant pairwise comparison being spring with both summer and autumn (P = 0.027). While this season overlapped with the broad group of winter, it was widely separated from summer and autumn (Figure 3.52). The fauna in spring did not contain species such as *R. sarba*, *A. truttaceus*, *A. georgianus*, *Ammotretis brevipinnis* and *Platycephalus laevigatus* that were caught in both summer and autumn. Moreover, *Platycephalus speculator* and *Pomatomus saltatrix* were only recorded in spring (Figure 3.53).

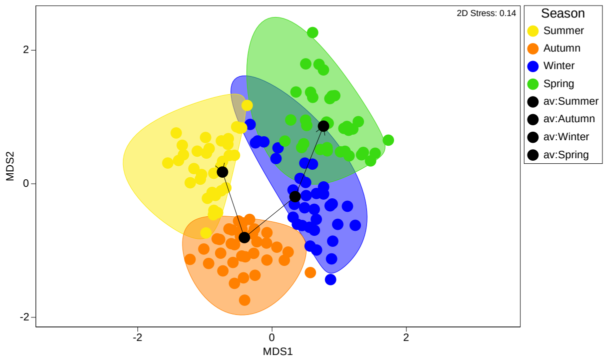

Figure 3.52. Bootstrapped mMDS ordination plots for season calculated from a Bray-Curtis resemblance matrix of the transformed catch rate of each offshore fish species in each sample from Cheyne Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown.

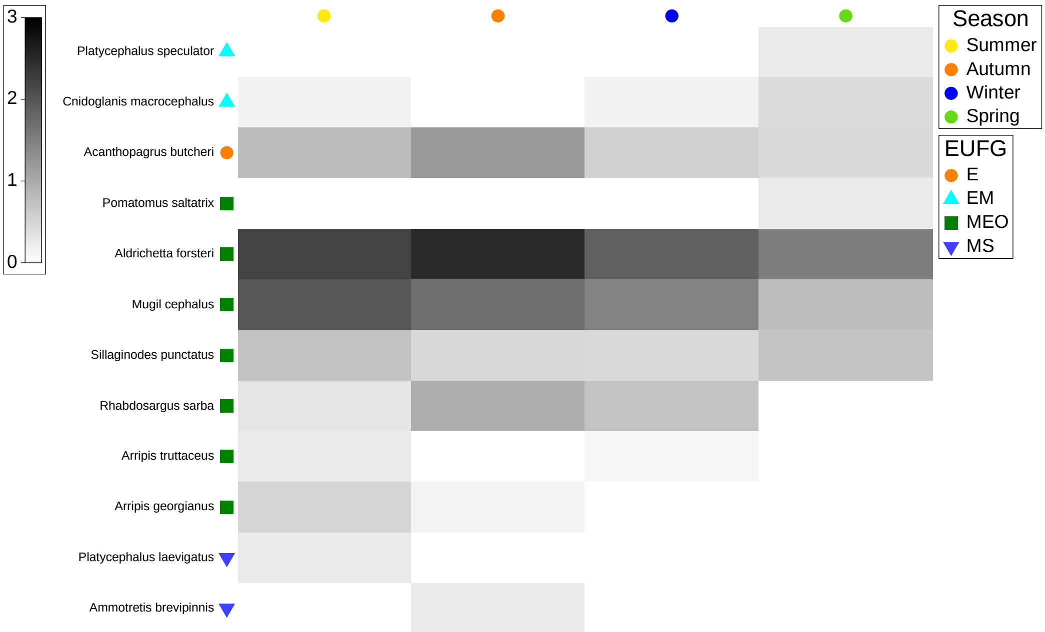

Figure 3.53. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Cheyne Inlet. Shading intensity is proportional to density. Samples (x axis) ordered by region and season and species (y axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Beaufort Inlet

Only three species were recorded in Beaufort, with the marine estuarine-opportunist *M. cephalus* representing 94% of all fish caught. This species was the most frequently caught, however, it was only present in 50% of samples (Table 3.8). Both the number of species and total catch rate differed markedly with season (Table 3.11). On average two species, representing 30 fish h^{-1} were recorded in summer, followed by one species with a catch rate of 9 fish h^{-1} in autumn after which no fish were recorded (Figure 3.54b). This is also reflected in the faunal composition where the significant difference was caused by *A. butcheri*, *A. forsteri* and *M. cephalus* being recorded in summer, only the last species present in autumn and no fish in the remaining two seasons (Figures 3.55, 3.56). Large numbers of deceased *A. butcheri* were observed washed up on the banks of the estuary in autumn and the same was true for *M. cephalus* in winter. Full description is given in (Supplementary Material 2).

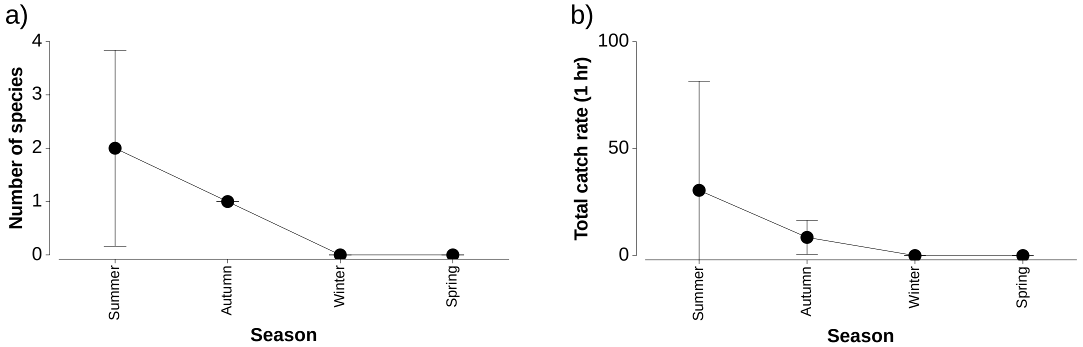

Figure 3.54. Mean and ± 95% confidence limits of total catch rate (h^{-1}) among seasons in Beaufort Inlet.

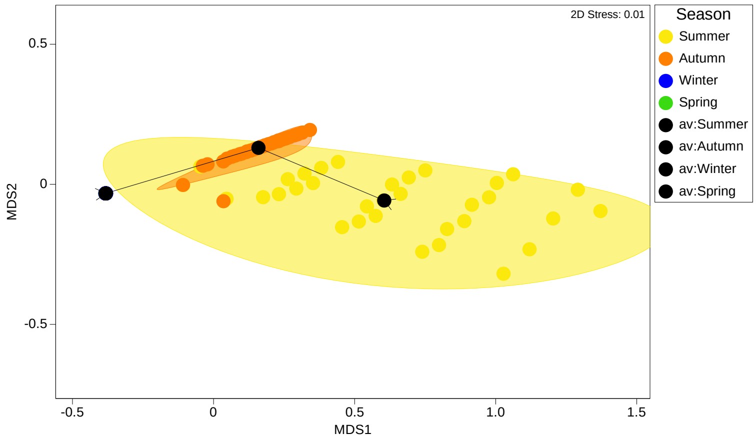

Figure 3.55. Bootstrapped mMDS ordination plots for season calculated from a Bray-Curtis resemblance matrix of the transformed catch rate of each offshore fish species in each sample from Beaufort Inlet. Group averages (black symbols) and 95% confidence regions (shaded areas) are also shown. Note no confidence regions for winter or spring as no fish were caught in any net in those seasons.

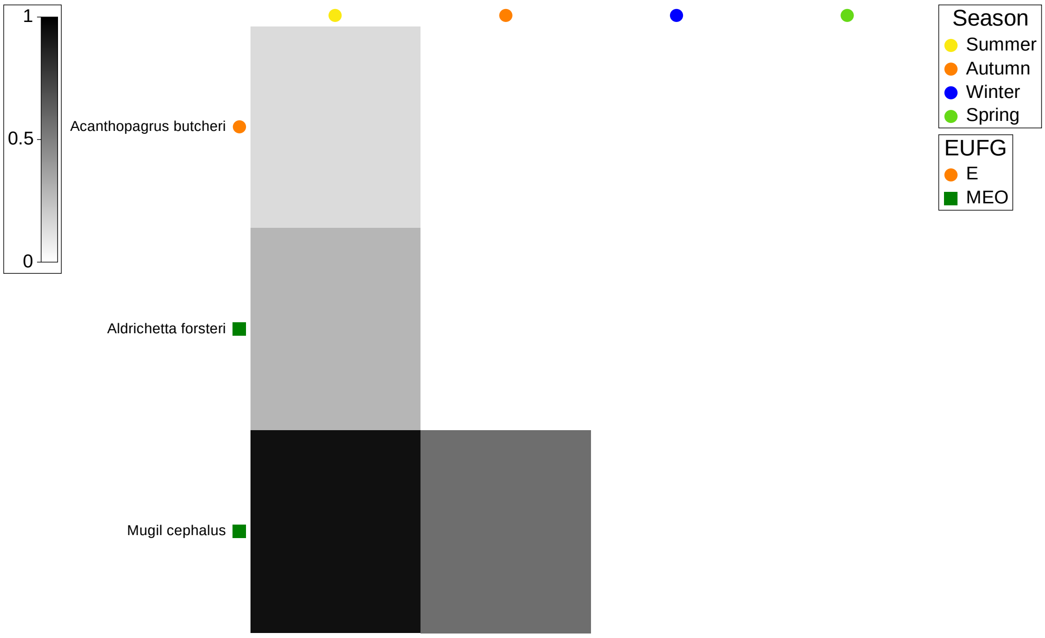

Figure 3.56. Shade plot of the dispersion-weighted and square-root transformed catch rate (h^{-1}) of each fish species found in Beaufort Inlet. Shading intensity is proportional to density. Samples (*x* axis) ordered by region and season and species (*y* axis) seriated and then constrained by their EUFG. EUFG codes given in Table 3.9.

Chapter 4. Discussion

This study has provided some of the first quantitative data on the fish faunas of the nearshore and offshore waters of eight estuaries in the Albany region on the south coast of Western Australia. It has investigated how the fish faunas in these systems differ from each other and are influenced by season, “bar status” (*i.e.*, open or closed), and physio-chemical variables (salinity, temperature and dissolved oxygen). This greater knowledge of the estuaries and their dynamic environments is particularly important as temperate estuaries are the most degraded aquatic ecosystems in the world (Jackson et al., 2001; Kennish, 2002). This is cause for concern as they are highly productive, provide crucial nurseries and habitats for aquatic fauna and frequently support important recreational and commercial fisheries and socio-economic ecosystem services (Barbier, 2007; Barbier et al., 2011). Gaining this additional understanding in south-western Australia is particularly important as the nature of estuaries are changing with declining rainfall and associated inflow to estuaries due to climate change (Hallett et al., 2018).

4.1. Physio-chemical environment

4.1.1. Number and duration of bar openings

Two of the estuaries in this study, Oyster and Waychinicup, are permanently-open, and the other six systems opened for varying lengths of time between February and November 2020, except for Beaufort, which remained closed. Previously, the five non-permanently-open estuaries were regarded as seasonally-open, with their bar breaching only once annually and typically in winter (Brearley, 2005; Hodgkin and Clarke, 1990). The use of logger data, corroborated with local knowledge and field observations, indicated that the bar of each of these five estuaries was breached between two and seven times, in response to rainfall events, such as those in May and particularly August, where 81 mm of rain fell in a single day (Bureau of Meteorology, 2021). This latter event contributed to monthly rainfall that was 69 mm above the 1991-2020 average for Albany (Bureau of Meteorology, 2021). The results from this study have shown that those estuaries previously termed “seasonally-open” can open in any season if heavy localised rainfall occurs. Thus, the term “annually open,” *i.e.*, typically open one or more times during a year and in any season, is proposed to more accurately reflect the bar status of these systems (see also Supplementary Material 1: Literature Review).

Bar breaches are caused by a combination of the volume of water in the estuary, the height and width of the bar and the volume of fluvial discharge entering the estuary, which is influenced by rainfall and catchment area (Hoeksema et al., 2018; Ranasinghe et al., 1999;

Rich and Keller, 2013). Although Beaufort was the largest of the eight catchments, it did not breach even after the unprecedented rainfall in August. This was due to the water level being so low as a result of previous years of low flow (see Krispyn et al., 2021) and where that the sand bar was 3.5 m high and >100 m thick. However, the rainfall did result in a significant decline in salinity from ~110 to ~59 and raised water levels. While this was not sufficient on this occasion to breach the bar, it may facilitate future breaching.

The duration of bar openings is related to the amount of river flow received in the estuary and the volume of water the estuary holds before breaching (Hoeksema et al., 2018). For example, Taylor had the smallest catchment (~10 km^2), is small in surface area (0.47 km^2) and had the shortest bar opening (maximum of 5 days). Given the same rainfall, larger catchments provide greater volumes of flow, which would take longer to travel from the catchment to the estuary, and thus, provide more protracted flows, facilitating greater scouring. Therefore, once breached, such estuaries would remain open for longer. A combination of the magnitude of rainfall, catchment size, and water volume influencing bar breaches, parallels that recorded for similar estuaries in both South Africa (Slinger, 2017) and California, USA (Elwany et al., 1998).

4.1.2. Salinity, dissolved oxygen and temperature

Principle coordinate analysis determined that the main physico-chemical difference between the eight estuaries was the varying salinity. Beaufort had the highest salinity (mean = 94; maximum = 122), with values exceeding 100 present for at least six months. The extreme hyper-salinity in Beaufort was due to below-average rainfall in 2018, 2019 and, to a lesser extent, early in 2020. This led to a pronounced decrease in discharge, which, except for August 2020, was always <0.5 $m^3 s^{-1}$. During these three years, salinities at the Pallinup River gauging station, located 34 km upstream from the bar of the estuary, typically increased, rising from 15 in January 2018 to a maximum of 81 in February and 53 in June 2020. Salinities in the river declined to ~32 after August 2020, following the heavy rainfall in the region (Krispyn et al., 2021). Therefore, all the ‘freshwater’ that the Beaufort Inlet received from its river was saline and even hypersaline at times, which explains why salinity in Beaufort only decreased to 60 in the estuary after August 2020. Cheyne Inlet was the only other estuary to record hypersaline conditions (54 in summer), declining to less than 40 in spring.

Salinities over 100 have only been recorded in a small number of estuaries *e.g.*, Laguna Madre (USA), St Lucia and Groen (South Africa), Casamance and Sine-Saloum (Senegal) and Coorong, Culham, Hamersley, Gordon and Wellstead (Australia;

(Australia; Tweedley et al., 2019b; Wooldridge et al., 2016). These systems are generally shallow and located in areas with low and/or highly seasonal rainfall, low tidal ranges, high rates of evaporation and are regarded as normally-closed (see Supplementary Material 1: Literature Review; Tweedley et al., 2019b). The fact that south-western Australia has become a global hotspot for hypersaline systems reflects increases in air temperatures, evaporation rates and decreasing rainfall due to climate change and secondary salinisation (Hallett et al., 2018).

Normans had the lowest mean salinity (~4), which was stable throughout the study. This low salinity is thought to be related to the shallow depth of the basin relative to sea level (K. Krispyn, personal observations, Hodgkin and Clarke (1990)). Thus, any flow flushes out any remaining saline water and prevents increases in salinity due to evapoconcentration.

Hypoxia, *i.e.*, dissolved oxygen concentrations <2 mgL^{-1}, is known to occur in south-western Australian estuaries (Kurup and Hamilton, 2002; Tweedley et al., 2014a; Tweedley et al., 2016a) and can influence the biology and ecology of the fish communities (Cottingham et al., 2018; Watsham, 2016). However, no hypoxia was detected in the nearshore waters, likely due to the shallow basins that are well mixed by the wind and so are not stratified. While these values were obtained during the day when oxygen values are greatest (Tweedley et al., 2019a), additional sampling done at night at the surface and bottom of the water column only rarely detected hypoxic conditions and no anoxia (Krispyn, K., Murdoch University, unpublished data). Temperatures did not differ among estuaries and changed seasonally as is expected of a Mediterranean climate.

4.2. Nearshore fish communities

4.2.1. Inter-estuarine differences

As hypothesised, the characteristics of the nearshore fish faunas were distinctly different across the eight estuaries, however, all were dominated by estuarine residents from the Atherinidae (*e.g., Atherinosoma elongata* and *Leptatherina wallacei*) and Gobiidae (*e.g., Pseudogobius olorum*). These three species collectively represented 79% of the fish recorded in all estuaries. The dominance of these species is typical for the shallow waters of estuaries in south-western Australia, particularly in those that become disconnected from the ocean for periods by a sand bar (Hoeksema et al., 2009; Valesini et al., 2014). Moreover, species in these two families also dominate the shallow water fish fauna elsewhere in temperate Australia (Connolly, 1994; Griffiths, 2001; Molsher et al., 1994;

Pollard, 1994) and in southern Africa (Bennett, 1989; Harrison and Whitfield, 2008; Potter et al., 1990).

Atherinosoma elongata, *L. wallacei* and *P. olorum* have a short life cycle of around a year and complete their life cycles within estuaries (Gill et al., 1996; Prince and Potter, 1983). Thus, unlike marine species, individuals in these estuarine populations do not need to migrate from the estuary to the ocean to reproduce (Gill et al., 1996; Potter and Hyndes, 1999) and are therefore able to dominate estuaries that become disconnected to the ocean. The high abundances of each atherinid and gobiid species in the broad range of salinities present in the eight estuaries over this study highlight the adaptation of these species to these environments and their tolerance to changing physio-chemical conditions (Potter and Hyndes, 1999; Potter et al., 2015a). These species were found in far greater abundances in the five annually-open (Cheyne, Taylor, Normans, Cordinup and Torbay), than two permanently-open (Oyster and Waychinicup) systems. The high densities of *A. elongata*, *L. wallacei* and *P. olorum* is related to the higher accumulation of nutrients in annually-open estuaries due to the longer water residency time than permanently-open estuaries, which can be export nutrients out on a tidal cycle or riverine flow (Ranasinghe et al., 1999; Tweedley et al., 2016b). *Ruppia megacarpa* are one of the species that utilise the high nutrients in the annually-open estuaries and very substantial growths occurred in these systems (Newman, D., Murdoch University, unpublished data; Brearley, 2005). *Ruppia megacarpa* has been shown to be an important habitat and source of prey for *A. elongata*, *L. wallacei* and *P. olorum* and often support higher densities of fish (Humphries and Potter, 1993; Humphries et al., 1992; Pollard, 1994).

Although the nearshore fish faunas were dominated by estuarine residents, they only constituted a small percentage of the total number of species due to the small number of estuarine species locally (Potter et al., 2016; Valesini et al., 2014). Conversely, marine species constituted 83% of the total number of species. Thus it is not surprising that the permanently-open Waychinicup (58) and Oyster (36) contained a far greater number of species than the annually-open estuaries (4–19) and the normally-closed Beaufort (3). Other studies in south-western Australia have reported the same pattern (Hoeksema et al., 2009; Potter et al., 2015b; Tweedley et al., 2017), as have studies in South Africa (Harrison and Whitfield, 2008; Whitfield, 1980). The greater connectivity of permanently-open estuaries increases their potential for marine spawning species to recruit into these systems. For example, the number of marine stragglers in the nearshore waters of the Peel-Harvey Estuary further north, increased from 6 (1980s) to 13 (1990s) and 23 (2000s), using an identical sampling regime due to the presence of a second permanently-open entrance channel and increased salinities (Potter et al., 2016). Furthermore, the presence of stenohaline marine species in permanently-open estuaries is facilitated by their relatively stable salinities (Aguilar-Medrano et al., 2019; Harrison, 2004).

The increased number of species in permanently-open estuaries may also be related to the typically greater diversity of habitats, *e.g.*, seagrass beds or rocky algal reefs, particularly near the clearer waters of the entrance channel (Claridge et al., 1986; Lefcheck et al., 2019; Whitfield et al., 2022; Whitfield, 2017). For example, Waychinicup and Oyster, which contain extensive *Posidonia* beds (Phillips and Lavery, 1997; Thomson, 2018), harboured 41 and 17 marine straggler species, respectively, most of which were associated with seagrass. Seagrass is integral to providing habitat and food for these species (Whitfield, 2017). The most abundant species in these two estuaries was the estuarine & marine *L. presbyteroides* that were either absent or present in very low densities in the annually-open estuaries. This species previously found to be the most abundant in Oyster Harbour (Hoeksema et al., 2009) and also in the nearby permanently-open Nornalup–Walpole Estuary (Potter and Hyndes, 1994). This species is known to occupy the downstream reaches of estuaries where salinities are relatively constant and close to those of seawater (Hoeksema et al., 2009; Prince and Potter, 1983), conditions more readily available in permanently-open estuaries.

The distinct differences in faunal composition between Waychinicup and Oyster is probably related to their very different morphologies and habitats. Waychinicup is the only fjord type estuary in south-western Australia (Hodgkin and Clarke, 1990) with a very deep entrance channel (~22 m) and substrates that support a unique suite of different habitats, *i.e.*, large beds of the macroalgae *Ecklonia radiata*, granite boulders, corals, caves, sponges, and range of seagrass species (Phillips and Lavery, 1997). These habitats and the diversity of depths were found to support species that have rarely or never been caught in estuaries before *e.g.*, *Centroberyx lineatus* (Chubb et al., 1979). Moreover, systems with deep, wide mouths tend to contain more species, possibly due to possessing deeper open water channels allowing greater tidal exchange, hence more larval recruitment from the ocean and a greater diversity of habitats (Blaber, 2008; Horn and Allen, 1976; Whitfield, 2019).

Normans and Beaufort were the most depauperate estuaries, with both containing a single species in three of the four seasons, a total of four and three species, respectively. The low diversity in Beaufort was caused by the extreme hypersalinity. Such environments are among the harshest for survival due to the osmoregulatory challenges they pose to aquatic fauna (Brauner et al., 2012; Gonzalez, 2012). Of the three species recorded in Beaufort, only a total of three individuals of *Mugil cephalus* and *Aldrichetta forsteri* were recorded, leaving only the solely estuarine species *A. elongata.* This species dominated the nearshore waters, being caught throughout the study and was the only fish species caught in winter and spring, due to the deaths of the other species. This atherinid is very euryhaline and has been recorded in salinities of 122 in Wellstead Estuary, ~30 km west of Beaufort (Young and Potter, 2002). Moreover, its congener *Atherinosoma microstoma* was found in salinities of 160 in the Coorong Lagoon, South Australia (Wedderburn et al., 2016). A negative relationship between the number of species and magnitude of hypersalinity, like that in Beaufort, has been documented in estuaries in the USA, South Africa and an Australian salt pond as species die when their tolerances are exceeded (Molony and Parry, 2006; Tweedley et al., 2019b; Whitfield et al., 2006).

In contrast to Beaufort, the salinity in Normans is predominantly oligohaline and only *L. wallacei* was recorded until the bar breached before spring. This species is known to be abundant in regions of low salinity and can breed in estuaries and freshwater environments (Prince and Potter, 1983). It is not known whether the paucity of species recorded in Normans during the current study is typical for this and for other small oligohaline estuaries in south-western Australia. However, these results parallel the findings from a study of larval fish in Normans in 2003 and 2004 when salinities ranged between 10–50 (Close, 2008). While eight species were recorded, *L. wallacei* represented 96% of all fish caught followed by *Galaxias occidentalis* and *P. olorum* (2% each), both of which can complete their lifecycle in freshwater. The most likely cause of the lack of other estuarine species in Normans is that the salinities were consistently low throughout 2020. Under these conditions, the osmoregulatory costs are too great for eggs and early larval stages of euryhaline estuarine species such as *A. butcheri* (Hassell et al., 2008; Nicholson et al., 2008; Partridge and Jenkins, 2002).

Atherinids were abundant in all estuaries, except Cordinup, which is anomalous as these species are typically very abundant in south-western Australian estuaries (Potter and Hyndes, 1999). A possible explanation for their absence in Cordinup could be that large parts of the small catchment have been cleared to create a blue gum plantation, which has altered the water quality in the Cordinup river. Stewart (2011) found that the rivers in blue gum plantations in south-western Australia had lower diversity and densities of invertebrates than corresponding systems. The diet of atherinid *A. elongata* in Wilson Inlet comprised predominantly the shrimp *Palaemonetes australis* (Humphries and Potter, 1993), yet this and similar species of crustacean were not recorded in the seine nets samples from Cordinup but were in most other estuaries sampled (K. Krispyn, personal observation). It is hypothesised that food limitation may have played a role in the absence of atherinids, which feed mainly on invertebrates (Humphries and Potter, 1993; Poh et al., 2018; Prince et al., 1982). As the goby *P. olorum*, which was abundant in Cordinup, is a detritivore it would not be affected in the same way as the atherinids (Gill and Potter, 1993; Humphries and Potter, 1993).

Salinity and the duration of bar opening (*i.e.,* extent of connectivity with the ocean) were identified as the biggest environmental factors influencing the nearshore fish fauna. Among the annually-open estuaries, Taylor had the lowest number of days of water exchange with the ocean and the lowest number of species with no marine straggler species recorded. In contrast, Torbay had the higher connectivity with the ocean and yielded more species. The status of bar opening was also found to be the single most important factor influencing the composition of the fish fauna in ten estuaries in the Eastern Cape Province (South Africa; Vorwerk et al., 2003). The longer connectivity is thought to also provide a better immigration opportunity for marine species, but salinity also plays a crucial role. In general, prior to a bar breaching, freshwater fills the river and estuary and so, when the bar breaks, the parcels of freshwater fill the estuary before reaching the ocean. This lowers salinity in the estuary for a period of time, potentially inhibiting immigration from marine straggler species. This situation occurred in Torbay and only two marine straggler species were recorded, whereas more immigrated following a breach in Cheyne where salinities in the estuary were higher and a greater number of marine stragglers were recorded.

4.2.2. Seasonal differences within estuaries

The fish fauna in all eight estuaries underwent seasonal changes, albeit they varied between estuaries. For example, in Torbay and Taylor there was a decrease in number of species and density of fish during spring, while the reverse was true in Normans, Waychinicup, Cordinup and Cheyne. Seasonal changes in the fish faunas of annually-open estuaries have been related to the timing and duration of bar opening events (Bennett, 1989). Periods of bar closure prevent the immigration of marine species into these systems and reduce the diversity of species present (Hoeksema et al., 2009; Tweedley et al., 2018).

In this study seasonal changes were largely characterised by the immigration of juveniles of marine-estuarine-opportunists, in particular mugilids, which use the estuary as a nursery area. Juvenile recruits of *M. cephalus* and *A. forsteri* (<100 mm in total length and most <40 mm) were recorded in spring in all estuaries except Beaufort which remained closed throughout the study. This was expected as mugilids spawn in nearshore marine waters during winter and post-flexion larvae then migrate onshore and recruit into estuaries at between 10 and 40 mm total length (Chubb et al., 1981; Thomson, 1955, 1957; Whitfield et al., 2012). After entering the estuary they grow rapidly and move into the offshore, deeper waters as sub-adults within their first year (Chubb et al., 1981; Chuwen et al., 2009b). This latter movement provides an explanation of why only few mugilids were caught in nearshore waters in summer and autumn.

After the heavy rainfall and resultant bar breaching in winter and spring, mean fish densities declined in all estuaries, except in Taylor and Normans. This is likely driven by the flushing of small-bodied atherinid species from the estuary into marine waters. These changes, parallel findings in larger estuaries of south-western Australia such as Hardy Inlet and the Swan-Canning and Peel-Harvey estuaries (Loneragan and Potter, 1990; Loneragan et al., 1986; Prince et al., 1982; Valesini et al., 1997). The lack of this trend in Taylor could be related to the fact that the bar breaches for only short durations, possibly reducing the impact of flushing on the fish fauna. Another potential hypothesis is that increased water levels allowed fish to colonise recently inundated riparian vegetation, *e.g.*, salt-marsh, thus dispersing the fish fauna and reducing the density in a given spot. This occurs in the annually-open Vasse-Wonnerup Estuary and Hill Inlet (Tweedley et al., 2014a; Tweedley et al., 2020).

Fish densities are also influenced by extreme hypersalinity. In Beaufort, mean densities of *A. elongata* were ~270 fish 100 m^{-2} in summer and autumn but declined markedly to 18 fish 100 m^{-2} after being exposed to salinities in excess of 100 for six months. This mirrors the trend reported for its congener *A. microstoma*, whose densities declined by

50% after prolonged exposure to waters >100 in the Coorong, South Australia (Wedderburn et al., 2016). In Beaufort, salinities decreased in spring, around the spawning time of *A. elongata* (Prince and Potter, 1983) and consequently mean densities increased greatly to 850 fish 100 m^{-2}.

Acanthopagrus butcheri, which was typically commonly caught throughout the study, was absent or occurred in very low densities in winter in all estuaries. This is likely due to their movement patterns. Typically, before spawning in late autumn and early spring, *A. butcheri* move into the upper regions of estuaries (Sakabe and Lyle, 2010; Sarre and Potter, 1999). As these species rarely leave estuaries, it is proposed these fish moved to upstream spawning areas that were beyond the upper limit of sampling, which was inhibited by the presence of in water vegetation and snags.

4.2.3. Regional differences within estuaries

Regional differences in fish fauna were found in six of the eight estuaries, *i.e.,* all except the annually-open Normans or the normally-closed Beaufort. In those estuaries with regional differences, marine species were confined to only the lower regions in annually-open and lower and basin regions in permanently-open estuaries, while species with estuarine and freshwater affinities were more abundant in the upper regions. This distribution has primarily been related to changes in salinity, with stenohaline marine species limited to the high salinity areas of the lower reaches of the estuary and euryhaline estuarine species partitioning their distribution along the salinity gradient (Hogan-West et al., 2019; Loneragan et al., 1989; Loneragan et al., 1986; Prince et al., 1982; Valesini et al., 2018).

The physico-chemical environment was not the sole factor influencing the distribution of species as regional differences in the fish fauna were detected in Taylor, Cordinup and Cheyne, where salinity did not vary spatially. Habitat differences, therefore, may account for the differences in composition among regions. The fish fauna in seagrass (*Ruppia megacarpa*) habitat in the nearby Wilson Inlet differed from that on the bare substratum, with the atherinids *A. elongata* and *L. wallacei* and the gobiid *P. olorum* occurring in greater densities over patchy and dense *R. megacarpa* than bare sand (Humphries and

Potter, 1993). Finer sediments, *R. megacarpa* and/or decomposing seagrass and coarse woody debris was found in the upper regions of Torbay, Oyster, Waychinicup and Cordinup which would provide the preferred habitats for *P. olorum*, *A. brifrenatus, A. elongata* and *L. wallacei* (Gill and Potter, 1993; Humphries and Potter, 1993). Furthermore, in Cheyne and Taylor, *R. megacarpa* was most abundant in the lower and basin regions (Newman, D., Murdoch University, unpublished data), correlating with greater densities of those aforementioned atherinids and gobiids.

The estuaries where no regional differences were detected, *i.e.*, Beaufort and Normans, were each dominated by a single species and their physico-chemical environments were homogenous among regions within these systems. Moreover, in Beaufort the habitat, *i.e.,* bare substrate, remained consistent throughout the estuary. Thus, there is no environmental or habitat driver, nor sufficient species richness or inter-specific competition to elicit spatial partitioning (Potter et al., 2015a).

4.3. Offshore fish communities

4.3.1. Inter-estuarine differences

Overall, the majority of species recorded in the offshore waters were marine species and particularly marine stragglers. However, these species only represented 5% of the total catch, reflecting the fact that such species enter estuaries infrequently and in low numbers (Potter et al., 2015b; Whitfield et al., 2022). The contribution of marine stragglers varied markedly among estuaries, representing <1 % of the fish in annually-open estuaries to 61% in Waychinicup, which is unique for an estuary in south-western Australia with a permanently-open, wide and deep entrance channel (Hodgkin and Clarke, 1990). This and its marine-like physico-chemical environment encourage the presence of marine stragglers, compared to those permanently-open systems with narrow, shallow entrance channel and those estuaries that are annually-open or normally-closed (Tweedley et al., 2016b).

The dominance of the marine estuarine-opportunists with respect to the total catch in most systems is consistent with the findings from studies on other annually-open estuaries of south-western Australia (Chuwen et al., 2009b; Tweedley et al., 2014b) and South Africa

(Harrison and Whitfield, 2008; Whitfield et al., 2022). Marine estuarine-opportunists, such as *M. cephalus* and A. *forsteri* actively seek to immigrate in to estuaries as juveniles to make use of their productivity and facilitate rapid growth before emigrate back to the ocean as adults to spawn (Chubb et al., 1981; Whitfield et al., 2012). Given their lifecycle, the presence and/or abundance of marine estuarine-opportunists in an estuary is due, in part, to their bar status. In normally-closed estuaries, where recruitment and immigration opportunities are severely limited, estuarine species tend to dominate (Hoeksema et al., 2006a; Young and Potter, 2002). This was not the case in Beaufort, as mugilids entered the system in October 2017 (the last time the bar opened) and remained in the system out lasting the less euryhaline *A. butcheri* (Krispyn et al., 2021).

As in the nearshore waters, trends in faunal composition were significantly related to changes in salinity and the extent of connectivity with the ocean. Once again, diversity increased with salinity, as many of the species are marine and thus exhibit a preference for environmental conditions close to those found in the ocean (Chuwen et al., 2009b) and peak in those estuaries that were permanently-open facilitating immigration and emigration from a wide range of marine straggler species and providing a range of habitats, *e.g.*, rocky reefs in Waychinicup, not present in the annually-open estuaries (Hodgkin and Clarke, 1990). Diversity then declined as a result of hypersalinity, as has been reported in estuaries in Australia (Young and Potter, 2002) and elsewhere (Tweedley et al., 2019b; Whitfield et al., 2006).

4.3.2. Seasonal trends within estuaries

As in nearshore waters, any seasonal shifts in faunal composition in offshore waters, were related to the timing and duration of the bar openings, which allowed immigration and emigration of marine species. Following bar breaching in spring, catch rates decreased due to a reduction in the abundance of adult marine estuarine-opportunists that would have emigrated to their marine spawning grounds (Fairclough et al., 2000; Whitfield et al., 2012) as such species are unable to spawn in estuaries. Contrasting seasonal patterns in composition were recorded in the two permanently-open estuaries, with significant trends detected in Waychinicup but not Oyster. Seasonal differences in Waychinicup were the results of the presence of varying suite of marine stragglers that were not recorded in all seasons. This is characteristics of their lifecycle, being 'accidental' users of estuaries (Potter et al., 2015b; Whitfield et al., 2022). These species were less prevalent in Oyster, where marine estuarine-opportunists dominated catches (see also Chuwen et al., 2009b). The permanently-open nature of this system allows continuous immigration and emigration of individuals and thus the populations of these species are relatively consistent over time.

The pronounced seasonal changes in Beaufort were due to protracted extreme hypersalinity (> 100; Krispyn et al., 2021). This firstly resulted in the mass mortality of *A. butcheri*, which is known to die at salinities ~85 (Hoeksema et al., 2006b), and *A. forestri*. These species, together with *M. cephalus* were recorded in summer, with only individuals of *M. cephalus* surviving to be recorded in autumn, after which (winter and spring) no fish were recorded in the offshore water. This deleterious result was confirmed by commercial fisherman that tried fishing in Beaufort after autumn and did not catch any fish from much longer gill nets (Frank Thygesen, pers. comm.).

The successive loss of species as salinity increases in normally-closed estuary exceeding the tolerances of various species have been reported in the normally-closed Stokes, Hamersley and Culham inlets to the east of Beaufort, where mean salinities reached 64, 145 and 296, respectively (Hoeksema et al., 2006a; Tweedley et al., 2019b). A detailed explanation of the trends in Beaufort is given in Supplementary Material 2. In brief, the survival of *M. cephalus* in salinities in excess of 100 for six months, the highest salinity in which a marine species of fish has ever been recorded, is thought to be related to a suite of physiological adaptations that allow them to occupy environments from freshwater to extreme hypersaline conditions and their diet (Krispyn et al., 2021). As hypersalinity also affects invertebrate populations, reducing diversity and abundance, it limits food resources for piscivorous and zoobenthivorous fish (*e.g., A. butcheri* and *A. forestri*), however not for detritivores such as *M. cephalus*, thus they are better placed to cope with the increased metabolic costs of osmoregulation in hyperosmotic environments (Gonzalez, 2012).

4.4. Implications and future research

This study provided some of the first quantitative data on the fish communities present within eight estuaries in the Albany region on the south coast of Western Australia. It investigated the relationship between the fish community and physio-chemical variables and bar-opening regimes of those estuaries. All estuaries, even though they are located within a relatively short (130 km) stretch of coastline, were found to support a unique fish fauna, albeit they typically share a core suite of species. These findings enhance our knowledge on the fish communities of these systems and provide baseline data that are fundamental for management, particularly in regard to understanding and predicting the effects of climate change.

Results indicate that salinity and the duration of bar opening events strongly influence the fish fauna of the eight estuaries sampled in the current study. Both of these environmental variables are strongly influenced by the timing and magnitude of rainfall, which vary from year to year. Even though sampling was undertaken over essentially a year (four calendar seasons), rainfall in 2020 was higher than the average and several large storm events occurred. Thus, the salinities and profiles of the bar breaks would likely be different in other years. For example, a drier year, like Beaufort experienced in the two years prior, could result in the occurrence of hypersalinity in some of the smaller annually-open estuaries and a lower extent of connectivity with the ocean. Continuing the sampling into the future, even if it was restricted to regular water quality monitoring and the deployment of the loggers would detect bar breaches and the occurrence, magnitude and persistence of any hypersalinity.

Although the estuaries studies are located with 130 km of each other, rainfall declines eastward, with the catchment of Beaufort receiving a far lower median annual rainfall (410 mm) than the other catchments (range = 610-943; Table 2.1). As, in general, climate change in this region is forecast to reduce rainfall and flow (Hallett et al., 2018) the estuaries will be less likely to breach in the short term. Note this may change if sea-level rises to beyond the 1-2 m to exceed the height of the sand bars. Thus, there would be value in undertaking long-term monitoring using a similar methodology as applied here to conduct a space-for-time substitution approach (e.g. Blois et al., 2013; Lester et al., 2014; Pickett, 1989). This would facilitate the inference of future trajectories for these systems and their fish faunas and aid in adaptive management (Elliott et al., 2022).

The dramatic declines in the fish fauna of Beaufort, as a result of prolonged extreme hypersalinity, provide an insight of the potential future for estuaries along the southern coast of Western Australia. As, historically such hypersalinity has been an infrequent occurrence, and typically occurred in the less well-studied estuaries, there is a paucity of knowledge on its effect on the fish fauna and the environmental tolerances of key species. Moreover, little is known about the potential for these systems to recover from this defaunation. In the case of Beaufort, at the end of this study only a single species of fish and a single species benthic macroinvertebrate were present (Kyispyn et al., 2021). It would be valuable to continue to survey the fauna of Beaufort, particularly if the bar breaches, to assess the timing and duration of the breach and how this impacts the fauna and their recovery and hence determine the resilience of the ecosystems to hypersalinity. Moreover, as Beaufort is open to commercial fishing, monitoring the recruitment and immigration of fish following a breach is vital in helping inform fisheries management.

Waychinicup, with its unique geomorphology and suite of habitats, contains a very diverse and distinctive fish fauna compared with the other seven estuaries sampled in this study and, more generally, across south-western Australia (Supplementary Material 1: Literature Review). Although, the estuary is surrounded by the Waychinicup National Park, the protection stops at the high-tide mark and the system is open to recreational fishing. As Nornalup-Walpole is the only estuary on the southern coast of Western Australia formally designated as a marine park there is a paucity of protected estuarine habitat. Given the unique fish fauna present in Waychinicup and its strong cultural significance for the Menang Noongar people it would be value in considering this system as a priority for future conservation and potential designation as a Marine Protected Area.

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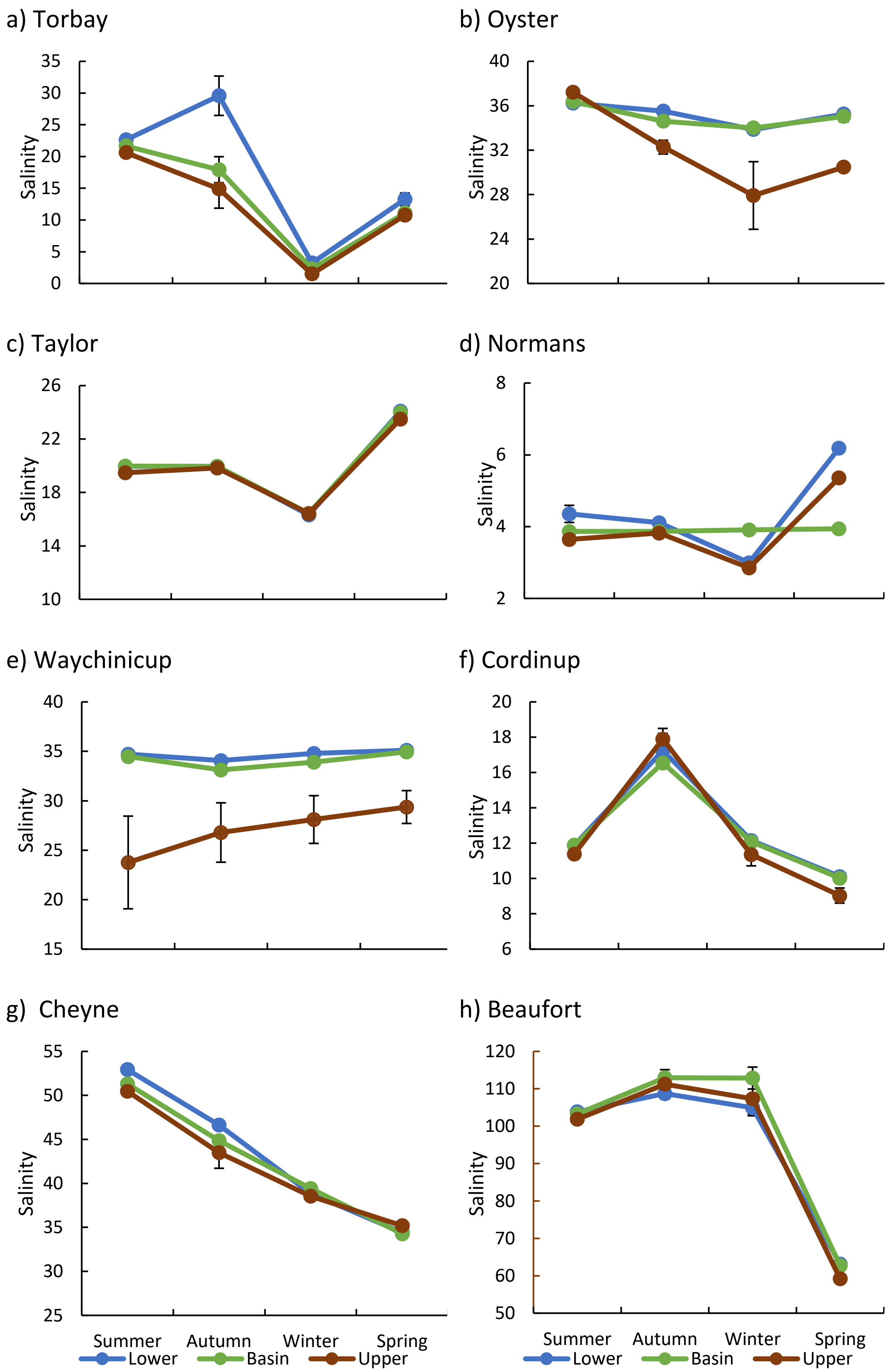
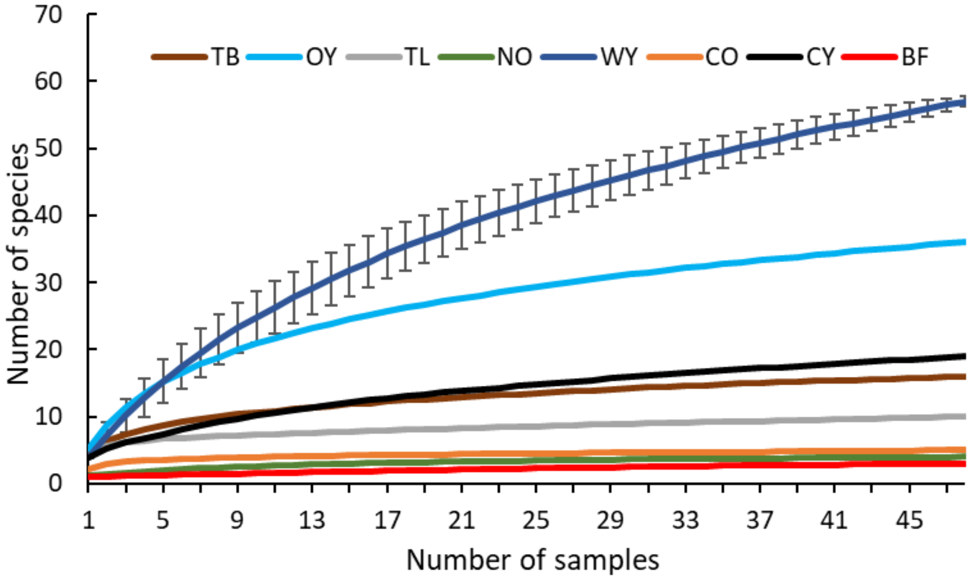
Appendices to main dissertation

Appendix 1. Mean salinity in each region of (a) Torbay, (b) Oyster, (c) Taylor, (d) Normans, (e) Waychinicup, (f) Cordinup, (g) Cheyne and (h) Beaufort in each season in 2020. Surface and bottom values were essentially the same in the offshore and therefore not shown. Error bars represent ±95% confidence limits.

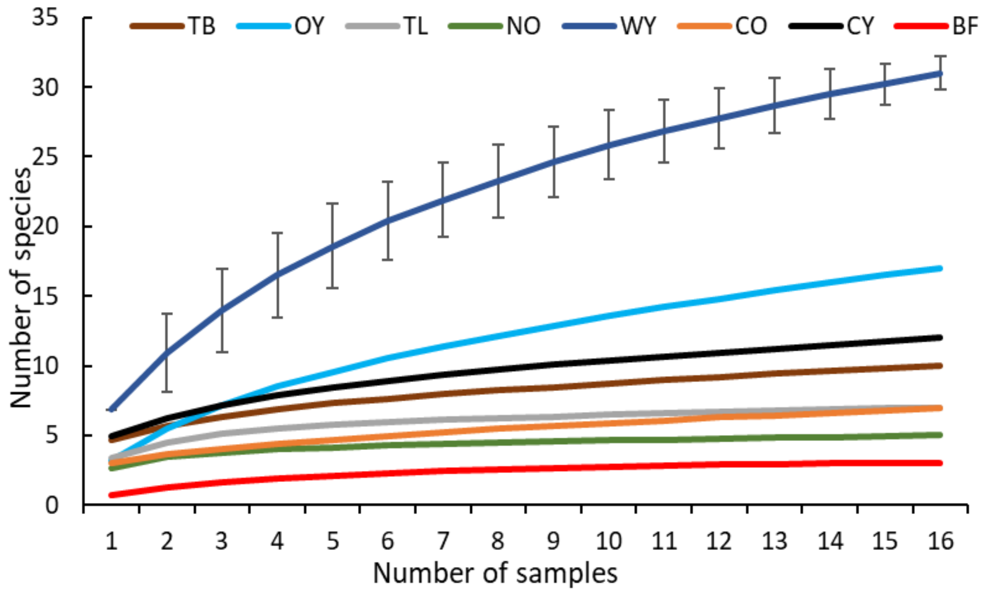


Appendix 2. Species accumulation curves for the number of species vs the number of samples for the (a) nearshore fish faunas and (b) offshore fish faunas in the eight estuaries in the Albany region, during four seasons in 2020. For clarity, the 95% confidence limits are provided only for Waychinicup as they were the most variable. TB = Torbay, OY = Oyster, TL = Taylor, NO = Normans, WY = Waychinicup, CO = Cordinup, CY = Cheyne and BF = Beaufort.

(a)



(b)



Supplementary Material 1. Literature review: Characteristics and classification of estuaries in microtidal southern Western Australia

Abstract

Estuaries are dynamic ecosystems located at the interface of freshwater and marine environments and are influenced by processes occurring in the catchment and ocean. These systems are therefore difficult to define and highly diverse, yet they support a distinct fauna and provide considerable ecosystem services. Numerous attempts have been made to classify estuaries, with most operating at the regional scale in South Africa and Australia. Classifications schemes have been developed for estuaries in south-western Australia, Victoria, New South Wales and for South Africa. This study aimed to identify all estuaries along the microtidal coastline of southern Western Australia using the literature and virtual globes. A total of 152 estuaries were identified and a suite of information on their characteristics measured and obtained from the literature. Using these data, estuaries were grouped into 10 categories, *i.e.*, ephemeral, micro-estuary, estuarine-lake, morphologically-open, permanently-open shallow, permanently-open deep, predominantly-open, annually-open basin, annually-open linear and normally-closed. These groups reflect differences in the size, shape, extent of connectivity to the ocean and permanency. The effectiveness of the proposed classification scheme was tested against four previous classification schemes using quantitative data on the physical characteristics of all 152 estuaries and, where data were available, on the fish and benthic macroinvertebrate faunas. The southern Western Australian classification performed more strongly than the schemes currently used locally, *i.e.*, estuary type and geomorphic type that focused predominantly on a single aspect of estuaries, *e.g.*, bar status and geomorphology, respectively. Moreover, they were more appropriate than schemes developed for microtidal estuaries in other parts of Australia and South Africa.

1. Introduction

Estuaries are transitional ecosystems located at the interface between freshwater and marine environments (Boyd et al., 1992; Cooper, 2001). The geomorphology of these systems and their physico-chemical environment are heavily influenced by the interaction between river flow, waves and tides (Dalrymple et al., 1992; McSweeney et al., 2017a). Estuaries provide considerable biological, social and economic values, including a range of ecosystem services, support a distinct endemic flora and fauna and play a crucial role in the life-cycle of other species (Whitfield and Elliott, 2011; Whittaker and Likens, 1975). Recent estimates using virtual globes indicate there are 53,618 estuaries globally (McSweeney et al., 2017b). The heterogeneity and global distribution of estuaries has made finding a universally appropriate definition difficult (Elliott and McLusky, 2002; Potter et al., 2010).

The American Society for the Advancement of Science addressed this problem and subsequently defined estuaries as "a semi-enclosed coastal body of water which has a free connection with the open sea, and within which seawater is measurably diluted with fresh water derived from land drainage" (Pritchard, 1967). However, it was largely based on the features of macrotidal and mesotidal systems (*i.e.*, tidal ranges of >4 m and 2-4 m, respectively) located in the northern hemisphere and did not consider estuaries that become disconnected from the marine environment for periods by the formation of a sand bar at their mouths (Day, 1980, 1981). These estuaries are typically found along microtidal coasts (tidal range <2 m) and in storm and swell wave environments (Tweedley et al., 2016b). To date, a minimum of 1,477 of such estuaries exist comprising 3% of estuaries globally (McSweeney et al., 2017b). Moreover, highly seasonal rainfall and thus flow (fluvial discharge) can cause some systems to become hypersaline (salinity >40) for extended periods (Tweedley et al., 2019b; Tweedley et al., 2016b). To include these systems in a definition of estuaries, Potter et al. (2010) defined estuaries as "a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which it receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural seawater and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible". This definition includes all systems with a well-defined river or creek that provide sufficient flow to breach any sand bar that may form at least once a decade. It thus does not include systems that are regarded as "permanently-closed", *e.g.*,, coastal salt lakes that never or rarely breach to the ocean (Hodgkin and Hesp, 1998).

In addition to estuaries being difficult to define, as transitional ecosystems, their upper and lower boundaries have long been debated (Elliott and McLusky, 2002). Pritchard (1967) for example, defined the upper limit as the point where the water becomes fresh. While this may be appropriate for estuaries that receive substantial ‘freshwater’ flow, it does not apply in systems that experience hypersalinity or where the soils in catchments have become secondarily salinized (Potter et al., 2010; Tweedley et al., 2016b). This study follows Fairbridge (1980) and Van Niekerk et al. (2020) in using the limit of tidal penetration under open mouth conditions to define the upper limit of an estuary. Likewise, the lower limits of estuaries can be difficult to define in systems with wide funnel-shaped mouths (typically macrotidal estuaries), and in tropical monsoonal climates where heavy river flow can dilute local marine waters (Blaber, 1997). Microtidal estuaries, however, tend to have clear morphological demarcations, such as prominent headlands and/or a well-defined narrow entrance channel (Cooper, 2001; Potter et al., 1990).

Despite their well-recognised values, estuaries in temperate environments are regarded as the most degraded of all aquatic ecosystems and their conservation is at a tipping-point (Jackson et al., 2001). The classification of these systems is challenging but fundamental to conservation planning at local, regional, national (*e.g.*, the Australian listed threatened species and ecological communities), multinational (e.g. European Nature Information System habitat types, EEA, 2007) and international (e.g. IUCN Global Ecosystem Typology, Bland et al., 2017) levels. Traditionally, high-level estuarine classification schemes have focused on a single variable or aspect, *e.g.*, water balance and circulation (Pritchard, 1967), geomorphology (Fairbridge, 1980; Pritchard, 1967), sedimentology (Rusnak, 1967), tidal range (Davies, 1964; Hayes, 1975) and the influence and interplay between marine and fluvial processes (Dalrymple et al., 1992), but are designed to be applicable globally. Due to their simplicity, such classifications have been useful, however, they lack the nuance to be effective at more localised scales. Therefore, most existing classification schemes have been developed for the national or regional scales (Whitfield and Elliott, 2011) and often incorporate multiple abiotic features (Edgar et al., 2000; Hume et al., 2007; Whitfield, 1992).

Examples of classifications schemes for microtidal estuaries include Van Niekerk et al. (2020) for South Africa and, in Australia, Roy et al. (2001) for New South Wales, McSweeney et al. (2017a) for Victoria. Van Niekerk et al. (2020) utilised data and observations on geomorphology, hydrology, biota, salinity, climate and biogeography and an expert panel to categorise 492 South African estuaries into nine estuary types and three microsystem types, which were further subdivided using biogeographic zones. Roy et al. (2001) grouped estuaries in New South Wales into five groups and then into 13 types based on their geomorphology, waves, tides and physio-chemical characteristics. McSweeney et al. (2017a) classified estuaries that become disconnected from the ocean on the Victorian coastline into three types by subjecting data on the duration and frequency of bar opening and estuary size to multivariate statistical analyses.

Southern Western Australia (30’S to 34’S and 115’E to 123’E) has a microtidal coastline, ~2300 km in length and contains the two drainage divisions, *i.e.,* the south-west coast and south-western plateau (Figure 1). The region experiences a Mediterranean climate with warm to hot, dry summers and mild to cool, wet winters (Belda et al., 2014), with up to 80% of annual rainfall occurring between May and October (Hallett et al., 2018). Within the region, air temperatures increase and rainfall, and so also flow, decrease from the south-west corner to the South Australian border (Lester et al., 2014). The low tidal range, longshore and onshore transport of sediment and seasonal nature of flow can result in the formation of sand bars at the mouths of some estuaries, which can periodically disconnect them from the ocean (Ranasinghe et al., 1999). The level of connectivity with the ocean is determined by the amount of discharge the estuary receives relative to its area, with some always remaining open to the ocean and others being closed for various durations (Hoeksema et al., 2018; Tweedley et al., 2016b).

These levels of isolation from the ocean were used to classify estuaries in southern Western Australia into four categories; i) *permanently open* - the bars never, or rarely, close; ii) *seasonally-open* - the bars close for several months in summer–autumn and open annually following major river flow in winter; iii) *normally-closed* - the bars remain closed for years at a time and iv) *permanently-closed* - the bars never or rarely open and so are salt lakes rather than estuaries (Hodgkin and Hesp, 1998; Hodgkin and Lenanton, 1981). A fifth category, *intermittently-open*, was added by Young et al. (1997) to distinguish those systems with intermittent opening and closing of their mouth throughout the year. Another classification scheme, albeit less widely used in the region, was proposed by Hesp (1984) on the basis of geomorphology; who made a distinction between *riverine* estuaries and the three types of lagoonal-estuaries namely, *inter-barrier*, *valley* and *basin*.

The purpose of this study is three-fold: i) Synthesise existing knowledge on the characteristics of estuaries in southern Western Australia; ii) develop a classification scheme that adequately reflects their environmental and biological characteristics; and

(iii) validate the new classification scheme by using both enduring environmental variables and existing data on their fish and benthic invertebrate communities. The performance of the new classification is compared to/with existing schemes for local estuaries and microtidal systems in other regions of Australia and South Africa.

2. Materials and methods

2.1. Identification of estuaries and measurement of their characteristics

Estuaries in southern Western Australia were identified using a combination of scientific and grey literature, virtual globes, *i.e.,* Google Earth (see Yu and Gong, 2012), and Governmental Geographical Information System (GIS) data. The literature included publications by Hodgkin and Lenanton (1981), Hesp (1984), (Hodgkin and Hesp, 1998), (Brearley, 2005), reports by (Hodgkin and Clarke, 1987-1990) and the Land and Sea Audit (National Land and Sea Audit, 2002). The ~2,300 km of coastline in southern Western Australian was examined and where an estuary was thought to occur all historical satellite imagery examined (Google Earth). This method has been employed by other workers in microtidal regions to identify estuaries (e.g. McSweeney et al., 2017a; Van Niekerk et al., 2020). Digital elevation models and hydrological maps provided by the Department of Water and Environmental Regulation were examined in ARCMap 10.6 and the location of any watercourses (perennial and ephemeral) cross-checked against satellite imagery. Using this combination of data sources, 152 systems that meet the Potter et al. (2010) definition of an estuary were identified. Note that unlike Van Niekerk et al. (2020), artificially created estuaries, *i.e.,* diversion drains, were included in the classification, as although modified by anthropogenic change, they conform to the Potter et al. (2010) definition and can provide substantial habitat for fauna (Tweedley et al., 2018). Each estuary was assigned a number ranging from 1 in the north-west of the region down the west coast and from west to east on the southern coast to 152 (Figure. 1). Names for each estuary were sourced from the literature and, if no name could be found, allocated as "Unnamed" with a number. There is an intention to also provide, where possible, indigenous names for each estuary. For example Oyster Harbour is known as Miaritch (Miyaritj) to the Menang Noongar people and the Swan River Estuary is know as Derbarl Yerrigan by the Whadjuk Noongar people. However, this was beyond the scope of the review in its current form.

Key parameters that influence the geomorphology of estuaries were identified in a review of the literature. These 26 parameters were grouped into five broad categories: location and catchment, geomorphology, bar resilience, drying & hypersalinity and other classification schemes and the value for each parameter for each of the 152 estuaries in southern Western Australia sourced (SM1 Appendix 1). Note that data were not available for all estuaries. The first category (Location and catchment) included the latitude, longitude (Google Earth), Köppen-Geiger climate class (Kottek et al., 2006), Interim Biogeographic Regionalisation for Australia (IBRA) group (Thackway and Cresswell, 1997) as well as median rainfall (Brearley, 2005) and catchment size (Department of Water and Environmental Regulation, unpublished data).

Geomorphological variables included whether the estuary was natural or artificial, its geomorphological type ((Hodgkin and Hesp, 1998)Hodgkin and Hesp, 1998), whether it was dominated by riverine, tidal or wave processes (OzCoasts, 2020). The surface water area, perimeter, length of main source (from the bar to the upper limit of tidal flow [under open conditions] in the longest river if more than one was present), area:length and width of the entrance channel were measured using Google Earth (see example in Figure. S1). The bar resilience category included mean annual flow summed across all rivers, the number of rivers, estuary type, estimated number of days open annually, bar height and bar thickness (all Google Earth, Brearley, 2005).

Both the extent (*i.e., none, disconnected* [river(s)]) becomes disconnected from basin, delta exposed], *partial* [*1-25%*], *majority* [50-99%] and *ephemeral* [>99%]) and frequency of desiccation (*i.e., perennial, rare* [2-10+ years], *seasonal* [annually] and *frequent* [multiple times a year]) were assigned using historical imagery from Google Earth supported by local knowledge. The drying & hypersalinity category also include maximum salinity recorded from the literature, the Water Information Reporting database (Department of Water and Environmental Regulation, 2021) or during site visits conduced in this study (Krispyn, K., Murdoch University, unpublished data). It should be noted that the maximum salinity for some systems was based on only a single sampling occasion.

The final category (other classification schemes) compared information on the condition status of the estuary and its catchment (*i.e., near pristine*, *largely unmodified*, *modified* and *extensively modified*; (National Land and Sea Audit, 2002), the estuary classification described here and those for South Africa (Van Niekerk et al., 2020), New South Wales (Roy et al., 2001) and Victoria (McSweeney et al., 2017a). Note that these three classification schemes were not designed to be applied in southern Western Australia and so not all the 152 estuaries were able to be assigned to a type. In those cases were an estuary did not meet the criteria described in the source literature no type was assigned.

To maintain objectivity, classification decisions were reviewed by an independent researcher with considerable experience of southern Western Australian estuaries not involved in the current project.

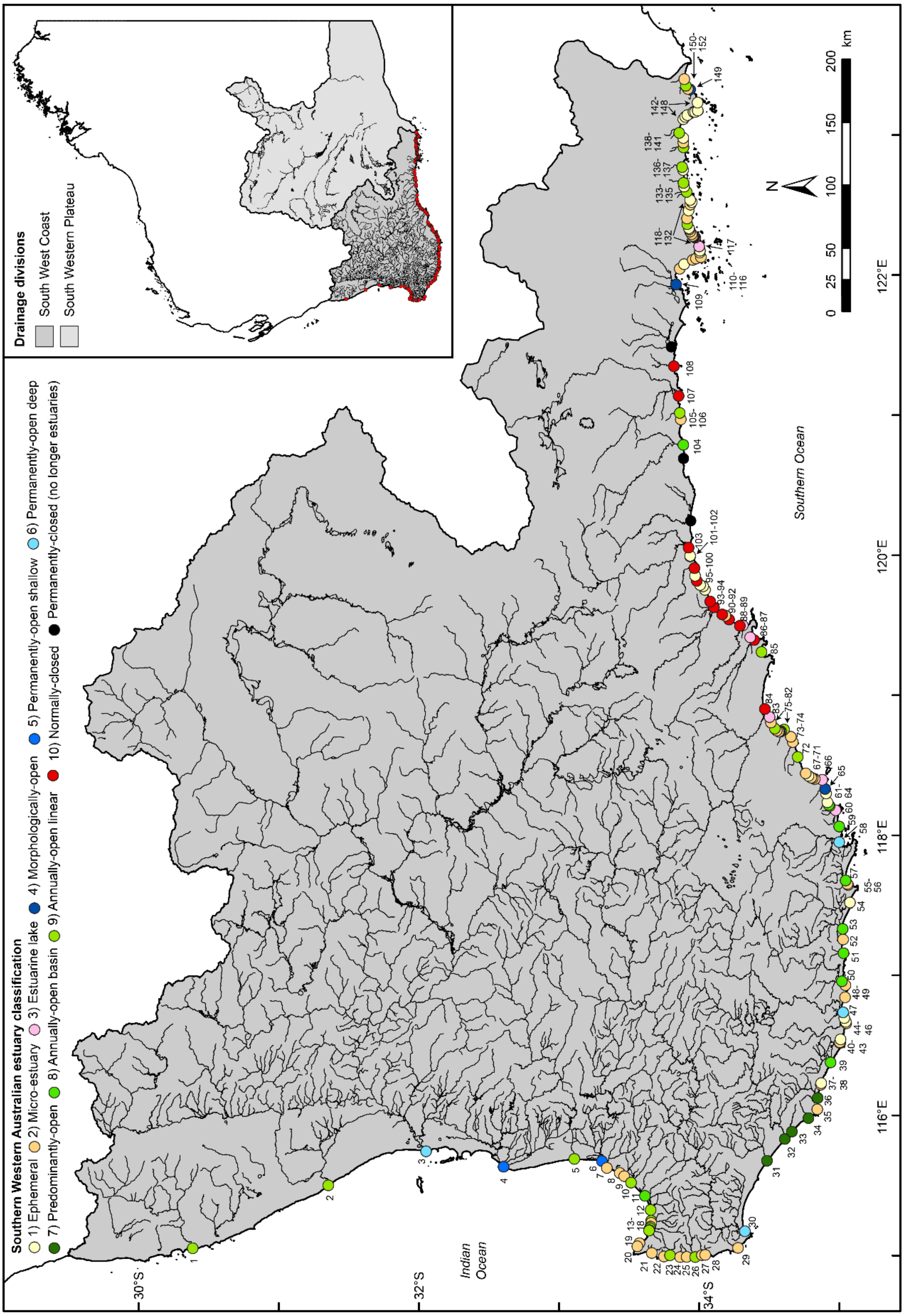


Figure 1. Maps of south-western Australia showing (a) the extent of the drainage basin in Western Australia and (b) the location and their classification of the 152 estuaries, all of which occur in the South West Coast Drainage Division (shaded grey area). Note that Princess Royal Harbour is not an estuary *sensu* Potter et al. (2010). Details of numbered estuaries given in SM1 Appendix 1.

2.2. Classification and validation of the estuaries

Using the information for each estuary (SM1 Appendix 1), examples of existing classification schemes (*e.g.*, van Niekerk et al. 2020) and personal observations recorded from site visits for less well-studied systems, K. Krispyn, J. Tweedley and N. Loneragan, all with between 5 and 35 year' experience in estuaries in the region, assigned estuaries to groups. For each of the 10 groups a definition was produced together with a dichotomous key with quantitative decision rules to allow any future estuary to be assigned to this scheme and to facilitate the use of this classification in other regions with similar characteristics (Figure 2).

The effectiveness of the new classification scheme against existing ones was determined objectively/quantitatively using a suite of multivariate statistical analyses in the PRIMER v7 software package (Clarke and Gorley, 2015). The existing schemes tested included coast (*i.e.*, west or south), IBRA groups, geomorphic type and estuary type (both Hodgkin and Hesp, 1998) and the classification schemes produced for South Africa, New South Wales and Victoria (McSweeney et al., 2017a; Roy et al., 2001; Van Niekerk et al., 2020). The first suite of analyses investigated the potential for the estuaries in the various classification schemes types to differ in their characteristics. As data were not available for all estuaries, a subset of 10 encompassing the range of parameters in SM1 Appendix 1 were selected covering each of the four main categories (*i.e.*, all except classification schemes). These were, surface water area, perimeter, area:length, length of main source, entrance channel width, days open annually, bar heights, bar thickness, catchment size and median rainfall.

A draftsman plot of the values for each pair of parameters was examined to assess whether the values for each parameter were skewed and, if so, which type of transformation would ameliorate that effect. This plot demonstrated that surface water area, perimeter, area:length, length of main source, bar height, catchment size and median rainfall needed to be $\log_e (x+1)$ transformed. As some parameters were measured in different units, data for each parameter were normalised to place all variables on a common scale (Clarke and Gorley, 2006). In order to ensure each of the four categories (*i.e.*, Geomorphology, Bar resilience, Drying & hypersalinity and Location & catchment) contributed equally to the estuary type classification, a weighting procedure was carried out to ensure each broad category had an arbitrary weight of 100, which was then divided equally amongst its component parameters.

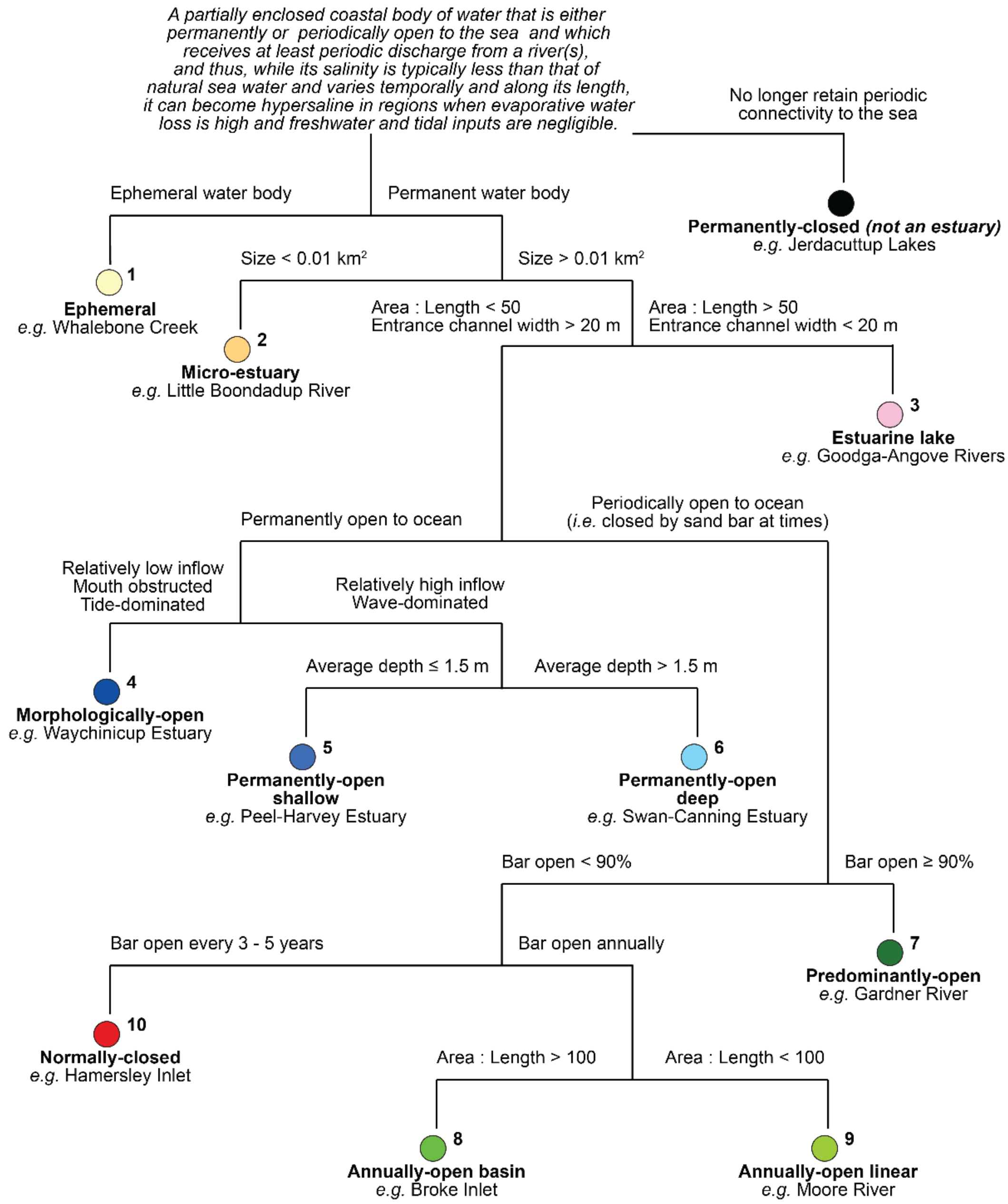


Figure 2. Graphical representation of a dichotomous key developed to classify the 152 estuaries identified in south-western Australia. Key shows the quantitative decision rules at each step using data able to be easily obtained from remotely-sensed data (*e.g.*, aerial photographs or GoogleEarth).

The pre-treated data were then used to construct a Manhattan distance matrix. Manhattan was selected rather than Euclidean distance as the distance coefficient operates with absolute and not squared differences and thus is less prone to distortion by outliers (Clarke et al., 2006). This matrix was subjected to eight one-way Analysis of Similarities (ANOSIM; Clarke and Green, 1988) tests, *i.e.*, one for each estuary classification scheme. The null hypothesis of no significant difference in characteristics among estuary types in each classification was rejected if P was <0.05. The magnitude of the test statistic R typically ranges from 1, when all samples within each group are more similar to each other than to any of the samples from other groups, down to ~0, when the average similarity among and within groups do not differ. Because *R* provides a universal measure of group separation, those classifications with the greater *R* are deemed to be more effective discriminators (Lek et al., 2011). Trends in the distributions of the estuaries in each category of the classifications were visualised using non-metric Multi-dimensional Scaling (nMDS; Clarke, 1993).

The same approach to comparing the effectiveness of each of the eight classification schemes was applied to biological data on the fish and benthic macroinvertebrate faunas from southern Western Australian estuaries. Abundance values were obtained from published sources for each fish species recorded in the nearshore, shallow (<1.5 m deep) and offshore, deeper (>1.5 m deep) waters at sites throughout 23 and 24 estuaries, respectively (SM1 Appendix 2). Benthic macroinvertebrate data were available for a subset of eight of those systems, the systems studied in the main body of my Honours dissertation (Torbay, Normans, Oyster, Taylor, Cordinup, Waychinicup, Cheyne, and Beaufort, SM1 Appendix 2). These data had been collected seasonally from numerous sites throughout each system for at least a year. Nearshore waters were sampled during daylight hours using a 21.5m seine net, which comprised two 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m long cod-end (3 mm mesh), swept an area of 116 m^2 and fished to a maximum depth of 1.5 m. Offshore waters were sampled at night using a 160 m long, composite, sunken gill-net, which consisted of eight panels that were 20 m long and 2 m high, each with a different mesh size, ranging from 38 to 127 mm. Benthic macroinvertebrates were sampled using a cylindrical corer that was 11 cm in diameter and sampled to a depth of 15 cm (surface area = 95.07 cm^2) (estuaries and sources of benthic data). Samples were then sieved through a 500 μm mesh.

For each of the three biological data sets, the replicate abundance data for each species were initially averaged to produce a single value for each estuary, standardized to convert the percentage composition, square-root transformed and used to construct a Bray-Curtis similarity matrix. Each resemblance matrix was then subjected to one-way ANOSIM tests and nMDS ordination to test for differences among categories in each classification scheme.

3. Results and discussion

3.1 Number of estuaries

A total of 152 estuaries were identified, a substantial increase from the up to 50 estuaries recognised in the literature (e.g. Brearley, 2005; National Land and Sea Audit, 2002). This reflects the use of satellite imagery and GIS, which allowed the identification of systems in more remote areas of the extensive coastline, where scientists may be have visited and 85 micro and ephemeral estuaries and the inclusion of nine artificial estuaries, such as the Vasse Diversion Drain. Similarly, Whitfield (1992) recognised 289 estuaries in South Africa, but a recent reclassification using satellite and aerial imagery identified an additional 202 microsystems (Van Niekerk et al., 2020). Each of the 152 estuaries in southern Western Australia were located within the South West Coast drainage division (Figure 1). None were found in the South West Plateau. Around 80% of estuaries discharge onto the south coast of the state (Table 1). Each estuary was able to be assigned to an Interim Biogeographical Regionalisation for Australia (IBRA) group, geomorphic type and estuary type. Almost 60% of estuaries were located in the Esperance Plains IBRA regions: 70% were riverine in morphology and 38% were classed as intermittently-open and another 38% as normally-closed, whereas only 10 systems (7%) maintained a permanent-connection to the ocean (Table 1), as occurs in all macrotidal estuaries (Tweedley et al., 2016b). All southern Western Australian estuaries were able to be assigned to a category in the current classification, with 88, 47 and 12% able to be assigned using the schemes from South Africa, New South Wales and Victoria, respectively.

3.2. Characteristics of southern Western Australian estuaries

Median annual rainfall in the catchments of estuaries in southern Western Australia changed with latitude and longitude. Along the west coast rainfall was ~500 mm between 30-32 °S, but increased to 1,128 mm by 34 °S (Figure. 3a). The highest rainfall for south coast estuaries was at 115 °E, *i.e.*, 1,363 mm and declined sequentially in an eastward direction to only 483 mm by 119 °E, before increasing to 623 and 549 at 122 °E and 123 °E, respectively. Estuaries were present in each 1° latitude and longitude section of the coastline, with the largest concentration in 33°S (Geographe Bay and Cape Naturaliste) and 118 °E (Albany) and 122 °E (Esperance). In terms of the total area of estuaries, by far the largest extent of estuarine habitat was present at 32 °S, due to the Swan-Canning and Peel-Harvey estuaries, with the latter system being the largest in the region at ~137 km^2 and comprising ~29% of the total estuarine area (Figure 3b). Other extents of coastline with relatively large areas of estuarine habitat were 116 °E and 117 °E (Denmark) due to the Broke and Wilson inlets both of which are >45 km^2.

Estuaries on the west coast were generally of a single estuary type – permanently open, except for those at 33 °S, which were a mix of all four types with most being either intermittently-open or seasonally-open (Fig. 3c). On the south coast, however, estuaries in each degree of longitude generally belonged to multiple types. Intermittently-open and normally-closed systems were the most common, with those of the former category being more abundant to the west, *i.e.,* 115-117 °E and normally-closed systems to the east, *i.e.,* 118 to 123 °E.

Table 1. Number of southern Western Australian estuaries able to be assigned (A), unassigned (U) and their percentage (U%) contribution to each level in the classification scheme developed in the current study and those used in other microtidal regions.

Coast		**Interim Biogeographical Regionalisation for Australia[1]**		**Geomorphic type[2]**		**Estuary type[3]**	
Name	#	Name	#	Name	#	Name	#
West	29	Swan Coastal Plain 02 (SWA02)	18	Basin	18	Permanently open	10
South	123	Warren 01 (WAR01)	36	Inter-Barrier	7	Intermittently open	59
		Jarrah Forest 02 (JAF02)	9	Riverine	106	Seasonally open	26
		Esperance Plains 01 (ESP01)	40	Valley	21	Normally closed	57
		Esperance Plains 02 (ESP02)	49				
Assigned	152		152		152		152
Unassigned	0		0		0		0
Percentage unassigned	0.00		0.00		0.00		0.00

Western Australia[4]		**South Africa[5]**		**New South Wales[6] (Australia)**		**Victoria[7] (Australia)**	
Name	#	Name	#	Name	#	Name	#
Ephemeral Estuaries	34	(1) Micro-Outlet	33	(1) Ocean Embayments	0	(1) Intermittently open/closed estuary Type A	3
Micro-Estuary	51	(2) Micro-Estuary	58	(2) Funnel-shaped Estuary	2		
Estuarine Lakes	6	(3) Estuarine Lake	7	(3) Drowned Valley Estuary	1	(2) Intermittently open/closed estuary Type B	1
Tide dominated	3	(4) Estuarine Bay	3	(4) Tidal Basin	0		
Permanently Open Shallow	2	(5) Estuarine Lagoon	2	(5) Barrier Estuary	7	(3) Intermittently open/closed estuary Type C	4
Permanently Open Valley	4	(6) Predominantly Open	4	(6) Barrier Lagoon	0		
Predominantly open	5	(7) Large Temporarily Closed	4	(7) Interbarrier Estuary	0	(4) Barrier Type	3
Annually open basin	9	(8) Small Temporarily Closed	16	(8) Saline Coastal Lagoon	23	(5) Drowned River Valley	7
Annually open river	26	(9) Large fluvially Dominated	0	(9) Small Coastal Creeks	32		
Normally closed	12	(10) Small Fluvially Dominated	0	(10) Evaporative Lagoons	0		
		(11) Arid Predominantly Closed	7	(11) Brackish Barrier Lake	6		
		(12) Coastal Waterfall	0	(12) Perched Dune Lake	0		
				(13) Backswamp	0		
Assigned	152		134		71		18
Unassigned	0		18		81		134
Percentage unassigned	0.00		11.84		53.29		88.16

[1] = (Department of Water and Environmental Regulation, 2021); [2, 3] = (Hodgkin and Hesp, 1998); [4] = Current study; [5] = (Van Niekerk et al., 2020); [6] = (Roy et al., 2001); [7]= (McSweeney et al., 2017a).

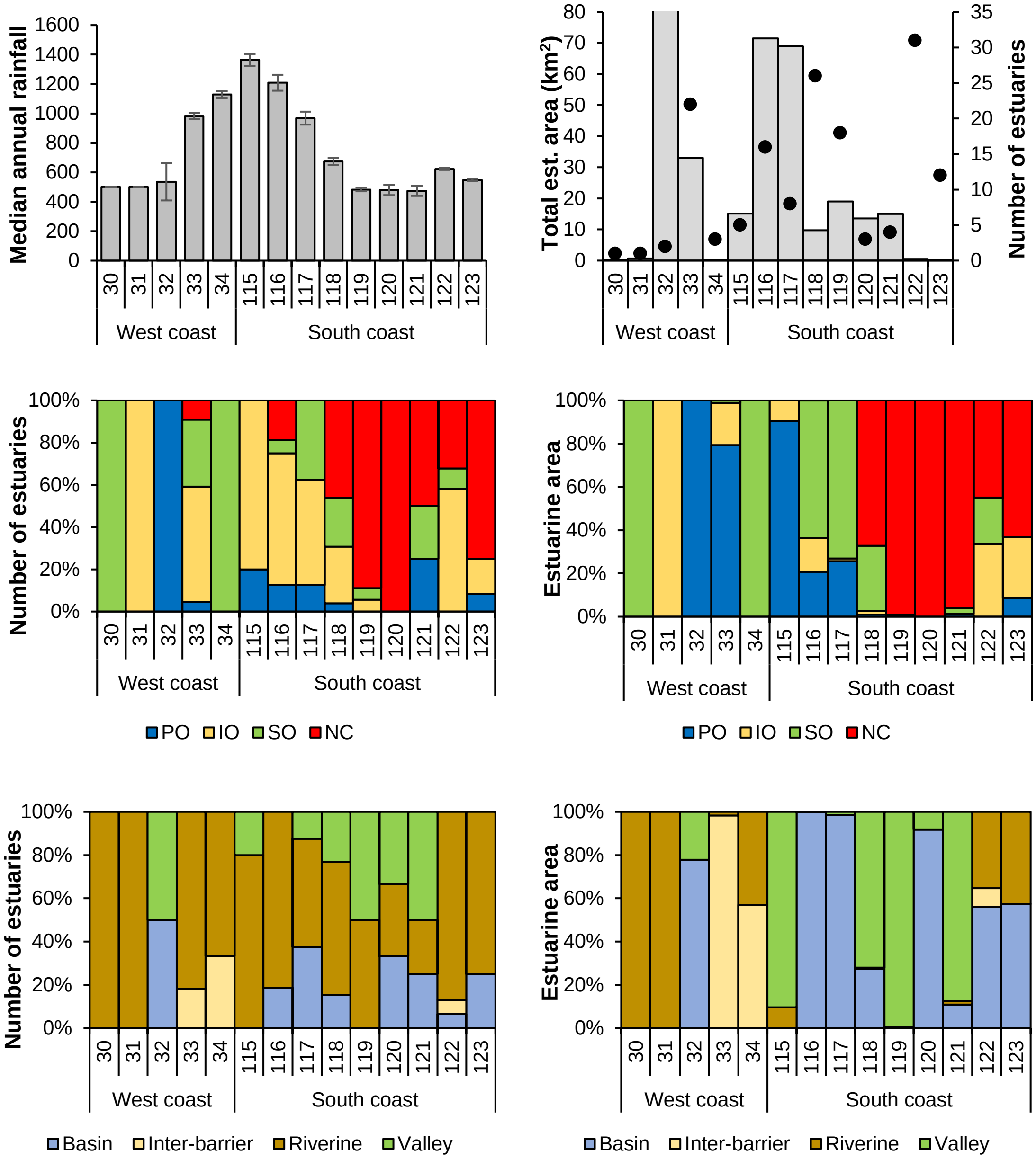


Figure 3. Bar charts of (a) median rainfall (±1 SE) and (b) number of estuaries and total estuarine area in each degree of latitude and longitude on the southern Western Australian coast. * value for 32°S in (b) = 172 km^2. Stacked bar charts of the percentage number of estuaries in each (c) estuary type and (e) geomorphic type and the percentage estuarine area in each (d) estuary type and (f) geomorphic type in each degree of latitude and longitude on the southern Western Australian coast.

(Figure 3c). A similar pattern is evident for estuarine area, with the exception that due to the relatively small size of the intermittently-open estuaries compared to permanently- and seasonally-open categories, these systems make a smaller contribution. East of 118 °E, 44-99% of all available estuarine habitat only maintains a very limited connection to the ocean, *i.e.*, being normally-closed (Fig 3d). These trends reflect, in part, the declining rainfall from the far west to ~121 °E as, on average, permanently-open systems received ~389,000 ML of flow, compared to ~60,300 ML for intermittently-open systems and ~24,900 and ~6, 800 ML for those that are seasonally-open and normally-closed, respectively (SM1 Appendix 1). The amount of flow a microtidal estuary receives is regarded as the primary driver in maintaining connectivity with the ocean (Elwany et al., 1998; Reddering, 1988; Rich and Keller, 2013; Whitfield et al., 2008). For example, the probability of the Carmel Estuary (California, USA) being open increases 10-fold as mean daily river flow increases from 0.2 to 1.0 $m^{3\ s-1}$ and is open on 98.5% of the days when flow is greater than 0.5 $m^{3\ s-1}$ (Rich and Keller, 2013). However, the tidal prism and magnitude of wave energy also play a supporting role (Elwany et al., 1998).

When classified according to geomorphic type, most estuaries in all sections of the coastline were riverine, with contributions from valley and basin systems, particularly along stretches of the south coast (Fig. 3e). Due to the small surface area of many riverine estuaries, when based on area, basin systems, which have a large, wide central region and represent more of the available habitat (Fig. 3f).

3.3. Morphological categories

The 152 estuaries identified throughout the coastline of southern Western Australian are considered to fall into one of ten categories (Table 2). The text below describes the features of estuaries in each category and a satellite image of a characteristic example is provided in Figure 4.

Table 2. Short definitions for each of the ten categories of estuaries found in southern Western Australia.

Estuary group type	Description
1. Ephemeral	Small linear estuary that dries up during periods of low flow
2. Micro-estuary	Small, permanent linear estuary
3. Estuarine lake	Estuary comprising one or more large circular water bodies connected to the ocean via a long narrow entrance channel
4. Morphologically-open	Estuary that is permanently open to the ocean only due to the presence of a natural or anthropogenic morphological feature
5. Permanently-open shallow	Estuary with a permanent connection to the ocean and wide, shallow basin region with an average depth of <1.5 m
6. Permanently-open deep	Estuary with a permanent connection to the ocean through a relatively deep wide entrance channel, with an average depth of >1.5 m and deep areas
7. Predominantly-open	Linear estuary that are almost always open to the ocean (90-99% of the time)
8. Annually-open basin	Estuary that breaches one or more times per year and have a relatively large circular basin
9. Annually-open linear	Estuary that breaches one or more times per year with a long, sinuous linear shape
10. Normally-closed	Estuary with a substantiable sand bar that remains closed for years at a time and only opens in response to large amounts of flow associated with heavy winter rainfall or cyclonic events

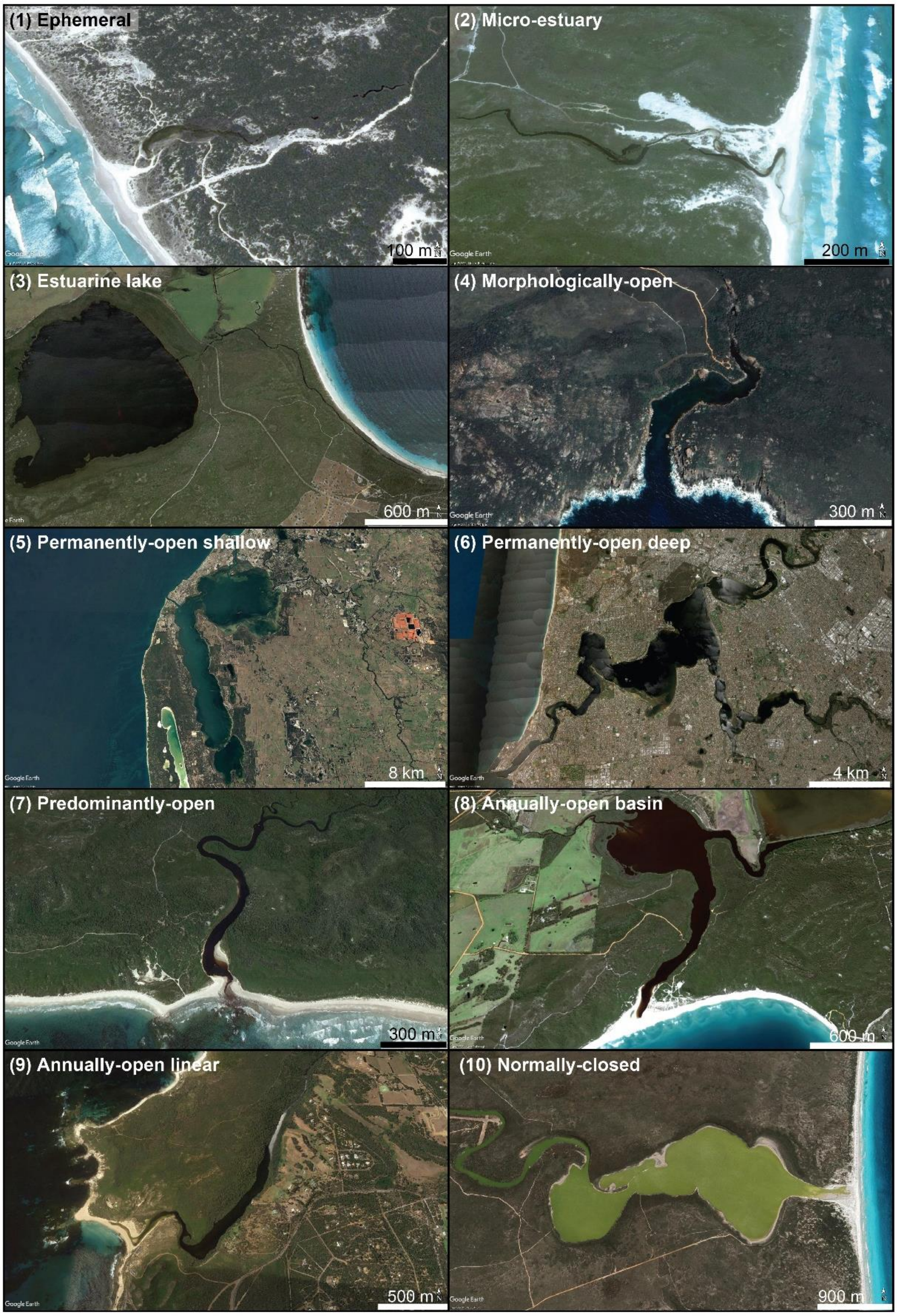


Figure 4. Satellite images showing an example of each of the types of southern Western Australian estuary. (1) Unnamed 33; (2) Bluff Creek; (3) Goodga-Angove; (4) Waychinicup; (5) Peel-Harvey; (6) Swan-Canning; (7) Gardner; (8) Torbay; (9) Margaret River; (10) Gordon. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

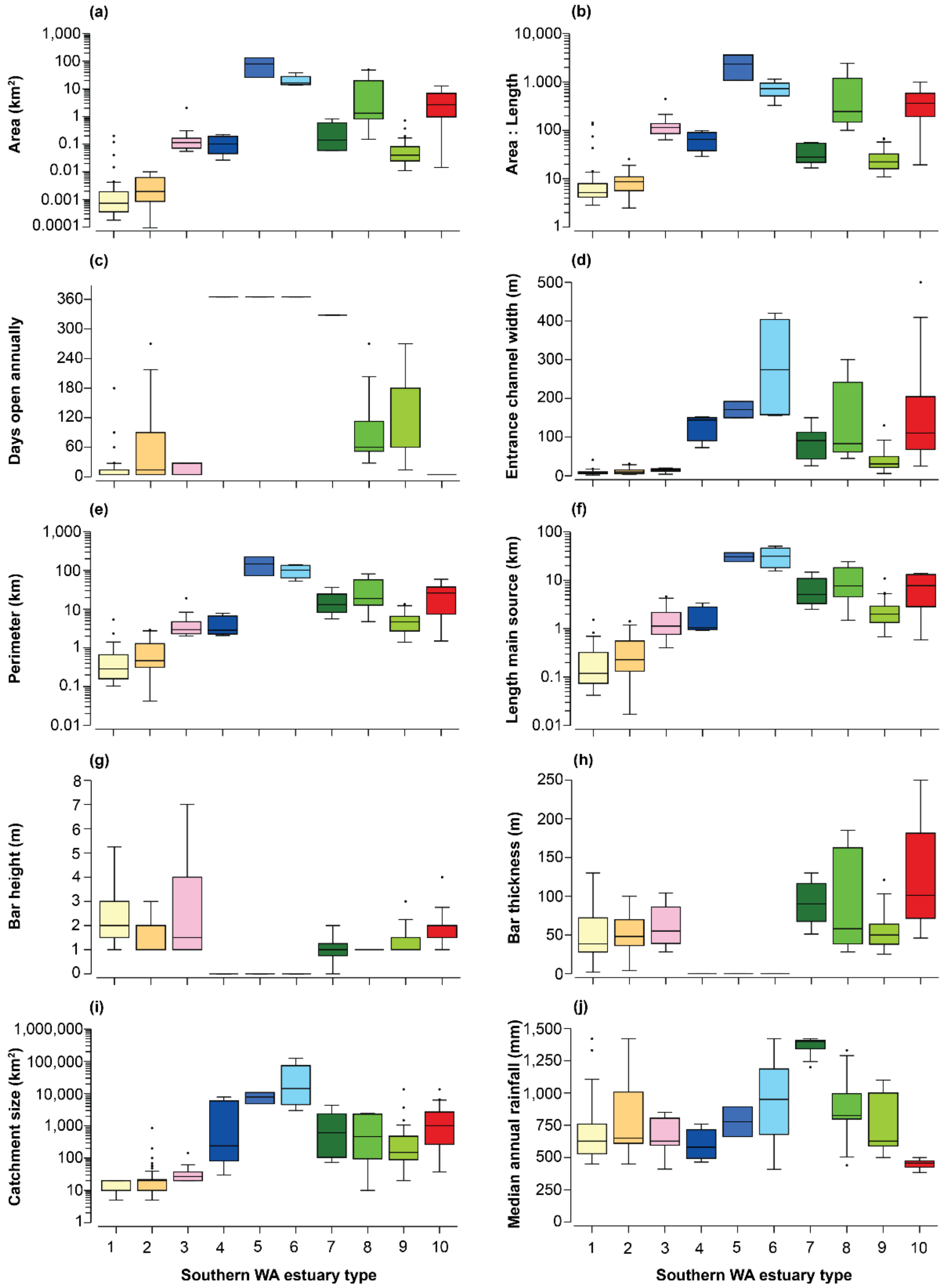


Figure 5. Box plots showing the distribution values of the subset of 10 estuarine characteristics in each of the ten categories of estuaries in southern Western Australia. n = 152. Full names of numbered estuary categories given in Table 1.

Ephemeral

These are typically, short (<500 m), shallow riverine systems <0.01 km^2 in area that can completely dry out during periods of low flow (Figures 4, 5a, SM 1 2). They occur along the south coast in a range of rainfall zones but are characterised by very small catchments (<20 km^2) and so only connect with the ocean during periods of high flow following localised rainfall or storm events. Ephemeral estuaries are generally elevated above mean sea level, with a relatively high bar (2 m). Their entrance channel is perched, which, when the estuary is open, limits the inflow of marine water and mixing. This combined with their shallow bathymetry results in them being generally oligohaline. Limited field observations indicate that most do not support a fish fauna, although some species that breed in freshwater have been recorded, but they do provide a refuge for numerous tadpoles. These observations are supported by quantitative sampling of the analogous micro-outlets in South Africa (Van Niekerk et al., 2020), where the nekton similarly was dominated by tadpoles rather than fish (Magoro et al., 2020a). The invertebrate fauna in the micro-outlets comprised mainly freshwater taxa such as chironomid and odonata larvae (Magoro et al., 2019).

Micro-estuary

These systems resemble ephemeral estuaries but are permanent waterbody (cf. Figures SM1 2, SM1 3). Micro-estuaries are likewise small (<0.01 km^2) riverine systems that can reach 1.5 km in length and possess a narrow an entrance channel (<35 m wide; Figure 5b). Most have a catchment <100 km^2 in area, although there are two systems with catchments of 200 and 847 km^2. The large catchment facilitates their greater connectively with the ocean than ephemeral estuaries. As such the exchange of freshwater and seawater can occur following the breaching of the bar and so typically have greater salinities. Observations of micro-estuaries (Krispyn, Murdoch University) indicate most contained a fish fauna, which is similar to estuaries in the same category in South Africa (Van Niekerk et al., 2020), where the limited range of freshwater, estuarine-resident and marine estuarine-opportunists fish species were recorded (Magoro et al., 2020a). South African micro-estuaries were also found to contain a more ‘estuarine’ benthic invertebrate that nearby ephemeral estuaries (Magoro et al., 2019).

Estuarine-lake

These estuaries comprise one or more large circular water bodies connected to the sea via a long narrow entrance channel (<20 m wide; Figure 4). The basin region is typically situated in a depression behind coastal dunes, however, in the case of the Goodga-Angove Rivers (SM1 Figure 4), the basin is above sea level. The freshwater flow is typically provided by small streams, but these systems in South Africa can also by fed by ground water aquifers (Van Niekerk et al., 2020). Limited sampling indicates than these are primarily oligohaline (SM1 Appendix 1) and the relatively high elevation of the basin of some systems would preclude the input of marine waters by the tide. However, Lake St. Lucia in South Africa has become markedly hypersaline following multiple years of drought and mouth closure, which dramatically influenced the fauna (Cyrus et al., 2011; Tweedley et al., 2019b).

Morphologically-open

These are systems that maintain a permanent connection to the ocean only due to the presence of a natural or anthropogenic morphological feature (Figure 4). Such estuaries would not naturally be permanently open (see below) as they do not receive sufficient flow to prevent the build-up of sand at the mouth. For example, Waychinicup Estuary and Bandy Creek receive an average of 8,000 and 6,400 ML of flow annually compared to 721,000 and 480,075 ML in permanently-open shallow and permanently-open deep estuaries, respectively (SM1 Appendix 1). There are three examples in southern Western Australia, *i.e.*, from west to east i) Waychinicup Estuary, ii) Bandy Creek and iii) Jorndee. Waychinicup lies in a gorge carved between two large granite headlands and Jorndee has an extensive rock bar (SM1 Supplementary Figure S5; (Hodgkin and Clarke, 1987-1990). Bandy Creek on the other hand, remains open due to the presence of two groynes constructed in 1983 as part of a boat harbour (Jones et al., 2009). The relatively wide entrance to Waychinicup Estuary resembles that of a macrotidal estuary making it the only tide dominated estuary in the region (OzCoasts, 2020). These systems exhibit a longitudinal salinity gradient due to mixing between fluvial and tidal inputs (Phillips and Lavery, 1997).

Permanently-open

The permanently-open estuary type of Hodgkin and Hesp (1998) was divided into two categories, *permanently-open shallow* and *permanently-open deep* (Table 2, Figure 4). These categories were primarily separated on their average and maximum depths, with a proposed demarcation of 1.5 m average depth of their basin, noting that the upper saline reaches of the systems, which can resemble rivers may contain deep holes. For example, the Swan-Canning Estuary, Blackwood Estuary, Walpole-Nornalup Inlet and Oyster Harbour (all permanently-open deep) have maximum depths of between 5 and 22 m in the basin regions (Brearley, 2005), compared to 1 and 1.5 m in the permanently-open shallow Peel-Harvey and Leschenault estuaries (Semeniuk et al., 2000; Valesini et al., 2019). The division between deep and shallow permanently open systems was based on the premise that deeper areas of systems may provide additional habitat not present in shallow basins and that the benthic environment of these deeper waters often comprise finer sediment and a different invertebrate fauna (e.g. Tweedley et al., 2011; Tweedley et al., 2017). Moreover, these areas are more susceptible to salinity and temperature stratification, which in microtidal estuaries often led to hypoxia and effects on faunal composition (Kurup and Hamilton, 2002; Tweedley et al., 2016a). Moreover, due to their bathymetry, permanently-open shallow estuaries are more likely to become hypersaline than deeper systems, due to a lack of rainfall and thus discharge in summer/autumn and evaporation in their wide shallow basin areas (Potter et al., 2016; Veale et al., 2014). The magnitude of hypersalinity in these systems is predicted to increase with a drying climate (Huang et al., 2020).

Both categories of permanently-open estuaries share some characteristics in that they have the largest mean area and perimeter (Figure 5) and drain water from a large catchment. For example, the catchment of the Swan-Canning Estuary extends 126,000 km^2, which is almost the area of Greece (Valesini et al., 2014). Subsequently, these estuaries receive the greatest quantities of flow (Tweedley et al., 2016b) and they typically exhibit longitudinal salinity gradients to which the fauna respond (Loneragan et al., 1989; Valesini et al., 2018). The entrance channel of both categories of estuaries tends to be relatively wide for a southern Western Australian estuary and deep. In some cases, anthropogenic modification, *i.e.*, dredging for port development (Swan-Canning) and the construction of the artificial entrance channel (Peel-Harvey) have resulted in additional deepening, with depth of 14 and 6.5 m, respectively (Nicholls, 2003; Valesini et al., 2019). These wide deep entrance channels provide opportunity for marine taxa to enter the estuaries and thus such systems often contain larger numbers of species of fish and invertebrates than estuaries with only a temporary connection to the ocean (Tweedley et al., 2016a; Wildsmith et al., 2011).

Predominantly-open

Predominantly-open estuaries (Figure 4) are connected to the ocean >90% of the time due. They typically occur in areas of high median annual rainfall (*i.e.*, >1,200 mm) and relatively high flow, but with catchment sizes more similar to annually-open than permanently-open estuaries (Figure 5). Predominantly-open estuaries are linear in morphology with a low area:length and fairly small surface area of <1 km^2 (SM1 Appendix 1). Salinities are predominantly oligohaline as their perched and narrow breaches attenuate much of the tidal inflow (SM1 Supplementary Figure S8), but stratified conditions are present in the lower reaches (Hodgkin and Clarke, 1987-1990).

Annually-open

The term annually-open refers to those systems that breach one or more times per year (*i.e.,* at least annually) and thus includes both the seasonally-open and intermittently-open categories used previously (e.g. Tweedley et al., 2016b). This was made on the basis that several estuaries classified previously as seasonally-open were breached multiple times (rather than once) in a given year (e.g. Krispyn et al., 2021). As many of such estuaries are located in remote and uninhabited areas, obtaining daily data of bar status *e.g.,* Cowley (1998) was not possible (e.g. Hoeksema et al., 2018). However, the use of data loggers enables data on indicators of a bar breach *e.g.,* water level, temperature and salinity to be obtained at fine temporal scales (seconds – hours) for protracted periods (up to years). Moreover, the original definition of intermittently-open was designed for the Moore River, which is unique in that breaches are a result of the effects of a substantial input from artesian springs, rather than of freshwater discharge derived from rivers (Young et al., 1997). The annually-open estuaries classified here are similar to the temporarily open/closed category of Whitfield (1992), large and small temporarily closed categories of (Van Niekerk et al., 2020) and intermittently closed/open lakes and lagoons (McSweeney et al., 2017a).

Breaches of the sand bar in annually-open estuaries tend to occur in winter, when average monthly rainfall is highest, however, these systems can breach at other times throughout the year if there is sufficient flow. In the Vasse-Wonnerup, 36 breaches occurred in the 75 months between July 2014 and November 2020, with between four and six breaches occurring in each month between May and October (Department of Water and Environmental Regulation, unpublished data). Hodgkin and Clarke (1987-1990) used local knowledge to determine that, between 1964 and 1988, the bar of Broke Inlet was breached in 19 of the 21 years and remained open for an average duration of 16 weeks and a maximum of 26 weeks.

Two categories of annually-open estuaries are recognised, those with a relatively large basin (*annually-open basin*) and those without (*annually-open linear*) (Table 2). Thus the basin category trend to have a larger area, perimeter and area:length, although there is considerable range in their area, from <0.2 to 49 km^2 (SM1 Appendix 1). Generally speaking, annually-open basin estuaries have a larger catchment and occur in areas with a greater median annual rainfall, than their linear counterparts. Breaches in annually-open linear estuaries, which are all <1 km^2 in area, are caused more by localised rainfall patterns that commensurate rapid increases in flow. This limits scouring resulting in the bar being open for an shorter period, albeit potentially more frequently. These features of annually-open linear estuaries are similar to those reported in small temporarily closed estuaries in South Africa (Van Niekerk et al., 2020).

Normally-closed

Normally-closed estuaries are principally characterised by sand bar that remains closed for several years at a time. The bars of these estuaries are only breached in response to large amounts of flow associated with heavy winter rainfall or cyclonic events (Hoeksema et al., 2018). For example, in the same 21 year period when Broke Inlet (annually-open basin) was breached in 19 years, the normally-closed Stokes and Hamersley inlets became open in six and five years , respectively and the normally closed Culham did not open at all (Hodgkin and Clarke, 1987-1990). Moreover, once breached the bar of Stokes Inlet was only recorded to by open to the ocean for between four and six weeks. Breaching in normally-closed estuaries is inhibited by the substantial bars that can reach 4 m above sea level and be several hundred meters thick (SM1 Appendix 1). The resilience of these bars to breaching is exemplified by Culham Inlet that remained closed for 53 years prior to 1972, causing the estuary at the time to be considered ‘permanently-closed’ (Hodgkin, 1997). However, land clearing in the catchment increased run-off and resulted in more frequent breaching (Hoeksema et al., 2018).

While the catchment sizes of these estuaries are, on average, greater than for all except the two permanently-open categories, they occur in areas where median annual rainfall is <500 mm (Figure. 5). The low rainfall is compounded by the high evaporative rates from pan evaporation which for Culham Inlet was estimated to be 1,490 mm and so three time greater than annual rainfall in the catchment (445 mm; Hodgkin, 1997; Hoeksema et al., 2018). The wide, shallow basin areas (high area:length) facilitates evaporation and during years of low flow these systems can become extremely hypersaline. Three years after breaching salinities, in Culham Inlet reached 313 (Hoeksema et al., 2018) and a value of 345 was recorded in Hamersley Inlet in November 2021 (Krispyn, K., Murdoch University, unpublished data). Furthermore, both Saint Mary and Hamersley inlets have been known to dry completely (Hodgkin and Clarke, 1987-1990).

Normally-closed estuaries harbour a depauperate fauna (Tweedley et al., 2019b; Tweedley et al., 2016b) as their limited connectivity with the ocean prevents the immigration of marine species and hypersaline conditions results in mass mortality events. For example, an estimated 1.3 million individuals of the sparid *Acanthopagrus* *butcheri* died in the upper reaches of Culham Inlet as salinities reached 85 and their attempted movement into less saline waters further upstream was prevented by the presence of rock bar across the river (Hoeksema et al., 2006b). Moreover, in Beaufort Inlet, only a single species of euryhaline fish (the atherinid *Atherinosoma elongata*) and invertebrate (larvae of the chironomid *Tanytarsus barbitarsis*) was able to survive in salinities of ~120 (Krispyn et al., 2021).

Distribution and physico-chemical parameters

Estuaries on the west coast of southern Western Australia belong to four of the ten categories, with those at 30 and 31 °S being exclusively annually-open linear systems (Figure 6a). Slightly further south lies a permanently open shallow and a permanently open deep estuary. Micro-estuaries are the most numerous systems at 33 and 34 °S along this coast. The western most part of the south coast contains all most all of the predominantly-open estuaries, with the coast eastern comprising a mix of mainly ephemeral, micro-estuaries, annually-open basin and linear estuaries and those that are normally-closed (Figure. 6a). However, when based on area, a slightly different pattern is evident. From north-west to south east across the regions, estuarine habitat on the west coast is mainly provided by annually-open linear (30-31 °S) then permanently-open shallow (32-33 °S) and then micro-estuaries (34 °S; Figure. 6b). On the south coast, permanently-open deep systems comprise most of the estuarine habitat at 115 °E, followed by annually-open basin (116-117 °E), normally-closed (118-121°E) and ephemeral (122-123°E). On the basis of this pattern in the area of different types of estuarine habitat opportunities are limited for the recruitment of marine species due to the protracted bar closures and ephemeral habitat which is often not conducive for fish populations (Magoro et al., 2020b).

The quantity of flow into the various categories of estuaries from their river(s) differs markedly, ranging from over 400,000 ML in permanently-open estuaries, to 171,000 in predominantly-open and 70,000 and 18,000 in annually-open basin and linear estuaries, respectively to <8,000 in the remaining categories (Figure 6c). The mean maximum salinity exhibited a different pattern being lowest in the estuarine lakes (3), mesohaline (7-9) in the ephemeral and micro-estuaries, euryhaline (31-39) in predominantly-open, annually-open linear, permanently-open deep, morphologically-open and hypersaline (>40) in the permanently-open shallow and annually-open basins systems and to extreme levels in normally-closed estuaries (145; Figure. 6d).

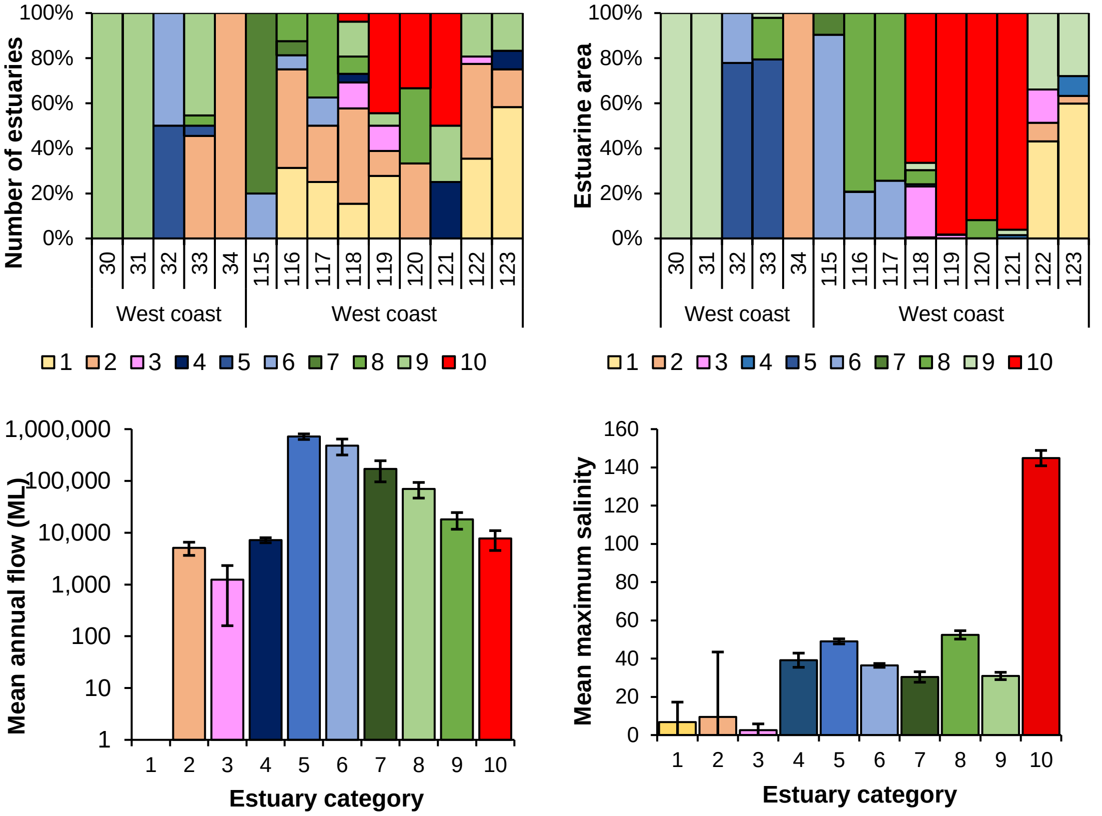


Figure 6. Stacked bar charts of the percentage (a) number of estuaries (b) estuarine area in each southern Western Australian estuary category in each degree of latitude and longitude on the southern Western Australian coast. Bar graph of the (c) mean annual flow (±1 SE) and (d) mean maximum salinity (±1 SE) in each southern Western Australian estuary. Note no flow data were available for ephemeral estuaries (1). Full names of numbered estuary categories given in Table 1.

3.4. Validation

Abiotic parameters

A one-way ANOSIM test confirmed that the environmental characteristics of the 152 southern Western Australian estuaries differed between the 10 categories in the proposed classification scheme (P = 0.001). The relatively high Global R-statistic value of 0.765 indicates that the differences in characteristics among the categories of estuaries is substantially less than the variability within a category. Thus, the proposed classification scheme adequately distinguishes between systems with different physical characteristics. Moreover, comparisons between each pairwise combination of estuary categories demonstrated that all differed significantly (all P<0.05) except for the comparison between permanently-open shallow and permanently-open deep estuaries (P>0.05, R = -0.179, Table 2). This result is not surprising as estuaries in these two groups are distinguished on the basis of their bathymetry (Table 2; Figure 2) and, as depth data was only available for a small number of the 152 estuaries, this variable was not used in the analyses. On the nMDS plot the samples for the various estuaries were arranged loosely in their categories and formed a linear trend from micro and ephemeral estuaries on the far right, to those with increasing connectivity to the ocean further left (*i.e.*, annually-open, predominantly-open and then morphologically-open and permanently-open; Figure 7). The points representing normally-closed estuaries formed a discrete group in the center bottom of the plot

ANOSIM tests for each of the other seven classification schemes also detected significant differences between their categories (P = 0.001-0.015; Figure 7). However, the magnitude of the Global R-statistic values varied markedly (0.110 – 0.697) but was always less than that for the southern Western Australian classification (Figure 7). Among the schemes used in WA, for which 100% of estuaries were assigned to a category, geomorphic type was the best, with riverine systems forming a relatively discrete group on the MDS plot, but estuaries in the other three categories (inter-barrier, valley and basin) intermingle (Figure. 7). With regard to estuary type the low Global R-statistic value reflects the marked overlap between intermittently-open and seasonally-open estuaries. As not all of the 152 estuaries were able to be assigned to a category using the classification scheme for South Africa (88%), New South Wales (47%) and, particularly Victoria (12%), some these tests were conducted with a smaller sample size (Table 1). The far higher number of estuaries assigned to the Van Niekerk et al. (2020) scheme reflects that fact that it incorporated micro-estuaries, which were not recognized in the other systems.

Table 3. R-statistic values derived from a one-way ANOSIM test on the geomorphological features of southern Western Australian estuaries. Grey shading denotes no significant difference (P >0.05). 1= Ephemeral estuary; 2= Micro-estuary; 3= Estuarine lakes; 4= Morphologically-open; 5= Permanently-open shallow; 6= Permanently-open deep; 7= Predominantly-open; 8= Annually-open basin; 9= Annually-open linear; 10= Normally-closed.

	Estuary category								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
2 -	0.555								
3	0.915	0.516							
4	1.000	0.940	0.864						
5	1.000	1.000	0.969	0.917					
6	1.000	1.000	0.976	0.778	-0.179				
7	1.000	0.955	0.936	0.990	1.000	0.894			
8	0.995	0.904	0.417	0.504	0.489	0.642	0.347		
9	0.944	0.623	0.415	0.571	0.961	0.968	0.500	0.494	
10	0.955	0.856	0.494	0.850	0.971	0.970	0.927	0.647	0.778

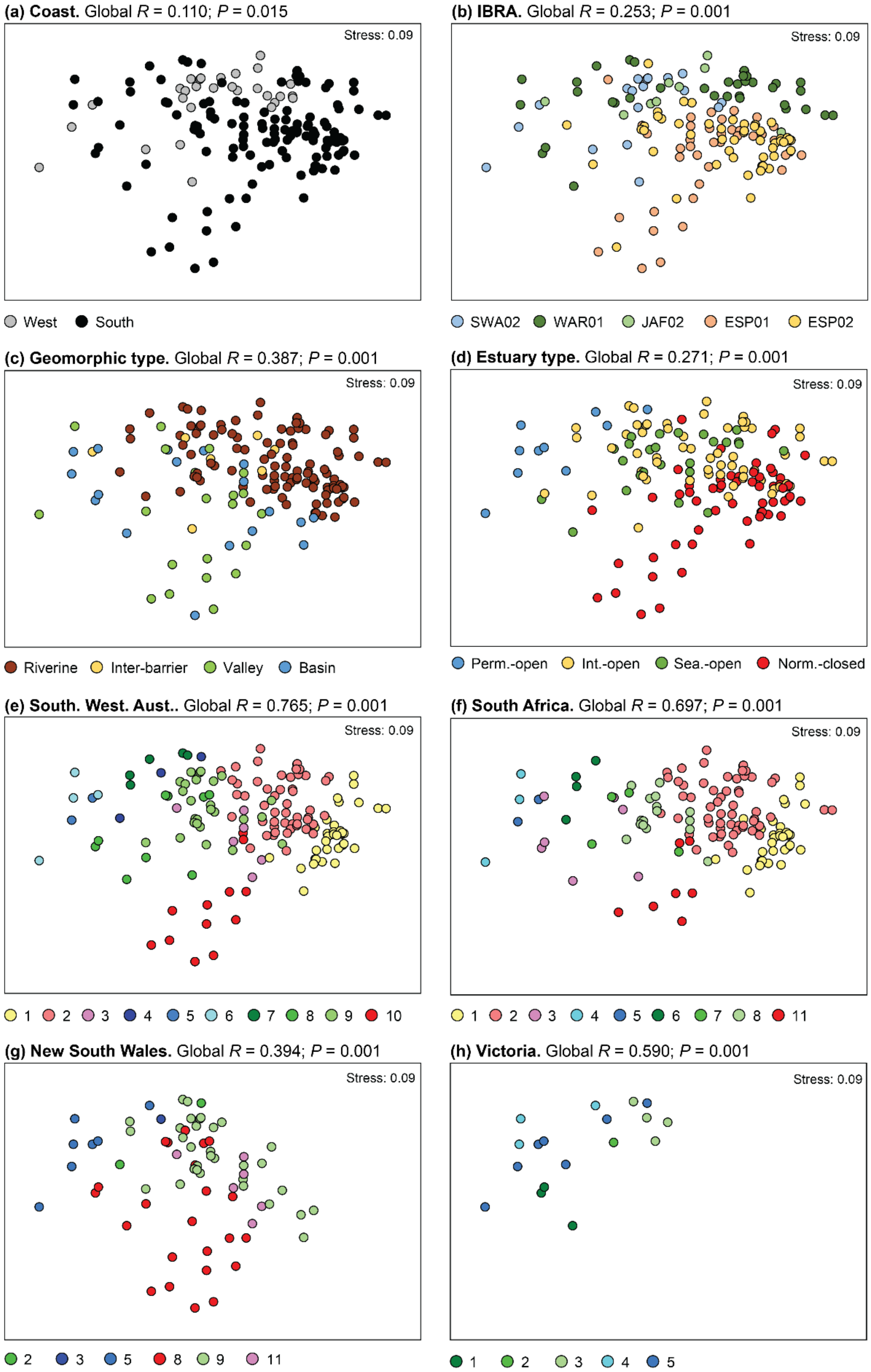


Figure 7. nMDS plots of the physical characteristics of the 152 estuaries in southern Western Australia coded for a suite of classifications. The Global *R*-statistic and associated *P*-value derived from a one-way ANOSIM test are provided on each plot. (a) located on the west or south coast of SWA, (b) located in the IBRA boundaries (Thackway and Cresswell, 1997), estuaries classified into (c) Geomorphic type and (d) Estuary type (Hodgkin and Hesp, 1998), (e) current study, (f) South Africa (Van Niekerk et al., 2020), (g) NSW, Australia (Roy et al., 2001) and (h) Vic, Australia, (McSweeney et al., 2017a). For codes see Table 1.

Biotic parameters

Fish faunal composition recorded from the nearshore (<1.5 m deep) waters of 23 estuaries in southern Western Australia where existing data were available differed significantly with six of the various classification schemes, *i.e.,* all except the coast and geomorphic type classifications (Figure 8). Among those six, the southern Western Australian scheme produced the highest Global *R*-statistic values (0.528), indicating it best discriminated among fish faunas. The next largest value was derived from the estuary type classification, however, examination on the nMDS plots suggest that the slightly lower value was due to the lack of segregation of the permanently-open estuaries which form three categories in the southern Western Australian scheme and, as with the physical environment validation, intermingling of the between intermittently-open and seasonally-open estuaries.

When the analysis was repeated using fish composition data from offshore waters (>1.5 m deep) of the same 23 estuaries and that of Hill Inlet, significant differences were detected among estuaries with five of the schemes (Figure 9). On this occasion the South African classification scheme had the highest Global *R*-statistic (0.469), although it should be noted that this did not include four of the estuaries. The next highest value was derived from the southern Western Australian scheme (0.382), followed by New South Wales (0.347; Figure 9). No significant difference was detected with the estuary type, geomorphic type or coast classifications.

The final validation test utilized data on the benthic macroinvertebrate fauna from the predominantly the nearshore waters of eight estuaries. Estuary type was the only classification scheme that generated a significant result (Global R = 0.673; P = 0.021), although that for the southern Western Australian scheme was close to significance (Global R = 0.542; P = 0.057; Figure 10). It should be noted here that the number of estuaries sampled is small and so this value may change if data were collected from more systems in the future. Examination of the nMDS plots for the estuary type and southern Western Australian schemes indicates that the likely point of difference between them is the classification of the permanently-open category in estuarine type to permanently-open shallow and permanently-open deep categories in the south Western Australian scheme. The lack of distinction in the benthic invertebrate compositions could be due to the fact that the data for these two systems were obtained from the nearshore waters only (Wildsmith et al., 2011; Wildsmith et al., 2009) and thus represents the invertebrates from only a subset of the potential habitat available. Work in the Broke and Wilson inlets (both annually-open basin systems) indicated that there was a significant difference in the sediment composition and benthic invertebrate fauna with depth (Platell and Potter, 1996; Tweedley et al., 2012). However, currently no such comparable data have been obtained from the nearshore and offshore waters on the basin areas of the Swan-Canning Estuary. Due to the paucity in the number of systems from which benthic data are available the current validation should be regarded as preliminary and reinvestigated if and when more data are available.

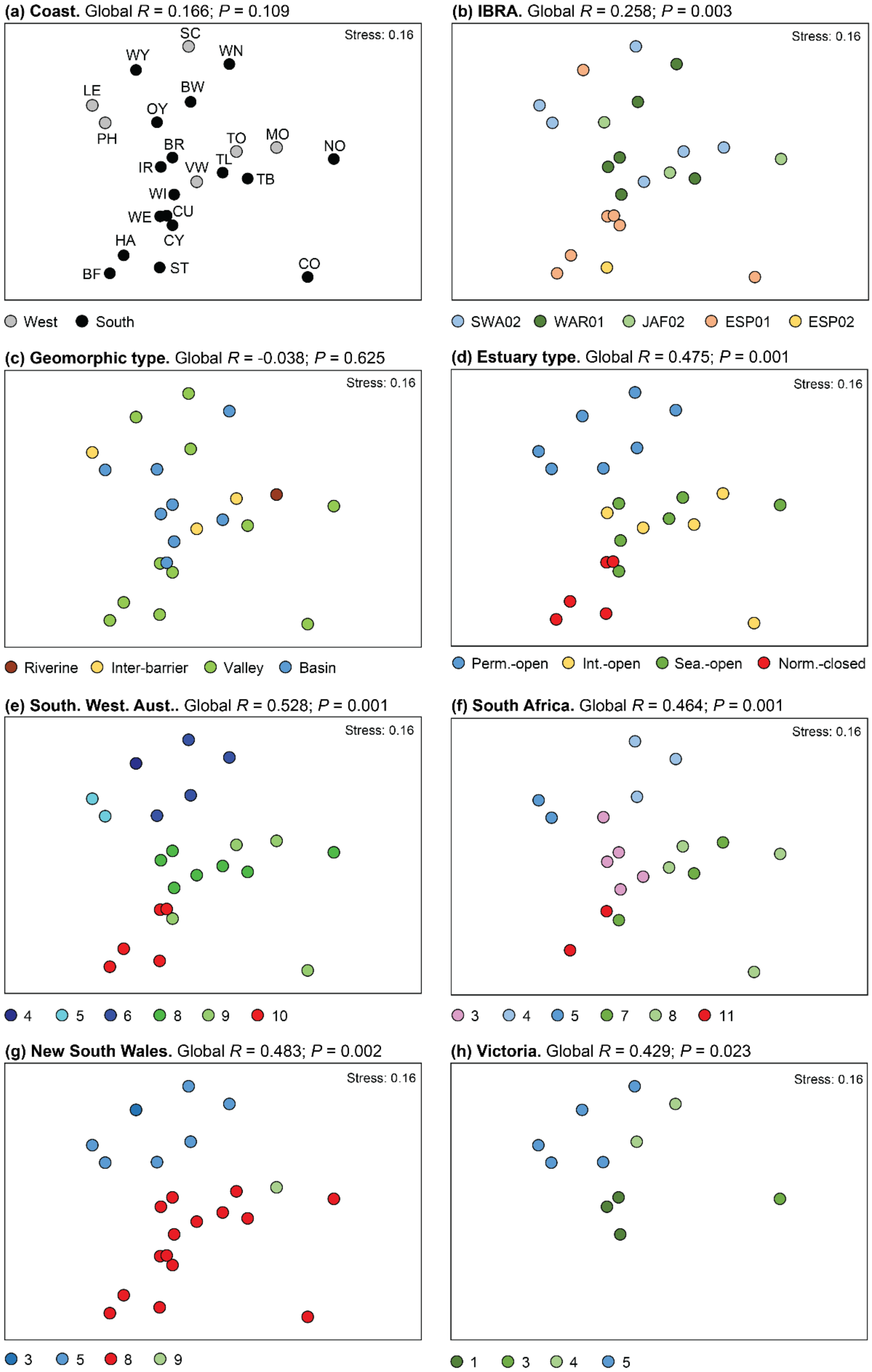


Figure 8. nMDS plots of the nearshore fish fauna of the 23 estuaries in southern Western Australia where studies have been conducted coded for a suite of classifications. The Global *R*-statistic and associated *P*-value derived from a one-way ANOSIM test are provided on each plot. (a) located on the west or south coast of SWA, (b) located in the IBRA boundaries (Thackway and Cresswell, 1997), estuaries classified into (c) Geomorphic type and (d) Estuary type (Hodgkin and Hesp, 1998), (e) current study, (f) South Africa (Van Niekerk et al., 2020), (g) NSW, Australia (Roy et al., 2001) and (h) Vic, Australia, (McSweeney et al., 2017a). For codes see Table 1.

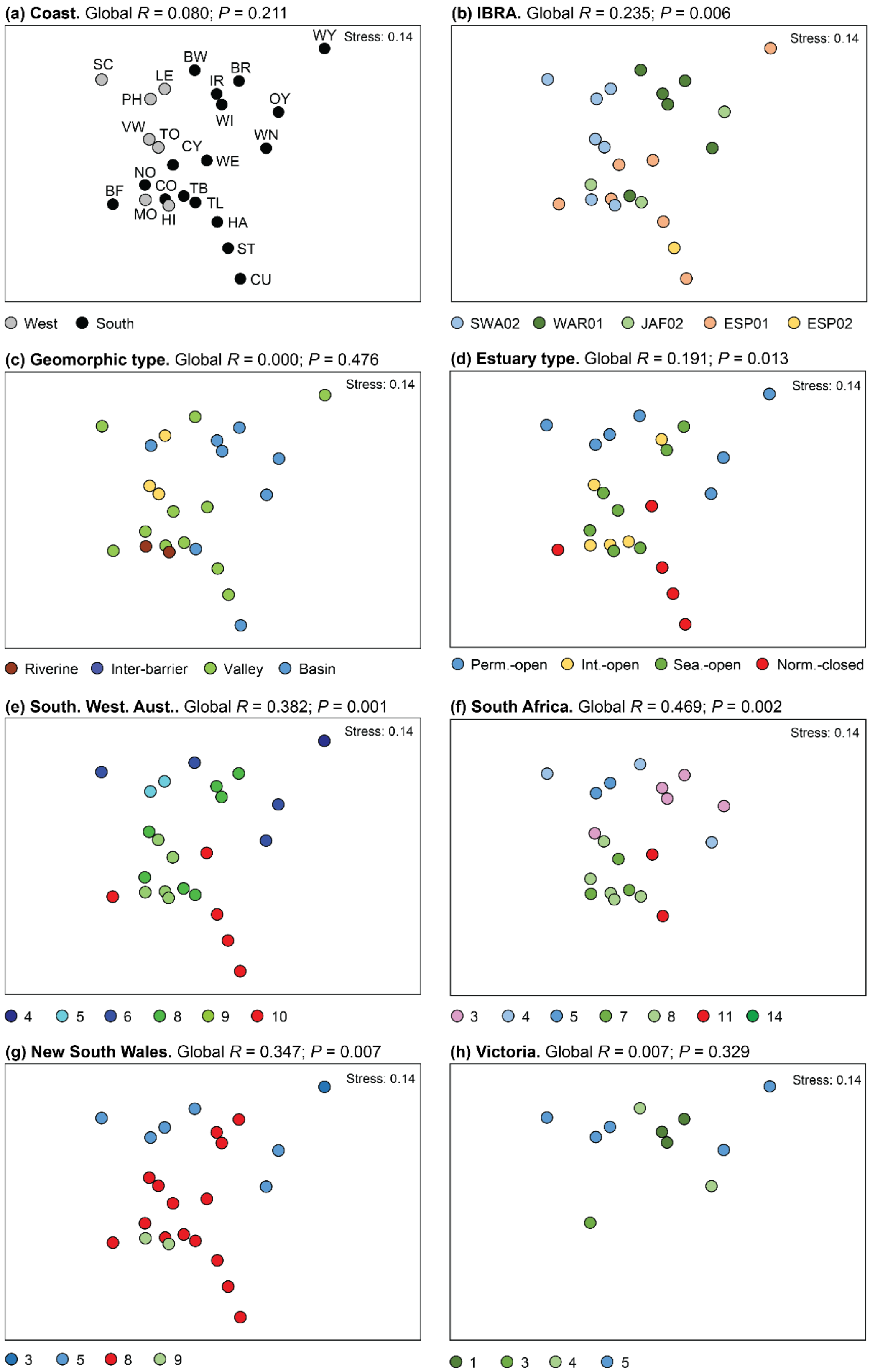


Figure 9. nMDS plots of the offshore fish fauna of the 24 estuaries in southern Western Australia where studies have been conducted coded for a suite of classifications. The Global *R*-statistic and associated *P*-value derived from a one-way ANOSIM test are provided on each plot. (a) located on the west or south coast of SWA, (b) located in the IBRA boundaries (Thackway and Cresswell, 1997), estuaries classified into (c) Geomorphic type and (d) Estuary type (Hodgkin and Hesp, 1998), (e) current study, (f) South Africa (Van Niekerk et al., 2020), (g) NSW, Australia (Roy et al., 2001) and (h) Vic, Australia, (McSweeney et al., 2017a). For codes see Table 1.

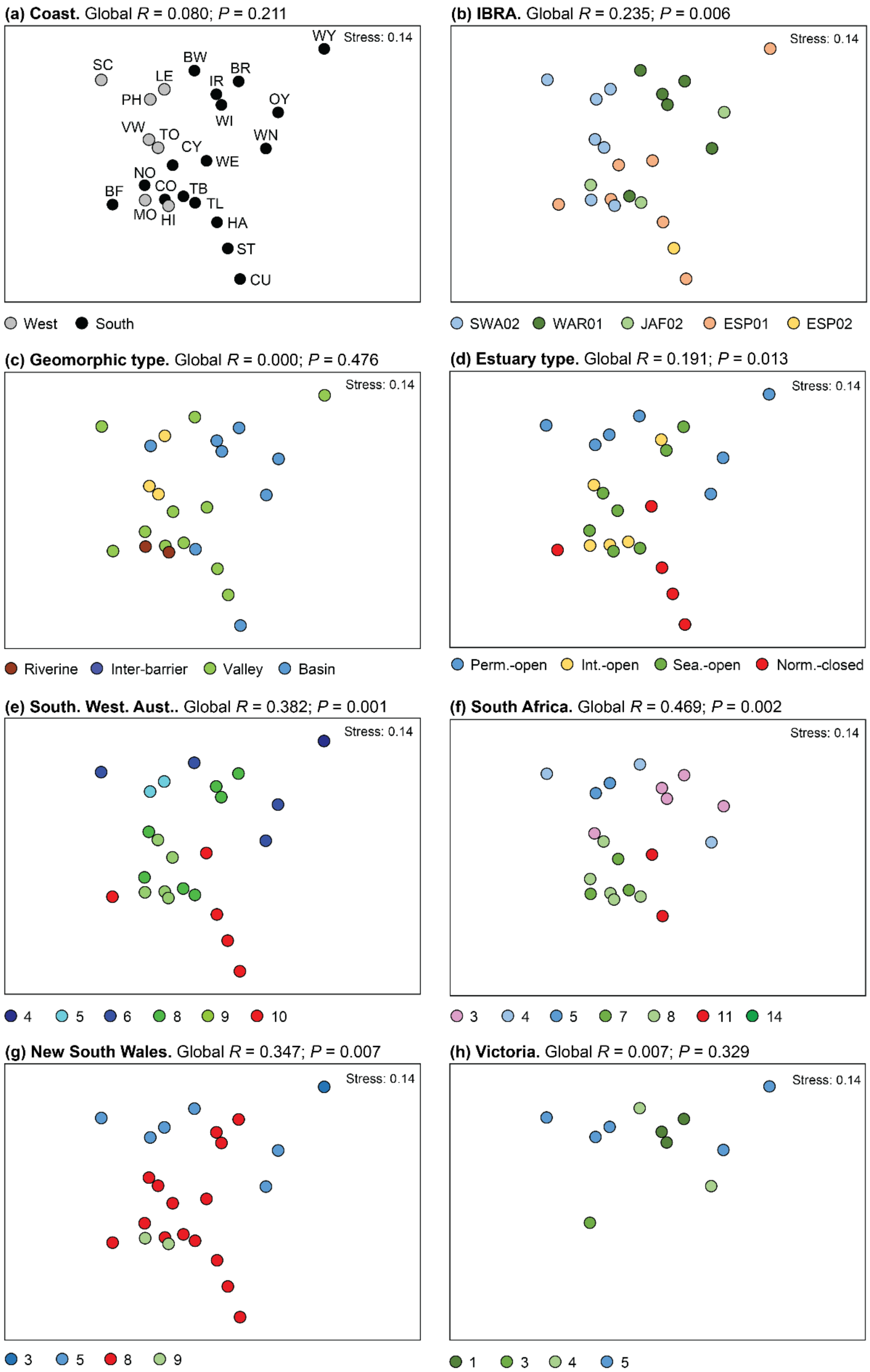


Figure 10. nMDS plots of the benthic macroinvertebrate fauna of the eight estuaries in southern Western Australia where studies have been conducted coded for a suite of classifications. The Global *R*-statistic and associated *P*-value derived from a one-way ANOSIM test are provided on each plot. (a) located on the west or south coast of SWA, (b) located in the IBRA boundaries (Thackway and Cresswell, 1997), estuaries classified into (c) Geomorphic type and (d) Estuary type (Hodgkin and Hesp, 1998), (e) current study, (f) South Africa (Van Niekerk et al., 2020), (g) NSW, Australia (Roy et al., 2001) and (h) Vic, Australia, (McSweeney et al., 2017a). For codes see Table 1.

4. Conclusions and future directions

The use of a range of data and methodologies enabled 152 estuaries that conform to the Potter et al. (2010) definition along the coastline of southern Western Australia to be identified. This represents a three-fold increase in the number of estuaries. Estuaries extend from Hill Inlet (30°S, 115°E) in the north-west to Weanerjungup (33°S, 123°E) in the south-east, all of which fall in the South West Coast drainage division. No estuaries were identified from the South Western Plateau as rainfall in this region is typically <300 mm a year (mean annual rainfall for Eucla = 275 mm; Bureau of Meteorology, 2021) and no rivers reach the coast. Any heavily localised rainfall and associated runoff could result in the temporary formation of a coastal waterfall type of micro-estuary described by Van Niekerk et al. (2020), *i.e.*, "*waterbodies elevated more than 10 m above mean sea level that have no direct channel connection with the sea*". Although not directly related, ephemeral waterfalls are commonly observed forming off Uluru in central Australia (25°20'39.94"S, 131° 2'12.78"E) (mean annual rainfall = 329 mm; Bureau of Meteorology, 2021) following heavy rain (Hudson, 2002).

Through analysis of their physical characteristics, the 152 estuaries were grouped in to 10 categories and a dichotomous key, definitions and a suite of satellite images of various systems provided to aid interpretation of these categories. These would also facilitate the use of this classification in other parts of the world. This study is unique amongst classification schemes in that the resultant categories have been statistically validated using both physical and biotic data. The southern Western Australian classification preformed more strongly that the scheme currently used locally, *i.e.*, estuary type and geomorphic type that focused predominantly on a single aspect of estuaries, *e.g.*, bar status and geomorphology, respectively. Moreover, they were more appropriate than the scheme developed for microtidal estuaries in other parts of Australia and South Africa.

While the validation process was as comprehensive as possible, it was limited by the availability of data. For example, comprehensive fish faunal data were available for 23 estuaries which represent only six of the 10 categories of estuary. No quantitative fish data are available for ephemeral and micro-estuaries, although visual observations and data from South Africa indicate that their faunas are depauperate and likely different from large, permanent waterbodies with greater connectivity from the ocean. Fewer data were available for invertebrates which highlights that this represents a knowledge gap that should be addressed. As more data become available on fish and particularly benthic macroinvertebrates, it would be valuable to repeat the validation of classification schemes. However, the current results suggest that the southern Western Australian classification is the most effective of the current schemes.

SM1 Appendices

Overleaf.

Appendix 1. Characteristics of the 152 estuaries identified in southern Western Australia.

		Location & catchment						Geomorphology							
#	Estuary	Latitude	Longitude	Koppen	IBRA	Median rainfall (mm)	Catchment size (km^2)	Natural/ Artificial	Geomorphic type	Domination	Area (km^2)	Perimeter (km)	Length (km)	Area: Length	Entrance channel width (m)
1	Hill Inlet	30°23'7.20"S	115° 3'2.96"E	Csa	SWA02	500	3,705	Natural	Riverine	River	0.07287	6.23	2.53	28.84	50
2	Moore River	31°21'7.77"S	115°29'58.03"E	Csa	SWA02	500	13,617	Natural	Riverine	River	0.71715	13.42	10.90	65.79	130
3	Swan-Canning Estuary	32° 2'59.50"S	115°44'33.73"E	Csa	SWA02	409	123,943	Natural	Valley	Wave	38.11915	141.55	50.70	751.93	420
4	Peel-Harvey Estuary	32°36'9.58"S	115°37'56.82"E	Csa	SWA02	662	10,843	Natural	Basin	Wave	133.60671	224.28	37.10	3601.55	192
5	Harvey River Diversion Drain	33° 6'29.89"S	115°41'18.27"E	Csa	SWA02	893	712	Artificial	Riverine	Wave	0.05277	6.90	3.38	15.61	20
6	Leschenault Estuary	33°18'16.53"S	115°40'21.64"E	Csa	SWA02	893	4,841	Natural	Inter-Barrier	Wave	26.21764	72.37	24.30	1079.09	150
7	Punchbowl canal	33°20'24.62"S	115°37'26.17"E	Csa	SWA02	653	5	Artificial	Riverine	Wave	0.00680	2.00	1.00	6.83	10
8	Five Mile Brook	33°25'55.45"S	115°35'18.14"E	Csa	SWA02	950	69	Artificial	Riverine	Wave	0.00620	2.89	1.42	4.36	6
9	Unnamed 1	33°27'49.56"S	115°33'53.14"E	Csa	SWA02	950	10	Natural	Inter-Barrier	Wave	0.00747	1.65	0.69	10.88	5
10	Capel River	33°30'44.42"S	115°31'10.59"E	Csa	SWA02	950	642	Natural	Riverine	Wave	0.08156	4.06	1.69	48.32	60
11	Vasse-Wonnerup	33°36'42.32"S	115°25'25.79"E	Csb	SWA02	905	461	Natural	Inter-Barrier	Wave	6.09150	51.85	18.09	336.75	60
12	Vasse Diversion Drain	33°39'6.18"S	115°19'25.54"E	Csb	SWA02	905	294	Artificial	Riverine	Wave	0.03174	2.70	1.33	23.83	30
13	Buayanyup River	33°39'24.86"S	115°14'51.37"E	Csb	SWA02	1010	131	Artificial	Riverine	Wave	0.03324	4.73	2.35	14.14	22
14	Unnamed 2	33°39'22.45"S	115°13'56.24"E	Csb	SWA02	1010	5	Artificial	Riverine	Wave	0.01000	2.84	1.41	7.10	6
15	Carbanup River	33°39'4.39"S	115°12'17.69"E	Csb	SWA02	1050	165	Artificial	Riverine	Wave	0.06754	6.51	2.92	23.16	22
16	Mary Brook	33°38'45.51"S	115°11'36.74"E	Csb	SWA02	1050	90	Artificial	Riverine	Wave	0.01156	2.55	0.72	16.12	6
17	Annie Brook Drain	33°38'30.69"S	115°10'46.49"E	Csb	SWA02	1050	90	Artificial	Riverine	Wave	0.04183	4.82	1.94	21.53	21
18	Toby Inlet	33°38'29.66"S	115°10'37.69"E	Csb	SWA02	1000	260	Natural	Inter-Barrier	Wave	0.17190	11.15	5.28	32.56	15
19	Meelup Brook	33°34'22.10"S	115° 5'12.85"E	Csb	JAF02	1000	5	Natural	Riverine	Wave	0.00107	0.20	0.08	13.74	4
20	Jingarmup Creek	33°33'27.71"S	115° 3'50.00"E	Csb	JAF02	1000	21	Natural	Riverine	Wave	0.00043	0.32	0.14	3.02	7
21	Gunyulgup Brook	33°39'35.38"S	115° 1'2.32"E	Csb	JAF02	975	48	Natural	Riverine	Wave	0.00619	1.37	0.66	9.36	10
22	Quinninup Brook	33°44'47.47"S	114°59'30.97"E	Csb	WAR01	1100	19	Natural	Riverine	Wave	0.00090	0.44	0.21	4.29	10
23	Wilyabrup Brook	33°47'25.38"S	114°59'60.00"E	Csb	WAR01	1100	89	Natural	Riverine	Wave	0.02490	2.72	1.34	18.55	39
24	Cowaramup Brook	33°51'47.31"S	114°59'17.42"E	Csb	WAR01	1030	24	Natural	Riverine	Wave	0.00089	0.36	0.17	5.13	6
25	Ellen Brook	33°54'31.38"S	114°59'18.35"E	Csb	WAR01	1060	28	Natural	Riverine	Wave	0.00065	0.39	0.19	3.45	5
26	Margaret River	33°58'15.45"S	114°59'14.58"E	Csb	WAR01	1075	477	Natural	Riverine	Wave	0.19493	9.06	4.35	44.83	30
27	Boodjidup Brook	34° 1'6.39"S	115° 0'5.55"E	Csb	WAR01	1105	58	Natural	Inter-barrier	Wave	0.00996	2.02	0.96	10.40	20
28	Calgardup Inlet	34° 2'30.71"S	115° 0'8.30"E	Csb	WAR01	1105	32	Natural	Riverine	Wave	0.00226	0.58	0.28	8.18	5
29	Turner Brook	34°16'35.06"S	115° 3'9.17"E	Csb	WAR01	1175	56	Natural	Riverine	Wave	0.00526	1.51	0.57	9.27	10
30	Blackwood River (Hardy Inlet)	34°19'27.65"S	115°10'16.24"E	Csb	WAR01	1421	22,521	Natural	Valley	Wave	13.69755	128.01	41.76	327.98	160
31	Donnelly River	34°28'58.25"S	115°40'32.55"E	Csb	WAR01	1200	1,677	Natural	Riverine	Wave	0.82806	36.47	14.70	56.32	100
32	Warren River	34°36'35.59"S	115°49'48.76"E	Csb	WAR01	1400	4,342	Natural	Riverine	Wave	0.51306	20.58	9.60	53.47	150
33	Meerup River	34°39'32.63"S	115°53'2.01"E	Csb	WAR01	1405	116	Natural	Riverine	Wave	0.05858	5.56	2.50	23.48	50
34	Doggerup Creek	34°46'43.32"S	115°58'49.37"E	Csb	WAR01	1390	74	Natural	Riverine	Wave	0.05959	9.14	3.56	16.72	26
35	Unnamed 3	34°50'27.39"S	116° 2'33.07"E	Csb	WAR01	1420	5	Natural	Riverine	Wave	0.00053	0.44	0.21	2.49	7
36	Gardner River	34°50'37.23"S	116° 7'26.53"E	Csb	WAR01	1420	607	Natural	Riverine	Wave	0.14232	13.15	5.09	27.98	91
37	Unnamed 4	34°51'58.18"S	116°13'4.85"E	Csb	WAR01	1420	5	Natural	Riverine	Wave	0.00084	0.21	0.10	8.66	4
38	Unnamed 5	34°52'8.81"S	116°13'48.02"E	Csb	WAR01	1420	5	Natural	Riverine	Wave	0.00027	0.16	0.08	3.58	5
39	Broke Inlet	34°56'7.63"S	116°22'41.01"E	Csb	WAR01	1331	970	Natural	Basin	Wave	45.55395	73.03	18.81	2421.79	246
40	Unnamed 6	35° 0'13.99"S	116°31'0.51"E	Csb	WAR01	1331	10	Natural	Riverine	Wave	0.00036	0.15	0.06	5.76	2
41	Unnamed 7	35° 0'3.43"S	116°31'8.22"E	Csb	WAR01	1331	10	Natural	Riverine	Wave	0.00071	0.23	0.10	6.89	8
42	Unnamed 8	35° 0'3.74"S	116°31'19.11"E	Csb	WAR01	1331	10	Natural	Riverine	Wave	0.00068	0.22	0.10	6.90	6
43	Unnamed 9	35° 0'23.92"S	116°32'30.14"E	Csb	WAR01	1331	10	Natural	Riverine	Wave	0.00049	0.20	0.09	5.40	8
44	Unnamed 10	35° 2'51.23"S	116°39'24.60"E	Csb	WAR01	1331	10	Natural	Riverine	Wave	0.00100	0.28	0.13	7.61	8
45	Unnamed 11	35° 2'39.76"S	116°40'5.05"E	Csb	WAR01	952	10	Natural	Riverine	Wave	0.00068	0.27	0.13	5.24	4
46	Unnamed 12	35° 2'1.51"S	116°41'41.92"E	Csb	WAR01	952	10	Natural	Riverine	Wave	0.00022	0.11	0.05	4.49	4
47	Walpole-Nornalup Estuaries	35° 1'31.62"S	116°44'4.00"E	Csb	WAR01	952	6,109	Natural	Basin	Wave	14.73949	75.64	21.06	700.05	388
48	Conspicuous	35° 2'20.29"S	116°50'30.39"E	Csb	WAR01	996	10	Natural	Riverine	Wave	0.00064	0.31	0.15	4.22	10
49	Unnamed 13	35° 2'29.81"S	116°55'44.78"E	Csb	WAR01	996	10	Natural	Riverine	Wave	0.00029	0.14	0.06	5.29	5
50	Irwin Inlet	35° 1'1.13"S	116°57'23.18"E	Csb	WAR01	825	2,346	Natural	Basin	Wave	11.08483	42.20	12.11	915.27	300
51	Parry Inlet	35° 1'42.46"S	117° 9'27.93"E	Csb	WAR01	1150	119	Natural	Basin	Wave	1.32315	15.19	5.40	245.21	80

Koppen Climate Classification; Csa = Hot-summer Mediterranean climate, Csb = Warm-summer Meditterranean climate, Cfa = Humid subtropical climate, Bsk = Cold semi-arid (steppe) climate, Cfb = Temperate oceanic climate (Kottek et al., 2006). Interim Biogeographic Regionalisation for Australia (IBRA); SWA02 = Perth, JAF02 = Southern Jarrah Forrest, WAR01 = Warren, ESP01 = Fitzgerald, ESP02 = Recherche (Thackway and Cresswell, 1997), Rainfall (Brearley, 2005), Catchment (Department of Water and Environmental Regulation, 2021), Geomorphic type (Hodgkin and Hesp, 1998), Domination (OzCoasts, 2020), other Geomorphology (Google Earth).

Appendix 1. Continued.

		Location & catchment						Geomorphology							
#	Estuary	Latitude	Longitude	Koppen	IBRA	Median rainfall (mm)	Catchment size (km^2)	Natural/ Artificial	Geomorphic types	Domination	Area (km^2)	Perimeter (km)	Length (km)	Area: Length	Entrance channel width (m)
52	Unnamed 14	35° 1'29.61"S	117°15'18.14"E	Csb	WAR01	1150	10	Natural	Riverine	Wave	0.00063	0.22	0.10	6.21	5
53	Wilson Inlet	35° 1'19.63"S	117°19'48.79"E	Csb	WAR01	792	2,290	Natural	Basin	Wave	49.07940	81.39	24.25	2024.23	220
54	Unnamed 15	35° 4'26.95"S	117°31'7.57"E	Csb	WAR01	875	5	Natural	Riverine	Wave	0.00046	0.23	0.11	4.18	6
55	Unnamed 16	35° 3'38.11"S	117°38'43.82"E	Csb	WAR01	943	5	Natural	Riverine	Wave	0.00040	0.17	0.08	5.10	5
56	Unnamed 17	35° 3'23.83"S	117°39'5.14"E	Csb	WAR01	943	10	Natural	Riverine	Wave	0.00218	0.69	0.32	6.82	15
57	Torbay Inlet	35° 2'37.04"S	117°40'35.60"E	Csb	WAR01	943	287	Natural	Valley	Wave	0.92787	17.60	6.15	150.85	83
	Princess Royal Harbour	35° 2'28.39"S	117°54'39.50"E	Csb	JAF02	940	101	Natural	Embayment	Tide	28.40029	29.99	7.92	3587.25	550
58	Oyster Harbour	34°59'50.05"S	117°56'59.83"E	Csb	JAF02	949	2,983	Natural	Basin	Wave	17.66671	52.57	15.49	1140.23	156
59	Taylor Inlet	34°59'52.12"S	118° 3'44.12"E	Csb	JAF02	800	10	Natural	Basin	Wave	0.46782	4.77	1.93	242.65	62
60	Goodga-Angove	34°58'21.33"S	118°10'42.80"E	Csb	JAF02	850	145	Natural	Basin	Wave	2.05548	19.08	4.61	445.49	13
61	King Creek	34°55'44.83"S	118°12'32.14"E	Csb	JAF02	810	22	Natural	Riverine	Wave	0.01308	2.46	1.20	10.88	25
62	Normans Inlet	34°55'23.92"S	118°12'58.36"E	Csb	JAF02	810	23	Natural	Valley	Wave	0.15002	5.07	1.50	100.15	45
63	Unnamed 18	34°54'51.87"S	118°14'5.45"E	Csb	JAF02	810	10	Natural	Riverine	Wave	0.00133	0.38	0.18	7.36	15
64	Unnamed 19	34°54'12.79"S	118°17'54.58"E	Csb	ESP01	760	10	Natural	Riverine	Wave	0.00103	0.30	0.09	11.06	10
65	Waychinicup Estuary	34°53'51.57"S	118°19'48.90"E	Csb	ESP01	760	242	Natural	Valley	Tide	0.10214	2.85	1.04	98.40	144
66	Maitland River	34°52'32.16"S	118°23'46.37"E	Csb	ESP01	805	20	Natural	Basin	Wave	0.08876	2.53	1.03	86.01	12
67	Bluff Creek	34°49'23.55"S	118°24'3.22"E	Csb	ESP01	805	20	Natural	Riverine	Wave	0.00999	2.73	1.03	9.69	11
68	Little Bluff Creek	34°48'27.87"S	118°24'23.79"E	Csb	ESP01	710	22	Natural	Riverine	Wave	0.00736	1.39	0.67	11.00	15
69	Coal Creek	34°47'51.60"S	118°24'39.87"E	Csb	ESP01	710	10	Natural	Riverine	Wave	0.00133	0.54	0.25	5.22	4
70	Unnamed 20	34°46'40.01"S	118°25'27.32"E	Csb	ESP01	710	10	Natural	Riverine	Wave	0.00191	0.65	0.31	6.15	10
71	Wongerup Creek	34°45'31.93"S	118°26'28.50"E	Csb	ESP01	650	200	Natural	Riverine	Wave	0.00511	0.42	0.32	15.97	15
72	Cordinup Inlet	34°42'4.12"S	118°33'33.75"E	Csb	ESP01	610	131	Natural	Valley	Wave	0.11500	5.83	2.18	52.80	88
73	Willyun Inlet	34°39'58.75"S	118°39'54.45"E	Csb	ESP01	610	847	Natural	Riverine	Wave	0.00973	2.24	0.64	15.20	10
74	Cowla Creek	34°39'11.96"S	118°42'11.12"E	Csb	ESP01	610	20	Natural	Riverine	Wave	0.00179	0.48	0.23	7.85	12
75	Cheyne Inlet	34°36'14.51"S	118°45'17.01"E	Csb	ESP01	610	98	Natural	Valley	Wave	0.17152	7.81	3.43	50.08	90
76	Unnamed 21	34°34'59.92"S	118°44'28.35"E	Csb	ESP01	610	20	Natural	Riverine	Wave	0.00061	0.18	0.07	8.26	10
77	Unnamed 22	34°34'35.28"S	118°44'20.04"E	Csb	ESP01	610	20	Natural	Riverine	Wave	0.00080	0.18	0.08	10.39	15
78	Unnamed 23	34°34'10.53"S	118°44'22.42"E	Csb	ESP01	610	10	Natural	Riverine	Wave	0.00041	0.09	0.04	10.02	15
79	Unnamed 24	34°33'56.71"S	118°44'26.97"E	Csb	ESP01	610	20	Natural	Riverine	Wave	0.00162	0.23	0.09	17.55	17
80	Unnamed 25	34°33'7.50"S	118°44'51.69"E	Csb	ESP01	610	20	Natural	Riverine	Wave	0.00198	0.32	0.15	13.11	23
81	Swan Gully	34°32'17.84"S	118°45'41.60"E	Csb	ESP01	610	30	Natural	Valley	Wave	0.02023	1.82	0.87	23.33	35
82	Unnamed 26	34°30'38.98"S	118°48'16.39"E	Csb	ESP01	610	20	Natural	Riverine	Wave	0.00660	1.23	0.49	13.41	25
83	Unnamed 27	34°29'56.51"S	118°50'34.71"E	Csb	ESP01	410	20	Natural	Basin	Wave	0.05495	2.31	0.40	137.04	17
84	Beaufort Inlet	34°28'2.90"S	118°54'5.39"E	Csb	ESP01	410	6,576	Natural	Valley	Wave	6.49308	38.51	13.97	464.82	500
85	Bitter Water Creek	34°26'38.40"S	119°18'32.72"E	Csb	ESP01	536	164	Natural	Riverine	Wave	0.03011	3.67	1.75	17.16	73
86	Wellstead Estuary	34°23'27.33"S	119°23'34.76"E	Csb	ESP01	465	749	Natural	Valley	Wave	3.00175	35.93	8.04	373.26	233
87	Hunter River	34°21'49.63"S	119°24'48.01"E	Csb	ESP01	610	37	Natural	Valley	Wave	0.16423	3.37	1.22	134.72	20
88	Kellys Creek	34°18'33.88"S	119°29'51.30"E	Csb	ESP01	595	34	Natural	Valley	Wave	0.13829	4.71	2.17	63.79	18
89	Gordon Inlet	34°17'18.72"S	119°29'43.07"E	Csb	ESP01	430	1,698	Natural	Valley	Wave	3.60009	32.58	13.62	264.38	176
90	Boondadup Inlet	34°12'43.78"S	119°32'22.16"E	Cfa	ESP01	500	76	Natural	Riverine	Wave	0.01424	1.50	0.73	19.42	25
91	Little Boondadup Inlet	34°11'4.88"S	119°34'4.47"E	Cfa	ESP01	500	20	Natural	Riverine	Wave	0.00609	1.00	0.48	12.71	25
92	St. Mary Inlet	34° 9'45.99"S	119°34'34.40"E	Bsk	ESP01	480	231	Natural	Valley	Wave	0.30080	6.22	2.45	123.03	75
93	Fitzgerald Inlet	34° 6'16.08"S	119°37'34.17"E	Bsk	ESP01	420	1,548	Natural	Valley	Wave	7.21478	28.47	10.83	666.49	111
94	Dempster Inlet	34° 4'38.19"S	119°40'8.56"E	Bsk	ESP01	470	372	Natural	Valley	Wave	2.22061	18.19	6.22	356.95	50
95	Unnamed 28	34° 2'22.83"S	119°45'6.97"E	Bsk	ESP01	470	10	Natural	Riverine	Wave	0.00046	0.22	0.10	4.56	5
96	Unnamed 29	34° 1'35.05"S	119°46'39.97"E	Bsk	ESP01	470	10	Natural	Riverine	Wave	0.00019	0.10	0.04	4.57	4
97	Unnamed 30	34° 0'18.85"S	119°47'15.57"E	Bsk	ESP01	470	10	Natural	Riverine	Wave	0.00102	0.33	0.16	6.46	4
98	Quion Head Inlet	33°58'55.56"S	119°48'57.23"E	Bsk	ESP01	470	37	Natural	Valley	Wave	0.02057	1.60	0.59	35.05	61
99	Whalebone Creek	33°58'8.09"S	119°51'9.62"E	Bsk	ESP01	470	10	Natural	Riverine	Wave	0.00130	0.56	0.27	4.82	15
100	Hamersley Inlet	33°57'52.17"S	119°54'25.41"E	Bsk	ESP01	440	1,268	Natural	Valley	Wave	2.33160	23.49	7.52	309.89	100
101	Mileys Creek	33°56'2.74"S	119°59'26.66"E	Bsk	ESP01	450	20	Natural	Riverine	Wave	0.00218	0.50	0.23	9.48	23
102	Unnamed 31	33°55'58.50"S	119°59'40.19"E	Bsk	ESP01	450	20	Natural	Riverine	Wave	0.00267	0.40	0.19	14.27	16

Appendix 1. Continued.

#	Estuary	Location & catchment						Geomorphology							
		Latitude	Longitude	Koppen	IBRA	Median rainfall (mm)	Catchment size (km^2)	Natural/ Artificial	Geomorphic types	Domination	Area (km^2)	Perimeter (km)	Length (km)	Area: Length	Entrance channel width (m)
103	Culham Inlet	33°55'24.63"S	120° 3'12.51"E	Bsk	ESP01	450	3,658	Natural	Basin	Wave	12.44613	44.57	12.63	985.68	140
	Jerdacuttup Lakes	33°55'55.83"S	120°15'25.27"E	Bsk	ESP02	415	2,151	Natural	Basin	Wave	5.90223	31.69	10.55	559.72	975
104	Oldfield Estuary	33°53'8.94"S	120°47'14.07"E	Bsk	ESP02	440	2,420	Natural	Valley	Wave	1.10920	18.74	7.63	145.33	240
105	Unnamed 32	33°52'0.64"S	120°58'7.48"E	Bsk	ESP02	550	35	Natural	Riverine	Wave	0.00490	0.95	0.45	10.85	19
106	Torradup Estuary	33°51'34.85"S	121° 0'56.10"E	Csb	ESP02	550	97	Natural	Valley	Wave	0.36640	13.23	5.41	67.75	91
107	Stokes Inlet	33°51'9.77"S	121° 8'11.15"E	Csb	ESP02	384	13,612	Natural	Valley	Wave	12.79619	58.98	13.88	921.78	296
108	Barker Inlet	33°49'5.63"S	121°20'55.06"E	Csb	ESP02	500	305	Natural	Basin	Wave	1.63355	8.59	3.25	502.01	110
109	Bandy Creek	33°50'8.42"S	121°55'58.45"E	Csb	ESP02	465	7,837	Natural	Riverine	Tide	0.22015	7.88	3.39	64.88	152
110	Stockyard Creek	33°51'34.83"S	122° 2'43.23"E	Csb	ESP02	540	30	Natural	Riverine	Wave	0.00926	1.30	0.62	15.01	31
111	Unnamed 33	33°53'25.39"S	122° 4'38.42"E	Csb	ESP02	540	20	Natural	Riverine	Wave	0.00437	0.69	0.33	13.07	10
112	Unnamed 34	33°57'7.90"S	122° 6'29.70"E	Csb	ESP02	540	20	Natural	Riverine	Wave	0.00267	0.71	0.48	5.58	15
113	Unnamed 35	33°58'32.21"S	122° 7'5.14"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00226	0.60	0.27	8.36	8
114	Unnamed 36	34° 0'37.65"S	122° 7'39.25"E	Csb	ESP02	645	10	Natural	Riverine	Wave	0.00130	0.45	0.22	5.97	4
115	Unnamed 37	34° 0'7.71"S	122° 9'42.40"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00079	0.49	0.24	3.36	9
116	Unnamed 38	34° 0'16.21"S	122°10'24.00"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00045	0.22	0.11	4.16	5
117	Unnamed 39	33°59'53.30"S	122°12'16.03"E	Csb	ESP02	645	20	Natural	Basin	Wave	0.07160	2.03	0.76	93.96	4
118	Unnamed 40	33°58'15.66"S	122°16'4.26"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00050	0.32	0.15	3.23	5
119	Unnamed 41	33°57'47.55"S	122°16'15.48"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00009	0.04	0.02	5.53	5
120	Unnamed 42	33°57'32.87"S	122°16'26.33"E	Csb	ESP02	645	20	Natural	Inter-barrier	Wave	0.01117	1.40	0.68	16.50	22
121	Unnamed 43	33°57'24.71"S	122°16'34.23"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00091	0.39	0.18	5.03	5
122	Unnamed 44	33°57'10.34"S	122°16'49.18"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00195	0.47	0.11	17.58	8
123	Unnamed 45	33°56'44.89"S	122°17'32.19"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00637	1.33	0.63	10.09	22
124	Unnamed 46	33°56'4.72"S	122°18'38.13"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00137	0.36	0.15	8.95	15
125	Unnamed 47	33°55'41.54"S	122°19'33.11"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00022	0.12	0.06	3.88	5
126	Unnamed 48	33°55'33.84"S	122°20'4.24"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00023	0.15	0.07	3.53	8
127	Unnamed 49	33°54'45.24"S	122°21'48.37"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.01869	3.41	1.59	11.77	15
128	Unnamed 50	33°54'39.83"S	122°24'16.08"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00653	0.60	0.26	25.39	30
129	Unnamed 51	33°55'22.80"S	122°27'42.32"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00091	0.66	0.32	2.84	10
130	Unnamed 52	33°56'9.56"S	122°30'11.48"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00568	1.59	0.73	7.78	12
131	Unnamed 53	33°56'43.90"S	122°31'17.29"E	Csb	ESP02	645	20	Natural	Basin	Wave	0.20065	5.35	1.52	131.75	18
132	Unnamed 54	33°56'2.72"S	122°32'13.88"E	Csb	ESP02	645	20	Natural	Riverine	Wave	0.00018	0.13	0.06	3.07	6
133	Dailey River	33°54'32.01"S	122°35'39.03"E	Csb	ESP02	610	136	Natural	Inter-barrier	Wave	0.03110	3.91	1.91	16.26	18
134	Unnamed 55	33°53'25.26"S	122°37'54.44"E	Csb	ESP02	610	10	Natural	Riverine	Wave	0.00079	0.33	0.16	5.03	8
135	Mungliginup Inlet	33°53'13.84"S	122°39'28.68"E	Csb	ESP02	590	648	Natural	Riverine	Wave	0.05874	4.91	2.43	24.15	23
136	Unnamed 56	33°53'2.36"S	122°45'1.94"E	Csb	ESP02	595	10	Natural	Riverine	Wave	0.00027	0.16	0.07	4.09	5
137	Alexander River	33°52'36.18"S	122°46'13.16"E	Csb	ESP02	595	1,473	Natural	Riverine	Wave	0.02930	4.24	2.04	14.34	36
138	Blackboy Creek	33°53'13.25"S	122°54'41.99"E	Csb	ESP02	595	197	Natural	Riverine	Wave	0.01617	2.60	1.24	13.04	31
139	Unnamed 57	33°53'4.54"S	122°56'41.18"E	Csb	ESP02	595	10	Natural	Riverine	Wave	0.00129	0.26	0.12	10.55	10
140	Unnamed 58	33°53'8.12"S	122°58'42.51"E	Csb	ESP02	595	10	Natural	Riverine	Wave	0.00056	0.20	0.09	6.08	7
141	Thomas River	33°51'20.22"S	123° 0'55.53"E	Cfb	ESP02	560	405	Natural	Riverine	Wave	0.04687	6.08	2.80	16.72	41
142	Unnamed 59	33°53'9.11"S	123° 6'48.38"E	Cfb	ESP02	529	20	Natural	Basin	Wave	0.11928	2.35	0.83	144.40	6
143	Unnamed 60	33°53'54.56"S	123° 7'46.62"E	Cfb	ESP02	529	20	Natural	Basin	Wave	0.04007	1.32	0.54	74.75	41
144	Jenamullup Creek	33°54'53.90"S	123° 8'33.52"E	Cfb	ESP02	529	20	Natural	Riverine	Wave	0.00255	0.74	0.32	7.92	7
145	Unnamed 61	33°57'25.52"S	123° 9'52.97"E	Cfb	ESP02	529	20	Natural	Riverine	Wave	0.00314	1.04	0.49	6.44	7
146	Cape Arid Creek	33°58'8.58"S	123° 9'51.93"E	Cfb	ESP02	529	20	Natural	Riverine	Wave	0.00144	0.71	0.33	4.42	5
147	Unnamed 62	33°59'15.97"S	123°10'26.29"E	Cfb	ESP02	529	10	Natural	Basin	Wave	0.01479	0.87	0.34	43.00	5
148	Unnamed 63	33°59'15.67"S	123°13'52.81"E	Cfb	ESP02	529	20	Natural	Riverine	Wave	0.00019	0.11	0.05	3.74	5
149	Jorndee Creek	33°56'2.59"S	123°19'29.81"E	Cfb	ESP02	580	30	Natural	Riverine	Wave	0.02654	2.08	0.92	28.97	73
150	Seal Creek	33°55'4.70"S	123°19'45.41"E	Cfb	ESP02	580	10	Natural	Riverine	Wave	0.00164	0.32	0.13	12.35	7
151	Poison-Fern Creek	33°54'12.50"S	123°21'4.35"E	Cfb	ESP02	580	78	Natural	Riverine	Wave	0.03806	4.56	1.52	25.05	43
152	Weanerjungup	33°53'31.57"S	123°23'54.04"E	Cfb	ESP02	580	100	Natural	Riverine	Wave	0.00862	1.09	0.52	16.57	20

Appendix 1. Continued.

#	Estuary	Bar resilience						Drying & hypersalinity			Other classification schemes				
		Mean annual flow (ML)	Number of tributaries	Estuary type	Estimated number of open days	Bar height (m)	Bar width (m)	Frequency of desiccation	Extent of desiccation	Maximum salinity	Condition	WA	SA	NSW	Vic
1	Hill Inlet		1	SO	28	2	50	Perennial	None	31.0	M	9	8	9	
2	Moore River	98,000	2	IO	90	1	30	Perennial	None	35.9	EM	9	7	9	
3	Swan-Canning Estuary	600,000	2	PO	365	0	0	Perennial	None	37.8	EM	6	4	5	5
4	Peel-Harvey Estuary	810,000	3	PO	365	0	0	Perennial	None	48.0	EM	5	5	5	5
5	Harvey River Diversion Drain		1	IO	28	3	63	Perennial	None	14.9		9		9	
6	Leschenault Estuary	632,000	3	PO	365	0	0	Perennial	None	50.0	EM	5	5	5	5
7	Punchbowl canal		1	IO	90	1	53	Perennial	None	24.0		2	2		
8	Five Mile Brook		1	IO	180	1	40	Perennial	None	0.5		2	2		
9	Unnamed 1		1	NC	5	1	37	Seasonally	Partial	36.4		2	2		
10	Capel River		2	IO	270	1	38	Perennial	None	36.5		9		9	
11	Vasse-Wonnerup	40,300	3	IO	90	1	58	Rare	Majority	132.0	EM	8	3	8	
12	Vasse Diversion Drain		1	IO	270	1	55	Perennial	None	35.9		9		9	
13	Buayanyup River	30,000	1	IO	270	1	36	Perennial	None	37.1		9		9	
14	Unnamed 2		1	NC	5	1	60	Perennial	None			2	2		
15	Carbanup River	30,000	1	IO	270	1	25	Perennial	None	37.0		9		9	
16	Mary Brook	15,000	2	IO	14	1	38	Seasonally	Majority			9	2	9	
17	Annie Brook Drain	15,000	1	IO	270	1	41	Perennial	None	50.0		9		9	3
18	Toby Inlet	48,000	1	SO	180	1	44	Perennial	None	48.0	EM	9	8	8	
19	Meelup Brook		1	IO	14	1	4	Perennial	None	2.7		2	2		
20	Jingarmup Creek		1	IO	14	1	45	Perennial	None	2.0		2	2		
21	Gunyulgup Brook	8,000	1	SO	28	1	65	Perennial	None	0.5		2	2		
22	Quinninup Brook		1	SO	28	2	70	Seasonally	Partial			2	2		
23	Wilyabrup Brook	8,000	1	SO	60	2	62	Perennial	None	0.8		9	8	9	
24	Cowaramup Brook	3,800	1	SO	14	2	38	Seasonally	Partial	0.5		2	2		
25	Ellen Brook	5,000	1	SO	180	2	40	Seasonally	Partial	2.7		2	2		
26	Margaret River	65,000	1	SO	60	1	40	Perennial	None	34.0	M	9	7	9	
27	Boodjidup Brook	11,000	1	SO	180	1	79	Seasonally	Partial	0.6		2	2		
28	Calgardup Inlet	4,800	1	SO	28	1	81	Seasonally	Partial			2	2		
29	Turner Brook	14,000	1	SO	28	1	58	Seasonally	Partial	0.6		2	2		
30	Blackwood River (Hardy Inlet)	860,000	2	PO	365	0	0	Perennial	None	31.0	M	6	4	5	4
31	Donnelly River	310,000	1	IO	328	1	130	Perennial	None	33.2	LU	7	6	9	
32	Warren River	380,000	1	IO	328	1	51	Perennial	None	24.9	LU	7	6	9	
33	Meerup River	24,000	1	IO	328	2	112	Perennial	None			7		9	
34	Doggerup Creek	14,000	1	IO	328	1	90	Perennial	None			7		9	3
35	Unnamed 3		1	NC	5	3	48	Seasonally	Majority			2	2		
36	Gardner River	125,000	1	PO	328	0	73	Perennial	None	33.0	LU	7	6	5	4
37	Unnamed 4		1	NC	5	2	59	Seasonally	Majority			2	2		
38	Unnamed 5		1	IO	60	3	72	Seasonally	Ephemeral			1	1		
39	Broke Inlet	162,000	3	SO	60	1	185	Perennial	None	41.0	NP	8	3	8	1
40	Unnamed 6		1	IO	180	1	2	Frequently	Ephemeral	0.3		1	1		
41	Unnamed 7		1	IO	180	1	52	Seasonally	Partial	0.4		2	2		
42	Unnamed 8		1	IO	180	1	56	Seasonally	Partial	0.4		2	2		
43	Unnamed 9		1	NC	5	2	124	Frequently	Ephemeral			1	1		
44	Unnamed 10		1	IO	14	3	43	Seasonally	Partial			2	2		
45	Unnamed 11		1	IO	14	30	29	Frequently	Ephemeral			1	2		
46	Unnamed 12		1	IO	14	30	44	Frequently	Ephemeral			1	2		
47	Walpole-Nornalup Estuaries	363,100	2	PO	365	0	0	Perennial	None	37.0	LU	6	4	5	4
48	Conspicuous		1	IO	180	2	9	Seasonally	Partial	0.4		2	2		
49	Unnamed 13		1	IO	180	1	25	Seasonally	Partial	1.2		2	2		
50	Irwin Inlet	164,000	2	IO	270	1	185	Perennial	None	42.1	LU	8	3	8	1
51	Parry Inlet	28,000	1	SO	90	1	85	Perennial	None	51.9	LU	8	3	8	2

Mean annual flow, Number of tributaries (Brearley, 2005), Estuary type (Hodgkin and Hesp, 1998), Est # of open days, bar height, bar width, frequency and dessication (Google Earth), Max salinity (Krispyn, K., unpublished data) & (Department of Water and Environmental Regulation, 2021), Condition M = modified, EM = Extensively modified, LU = Largely unmodified, NP = near pristine (Brearley, 2005). WA = southern Western Australia, SA = South Africa (Van Niekerk et al., 2020), NSW = New South Wales, Australia (Roy et al., 2001), Vic = Victoria, Australia (McSweeney et al., 2017a).

Appendix 1. Continued.

#	Estuary	Bar resilience						Drying & hypersalinity			Other classification schemes				
		Mean annual flow (ML)	Number of tributaries	Estuary type	Estimated number of open days	Bar height (m)	Bar width (m)	Frequency of desiccation	Extent of desiccation	Maximum salinity	Condition	WA	SA	NSW	Vic
52	Unnamed 14		1	IO	180	1	32	Seasonally	Partial	32.0		2	2		
53	Wilson Inlet	149,700	3	SO	60	1	155	Rare	Disconnected	38.9	M	8	3	8	1
54	Unnamed 15		1	IO	90	3	44	Seasonally	Ephemeral			1	1		
55	Unnamed 16		1	SO	90	2	39	Seasonally	Ephemeral	0.4		1	1		
56	Unnamed 17		1	IO	270	1	23	Seasonally	Partial	0.6		2	2		
57	Torbay Inlet	75,000	2	IO	180	1	28	Perennial	None	36.6	M	8	7	8	
	Princess Royal Harbour	3,600	0	PO	365	0	0	Perennial	None	35.0	M			1	
58	Oyster Harbour	97,200	2	PO	365	0	0	Perennial	None	40.0	M	6	3	5	5
59	Taylor Inlet	1,400	1	SO	28	1	50	Perennial	None	28.2	M	8	8	8	
60	Goodga-Angove	3,400	2	SO	28	1	28	Perennial	None	2.6		3	3	11	
61	King Creek	2,320	1	IO	270	1	50	Perennial	None	21.8		9	2	9	3
62	Normans Inlet	1,800	1	SO	60	1	31	Perennial	None	38.9	M	8	8	8	3
63	Unnamed 18		1	NC	5	2	85	Frequently	Ephemeral			1	1		
64	Unnamed 19		1	NC	5	2	24	Seasonally	Ephemeral			1	1		
65	Waychinicup Estuary	8,000	1	PO	365	0	0	Perennial	None	35.6	M	4		3	5
66	Maitland River		1	SO	28	1	39	Frequently	Disconnected	0.8		3	8	11	
67	Bluff Creek	532	1	IO	90	1	48	Seasonally	Partial	0.8		2	2		
68	Little Bluff Creek	610	1	IO	90	1	18	Frequently	Partial	2.2		2	2		
69	Coal Creek		1	IO	90	1	79	Seasonally	Partial	1.0		2	2		
70	Unnamed 20		1	IO	14	1	62	Seasonally	Ephemeral	4.2		1	1		
71	Wongerup Creek	1,150	1	IO	90	1	75	Seasonally	Partial	26.5		2	2		
72	Cordinup Inlet	1,700	1	IO	60	1	88	Perennial	None	27.5	M	9	8	8	
73	Willyun Inlet	2,110	1	NC	5	2	88	Seasonally	Partial	6.4		2	2		
74	Cowla Creek		1	NC	5	1.5	92	Seasonally	Partial	3.6		2	2		
75	Cheyne Inlet	1,800	1	SO	28	1.5	74	Seasonally	Partial	54.3	M	9	7	8	
76	Unnamed 21		1	NC	5	3	45	Seasonally	Ephemeral			1	1		
77	Unnamed 22		1	NC	5	2	66	Seasonally	Majority	5.4		2	2		
78	Unnamed 23		1	NC	5	1	20	Rare	Majority	0.8		2	2		
79	Unnamed 24		1	NC	5	1.5	60	Frequently	Partial	26.4		2	2		
80	Unnamed 25		1	NC	5	1.5	100	Frequently	Partial	34.9		2	2		
81	Swan Gully		1	SO	60	1	64	Seasonally	Disconnected	7.9		9	8	9	
82	Unnamed 26		1	NC	5	2	71	Seasonally	Partial			2	2		
83	Unnamed 27		1	NC	5	7	70	Frequently	Disconnected			3		11	
84	Beaufort Inlet	36,000	1	NC	5	4	100	Rare	Partial	121.8	M	10		8	
85	Bitter Water Creek		1	IO	60	1.5	121	Perennial	None			9	8	9	
86	Wellstead Estuary	14,000	2	NC	5	1	200	Rare	Partial	84.2	M	10	11	8	
87	Hunter River	191	1	NC	5	4	40	Seasonally	Disconnected	1.0		3	11	11	
88	Kellys Creek	129	1	SO	28	1.5	104	Seasonally	Majority	7.7		3	8	11	
89	Gordon Inlet	10,700	1	NC	5	2	106	Seasonally	Majority	280.2	M	10		8	
90	Boondadup Inlet	146	1	NC	5	1.5	62	Seasonally	Disconnected	54.8		10	2	9	
91	Little Boondadup Inlet		1	NC	5	1.5	80	Seasonally	Partial	34.9		2	2		
92	St. Mary Inlet	360	1	NC	5	1	102	Frequently	Majority	74.7		10	11	8	
93	Fitzgerald Inlet	5,400	1	NC	5	2	250	Frequently	Majority	135.0	LU	10		8	
94	Dempster Inlet	750	2	NC	5	2	163	Frequently	Majority		M	10	11	8	
95	Unnamed 28		1	NC	5	1.5	26	Frequently	Ephemeral			1	1		
96	Unnamed 29		1	NC	5	3	37	Frequently	Ephemeral			1	1		
97	Unnamed 30		1	NC	5	2	17	Frequently	Ephemeral			1	1		
98	Quion Head Inlet		1	NC	5	2	46	Seasonally	Disconnected	56.7		10	11	9	
99	Whalebone Creek		1	NC	5	2	130	Frequently	Ephemeral	16.1		1	1		
100	Hamersley Inlet	1,160	1	NC	5	2	90	Rare	Majority	345.0	M	10	11	8	
101	Mileys Creek		1	NC	5	1.5	84	Seasonally	Disconnected	55.9		2	2		
102	Unnamed 31		1	NC	5	2	100	Seasonally	Ephemeral	40.3		1	1		

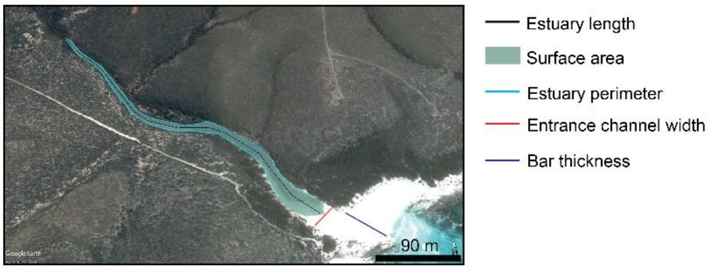
Appendix 1. Continued.

#	Estuary	Bar resilience						Drying & hypersalinity			Other classification schemes				
		Mean annual flow (ML)	**Number of tributaries**	**Estuary type**	**Estimated number of open days**	**Bar height (m)**	**Bar width (m)**	**Frequency of desiccation**	**Extent of desiccation**	**Maximum salinity**	**Condition**	**WA**	**SA**	**NSW**	**Vic**
103	Culham Inlet	3,400	1	NC	5	4	250	Seasonally	Majority	313.0	EM	10		8	
	Jerdacuttup Lakes	8,800	1	PC	0	12	250	Seasonally	Majority		M			12	
104	Oldfield Estuary	8,100	1	NC	28	1	41	Perennial	None	62.0	M	8		8	
105	Unnamed 32		1	NC	5	3	61	Rare	Partial			2	2		
106	Torradup Estuary	1,200	2	SO	28	1.5	41	Rare	Disconnected	40.0	M	9		8	
107	Stokes Inlet	11,880	2	NC	5	1.5	78	Rare	Majority	96.0	EM	10		8	
108	Barker Inlet	1,400	2	NC	5	1.5	65	Seasonally	Majority	32.0	M	10	11	8	
109	Bandy Creek	6,400	1	PO	365	0	0	Perennial	None	46.6	EM	4	6	2	5
110	Stockyard Creek		1	NC	5	2	86	Perennial	None	2.2		2	2		
111	Unnamed 33		1	NC	5	4	85	Frequently	Ephemeral	1.4		1	1		
112	Unnamed 34		1	IO	28	1	30	Perennial	None	2.0		2	2		
113	Unnamed 35		1	IO	28	1.5	31	Seasonally	Majority	3.9		2	2		
114	Unnamed 36		1	NC	5	1	17	Frequently	Majority			2	2		
115	Unnamed 37		1	IO	14	1.5	32	Frequently	Ephemeral	1.5		1	1		
116	Unnamed 38		1	NC	5	1	42	Frequently	Ephemeral	1.1		1	1		
117	Unnamed 39		1	IO	28	1.5	86	Seasonally	Disconnected	0.8		3	8	11	
118	Unnamed 40		1	IO	14	1	16	Seasonally	Majority	10.9		2	2		
119	Unnamed 41		1	NC	5	2	50	Seasonally	Majority	0.9		2	2		
120	Unnamed 42		1	IO	90	1.5	44	Rare	Partial	3.9		9	2	9	
121	Unnamed 43		1	IO	14	2	41	Frequently	Partial	10.9		2	1		
122	Unnamed 44		1	IO	28	1	41	Seasonally	Majority	5.8		2	2		
123	Unnamed 45		1	IO	90	1	36	Perennial	None	1.8		2	2		
124	Unnamed 46		1	IO	28	1	44	Seasonally	Partial	1.4		2	2		
125	Unnamed 47		1	NC	5	2	34	Frequently	Ephemeral	1.6		1	1		
126	Unnamed 48		1	IO	14	1	22	Frequently	Ephemeral	0.9		1	1		
127	Unnamed 49		1	IO	28	1	72	Frequently	Majority			9	2	9	
128	Unnamed 50		1	IO	28	1	80	Seasonally	Majority			2	2		
129	Unnamed 51		1	IO	14	2	60	Frequently	Ephemeral			1	1		
130	Unnamed 52		1	IO	28	2	68	Seasonally	Partial			2	2		
131	Unnamed 53		1	NC	5	1	38	Rare	Ephemeral			1	1	9	
132	Unnamed 54		1	IO	14	2	28	Frequently	Ephemeral			1	1		
133	Dailey River	2,670	2	IO	90	1	32	Perennial	None	12.3		9	8	9	
134	Unnamed 55		1	IO	28	1.5	23	Frequently	Ephemeral			1	1		
135	Mungliginup Inlet	3,170	1	SO	60	1.5	58	Perennial	None	46.0		9	8	9	
136	Unnamed 56		1	NC	5	1	32	Frequently	Ephemeral			1	1		
137	Alexander River	980	1	SO	60	1.5	73	Perennial	None	26.0		9	8	9	
138	Blackboy Creek	1,100	1	SO	60	1.5	60	Perennial	None			9	2	9	
139	Unnamed 57		1	NC	5	3	10	Rare	Majority			2	2		
140	Unnamed 58		1	NC	5	1.5	37	Frequently	Ephemeral			1	1		
141	Thomas River	1,500	1	IO	60	1.5	82	Perennial	None	28.3		9	8	9	
142	Unnamed 59		1	NC	5	4	120	Frequently	Ephemeral			1	1	9	
143	Unnamed 60		1	NC	5	1	33	Frequently	Ephemeral			1	1	9	
144	Jenamullup Creek		1	NC	5	3	123	Seasonally	Ephemeral			1	1		
145	Unnamed 61		1	NC	5	1	46	Frequently	Ephemeral			1	1		
146	Cape Arid Creek		1	NC	5	1.5	8	Frequently	Ephemeral			1	1		
147	Unnamed 62		2	NC	5	1.5	84	Frequently	Ephemeral			1	1	9	
148	Unnamed 63		1	NC	5	1.5	28	Frequently	Ephemeral			1	1		
149	Jorndee Creek		1	PO	365	0	0	Perennial	None	35.2		4		2	5
150	Seal Creek		1	NC	5	2	41	Frequently	Majority	13.9		2	2		
151	Poison-Fern Creek	100	2	IO	60	1	31	Perennial	None	51.0		9	8	9	
152	Weanerjungup		1	NC	5	2	37	Frequently	Majority	11.7		2	2		

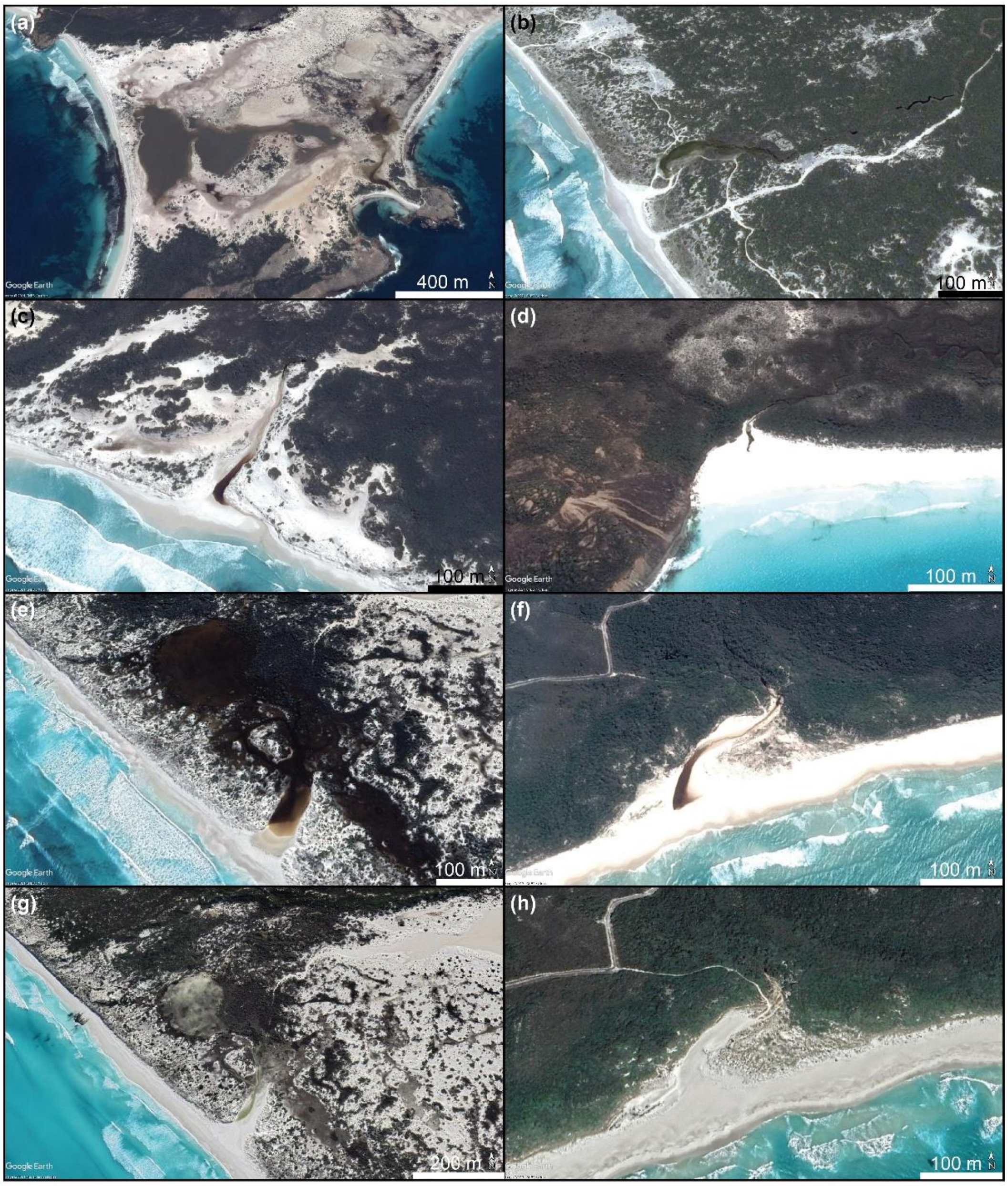
Appendix 2. Sources of data for each estuary in southern Western Australia where quantitative sampling of fish faunas in nearshore (<1.5 m deep) and offshore (>1.5 m deep) waters and benthic macroinvertebrates has occurred.

Estuary	Code	Nearshore fish	Offshore fish	Benthic macroinvertebrates
Hill Inlet	HI		Tweedley et al. (2019)	Tweedley et al. (2019)
Moore River	MO	Young et al. (1997)	I. Potter, unpublished data	
Swan-Canning Estuary	SC	Valesini et al. (2009; 2014)	Loneragan et al. (1989)	Wildsmith et al. (2011)
Peel-Harvey Estuary	PH	Valesini et al. (2009; 2014)	Loneragan et al. (1987)	Wildsmith et al. (2009)
Leschenault Estuary	LE	Veale et al. (2014)	Potter et al. (2000)	
Vasse-Wonnerup	VW	Tweedley et al. (2014)	Cottingham et al (2019)	Tweedley et al. (2020)
Toby Inlet	TO	Tweedley et al. (2018)	Tweedley et al. (2018)	Tweedley et al. (2018)
Blackwood Estuary	BW	Valesini et al. (1997)	Valesini (1995)	
Broke Inlet	BR	Tweedley (2011)	Tweedley (2011)	Tweedley et al. (2012)
Walpole-Nornalup Estuary	WN	Yeoh et al., (2017)	Yeoh (2018)	
Irwin Inlet	IR	Hoeksema et al. (2009)	Chuwen et al. (2009)	
Wilson Inlet	WI	Valesini et al. (2009; 2014)	Chuwen et al. (2009)	Tweedley et al. (2012)
Torbay Inlet	TB	K. Krispyn, unpublished data	K. Krispyn, unpublished data	
Oyster Harbour	OY	Hoeksema et al. (2009)	Chuwen et al., (2009)	
Taylor Inlet	TL	K. Krispyn, unpublished data	K. Krispyn, unpublished data	
Normans Inlet	NO	K. Krispyn, unpublished data	K. Krispyn, unpublished data	
Waychinup Estuary	WY	K. Krispyn, unpublished data	K. Krispyn, unpublished data	
Cordinup River	CO	K. Krispyn, unpublished data	K. Krispyn, unpublished data	
Cheyne Inlet	CY	K. Krispyn, unpublished data	K. Krispyn, unpublished data	
Beaufort Estuary	BF	Krispyn et al. (2021)	Krispyn et al. (2021)	Krispyn et al. (2021)
Wellstead Estuary	WE	Valesini et al. (2009; 2014)	Chuwen et al. (2009)	
Hamersley Inlet	HA	Hoeksema et al. (2006)	Hoeksema et al. (2006)	
Culham Inlet	CU	Hoeksema et al. (2006)	Hoeksema et al. (2006)	
Stokes Inlet	ST	Hoeksema et al. (2006)	Hoeksema et al. (2006)	

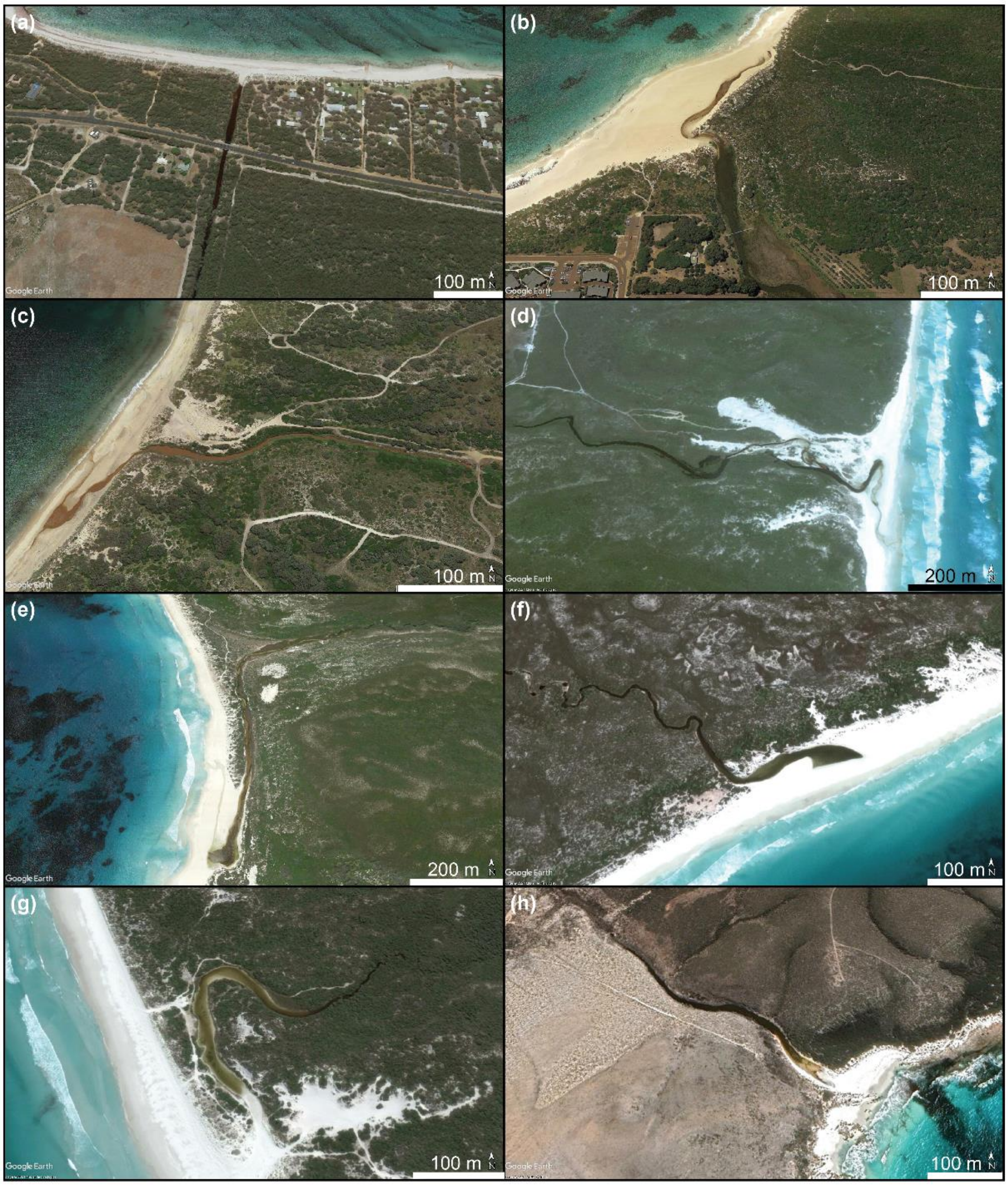
SM1 Supplementary information



Supplementary figure 1. Example measurements of; entrance channel width, surface water area, perimeter, length of main source, bar height and bar width at Little Boondadup Estuary. Image from GoogleEarth[TM] (CNES/Airbus).



Supplementary figure 2. Satellite images of a range of ephemeral estuaries. (a) Unnamed 53; (b) Unnamed 33; (c) Unnamed 51; (d) Unnamed 37; (e) Unnamed 60 containing water; (f) Unnamed 18 containing water; (g) Unnamed 60 when dry; (h) Unnamed 18 when dry. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.



Supplementary figure 3. Satellite images of micro-estuaries. (a) Unnamed 2; (b) Gunyulgup Brook; (c) Five Mile Brook; (d) Bluff Creek; (e) Boodjidup Brook; (f) Unnamed 45; (g) Stockyard Creek; (h) Little Boondadup. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 4. Satellite images of estuarine lake estuaries. (a) Goodga-angove; (b) Goodga-angove bar when open (c); Maitland River; (d) Maitland River bar when open; (e) Unnamed 27; (f) Kelly Creek; (g) Unnamed 39; (h) Hunter River. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 5. Satellite images of morphologically-open estuaries. (a) Waychinicup Estuary; (b) Waychinicup Estuary bar region; (c) Bandy Creek Inlet; (d) Bandy Creek Inlet bar region; (e) Jorndee Inlet; (f) Jorndee Inlet bar region. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 6. Satellite images of permanently-open shallow estuaries. (a) Peel-Harvey Estuary; (b) Mandurah Channel in the Peel-Harvey Estuary; (c) Leschenault Estuary; (d) Leschenault Estuary entrance channel. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 7. Satellite images of permanently-open deep estuaries. (a) Swan-Canning Estuary; (b) Swan-Canning Estuary bar region; (c) Blackwood River (Hardy Inlet); (d) Blackwood River (Hardy Inlet) bar region; (e) Walpole-Nornalup Estuary; (f) Walpole-Nornalup Estuary bar region; (g) Oyster Harbour; (h) Oyster-Harbour bar region. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 8. Satellite images of predominantly-open estuaries. (a) Gardner River 53; (b) Gardner River bar region; (c) Donnelly River; (d) Donnelly River bar region; (e) Warren River; (f) Warren River bar region; (g) Doggerup Creek; (h) Doggerup Creek bar region. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 9. Satellite images of annually-open basin estuaries. (a) Wilson Inlet; (b) Torbay Inlet; (c) Taylor Inlet; (d) Irwin Inlet; (e) Normans Inlet; (f) Parry Inlet; (g) Broke Inlet; (h) Parry Inlet bar when open. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 10. Satellite images of annually-open riverine estuaries. (a) Cheyne Inlet; (b) Poison-Fern Creek; (c) Moore River; (d) Mungliginup Inlet; (e) Margaret River; (f) Tooradup Estuary; (g) Hill Inlet; (h) Thomas River. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary figure 11. Satellite images of normally-closed estuaries. (a) Beaufort Inlet; (b) Fitzgerald Inlet (Left) Dempster Inlet (Right); (c) Hamersley Inlet; (d) Gordon Inlet; (e) Barker Inlet; (f) Stokes Inlet; (g) Quion Head Inlet; (h) St Mary Inlet. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe, and CNES/Astrium.

Supplementary Material 2. Salted Mullet: protracted occurrence of *Mugil cephalus* under extreme hypersaline conditions

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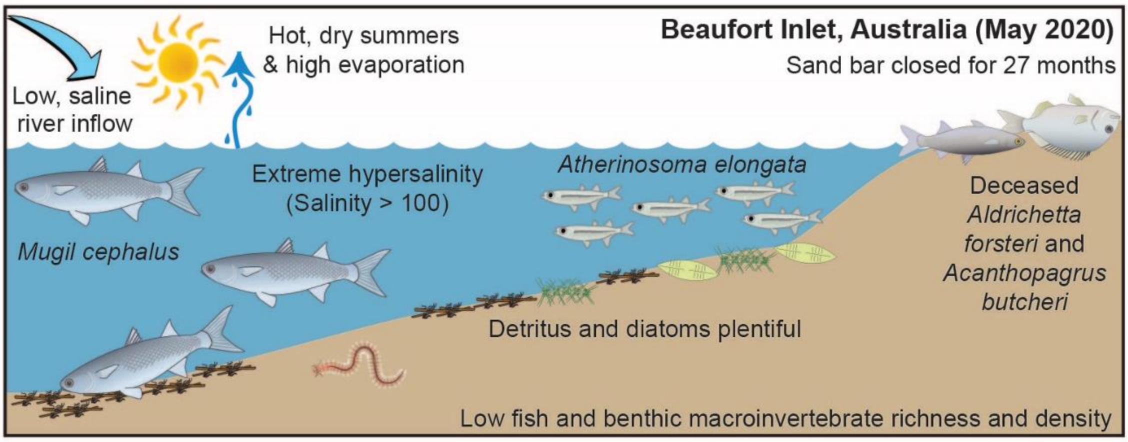
Graphical abstract



Highlights

- Salinities in Beaufort Inlet reached 122 due to low 'freshwater' flow and bar closure.
- Fish and invertebrate fauna depauperate, exacerbated by multiple fish kills.
- Protracted occurrence of *Mugil cephalus* in salinities >100.
- Detritus provided abundant food source for *M. cephalus* assisting survival.
- Highest salinity in which a marine-spawning species of fish has been recorded.

Abstract

Sampling of the fish faunas of eight estuaries along 130 km of the south coast of Western Australia was conducted seasonally for one year, during which Beaufort Inlet became markedly hypersaline (salinities up to 122 and >100 for six months). These conditions were caused by a combination of low amounts of saline river flow, the bar of this shallow estuary remaining closed for 27 months and high rates of evaporation. Fish faunas in the nearshore, shallow and offshore, deeper waters of Beaufort Inlet were depauperate compared to nearby estuaries. The number of fish species declined as salinity increased, with the highly euryhaline, estuarine-resident atherinid *Atherinosoma elongata* being the only fish to survive throughout the study. The cosmopolitan flathead mullet *Mugil cephalus* survived for the next longest period, living in salinities in excess of 100 for at least four months and in a maximum salinity of 122. This is the highest known salinity in which a marine-spawning fish species has been found globally and provides support for the cryptic species complex hypothesis pertaining to *M. cephalus*. The survival of these species for a relatively protracted time reflects the fact that they are euryhaline and have a suite of adaptations that allow them to occupy environments from freshwater to extreme hypersaline conditions. The longer occurrence of *M. cephalus* in the extreme salinities than *Acanthopagrus butcheri* and *Aldrichetta forsteri*, is likely also related to their primary diet of detritus, particulate organic matter and diatoms, all of which are abundant in this estuary. In contrast, piscivorous and zoobenthivorous fish were depauperate and in low abundances, which may reflect limited suitable food resources and/or more reduced euryhalinity by these species. Clearly, hypersalinity has a marked effect on the faunas and thus ecosystem functioning of estuaries, and with declines in rainfall and hotter temperatures projected in future climate change scenarios, more estuaries are likely to become increasingly hypersaline.

Keywords: climate change, closed estuary, fish kill, hyperhaline, osmoregulation, species complex

1. Introduction

Due to the relatively low range of salinities found in oceans, marine species (*i.e.*, those that spawn in marine waters) are typically stenohaline (*i.e.*, marine stragglers sensu Potter et al., 2015; Whitfield et al., 2022). An exception is provided by those marine fish taxa, such as some mugilids, that use estuaries as nursery areas (*i.e.*, marine estuarine-opportunist and marine estuarine-dependent species). For example, the cosmopolitan flathead mullet *Mugil cephalus*, spawns in nearshore marine waters, after which postflexion larvae undertake an onshore migration and recruit into estuaries at between 10 to 40 mm total length (Chubb et al., 1981; Whitfield et al., 2012). Some of these recruits move beyond the upper estuarine reaches into rivers and associated 'freshwater' environments (Bok, 1979). Growth is relatively rapid, and adults emigrate to the ocean at about three years of age to spawn, with some individuals then returning to estuaries in a spent condition (Whitfield et al., 2012). Given the dynamic physico-chemical conditions in estuaries, especially salinity variations, *M. cephalus* and other species with this life-history strategy need to be euryhaline.

Salinities in most estuaries range from 5 to 40, depending on the extent of river flow and marine connectivity. However, a global meta-analysis of hypersaline systems (salinity >40) identified at least 37 estuaries and 58 lagoons that experience these conditions (Tweedley et al., 2019). Such systems were found on all continents except Antarctica and occurred mainly in tropical, arid and warm temperate climates with low and/or highly seasonal rainfall. Microtidal estuaries (tidal range <2 m), where low tidal ranges and hence water volume exchanges prevent dilution of hypersaline waters by the ocean, are particularly susceptible to such conditions. In extreme cases, like the Culham Inlet in south-western Australia, salinities during drought conditions can reach in excess of 300 following the closure of the sand bar at the estuary mouth for several years (Hoeksema et al., 2018).

Most teleost species cannot survive in salinities >50 (Gonzalez, 2012) and so, as the magnitude of hypersalinity increases, the number of species decreases. Under extreme hypersaline conditions, mass mortalities and even the local extirpation of flora and fauna can occur (Hoeksema et al., 2006; Molony and Parry, 2006). A small suite of fish are, however, able to tolerate salinities >80, including species of atherinids (hardyheads), clupeids (herring), fundulids (killifish), cyprinodontids (pupfish), cichlids (tilapias), sparids (breams) and mugilids (mullets) (Whitfield et al., 2006; Brauner et al., 2012). In particular, *Cyprinodon variegatus* has been recorded in salinities of 142 in the USA and

Atherinosoma microstoma in 160 in the Coorong in southern Australia (Haney et al., 1999; Wedderburn et al., 2016). As both of these species complete their life cycle within estuaries (obligate users), there is strong selection pressure to be highly euryhaline or risk extinction from systems that become hypersaline.

Mugil cephalus on the other hand is a facultative user of estuaries and utilises these systems as nursery areas but can also occupy sheltered coastal waters (*e.g.,* embayments) as alternative habitats for their juveniles in regions where estuaries are absent (Lenanton and Potter, 1987). Thus the ‘trapping’ of individuals in an estuary through prolonged bar closure, and their subsequent exposure to extreme salinities, has a far less profound effect on the population than for estuarine species sensu stricto. That being said, *M. cephalus* has been recorded in salinities of up to 70 in the Laguna Madre (USA) and Casamance Estuary (Senegal) and 90 in Lake St Lucia (South Africa) although the durations of time individuals spent in these extreme salinities is unknown (Kantoussan et al., 2012; Nordlie, 2016). In Lake St Lucia, the populations of *M. cephalus* had the opportunity to retreat from the extreme hypersaline conditions in North Lake and False Bay, to the more euhaline conditions prevailing in South Lake (Wallace, 1975a). This species can, however, form the basis of substantial fisheries under moderately hypersaline conditions. For example, in the Mar Menor, a coastal lagoon in Spain where salinities have ranged from 43 to 70, the ‘mugilids’ (which included *M. cephalus*) was the only taxa present throughout the last 200 years (Marcos et al., 2015).

This study investigated the fish faunas of eight estuaries located within a 130 km stretch of the Western Australian south coast, focusing on one system, Beaufort Inlet, which became extremely hypersaline (up to 122). *Mugil cephalus* survived in this estuary for a relatively protracted period, during which all other marine-spawning fish died and the only fish species remaining in the system was the estuarine-resident species *Atherinosoma elongata*. Based on these results we conclude that *M. cephalus* is a highly euryhaline marine fish species and discuss the possible mechanisms and reasons for their survival under extreme hypersaline conditions.

2. Materials and methods

2.1. Study sites

Beaufort Inlet is a 6.5 km^2 estuary (34°27'33"S, 118°53'14"E) located on the microtidal (mean daily maximum tidal range = 0.7 m) southern coast of Western Australia (Fig. 1a).

The system is generally shallow, *i.e.*, <2 m below sea level and has a volume of 6.5 GL (Hodgkin and Clark, 1988). The mouth of the estuary is disconnected from the Southern Ocean by a sand bar that is 500 m long, 100 m wide and can be up to 3.5 m high (Table 1; Supplementary Fig. 1). Due to the size of the bar, the estuary is classified as 'normally-closed', *i.e.*, opens every three to five years, breaching on eight occasions in the 35 years between 1954 and 1998, and typically remains open for a few weeks (Hodgkin and Clark, 1988).

The bar was last breached following heavy cyclonic rain in February 2017 and again in September of that year following above average rainfall (Supplementary Table 1). Thus, at the commencement of faunal sampling in February 2020, the estuary had remained closed for 27 months. Mean seasonal salinities, recorded between 2003 and 2008, showed little variation between five sites spread throughout the estuary but ranged from 10 to 69 over this time (Department of Water and Environmental Regulation, 2021).

The estuary is fed by the 250 km long Pallinup River that drains an area of 4 970 km^2, of which 84 % had been cleared for cereal production and sheep grazing by 1984 (Hodgkin and Clark, 1988). The river was regarded as 'naturally saline', the extent of which has increased since land clearing occurred in the 1950s (Waters and River Commission, 2003). Salinity in the river varies between 3 when the water is flowing, to >50 during summer when the remaining water forms stagnant pools (Hodgkin and Clark, 1988). Beaufort Inlet experiences a Mediterranean climate, with hot, dry summers and warm, wet winters (Hallett et al., 2018). Median annual rainfall in the catchment (Ongerup; 1914-2020) is 388 mm, with 75 % falling between May and October (Bureau of Meteorology, 2021). Freshwater discharge from the Pallinup River (1974-2020) undergoes marked interannual variation, ranging from 0.5 to 151.4 GL (median = 9.7 GL; Department of Water and Environmental Regulation, 2021). Pan evaporation in south-western Australia is ~ 1 800 mm per year and is increasing with climate change (Bureau of Meteorology, 2021).

Beaufort Inlet is one of 13 estuaries along the Western Australian south coast open to commercial gill net and haul net fishing. Fishers target species such as the sparid *Acanthopagrus butcheri*, the plotosid catfish *Cnidoglanis macrocephalus*, the arripid *Arripis georgianus* and the mugilid *M. cephalus*. The estuary is also an iconic location for recreational fishers, who mainly target *A. butcheri* (Smallwood and Sumner, 2007). Large fish kills were recorded in 1998 and 2000, with the first thought to be due to the effects of an algal bloom and the second to low dissolved oxygen and hydrogen sulphide (Waters and River Commission, 2003).

Seven other estuaries were sampled in the study, all located <130 km to the west of Beaufort Inlet (Fig. 1b). Among these, Oyster Harbour and Waychinicup Estuary are 'permanently-open' to the ocean, while the Torbay, Normans, Cheyne and Taylor inlets and Cordinup River are 'seasonally-open', *i.e.,* their bars break annually, usually in winter (Table 1; Hodgkin and Clark, 1990; Brearley, 2005). Except for Oyster Harbour, which is ~ 18 km^2 in size, the other estuaries are <1 km^2 in area.

2.2. Sampling regime

Four sites in the nearshore, shallow waters (<1.5 m deep) in each of the entrance channel (lower estuary), basin (middle estuary) and saline lower reaches of the main river (upper estuary) were sampled in each system during February (summer), May (autumn), July (winter) and November (spring) 2020 (Fig. 1a,b,c). Sampling in these waters was undertaken using a 21.5 m seine net, consisting of two 10 m long wings, each comprising 6 m of 9 mm mesh and 4 m of 3 mm mesh, and a 1.5 m wide bunt made of 3 mm mesh. This net fished to a maximum depth of 1.5 m and swept an area of ~ 116 m^2. All fishes were euthanised in an ice slurry immediately after capture and frozen (Animal Ethics Permit RW3212/20).

Fish in offshore, deeper waters were sampled using composite sunken gill nets (2 m deep), each comprising eight 20 m panels with stretched mesh sizes of 35, 51, 63, 76, 89, 102, 115 and 127 mm. Due to the small size of the estuaries and ethical concerns over potentially high catches, four offshore sites were sampled spread throughout the distribution of nearshore sites (Fig. 1c). Gill nets were set for 1 h and upon capture each fish was identified to species, measured (total length [TL] in mm) and returned to the water.

A core of sediment was collected from each of the 12 nearshore sites in Beaufort Inlet on each sampling occasion, using a cylindrical corer that was 11 cm in diameter (area = 96 cm^2) and sampled to a depth of 15 cm. Cores were preserved in 5% formalin buffered in estuary water and subsequently wet sieved through a 500 μm mesh. Invertebrates were removed from any sediment retained on the mesh and identified to the lowest possible taxonomic level under a dissecting microscope.

Salinity, dissolved oxygen concentration (mg L^{-1}) and temperature (°C), were recorded in the middle of the water column at each nearshore site, on each sampling occasion, using a Yellow Spring Instrument 556 Handheld Multiparameter Instrument. Additional measurements at a limited range of sites were also taken in December 2019 and January, March and September 2020. As the instrument was calibrated to a maximum salinity of 70, when waters exceeded this value readings were calculated using dilutions of freshwater (Hoeksema et al., 2018).

A HOBO 24-002-C data logger was attached to a small concrete mooring and placed at a depth of 1-2 m at the upstream end of the entrance channel region of each estuary except Oyster Harbour. The logger recorded conductivity (maximum = 55 000 uS/cm) and temperature on an hourly basis throughout the study and the resultant data used to detect any breaches of the sand bar that might have occurred between sampling occasions. Salinity data for Beaufort Inlet and salinity and discharge data for the Pallinup River were provided by the Department of Water and Environmental Regulation (2021).

2.3. Data analyses

Mean values (± 1 SE) were calculated for each environmental variable in each month, and number of species and density (100 m^{-2})/catch rate (h^{-1}) of fish in the nearshore and offshore waters of each estuary overall and in each season in Beaufort Inlet. Shade plots (Clarke et al., 2014) were constructed using PRIMER v7 to visually highlight changes in the nearshore and offshore fish fauna seasonally in Beaufort Inlet. White space for a species demonstrates that it was not collected, while the depth of shading from grey to black is linearly proportional to the abundance of the species. Length frequency distributions were plotted for *M. cephalus* in 20 mm length classes for each of the estuaries in which ≥ 100 individuals were caught. Mean values for the number of benthic macroinvertebrates species and density (100 cm^{-2}) in Beaufort Inlet were calculated in each season.

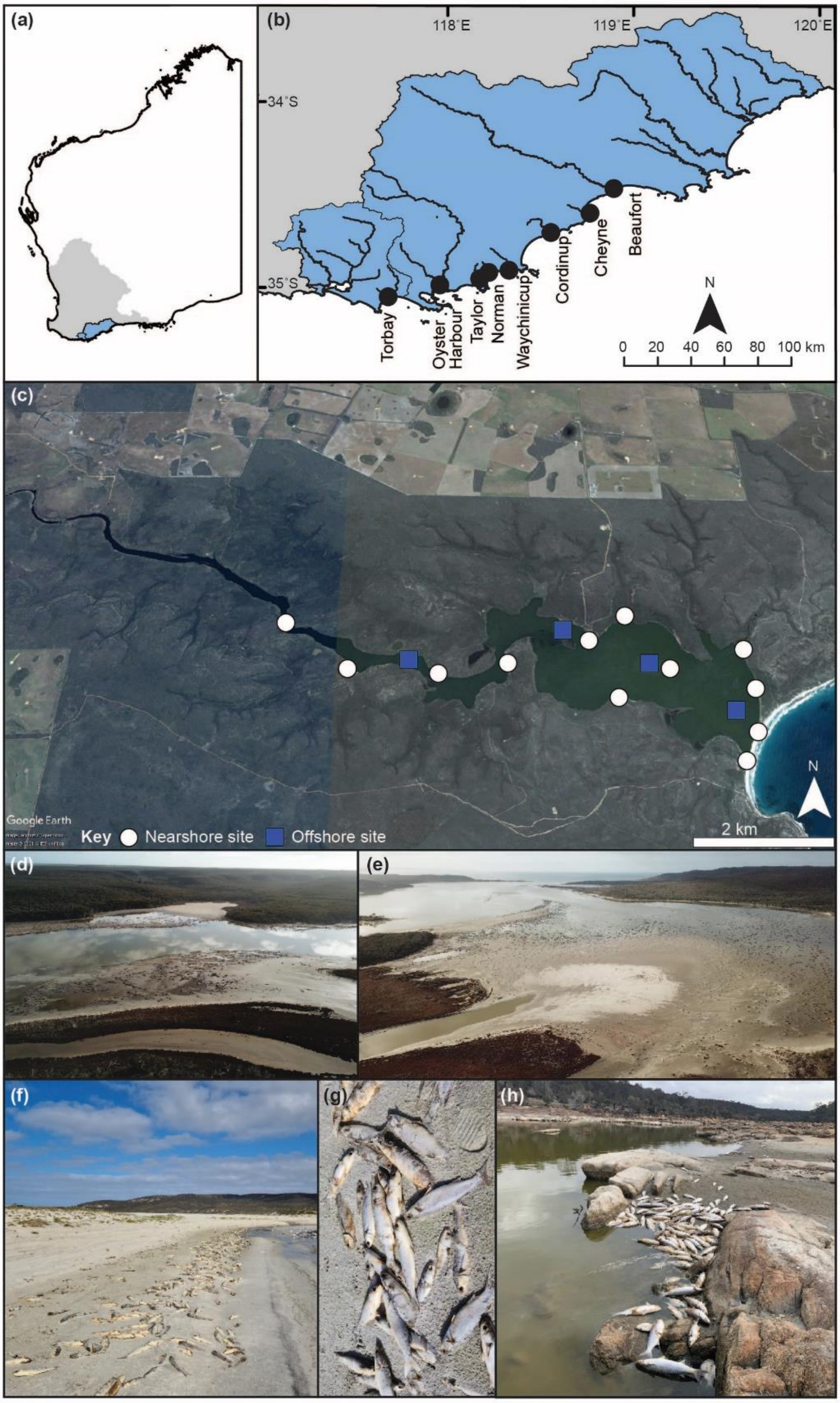


Fig. 1. Map of (a,b) Western Australia showing the south-western drainage division (grey shading) and catchments in the Denmark and Albany coasts (blue shading) including those of the eight estuaries sampled. (c) Satellite image of Beaufort Inlet showing sites in the nearshore and offshore waters. Photos showing the (d,e) extremely low water levels on the south-western shores of Beaufort Inlet in July 2020 and fish kills (f,g) at the bar and in the (h) lower reaches of the Pallinup River. Image in (c) provided by Google Earth and CNES / Airbus.

Table 1. Summary of environmental conditions and characteristics of their nearshore and offshore fish faunas in eight estuaries along the south coast of Western Australia. Data sources; [1] Brearley (2005), [2] Hodgkin and Clarke (1988, 1990); [3] Department of Water and Environmental Regulation (2021).

	Torbay Inlet	**Oyster Harbour**	**Taylor Inlet**	**Normans Inlet**	**Waychinicup Estuary**	**Cordinup River**	**Cheyne Inlet**	**Beaufort Inlet**
Estuary characteristics								
Estuary type [1]	SO	PO	SO	SO	PO	SO	SO	NC
Longitude	117°40'36"E	117°56'60"E	118° 3'44"E	118°12'58"E	118°19'49"E	118°33'34"E	118°45'17"E	118°54'5"E
Latitude	35° 2'37"S	34°59'50"S	34°59'52"S	34°55'24"S	34°53'52"S	34°42'4"S	34°36'15"S	34°28'3"S
Area (km^2)	0.93	17.67	0.47	0.15	0.10	0.11	0.17	6.49
Number of bar breaches in 2020	5	N/A	2	2	N/A	2	2	0
% of days were bar was breached	15	100	4	16	100	11	10	0
Bar height (m) [2]	1.5	N/A	1.0	1.5	N/A	2.0	1.5	3.5
Bar width (m) [2]	28	N/A	50	31	N/A	88	74	100
Average and (maximum) depth (m) [2]	1.5 (5.0)	5.0 (12.5)	2.0 (5.0)	1.0 (2.0)	2.0 (22.0)	2.0 (3.0)	1.0 (2.0)	1.5 (2.0)
Catchment size (km^2) [3]	287	2,983	10	23	242	131	98	6,576
Catchment clearing (%)[1]	74	81	70	46	41	27	40	80
Median rainfall (mm) [1]	943	721	800	800	760	610	610	410
Total annual flow (GL) [1]	75	97.2	1.4	1.8	8.0	1.7	1.8	9.7
Environmental conditions								
Mean salinity (±1SE)	14.12 (1.31)	34.06 (0.46)	19.99 (0.39)	4.17 (0.16)	30.72 (1.07)	12.64 (0.43)	42.53 (0.96)	94.34 (3.12)
Maximum salinity	34.74	37.56	24.16	6.21	35.43	19.26	54.25	121.78
Mean dissolved oxygen (±1SE; mgL^{-1})	8.02 (0.19)	8.31 (0.26)	9.58 (0.26)	8.37 (0.17)	8.00 (0.13)	8.43 (0.22)	7.61 (0.21)	5.39 (0.15)
Mean water temperature (±1SE; °C)	19.12 (0.58)	17.59 (0.42)	17.47 (0.50)	16.86 (0.49)	18.13 (0.25)	17.58 (0.39)	18.02 (0.56)	17.61 (0.53)
Nearshore fish								
Total number of species	16	36	10	4	58	5	19	3
Mean number of species (±1SE)	4.5 (0.23)	5.13 (0.4)	4.19 (0.19)	1.24 (0.07)	3.36 (0.27)	2.08 (0.14)	3.88 (0.29)	1.02 (0.05)
Mean density (±1SE; fish 100 m^2)	320.1 (57.82)	153.92 (33.84)	467.4 (88.1)	203.49 (41.91)	31.03 (7.86)	329.56 (98.95)	2 815.81 (689.98)	352.71 (167.44)
Offshore fish								
Total number of species	10	16	7	5	27	7	12	3
Mean number of species (±1SE)	4.63 (1.64)	3.13 (1.11)	3.38 (1.19)	2.63 (0.93)	6.56 (2.32)	3.06 (1.08)	4.94 (1.75)	0.75 (0.27)
Mean catch rate (±1SE ; fish h^{-1})	124.13 (43.88)	13.75 (4.86)	46.63 (16.48)	19.31 (6.83)	33.81 (11.95)	64.88 (22.94)	116.45 (41.17)	9.75 (3.45)
Mugil cephalus								
Number of fish caught	586	21	87	175	13	612	1,070	147
Total length range (mm)	120 - 490	208 - 474	247 - 447	152 - 420	270 - 440	160 - 509	132 - 515	270 - 463
Median total length (mm)	270	374	338	331	290	328	338	392

3. Results

3.1. Environmental conditions in Beaufort Inlet

During 2020 and the five years prior, the sand bar at the mouth of Beaufort Inlet was breached on three occasions, *i.e.*, January 2016, February 2017 and October 2017, when the mean monthly discharge from the Pallinup River was 8.3, 40.8 and 6.2 m^3s^{-1}, respectively (Fig. 2a). Rainfall in each of 2016 and 2017 was ~ 120 mm above average; however, below average rainfall occurred in 2018, 2019 and, to a lesser extent, in 2020 (Supplementary Table 1). This led to a pronounced decrease in discharge, which, except for August 2020, was always <0.5 m^3/s (Fig. 2a). During these three years, salinities at the Pallinup River gauging station located 34 km upstream from the bar of the estuary typically increased, rising from 15 in January 2018 to a maximum of 53 in June 2020, although salinities did decline to ~ 32 after August 2020 (Fig. 2a). Therefore, all the 'freshwater' that the Beaufort Inlet received from its river was saline and even hypersaline at times.

Mean salinities in Beaufort Inlet increased essentially sequentially from 70 in December 2019 to 109 in May and July 2020, before declining to ~ 60 in September and November 2020 (Fig. 2b). Maximum individual salinities of 120 and 122 were recorded in May and July, respectively. For at least the six months between February and July 2020, salinities at each site exceeded 100 (Fig. 2b). The increase in salinity reflected a marked drop in water levels, exposing marginal shoals and mounds of the serpulid polychaete *Ficopomatus enigmaticus* (cf. Fig. 1c, 1d and 1e). The overall mean salinity during the study (94) and maximum (122) in Beaufort Inlet exceeded those in each of the other seven estuaries located nearby, with their mean salinities ranging from 4 to 43, and maxima reaching between 6 and 54 (Table 1). Cheyne Inlet was the only other estuary where hypersaline conditions were recorded and then only in February and May.

Mean seasonal water temperature in Beaufort Inlet underwent a sinusoidal pattern ranging from ~ 23 °C in February to 13 °C in July before increasing to 18 °C in November 2020 (Fig. 2c). Mean dissolved oxygen concentrations were always normoxic, *i.e.*, 4.4 to 6.8 mg L^{-1} (Fig. 2c). The data logger recorded salinity values in Beaufort Inlet as 'over range' (*i.e.*, >55,000 uS/cm) throughout the entire study, suggesting that the bar at the mouth of the estuary was not breached, unlike those of the seven nearby estuaries that all broke at least twice or are permanently-open to the ocean (Table 1).

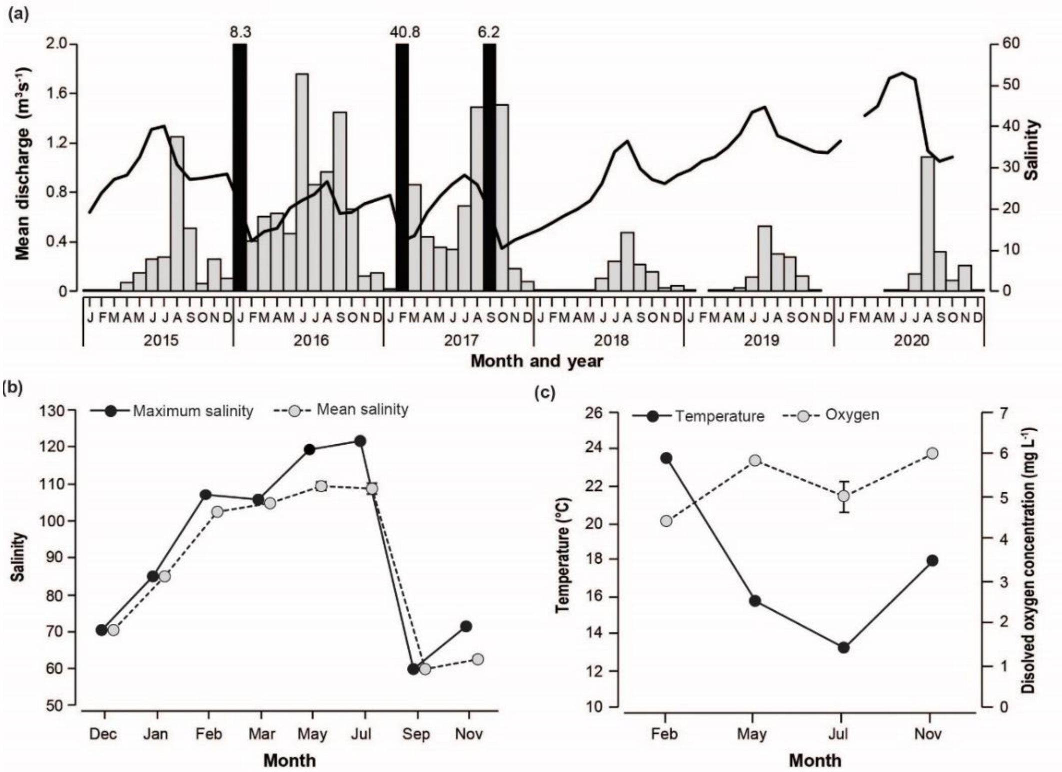


Fig. 2. (a) Mean discharge from the Pallinup River (m^3s^{-1}; histograms) and salinity of that water (line) in each month between January 2015 and December 2020. Black histograms denote months in which the bar at the mouth of Beaufort Inlet broke. Note the relatively very large flows in January 2016 and February and September 2017 shown as numbers as their values exceed the scale on the axis. Data provided by the Department of Water and Environmental Regulation (2021). (b) Maximum salinity and mean salinity, (c) mean water temperature (°C) and mean dissolved oxygen concentration (mgL^{-1}) in Beaufort Inlet. Error bars represent ±1 standard error.

3.2. Changes in fish faunal composition

Three species of fish were caught in seine nets in the nearshore waters of Beaufort Inlet, *i.e.,* the atherinid *Atherinosoma elongata* and the mugilids *M. cephalus* and *Aldrichetta forsteri.* The mean number of species in each season was ~ 1, with the mean density of fish (100 m^{-2}) increasing from 207 (February) to 260 (May) before decreasing markedly to 17 in July and then rising dramatically to 732 in November 2020 (Fig. 3a). *Atherinosoma elongata* dominated the assemblage in each season, representing >99.9 % of the total number of fish caught, while very low numbers of *A. forsteri* and *M. cephalus* were recorded in February and May, respectively (Fig. 3b). Only *A. elongata* was caught in July and November 2020. A total of 86 species were recorded from the nearshore waters of all eight estuaries across the four seasons, ranging from 3 and 4 in Beaufort and Normans inlets to 36 and 58 in Oyster Harbour and Waychinicup Estuary, respectively (Table 1). While the mean number of fish species in Beaufort Inlet was the lowest of all eight estuaries, the density of fish in this system was the third highest.

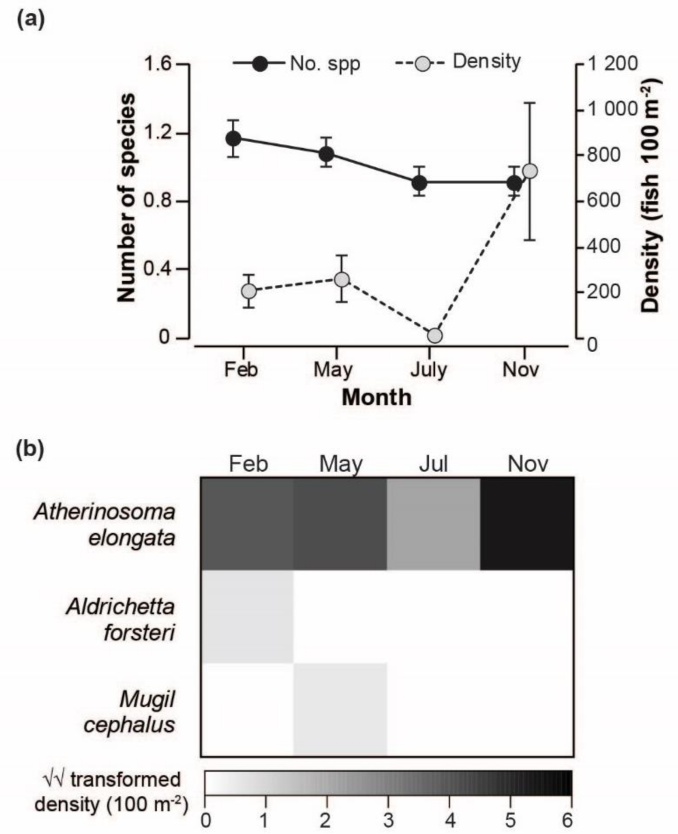


Fig. 3. Mean (a) number of species and density (fish 100 m^{-2}) of fish in the nearshore waters of Beaufort Inlet. Error bars represent ±1 standard error. (b) Shade plots of the nearshore fish fauna in each season in 2020.

Seasonal sampling of the offshore waters of Beaufort Inlet yielded three fish species, *i.e.*, *M. cephalus*, *A. forsteri* and *A. butcheri*, representing 94 %, 3 % and 3 % of the total catch, respectively. The mean number of species declined from 2 in February to 1 in May 2020, with a similar trend recorded for catch rate reducing from 31 to 9 fish h^{-1} between these seasons (Fig. 4a). This decline continued with no fish caught in July or November 2020. *Mugil cephalus* was the only species still recorded in offshore waters in May (Fig. 4b). By July *M. cephalus* was no longer caught and although salinity had decreased in November, no fish in the offshore waters were found in that season. A total of 43 species was recorded in the offshore waters of the eight estuaries, with the three species in Beaufort Inlet being lower than in any of the other systems (range = 5-27; Table 1). Furthermore, catches in the offshore waters of Beaufort Inlet also had the lowest mean number of species (cf. 0.75 and 2.63-6.65) and mean total catch rate (cf. 9.75 and 13.75-124.13).

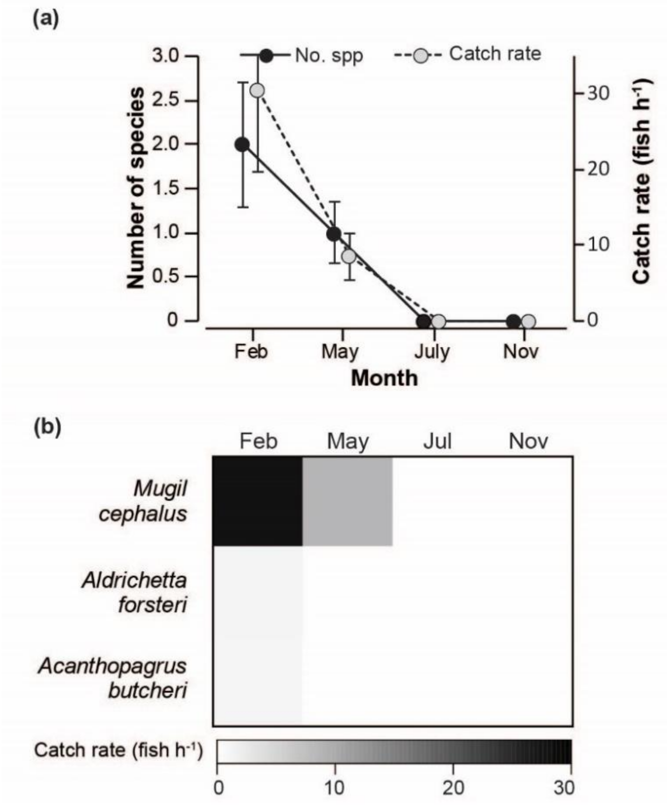


Fig. 4. Mean (a) number of species and catch rate (fish h^{-1}) of fish in the offshore waters of Beaufort Inlet. Error bars represent ±1 standard error. (b) Shade plots of the offshore fish fauna in each season in 2020.

A total of 147 *M. cephalus* were caught in Beaufort Inlet with their total lengths ranging from 270 to 463 mm and a median size of 392 mm (Table 1). The median size in this estuary was greater than that in any of the other seven estuaries sampled. Moreover, the dominant size class of *M. cephalus* in Beaufort Inlet was between 360 and 420 mm TL, comprising 90 % of all individuals (Fig. 5). Fish this large were not numerically abundant in the other estuaries, with the major peak in Normans, Cordinup and Cheyne comprising fish of around 320-340 mm TL and smaller in Torbay at 200-280 mm TL.

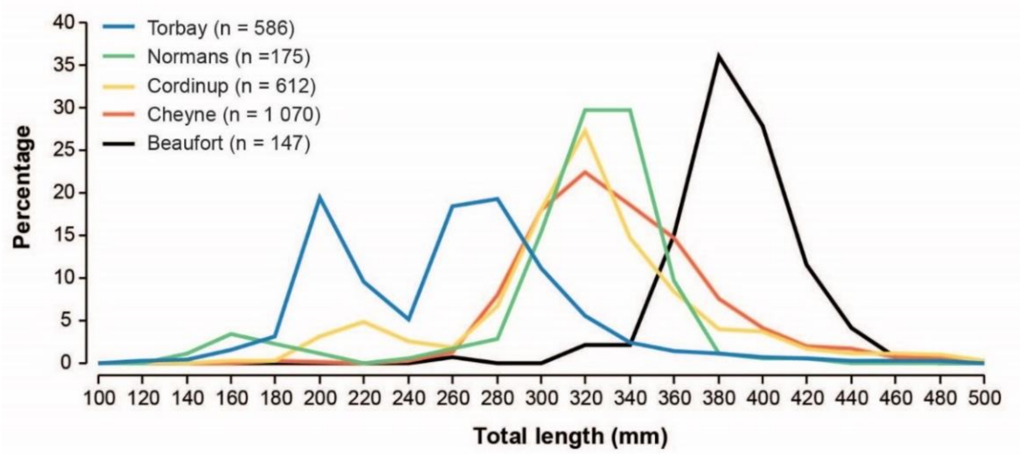


Fig. 5. Length frequency (percentage) distribution of *Mugil cephalus* recorded in each of the five estuaries on the southern coast of Western Australia where >100 individuals were caught.

3.3. Observations of mass mortalities of fish

In mid-January 2020 fishers observed *A. butcheri* with salt sores and ten days later visitors to the estuary reported seeing an estimated 50 000 fish dead on the banks. During sampling in February, dead fish were observed on the shoreline extending from the bar (Fig. 1f), through the basin to the lower parts of the upper reaches. Numbers were greater on the eastern shore, likely due to the prevailing westerly sea breeze, and the bar where full strength seawater seeps through, thus providing a localised refuge of 'diluted' hypersalinity. The majority of dead fish were *A. butcheri* and *A. forsteri*, with lower numbers of the sillaginid *Sillaginodes punctatus* and *A. georgianus*. An emaciated *A. butcheri* was observed swimming at the water's surface before dying (K. Krispyn, pers. obs.).

Another fish kill was reported by the public in April 2020 in the upper reaches of the estuary comprising mainly *M. cephalus* with some individuals of the sparid *Rhabdosargus sarba*. By May, water levels had declined further and fish from the kills in January and February were still visible and relatively intact (*i.e.*, had not started to undergo decomposition) in the basin and at the bar. Dead *M. cephalus* were observed washed up onto rocks in the upper reaches (Fig. 1g) and some were seen lethargically finning at the surface.

In July 2020, relatively high densities of dead *M. cephalus* extended throughout all regions of the estuary, with the greatest numbers at the bar and the upper reaches. Declining water levels exposed rocky granite outcrops, which disconnected the uppermost reaches of the estuary from the Pallinup River and would have prevented the movement of fish upstream. Water levels had risen in November and no new dead fish were observed. Previously deceased fish that had sunk were collected as bycatch from the seine netting and were decomposing.

3.4. Benthic macroinvertebrate composition

A total of 1 062 benthic macroinvertebrates, representing six taxa were extracted from the 48 samples with a mean density of only 23 individuals 100 cm^{-2}. Larval insects dominated the fauna, with larvae of the chironomid *Tanytarsus barbitarsis* contributing 98.7 % of all invertebrates recorded. The ostracod *Mytilocypris ambiguosa,* polychaete *Capitella capitata* (both 0.6 %) and larval Ceratopogonidae spp. (0.4 %) were the next most abundant, with a single individual of the polychaete *Psuedopolydora kempi* and amphipod *Grandidierella propendatata* also collected. The mean number of benthic macroinvertebrate species declined from 1.4 in February to 0.8 in May and June before increasing slightly to 1.1 in November 2020. Mean density (individuals 100 cm^{-2}) underwent the same trend decreasing from 39 in February, to 16 in May and June, and then 20 in November, driven by shifts in the abundance of *T. barbitarsis*.

4. Discussion

Apart from Beaufort Inlet, there are only a small number of estuaries globally, where salinities can exceed 100, including the Laguna Madre (USA), St Lucia and Groen (South Africa), Casamance and Sine-Saloum (Senegal) and Coorong, Culham, Hamersley, Vasse-Wonnerup and Wellstead (Australia; Wooldridge et al., 2016; Tweedley et al., 2019). These systems are generally shallow and located in areas with low and/or highly seasonal rainfall, low tidal ranges and high rates of evaporation (Tweedley et al., 2019). In Beaufort Inlet, the pronounced hypersalinity was caused by three years of below average rainfall, resulting in limited saline (mean salinity = 34) discharge from the Pallinup River and the bar being closed for 27 months prior to the start of the current study, including remaining closed throughout the 10 months of sampling. Given the paucity of hypersaline systems, periods of extreme hypersalinity provide a unique opportunity to investigate the effects of this environmental state on the faunas of these systems. The frequency of extreme hypersaline events in these systems, and the number of systems experiencing extreme hypersalinity, is likely to increase with changing climate, particularly along the southern coast of Australia.

4.1. Effect of hypersalinity on the fauna of Beaufort Inlet

Hypersaline environments are regarded as among the harshest to survive in due to the osmoregulatory challenges they pose (Gonzalez, 2012). As marine fish regulate their internal salt concentrations and osmotic pressure below that of seawater, they lose water osmotically, which is replaced by absorbing seawater (Brauner et al., 2012). Salts in that water must be removed to maintain a favourable osmotic gradient, with Na^+ and Cl^- excreted branchially by chloride cells (ionocytes) fuelled by the enzyme Na^+/K^+-ATPase (NAK) and protein co-transporters, and divalent salts (mainly Mg^{2+} and SO_4^{2-}) excreted renally in isotonic urine (Genz et al., 2011; Gonzalez, 2012).

As salinities become increasingly hypersaline, water absorption and salt excretion become more challenging. Gonzalez (2012) posed that, in theory, for a fish living in 3 x seawater (salinity = 105; *i.e.*, similar to that in Beaufort Inlet during the current study) the osmotic gradient across the gills is ~ 4 x greater and, if water loss is 4 x higher than in seawater, that fish would need to absorb 12 x more salt water. This would greatly increase salt excretion and lead to an associated increase in metabolic costs and oxygen consumption (Brauner et al., 2012).

The fish fauna of Beaufort Inlet was depauperate, harbouring only three species in each of the nearshore and offshore waters, compared to 5-58 (nearshore) and 5-27 (offshore) found in the other seven estuaries sampled. Moreover, as salinities increased from February to July, the number of species and density/catch rate of fish decreased. Simultaneously, the composition of fish that had died and washed up on the banks of Beaufort Inlet changed. Generally, marine estuarine-opportunist species were the first to die with *S. punctatus* and *A. georgianus* only observed dead on the banks in February (*i.e.,* they were not caught during sampling). While the marine estuarine-opportunist *A. forsteri* and solely estuarine *A. butcheri* were recorded in February, these species had become extirpated by May. *Mugil cephalus* was last recorded in May, following four months of existence in salinities >100.

Atherinosoma elongata remained present for the duration of the study and its density increased markedly in November following successful spawning as occurs at this time of year (Prince and Potter, 1983; Tweedley et al., 2014a). This atherinid is highly euryhaline having been recorded in salinities of 122 in the nearby Wellstead Estuary (Young and Potter, 2002) and its congener *A. microstoma* in salinities as high as 160 in the Coorong (Wedderburn et al., 2016). Chironomids are a key component of the diet of *A. microstoma* (Hossain et al., 2017) and therefore it is plausible that these atherinid species utilise this abundant food resource, subsidised from terrestrial environments, during periods of extreme hypersalinity.

The location of deceased fish on the banks in Beaufort Inlet, and those collected from seine nets, indicates that fish tried to move upstream into the moderately hypersaline Pallinup River (salinity = 42-53) as a refuge. However, movement into these waters was precluded by the presence of rock bars exposed by the low water levels and that obstructed water flow. Similar bars in the river of Culham Inlet 120 km north-west of Beaufort prevented the upstream movement of *A. butcheri*, and contributed to the death of an estimated 1.3 million fish when salinities exceed 85 (Hoeksema et al., 2006).

Sequential reductions in the richness and abundance of the fish fauna like those in Beaufort Inlet have been reported elsewhere in the world as salinities exceed the tolerance of particular species (Whitfield et al., 2006). In the study of a solar salt pond in northern

Australia, which ranged in salinity from ~ 35 to 116, Molony and Parry (2006) recorded a significant negative relationship between the number of species and salinity, with a reduction of one species for each increase of salinity by 16. In St Lucia, the number of fish species recorded declined from 39 at a salinity of 18, 18 at a salinity of 80, and 1 at a salinity of 120 (Whitfield et al., 2006). Moreover, declines in prey diversity with increasing salinities have been found to telescope the food chain (Deegan et al., 2010), thus creating food problems for fishes foraging at higher trophic levels. Fish species in temperate estuaries are known to exhibit low redundancy (Whitfield and Harrison, 2020), which the additional loss of species through hypersalinity would exacerbate, resulting in a reduction in ecosystem complexity and potentially also functionality.

4.2. Reasons for the protracted occurrence of Mugil cephalus

With the exception of *A. elongata*, *M. cephalus* persisted in the hypersaline conditions present in Beaufort Inlet longer than any other fish, with individuals surviving for at least four months (potentially six) in salinities of >100 and were recorded in a maximum salinity of 122. This value considerably exceeds the highest recorded for *M. cephalus* in other hypersaline estuaries, *e.g.*, the 70 in the Sine Saloum and Casamance (Trape et al., 2009; Kantoussan et al., 2012) and 75 in the Laguna Madre (Gunter, 1967). In St Lucia, *M. cephalus* was abundant in salinities between 60 and 70, present in salinities between 70 and 80, but either absent or undergoing mortalities above 80 (Wallace, 1975a).

While *M. cephalus* was recorded in a salinity of 110 in the upper reaches of Wellstead Estuary (50 km east of Beaufort Inlet), individuals were able to seek refuge further downstream where salinities were ~ 55 (Young and Potter, 2002). No such refuges were present in Beaufort Inlet during the current study due to wind-driven mixing of the shallow water and the presence of rock bars in the Pallinup River. The only known record of *M. cephalus* in salinities greater than those recorded in Beaufort Inlet was an experiment where fry were exposed to salinities of 126 and survived for four days (Khériji et al., 2003). As *M. cephalus* is known to frequent rivers in south-western Australia containing freshwater (salinity = 0; *i.e.*, those that have not been subjected to secondary salinization) for extended periods of months to years their salinity range is considered to be 0 to 122, the greatest recorded for any mugilid and also any other marine-spawning fish species.

The greater salinities in which *M. cephalus* is known to survive in southern Australia, together with limited dispersal and the isolation of this coastline relative to its global distribution could suggest that this is a separate species within the *M. cephalus* species complex. For example, tagged individuals in Western Australia were found to mainly migrate only a few kilometres from estuaries into coastal waters (Thomson, 1951). Phylogenetic analyses of mitochondrial DNA from *M. cephalus* collected globally suggested there were 14 species within this complex including one from Western Australia (Durand et al., 2012). This sample from the Peel-Harvey Estuary on the lower-west coast was unique from all other samples, including those from eastern Australia, New Zealand and South Africa. When the estuaries in south-western Australia were formed 7,000 years ago they were all permanently connected to the ocean, however, a reduction in sea level ~ 3,500 years ago resulted in many becoming isolated for periods of time (Hodgkin and Hesp, 1998). This isolation is thought to have been the selection pressure that resulted in these systems being dominated by species that are euryhaline and complete their lifecycle within estuaries (Potter et al., 1990). In a study of the genetic connectivity of seven fish species, including *M. cephalus*, Watts and Johnson (2004) concluded that estuaries in this region provide opportunities for genetic divergence and can increase the genetic subdivision of populations of inshore fishes, particularly those that utilise both marine and estuarine habitats.

Although little information is available on osmoregulatory mechanisms in mugilids there is some evidence to suggest that they possess some adaptations (see review by Nordlie, 2016). Higher NAK intensity and activity were found in the gills of *Liza aurata* that had been acclimated to salinities of 36 and 46 than 12 or 0 (Khodabandeh et al., 2009). Moreover, when individual *L. aurata* were subjected to hypersaline conditions the number of their chloride cells increased (Shahriari Moghadam et al., 2013). This facilitates the excretion of Na^+ and Cl^-, helping to mitigate the increases in these monovalent ions from drinking saline water. Moreover, the kidneys of mugilids are able to shift roles depending on the environment they are currently occupying (Nordlie, 2016). For example, in freshwater they excrete water gained osmotically from the hypoosmotic environment while conserving solutes, but in hypertonic waters, where body water is lost through osmotic flow, the kidney functions to conserve water and excrete divalent ions and other metabolic wastes (Nordlie, 2016).

Like other marine estuarine-opportunists *M. cephalus* spawns in marine waters and the juveniles recruit to the upper reaches of estuaries and even rivers, before returning to the ocean to spawn (Whitfield et al., 2012). In Western Australia, spawning and recruitment occurs between March and September (Chubb et al., 1981). The *M. cephalus* present in Beaufort Inlet in 2020 are hypothesised to have recruited to the estuary as 0+ fish following the most recent breaching of the bar in September 2017 and as the bar has remained closed since those individuals became trapped. This is supported by the length-frequency distributions where 90 % of the individuals were between 360 and 420 mm TL and thus estimated to be 3+ based on growth curves for male and female *M. cephalus* from the nearby Wellstead Estuary (Chuwen et al., 2008). As this size range is well above the length at sexual maturity, which starts at 270 mm and all are mature by 310 mm TL, fish were trapped in the estuary and thus unable to spawn.

In St Lucia, *M. cephalus* start maturing at much larger sizes than in Wellstead Estuary. Maturity begins at ~ 350 mm TL for both males and females, with at least 80 % of the sampled population being sexually mature at ~ 450 mm TL for males and 490 mm TL for females (Wallace, 1975b). The considerable difference in these values support the species complex hypothesis for *M. cephalus* discussed above. However, similar to the Wellstead Estuary example, the St Lucia mouth became constricted between June and August 1970 and resulted in adult *M. cephalus* resorbing their gonads due to an inability to access the marine environment where spawning occurs (Wallace, 1975b).

In Wellstead Estuary, *M. cephalus* would have been unable to spawn and there would have been a shift from reproductive to somatic growth, thus allowing the fish to grow larger and maintain a greater mass for their length (*i.e.,* a good body condition). Substantial energy reserves would help compensate for the increase in metabolic costs associated with osmoregulation in extreme salinities. Globally adult *M. cephalus* consume mainly detritus (including particulate organic matter), benthic microalgae (*e.g.,* diatoms), filamentous algae, foraminferans and small invertebrates (Odum, 1968; Blaber, 1976, Whitfield et al. 2012). Similarly, in Wilson Inlet on the south coast of Western Australia, *M. cephalus* ingested sediment and fine organic material almost exclusively (Platell et al., 2006). It is noteworthy that catches of *M. cephalus* decreased in the Mar Menor lagoon (Spain) following colonization of the alga (*Caulerpa prolifera*), which rendered the sediments anoxic and reduced the surface area covered with cyanbacteria and benthic diatoms (Marcos et al., 2015). The low energy environment of microtidal estuaries results in up to 80 % of the fine sediments that are transported into the estuary becoming trapped (Tweedley et al., 2016), which would provide a continual food source for this mugilid. As rates of digestion in *M. cephalus* increase with body size and salinity (Perera and De Silva, 1978), based on its diet, this species is well-adapted to survive in Beaufort Inlet.

The benthic macroinvertebrate component of non-hypersaline estuaries is typically dominated by crustaceans (*e.g.,* amphipods), polychaetes and molluscs (Tweedley et al., 2014b; 2015). However, a study in the Coorong showed that as salinity increases the number of taxa decreases and at a salinity of 64 the composition shifted markedly away from the 'traditional' fauna to one that is dominated by chironomids and ostracods (Dittmann et al., 2015). A similar pattern occurred in St Lucia, where only ostracods and chironomid larvae survived in salinities >50 (Boltt, 1975). These trends also reflect the invertebrate fauna of Beaufort Inlet, which was overwhelmingly dominated by *Tanytarsus barbitarsis* larvae (>98 % of all invertebrates). This species, which is found in salinities between 20 and 170, is a detritivore and regarded as the most salt-tolerant chironomid (Kokkinn, 1986). In addition to the limited range of taxa present, densities of macroinvertebrates were between 4 and 14 times lower than in other estuaries in south-western Australia (*i.e.,* 240 vs 960 to 3 195 individuals 100 cm^{-2}; Wildsmith et al., 2009; 2011).

The fact that *M. cephalus* survived for longer than the other mugilid *A. forsteri*, is also likely facilitated by their diet. The latter species is zoobenthivorous feeding on a range of taxa including crustaceans (*e.g.,* the carid prawn *Palaemonetes australis*), polychaetes, insects (beetle larvae) and gastropods (Thomson, 1954; Platell et al., 2006). The absence of these taxa in Beaufort Inlet could lead to the starvation of *A. forsteri* particularly given the increased metabolic demand in response to the hypersalinity. Consequently, zoobenthivorous fish are at greater risk from the effects of hypersalinity than detritivorous (iliophagous) feeders such as *M. cephalus*.

5. Conclusions

This study recorded the cosmopolitan flathead mullet *Mugil cephalus* living in salinities in excess of 100 for at least four months and in a maximum salinity of 122 in an estuary on the south coast of Western Australia. This is the highest known salinity in which a marine-spawning fish species has been recorded. The survival of these species for a relatively protracted time reflects the fact that they are highly euryhaline and have a suite of adaptations, the exact physiological mechanisms of which require further research, that allow them to occupy freshwater to extreme hypersaline conditions. The longer occurrence of *M. cephalus* than other species is also likely related to their diet of detritus, particulate organic matter and diatoms, all of which are abundant in this estuary. In contrast, fish species that are piscivores or zoobenthivores were depauperate and sparse, probably due to a combination of poor food resources and lack of euryhalinity under extreme hypersaline conditions. It is clear that hypersalinity has a marked effect on the faunas and thus ecosystem function of estuaries, and with declines in rainfall and increasing temperatures projected in the future, more estuaries are likely to become markedly hypersaline.

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SM2: Supplementary tables and figures

SM2: Supplementary table 1. Total monthly and annual rainfall 2015-2020 at Ongerup in the catchment of Beaufort Inlet. Mean and median rainfall between 1914 and 2020 are provided, together with their difference from the mean annual total. Grey shading denotes months where the bar at the mouth of the estuary was breached. Data provided by the Bureau of Meteorology (2021).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual	Difference
2015	1.2	20.0	16.4	30.4	31.8	34.4	45.0	43.8	22.2	22.6	31.8	29.8	329.4	-58.6
2016	108.6	8.4	56.4	36.8	34.8	49.2	24.8	74.2	36.6	24.8	8.0	42.6	505.2	117.2
2017	5.4	169.0	30.4	16.2	14.6	30.2	54.2	48.8	88.6	22.8	12.4	16.0	508.6	120.6
2018	19.6	9.1	16.4	14.3	10.6	40.5	34.3	57.2	11.1	28.8	26.6	16.6	285.1	-102.9
2019	1.3	0.6	41.7	19.8	18.5	64.1	37.4	55.1	15.5	40.4	3.1	0.6	298.1	-89.9
2020	0.6	48.3	16.1	14.8	38.2	29.4	29.4	73.6	37.6	13.6	51.7	7.8	361.1	-23.9
Mean	18.8	19.4	22.5	25.9	43.0	48.5	49.0	43.7	38.6	33.0	25.6	17.7	387.5	
Median	8.6	11.0	15.8	20.0	36.2	41.5	47.7	42.0	36.3	27.6	20.4	9.2	388.2	

SM2: Supplementary figure 1. Photographs showing the size of the bar of Beaufort Inlet in July 2020. For perspective the boat (located below the arrow) is 3.75m in length. Note the extensive vegetation present on the bar, further suggesting it breaks infrequently and, when it, does in discrete locations. The breach in February 2017 occurred on the left side of that vegetation.