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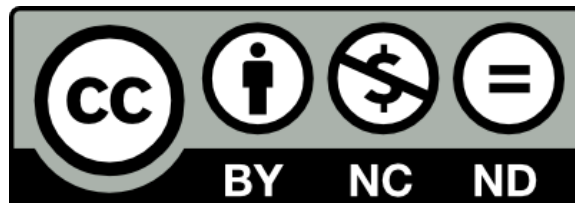
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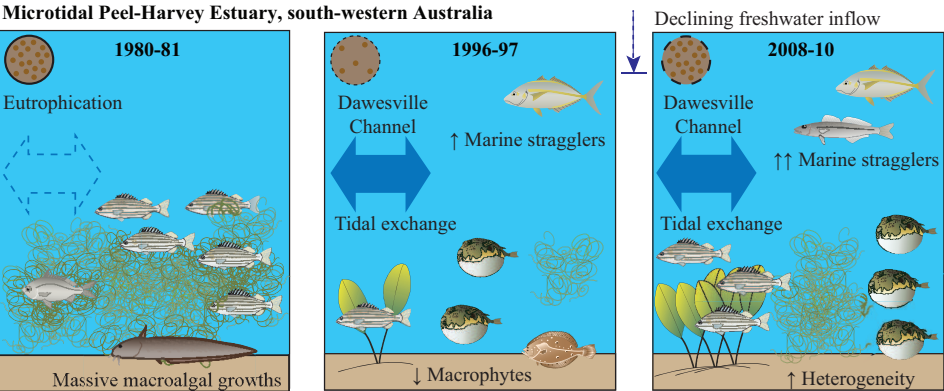
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Highlights

- Ichthyofauna of a eutrophic microtidal estuary following engineering intervention
- Species composition changed after opening of an artificial subsidiary entrance channel
- Increased tidal exchange and persistent high salinities influenced species composition
- Species composition also reflects extent of macrophyte abundance
- Great value of long-term data for predicting changes in estuarine ichthyofaunas

Decadal changes in the ichthyofauna of a eutrophic estuary following a remedial engineering modification and subsequent environmental shifts

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Keywords

Fish; ecoengineering; south-western Australia; microtidal; climate change

Abstract

This study has determined how the characteristics of the ichthyofauna of a large eutrophic microtidal estuary changed, initially in response to major structural remedial modifications, and then, during later years, as the environment became further modified, due mainly to effects of climate change. Data on the ichthyofauna of the Peel-Harvey Estuary, in south-western Australia, were derived firstly by seining in five regions over two consecutive twelve months (two years) in 2008-10. These data were then collated with those recorded previously using the same sampling regime throughout 1980 and 1981, when massive macroalgal growths were present, and throughout 1996 and 1997, soon after the opening, in 1994, of an artificial, deep and second entrance channel. The latter resulted in greater tidal flushing, consistently high salinities and reduced macroalgal biomass. Ichthyofaunal composition changed significantly overall and in four of the five regions across the three periods. Although increased tidal exchange did not lead to a rise in the number either of those marine species that typically use estuaries as nursery areas (marine estuarine-opportunists) or of those that complete their life cycle within the estuary (estuarine residents), the contributions made by the abundances of the representatives of those two groups to the total catch of fish varied markedly between periods. Those differences were largely responsible for the inter-period changes in species composition. In contrast to the situation with marine estuarine-opportunists, increased tidal exchange and higher salinities resulted in a greater number of marine straggler species entering the system, albeit in low numbers. The ichthyofauna during 1980-81 contained relatively large numbers of species that are typically associated with macrophytes, including marine estuarine-opportunists, e.g. *Pelates octolineatus*, and estuarine residents e.g. *Ostorhinchus rueppellii* and *Hyporhamphus regularis*. Following the opening of the artificial entrance channel, the relative abundances of these three macrophyte-associated species declined, whereas those of species, e.g. the marine estuarine-opportunist *Torquigener pleurogramma* and estuarine resident *Favonigobius lateralis*, which typically occur over unvegetated areas and in elevated salinities, increased. By 2008-10, such species had become more abundant, following declines in freshwater discharge and a longer persistence of high salinities, with macrophyte-associated species, e.g. the marine estuarine-opportunists *P. octolineatus*, *Gymnapistes marmoratus* and *Haletta semifasciata* and estuarine resident *O. rueppellii*, becoming more numerous as macroalgal and seagrass areas developed. This study demonstrates the great value of long-term data sets for detecting and predicting the effects of major structural changes and climate change on the faunas of estuaries.

Introduction

Estuaries are among the most productive of all aquatic ecosystems (Schelske and Odum, 1961; Heip et al., 1995; Costanza et al., 2007), with their high primary and secondary productivity providing a rich food source (Elliott and Hemingway, 2002; França et al., 2011; Potter et al., 2015a). This energy source is used by the wide range of marine fish species that enter estuaries in appreciable numbers, particularly during early life. Thus, in comparison with their natal environment, the juveniles of these species grow more rapidly and, through the presence of fewer large piscivores, are less susceptible to predation (Blaber, 1980; Le Pape et al., 2003; Yamashita et al., 2003; Veale et al., 2016). Estuaries have therefore often been considered as important nursery areas for fish (Blaber and Blaber, 1980; Beck et al., 2001; Able and Fahay, 2010; Sheaves et al., 2014). They also comprise the sole environment for the entire life of some species and act as an essential route for diadromous species during their migration from their main feeding areas in freshwater to their spawning regions in the marine environment or vice versa (Potter et al., 2015a,b).

Marine species dominate the ichthyofaunas of macrotidal estuaries in temperate regions, both in terms of number of species and overall abundance (Haedrich, 1983; Claridge et al., 1986; Dadswell and Rulifson, 1994; Thiel and Potter, 2001; Maes et al., 2005). Although marine fish species are also numerous in microtidal estuaries, such as those of south-western Australia and southern Africa, these estuaries contain a greater number of species that complete their life cycles and are abundant in these systems (Potter et al., 1990; Potter and Hyndes, 1999; Whitfield, 1999; Tweedley et al., 2016a). The success of these species in south-western Australian estuaries has been attributed to the conditions for spawning being particularly favorable in late spring to early summer, when breeding typically occurs in this Mediterranean climate (Potter et al., 2015a; Tweedley et al., 2016b). At this time, a combination of limited freshwater discharge and tidal action means that there is little water movement up and down the estuary and thus a far less turbulent and turbid environment than that produced by the strong tidal action in macrotidal estuaries. Furthermore, salinities in the main body of microtidal estuaries remain elevated during that

period and are thus at or near those of the marine environment in which these species presumably evolved (Potter and Hyndes, 1999).

As estuaries perform such an important ecological function for fishes and a range of other faunas, there has been widespread concern that, in temperate regions, they are regarded as the most degraded of all aquatic ecosystems (Jackson et al., 2001). In this context, eutrophication from increased nutrient input has become a major problem in many parts of the world, with, for example, 67% of the combined surface area of estuaries in the United States exhibiting moderate to high degrees of eutrophication, a trend also found elsewhere (Duarte, 2009; Rabalais et al., 2009; Paerl et al., 2014). The organic material, derived from eutrophication and other sources, tends to be retained in microtidal estuaries due to their long residence times (Patchineelam et al., 1999; Tweedley et al., 2012), thus leading to hypoxic conditions in deeper waters, but not necessarily in the shallows where substantial wind-induced mixing occurs (Eby and Crowder, 2002; Kurup and Hamilton, 2002; Tweedley et al., 2014)

The microtidal Peel-Harvey Estuary, which is by far the largest estuary in southwestern Australia, covers an area of ~136 km² and comprises two large, shallow basins (Peel Inlet and Harvey Estuary), a narrow, natural entrance channel at Mandurah and three main tributaries (Fig. 1). During the 1960s to 1980s, this estuary became increasingly eutrophic, through the input of large amounts of nutrients leached from the surrounding sandy soils following clearing for agriculture, and by entry from point sources such as piggeries (McComb and Humphries, 1992; McComb and Lukatelich, 1995). This eutrophication was reflected in the replacement of seagrasses by massive growths of macroalgae, belonging in particular to the genera *Cladophora*, *Chaetomorpha* and *Ulva* (McComb et al., 1981; Lukatelich and McComb, 1986).

As the large Peel-Harvey Estuary contains commercial and recreational fisheries and is widely used by residents and tourists for boating and other activities (Potter et al., 1983; Steckis et al., 1995; Lepesteur et al., 2008), it was decided to construct a deep second entrance channel to increase markedly the flushing of nutrients and organic material from this microtidal system and thereby reduce the extent of eutrophication (Gilles et al., 2004;

Brearley, 2005; Elliott et al., 2016). The opening of this so-called Dawesville Channel in 1994 led to a tripling in tidal water exchange with the ocean, a marked increase in salinity, a 2-4 fold decrease in total phosphorous and nitrogen concentrations and a flushing of 10% of the estuary volume each day (Brearley, 2005; Ruibal-Conti, 2014; Elliott et al., 2016). This resulted in a reduction in macroalgal growths (Wilson et al., 1997; 1999).

The presence of massive macroalgal growths in the Peel-Harvey Estuary in the 1980s was reflected in the domination of the fish fauna by two macrophyte-associated species, the Western Striped Grunter *Pelates octolineatus* (previously erroneously referred to as *Pelates sexlineatus*) and the Western Gobbleguts *Ostorhinchus rueppellii* (Potter et al., 1983; Loneragan et al., 1986). The reductions in macroalgal biomass in the late 1990s, following the opening of the Dawesville Channel (Wilson et al., 1997; 1999), were accompanied by a decline in the density of the above two species and changes in ichthyofaunal composition (Young and Potter, 2003b). However, marked reductions in freshwater discharge over recent years, due to declining rainfall, have reduced the effectiveness of freshwater flushing of the waters close to the mouths of tributaries, thereby leading to the development of macroalgal beds in those areas (Zammit et al., 2006; Pedretti et al., 2011). In contrast, regular strong tidal flushing in areas closer to the Dawesville Channel have increased water clarity and resulted in salinities remaining at or approaching that of the surrounding ocean, thus facilitating the development of seagrass beds (Pedretti et al., 2011). Substantial areas of unvegetated substrata still remain, however, in the Peel-Harvey Estuary.

This unique study explores how the characteristics of the fish fauna changed in the large, microtidal Peel-Harvey Estuary over ~30 years, during which (in 1994) this system underwent a major structural change (i.e. construction of Dawesville Channel). For this purpose, data on the fish fauna were collected seasonally for two consecutive twelve months (two years) in 2008-10 and compared with those recorded seasonally throughout 1980 and 1981 (Loneragan et al., 1986; Potter et al. unpublished data) and throughout 1996 and 1997 (Young and Potter, 2003a,b). Emphasis has been placed on determining how the structure and species composition of the ichthyofaunal community, throughout and within regions of the estuary, changed between the first two periods, in response to a reduction in eutrophication

and increase in salinity as a result of greater tidal exchange, and subsequently, through declining rainfall, to the maintenance of high salinities for longer during the year and the development of greater areas of seagrass and macroalgae. It is hypothesised that these changes would be accompanied by increases in the number of marine stragglers and that macrophyte-associated species, such as *P. octolineatus* and *O. rueppellii*, would be more numerous in 1980-81 and 2008-10 than in 1996-97, whereas species, such as *Torquigener pleurogramma*, which are typically found over unvegetated substrata and in high salinities, would be most abundant in the two most recent periods.

Materials and Methods

Sampling regime

During the present study, 102.5 and 21.5 m long seines were used to sample fishes at four sites, spread throughout nearshore, shallow waters in each of the five regions of the Peel-Harvey Estuary (Fig. 1), viz. Mandurah (Entrance) Channel (MC), Eastern Peel (EP), Western Peel (WP), Northern Harvey (NH) and Southern Harvey (SH). Each site was sampled using both seines in each season between winter (July) 2008 and autumn (April) 2010. Previously, one or two sites in each region were sampled using the 102.5 m seine twice in each season between summer 1980 and spring 1981 (Loneragan et al., 1986; Potter et al., unpublished data) and three sites in each region using both the 102.5 and 21.5 m seines between summer 1996 and spring 1997 (Young and Potter, 2003a,b). Samples were thus collected using the 102.5 m seine in eight consecutive seasons (i.e. over two years) in three decadal periods, i.e. 1980-81, 1996-97 and 2008-10, and with the 21.5 m seine during the last two of those periods.

The 102.5 m seine consisted of two wings, each comprising a 44.5 m (25.4 mm mesh) and 5.5 m panel (15.9 mm mesh), and a bunt measuring 2.5 m in width at the mouth (15.9 mm mesh), tapering to 0.4 m (9.5 mm mesh) over a distance of 2.5 m. This seine fished to a maximum depth of 1.8 m and swept an area of 1,600 m². The 21.5 m seine, 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 bunt (3 mm mesh), fished to a maximum depth of 1.5 m and swept an area of 116 m².

Salinity and water temperature in the middle of the water column were recorded at each site on each sampling occasion in 2008-10 using a Yellow Springs International Model 556 water quality meter (www.ysi.com). Comparable data were recorded in 1980-81 (Loneragan et al., 1986; Potter et al. unpublished data) and 1996-97 (Young and Potter, 2003a,b).

After their capture, the fish were immediately euthanised in an ice slurry and transported to the laboratory, where each was identified to species. The total number of individuals of each species in each sample was recorded and converted to a density (number 100 m⁻²).

Each species was assigned to a life cycle guild, based on the results of numerous studies of the biology of fish species in south-western Australian estuaries (Potter and Hyndes, 1999). The ways in which fish use estuaries are considered to comprise four categories, i.e. marine, estuarine, diadromous and freshwater, with each containing multiple guilds (Potter et al., 2015a,b). The first three categories are represented in the Peel-Harvey Estuary by between one and three guilds. The two guilds in the marine category are marine straggler (MS) and marine estuarine-opportunist (MEO). Marine stragglers are species that spawn at sea and typically enter estuaries sporadically and in low numbers and are most common in the lower reaches, where, for most of the year, salinities typically do not decline much below ~35. Marine estuarine-opportunists species are those that spawn at sea and regularly enter estuaries in substantial numbers, particularly as juveniles, but also use, to varying degrees, coastal marine waters as alternative nursery areas. The three guilds in the estuarine category are solely estuarine (E), estuarine & marine (E&M) and estuarine & freshwater (E&F). Solely estuarine species are typically found only in estuaries. In contrast, the estuarine & marine species and the estuarine & freshwater species are represented not only by populations whose individuals complete their life cycle in estuaries, but also by populations in coastal marine waters and fresh water, respectively. In south-western Australian estuaries, the anadromous category is represented by the semi-anadromous guild

(SA), which comprises species whose growth occurs mainly at sea, followed by a migration into the upper reaches of estuaries for spawning.

Statistical analyses

Multivariate statistical testing of the abundance data for the ichthyofaunal assemblages used a four-factor design (Period/Year/Season/Region), with three decadal periods for the 102.5 m seine samples (1980-81, 1996-97, 2008-10) and two decadal periods for the 21.5 m seine samples (1996-97, 2008-10) and, for each period, two consecutive years, five regions (MC, EP, WP, NH, SH) and all four seasons in each year. All factors were considered fixed and crossed, except for Year, which was nested in Period. The design was not balanced in terms of spatio-temporal replication, with, for example, 62, 120 and 155 replicate samples collected with the 102.5 m seine in the 1980-81, 1996-97, 2008-10 periods, respectively, noting however, that all but one of the 120 Year \times Region \times Season combinations had at least one replicate. All statistical analyses employed here are able to handle this degree of imbalance in replication without bias.

The accumulating number of different species, recorded as the number of samples increased, when using the 102.5m seine in 1980-81, 1996-97 and 2008-10 and the 21.5 m seine in the latter two periods, were plotted as species accumulation curves (Ugland et al., 2003; Clarke and Gorley, 2015). For this purpose, within each period and each size of seine, the full set of samples were randomly ordered and the curve of cumulative numbers of different species calculated. This computation was repeated for a further 999 random orderings of the samples, and the resulting curves averaged and plotted. The same procedure was then repeated having excluded marine stragglers, and finally for marine stragglers on their own.

Variability in the numbers of individual species in the replicate seine samples was used to carry out dispersion weighting for each species (Clarke et al., 2006). This downweights the densities of heavily-schooling species such as *Torquigener pleurogramma* and *Pelates octolineatus*, i.e. those whose numbers are erratic over replicates, relative to those which return more consistent values, as would be expected from individuals arriving in

the seine independently of one another. Dividing counts for each species by its mean index of dispersion (average of the variance to mean ratio in replicate seines) then ensures all species have equivalent variability structure, and prevents the analyses becoming dominated by strong outliers. In this case, it is then optimal to further transform the dispersion-weighted data, by a milder square-root transformation, as demonstrated by Clarke et al. (2014a) for fish communities, and particularly those in estuaries and nearshore coastal waters where the prevalence of juvenile and small schooling species are high.

Bray-Curtis similarity was then calculated on the dispersion-weighted, transformed data and input to permutational ANOVA, using the PERMANOVA routine in the PRIMER v7 package (Anderson, 2001; Anderson et al., 2008; Clarke and Gorley, 2015). Since the primary focus of this study was to compare fish communities across the three decadal periods, the appropriate ‘replicate’ variation for those period tests is obtained from the year-to-year variability within each decade (the Year factor is nested in the Period factor). PERMANOVA tested for the main effects of Period, Year, Season and Region, two-way interactions between each pair of these main effects, and also three-way interactions, all of which may be relevant to understanding the subtlety of changes between the three decadal periods.

Separate three-way crossed Analysis of Similarities (ANOSIM; Clarke and Green, 1988; Clarke et al., 2014b) were used to interpret the relative size of the overall Period, Year, Season and Region effects on the fish compositions derived from the 102.5 and 21.5 m seine samples, using the same resemblances as for the PERMANOVA tests. All pairs of these four factors are crossed with each other (i.e. the same Regions are examined in the same Seasons in the same Years and Periods), with the one exception that Year is nested within Period (each period contains different years, naturally). This is conventionally denoted as the design $\text{Season} \times \text{Region} \times \text{Year}(\text{Period})$. It is handled here in two stages, first testing the crossed/nested three-factor ANOSIM design ($B \times C(A)$; see Table 6.4 in Clarke et al., 2014b), in which Year C (nested in Period A) is crossed with the “flattened” factor B, consisting of all 20 combinations of Season and Region, to obtain ANOSIM \bar{R} values for Period and Year. Then a three-factor fully crossed design ($A \times B \times C$; see Table 6.4 in Clarke et al., 2014b) of

Season \times Region \times Time computes Region and Season \bar{R} values for comparing with those for Year and Period. Here the “Time” factor consists of the 6 levels of all years in all periods, and thus combines both differences between years within each period and changes over periods.

The ANOSIM R -statistics provide a robust and universally scaled measure of effect sizes, ranging from ~ 0 , when the average similarities among and within groups do not differ, up to 1, when the compositions of all samples within each group are more similar to each other than to those of any sample from other groups (Clarke and Warwick, 2001). The same combination of ANOSIM designs was utilised for analysing the data derived from the 21.5 m seine samples as for the 102.5 m seine, recognizing however, that, as the 21.5 m seine was not used in 1980-81, comparisons are restricted to 1996-97 vs 2008-10.

As four-way PERMANOVA detected strong Period \times Region interactions (and no significant Period \times Season interaction) with the data for either seine (see Results), separate Bray-Curtis similarity matrices were extracted for each region from the resemblance matrix. When assessing the relative size of effects within a single region, both globally for Period and Season factors and between specific pairs of periods or seasons, it is more efficient and meaningful to work with averages (in some form) over the lowest level of variability in the design, i.e. over spatio-temporal samples taken within a specific region in a particular season and year. This is possible since there is no necessity in this case to remove a year effect (a consistent and strong year difference over seasons is not present, see Results), so simpler 2-way crossed ANOSIMs are performed, in which the two years in each period become the replicate level for tests of Period and Season within each Region, and for Region and Season within each Period.

Non-metric Multidimensional Scaling (nMDS) ordination then used data at this same level of averaging over samples for each Region, Season and Year(Period) combination, to visualise the extents to which ichthyofaunal composition differed across seasons and periods for the separate regions. Further nMDS ordinations were then constructed at a higher level, averaging now over both the years and seasons in order to display, on a single plot for each seine, the scale of (significant) Period \times Region interactions in the context of Period and

Region main effects. All of these plots were constructed by calculating the distances between each pair of group centroids, *i.e.* the relevant average in the ‘Bray-Curtis space’ of all samples (Anderson et al., 2008; Lek et al., 2011). This is preferable here to calculating averages in the (transformed) ‘species space’ of the original data matrix because of the imbalance in numbers of replicates among groups.

Segmented bubbles of proportional sizes, representing the dispersion-weighted and square-root transformed abundances of six selected species, those pre-treated abundances for each species having been averaged over all seasons and years in each period, were overlaid on the corresponding centroid nMDS plot for the 102.5 m seine samples. This illustrates the abundance trends exhibited by some of the species, which varied conspicuously between period and/or regions, and thus how they contribute to the structure of this nMDS plot. For visual clarity, however, the data are restricted to those for the Mandurah Channel, Eastern Peel and Southern Harvey.

Data for a suite of species recorded in at least five samples, obtained using the 102.5 m seine across 1980-81, 1996-97 and 2008-10, and for the 21.5 m seine across the last two periods, were used to produce separate shade plots (*sensu* Clarke et al., 2014a), with species clustered using the Index of Association (Whittaker, 1952; Somerfield and Clarke, 2013) and placed in optimum serial order, constrained by the cluster dendrogram (Clarke et al., 2014b). These plots illustrate the trends exhibited by the abundance of each of those species with respect to Period, Region and Season. For this purpose, the number of individuals of each species in each sample were dispersion weighted and square-root transformed, and those for each Period, Region and Season combination then averaged. The shade plot is then a simple visualization of this averaged data matrix, where a white space for a species demonstrates that the species was not collected, while the depth and colour of shading, ranging from blue shades through the spectrum to black, represents increasing values for the (dispersion-weighted and transformed) abundance of that species (Clarke et al., 2014a; Valesini et al., 2014). The averaged samples (on the *x* axis of the plot) are ordered according to season in each region in each period.

Results

Salinity and water temperature

The mean seasonal salinity in the Peel-Harvey Estuary underwent similar seasonal changes in 1980-81, 1996-97 and 2008-10, peaking in summer and autumn and declining in winter and spring (Fig. 2a-c). The extent to which salinity declined in winter varied, however, more among regions in both years of 1980-81, than in those of either 1996-97 or 2008-10. Thus, in the winter of both years in 1980-81, mean salinities in the Southern Harvey and Eastern Peel fell to less than 5-10, compared with only 18 to 25 in the Mandurah Channel and Western Peel. The particularly low salinities in the first two regions in the winter and spring of 1980-81 are due to the major tributaries discharging directly into those regions (Fig. 1) and for such flow to be greatest during those seasons, as a consequence of highly seasonal rainfall. The presence of more pronounced variations in salinity among regions in all seasons in 1980-81 than in 1996-97 and 2008-10 (Fig. 2) is also related to tidal water exchange occurring only through the natural entrance channel in the first period, whereas it was augmented by that through the Dawesville Channel in the last two periods, which led to far greater mixing within the estuary. Minimum salinities (i.e. in winter) were far lower in 1996 than in 1997, 2008/9 and 2009/10, due to far greater discharges of freshwater into the estuary as a result of much higher rainfall in that year (Veale, 2013). Note, however, that salinities remained low for a shorter time in 1996, than in the two pre-Dawesville Channel years of 1980-81, because, following the opening of that channel, tidal influence increased far more rapidly as fresh water discharge declined.

Mean water temperature exhibited similar pronounced seasonal changes at all sites and in each year, declining from maxima of ~25 °C in summer to minima of ~14 °C in winter and then rising in spring (Veale et al., 2016).

Ranking and contributions of fish species

On the basis of the 102.5 m seine samples, the mean overall density of fish in the Peel-Harvey Estuary over two consecutive years in both 1980-81 and 2008-10 was the same,

348 i.e. 44 fish 100 m⁻², which was far greater than the 13 fish 100 m⁻² recorded in 1996-97
349 (Table 1). Although the total number of species recorded increased progressively with period,
350 it should be recognised that the number of samples also increased with period (Table 1). The
351 mean density of fish, derived from the 21.5 m seine samples, was also greater in 2008-10,
352 i.e. 283 fish 100 m⁻², than in 1996-97, i.e. 224 fish 100 m⁻² (Table 2). Although the number of
353 samples was less in 2008-10 than in 1996-97, the total number of species recorded rose
354 slightly from 43 to 46 between those periods.

355 Although eight of the ten most abundant species caught using the 102.5 m seine in
356 2008-10 also ranked among the ten most abundant in both 1980-81 and 1996-97, the ranking
357 by abundance and relative contribution of some species to the total catch differed markedly
358 between periods (Table 1). For example, *T. pleurogramma* ranked first in both 2008-10 and
359 previously 1996-97, when its contribution to total fish numbers was as high as 31 and 42%,
360 respectively, compared with sixth and only 6% in 1980-81. The overall density of this marine
361 estuarine-opportunist was also greater in the two most recent periods. *Ostorhinchus rueppellii*
362 ranked second in both 1980-81 and 2008-10, with respective contributions of 14 and 25%,
363 whereas this estuarine & marine species was the sixth most abundant species and constituted
364 only 3% of the total catch in 1996-97, trends that reflect those of density. The marine
365 estuarine-opportunist *P. octolineatus*, which was the most abundant species in 1980-81, when
366 it contributed as much as 37% to the total catch, was the seventh most numerous species in
367 2008-10 with a contribution of 2.5%, which, in turn, exceeded the tenth ranking and
368 contribution of only 1.0 % in 1996-97 (Table 1). These trends again parallel those of density.
369 The marine estuarine-opportunist *Hyperlophus vittatus* ranked among the four most abundant
370 species in each period, with contributions ranging from 7 to 17 %. The atherinids
371 *Atherinosoma elongata* and *Leptatherina presbyteroides* both ranked among the five most
372 abundant species in 1996-97 and 2008-10, but only tenth and eleventh in 1980-81, when their
373 densities were also lower. The tropical atherinid *Craterocephalus mugiloides* ranked ninth
374 and contributed 1.9% in 2008-10, the latter being far greater than in 1980-81 (0.3%) and
375 1996-97 (<0.1%).

The trends exhibited by the ranking of the most abundant species caught using the 21.5 m seine in 1996-97 and 2008-10 were similar to those recorded with the 102.5 m seine during the same two periods (Table 2). Thus, the macrophyte-associated species *O. rueppellii* likewise ranked higher and made a greater contribution in the more recent of those two periods, i.e. 5 and 7.0% vs 7 and 1.7%, and the same was true for *C. mugiloides*, i.e. 4 and 11.3% vs 22 and <0.1%. Although the contributions made by *T. pleurogramma* to the catches obtained using the 21.5 m seine in 1996-97 and 2008-10 were both less than those with the 102.5 m seine in those years (in which this marine estuarine-opportunist was the most abundant species), this tetraodontid still ranked fourth and sixth in the samples taken with the smaller seine in 1996-97 and 2008-10 (Table 2). *A. elongata*, *H. vittatus* and *L. presbyteroides* were very abundant and ranked in the top three species in the 21.5 m seine samples in both 1996-7 and 2008-10 (Table 2). While these three species were also abundant in the 102.5 m seine samples in 1996-97 and 2008-10, ranking in the top five species in both periods, their collective contribution to the total number of fish caught by the 21.5 m seine was far greater in both of those two periods. This trend is attributable to these species being relatively small and most abundant in shallow waters along the shore line and thus more susceptible to capture by the 21.5 m seine as this seine has smaller meshes and sampled just the waters close to the shore line.

Contributions of life cycle categories and guilds

In terms of life cycle guild, the number of marine straggler species taken by the 102.5 m seine in 1980-81, 1996-97 and 2008-10 increased sequentially from 6 to 13 to 23 (Table 3). In contrast, the number of marine estuarine-opportunist species was similar in each of those three periods, i.e. 17 or 18, as also were the numbers of estuarine & marine species, i.e. 8 or 9, and solely estuarine species, i.e. 4. The number of species representing the marine estuarine-opportunist, estuarine & marine and solely estuarine life cycle guilds in the 21.5 m seine samples from 1996-97 and 2008-10 were each the same or very similar to those of the corresponding guilds in the 102.5 m seine samples (Table 3). Although fewer species of

marine straggler were caught in the smaller than larger seine, their number likewise increased between 1996-97 and 2008-10.

In terms of number of individuals, the 102.5 m seine samples were dominated by marine estuarine-opportunists and estuarine & marine species collectively, with their combined contributions ranging from 84% in 1996-97 to 93% in 1980-81 (Table 3). The contributions of marine estuarine-opportunists in 1980-81 and 1996-97 were 68-70% and still as high as 56% in 2008-10, while those for the estuarine & marine guild in those three periods ranged from 23-32%. The densities of both life cycle guilds were least in the intervening period. The contributions by the solely estuarine guild ranged from 3.2 to 8.2% (Table 3).

In the 21.5 m seine samples, the contributions of marine estuarine-opportunists ranged widely from 37% in 2008-10 to 70% in 1996-97, reflecting, in particular, exceptionally large numbers of a single species, i.e. *H. vittatus*, in the earlier period (Table 2). Conversely, but not to the same extreme degree, the estuarine & marine species made greater contributions in 2008-10 than in 1996-97. In comparison with the 102.5 m seine, the relative abundance of solely estuarine species in the 21.5 m seine catches were greater in both 1996-97 and particularly 2008-10, when they contributed as much as 38% to the total catch, which was due almost entirely to large numbers of the atherinids *A. elongata* and *C. mugiloides* (Table 2).

Although relatively small, the contributions by marine stragglers to the 102.5 m seine catches in the three periods, 2.6-3.0%, far exceeded the 0.3% by those in the 21.5 m seine (Table 3). The estuarine & freshwater species, and single semi-anadromous species, made only small contributions to the catches by either seine in any period.

The species-accumulation curve, derived from the 102.5 m samples, displayed a less pronounced asymptote in 1996-97 and 2008-10 than in 1980-81 (Fig. 3a). Furthermore, in comparison with 1980-81, the total number of species in 62 samples (the maximum number of samples recorded in 1980-81) was slightly greater in 1996-97 and, to an even more marked extent, in 2008-10. The curves constructed from the same samples, but excluding marine stragglers, were very similar in 1996-97 and 2008-10 (Fig. 3b). While the curve for the

corresponding samples in 1980-81 rose more rapidly to an asymptote, the number of species at 62 samples in that period was very similar to those in 1996-97 and 2008-10. Conversely, when the curves were restricted to data solely for marine stragglers, the curve for 1980-81 lay well below that for 1996-97, and even more particularly that for 2008-10 (Fig. 3c).

The relationship between the trends in the species-accumulation curves constructed for the 21.5 m seine samples in 1996-97 and 2008-10, using firstly all species (Fig. 3d), then all species except marine stragglers (Fig. 3e) and finally just marine stragglers (Fig. 3f) closely parallel those exhibited using the 102.5 m seine in those two periods (Fig. 3a-c). Thus, the curve for all species and for just marine stragglers in 2008-10 lay above the corresponding curves for 1996-97, whereas the curves for all species except marine stragglers were very similar in those periods.

Variations in ichthyofaunal composition with period, region and season

On the basis of PERMANOVA, the ichthyofaunal compositions in the Peel-Harvey Estuary, derived from the 102.5 m seine samples in 1980-81, 1996-97 and 2008-10 and for the 21.5 m seine samples in the last two periods, differed significantly for Period, Season, Region and Year(Period) (Table 4a,b). The interactions for Period \times Region and Year(Period) \times Season were also significant for the samples obtained with both seines. Although, in the case of the 21.5 m seine samples, the pseudo-F (pF) value for Period was the second greatest, this main effect was not significant ($P = 0.339$) because the number of possible permutations (45) was small for a test based on (1, 2) degrees of freedom. However, Monte Carlo testing, using the asymptotic permutation distribution (Anderson et al., 2008), suggested a high level of significance, i.e. $P = 0.003$ (Table 4b). There was a smaller Period \times Region interaction, though more strongly significant since it was based on (4, 8) degrees of freedom, and with many possible permutations.

Separate three-way crossed ANOSIM tests for the 102.5 and 21.5 m seine catches yielded respective \bar{R} values of 0.585 and 0.375 for Period, 0.235 and 0.249 for Region, 0.241 and 0.251 for Season and 0.147 and 0.132 for Year. This confirms the relatively large size of the Period effect and that Year was far less influential than Region and Season.

On the nMDS ordination plots, derived from the distance among centroids matrices for the 102.5 m seine samples, the points for the samples for each period in 1980-81, 1996-97 and 2008-10 progressed sequentially from left to right and then upwards (Fig. 4a). Furthermore, in each period, the point for the Mandurah Channel typically lay above those for the other four regions and that for the Southern Harvey lay below those for all other regions. On the corresponding ordination plot, derived from data using the 21.5 m seine, the point for the sample from each region in 2008-10 lay to the right of that for the corresponding region in 1996-97 (Fig. 4b).

Two-way crossed ANOSIM tests demonstrated that the composition of the fish fauna was significantly related to Region in 1980-81 and 2008-10, but not in 1996-97, and was significantly related to Season only in 2008-10 (Table 5). The composition of the fish fauna in the 21.5m seine samples was influenced significantly by Region and Season in both 1996-97 and 2008-10.

Two-way crossed Period \times Season ANOSIM tests demonstrated that the compositions of the fish faunas in the Mandurah Channel, Eastern Peel, Northern Harvey and Southern Harvey differed significantly between periods, with the \bar{R} statistics for those regions ranging upwards from 0.508 in the Southern Harvey and 0.583 in the Northern Harvey to as high as 0.833 in the Mandurah Channel and 0.883 in the Eastern Peel (Table 6). In each region, the \bar{R} -statistic values for each pairwise comparison between the ichthyofaunal compositions in the three periods exceeded 0.500 in all cases except those involving the Western Peel (Table 6). In the case of seasons in each region, the \bar{R} statistic was always < 0.500 and the differences were significant only in the Mandurah Channel and Eastern Peel (Table 6).

The basis for the differences between the composition in 1980-81 and both 1996-97 and 2008-10, derived from the data for the 102.5 m seine, can be seen visually on the respective regional MDS ordination plots, with the points for the samples in the first period in each region showing a very marked tendency to lie to the left of those for the last two periods (Fig. 5a-e). Furthermore, the samples for 2008-10 formed particularly tight and essentially discrete groups on the plots for each region, except the Mandurah Channel.

In two-way crossed Period \times Season ANOSIM tests, using data derived from the 21.5 m seine samples in each region in 1996-97 and 2008-10, the \bar{R} -statistic value for Period exceeded 0.500 in the Mandurah Channel, Northern Harvey and Southern Harvey (Table 7). These inter-period differences are reflected, on the MDS ordination plots, by the discreteness of the samples for the two periods being greatest in those three regions (Fig. 5f-h).

Species responsible for period, regional and seasonal differences

The trends exhibited by the abundance of the various fish species on the shade plot, derived from the 102.5 m seine samples, provide a visual demonstration of the species mainly responsible for the differences between the ichthyofaunal compositions of the estuary in 1980-81, 1996-97 and 2008-10 (Fig. 6). Thus, for example, species such as *Hyporhamphus regularis*, *Sillago schomburgkii*, *Gerres subfasciatus* and *Contusus brevicaudus* were far more abundant in 1980-81 than in 1996-97 and 2008-10. The fauna in 1996-97 was characterised by a small suite of species, comprising *Pseudorhombus jenynsii*, *Favonigobius lateralis*, *T. pleurogramma* and *L. presbyteroides*, that were consistently abundant throughout the estuary. Species such as *Gymnapistes marmoratus*, *Ostorhinchus rueppellii*, *Haletta semifasciata* and *Pelates octolineatus* were numerous in 2008-10 and 1980-81, but present in only low numbers in 1996-97 (Fig. 6).

The strong regional effect on the ichthyofaunal compositions in 1980-81 and 2008-10 reflected, in part, the marked tendency for species such as *Aldrichetta forsteri* and *H. vittatus* to occur predominantly in the Mandurah Channel in both of these periods and in the Eastern Peel in the first period (Fig. 6). While *G. marmoratus*, *O. rueppellii* and *Haletta semifasciata* were caught mainly in the Western Peel and Northern Harvey in 1980-81 and 2008-10, they were more widely distributed in the latter period. The significant and marked seasonal effect in 2008-10 was attributable, in particular, to *P. octolineatus*, *Sillaginodes punctatus*, *G. marmoratus*, *O. rueppellii* and *H. semifasciata* being represented by large densities in summer and autumn and either fewer or no fish in winter (Fig. 6).

In the 21.5 m seine catches, species such as *F. lateralis*, *T. pleurogramma* and *L. presbyteroides* were particularly abundant in both 1996-97 and 2008-10, whereas species

such as *Stigmatopora argus*, *O. rueppellii*, *H. semifasciata* and *G. marmoratus* were far more numerous in 2008-10 (Fig.7). The regional effect in both periods was due, in particular, to species such as *S. schomburgkii*, *Atherinomorus vaigiensis* and *Sillago vittata* being largely confined to the Mandurah Channel. In 2008-10, *Hyporhamphus melanochir* and *C. mugiloides* were most abundant in the Northern Harvey and Southern Harvey, whereas the densities of *S. punctatus* were greatest in the Western Peel and Northern Harvey (Fig. 7). In terms of season, *H. vittatus*, *O. rueppellii* and *G. marmoratus* were absent or in very low numbers during winter in 1996-97 and 2008-10 in certain regions, in which these species were abundant in other seasons. In 1996-97, *A. elongata* was most abundant in summer, whereas *Leptatherina wallacei* was most abundant in winter.

The trends exhibited in the segmented bubble plots in Fig. 8 emphasize how the relative contributions of six key species in three regions (Mandurah Channel, Eastern Peel and Southern Harvey) changed between 1980-81, 1996-97 and 2008-10. Thus, for example, while *T. pleurogramma* was recorded only in the Mandurah Channel in 1980-81 (but in substantial numbers), it was abundant in each region in 1996-97 and 2008-10. Although *F. lateralis* was recorded in each region in each period, its relative contribution increased markedly in the Eastern Peel and Southern Harvey in 2008-10. The abundance of *H. regularis* in those same two regions declined between 1980-81 and 2008-10.

Discussion

This study has demonstrated statistically the ways in which the ichthyofaunal characteristics of a large microtidal estuary changed over three decades, during which part of that system was subjected to radical structural changes aimed at reducing the extent of eutrophication, and which led to major environmental changes in the estuary as a whole. Particular emphasis was placed on elucidating the influence of the construction of a large additional entrance channel, which increased flushing and salinity, and that of subsequent changes brought about by more persistently high salinities, caused by reductions in rainfall, and increases in seagrass and macroalgal biomass. As the large basins of the Peel-Harvey Estuary have water depths

less than ~2 m and mostly < 1 m (Hale and Bucher, 2007), they do not contain substantial numbers of large, mobile fish species. Thus, the use of a small (21.5 m long) and far larger (102.5 m long) seine, both of which sample to a depth of 1.5 m, is regarded as having sampled relatively effectively the fish species present throughout the water column within the dominant component of this estuary, i.e. the basins.

Numbers of species and individuals in the various guilds

Species accumulation curves, derived from the 102.5 m seine samples, demonstrate that the number of species in the Peel-Harvey Estuary increased progressively between 1980-81, 1996-97 and 2008-10 and that this rise was almost exclusively due to increases in the number of species of marine straggler. The rise in the number of these stragglers following the opening of the Dawesville Channel, some distance from the natural Mandurah entrance channel, is precisely what would be expected as this construction resulted in increases in tidal exchange with the ocean and the persistence, for longer during the year, of high salinities throughout the large basins of this estuary (Brearley, 2005; Ruibal-Conti, 2014). This trend closely parallels the increase that occurred in the number of species of benthic macroinvertebrates from 28 in 1986-87 to 63 in 2003-04, with the previously unrecorded species in the latter period being low in abundance and typically representing marine species, which had probably been transported into the estuary as planktonic larvae through tidal action (Wildsmith et al., 2009; Tweedley et al., 2012). The increase in the number of marine straggler fish species, recorded in the 102.5 m seine samples between 1996-97 and 2008-10, was paralleled by the corresponding trend in the 21.5 m seine samples. This increase was probably attributable to the maintenance of high salinities throughout both years in 2008-10 (Fig. 2) and an increase in habitat complexity through the development of appreciable areas of macrophytes. Thus, macroalgal growths became particularly prominent near the point where rivers discharge into the basins and seagrass beds developed near the Dawesville Channel, where water clarity and thus light penetration was greatest (Pedretti et al., 2011). As rainfall and thus the volume of freshwater discharge is declining (Veale, 2013) and salinities

are consistently higher, it seems likely that the overall number of marine stragglers will continue to increase.

In contrast to the trend exhibited by marine stragglers, the species representing the marine estuarine-opportunist guild in the 102.5 m seine samples were very similar in 1980-81, 1996-97 and 2008-10. Thus, among the 18 marine estuarine-opportunists recorded in the Peel-Harvey Estuary, as many as 16, i.e. all except *Arripis georgianus* and *Arripis truttaceus*, were caught in each period and were often relatively abundant in at least two of the three periods. The finding that, unlike the situation with marine stragglers, the number of marine estuarine-opportunist species did not increase between the three periods was predictable as, by definition, these species are those that regularly use estuaries as nursery areas (Potter et al., 2015b) and would thus always tend to be found in permanently-open systems, such as the Peel-Harvey Estuary. The number of marine estuarine-opportunists species in the 21.5 m seine samples in 1996-97 (19) and 2008-10 (17) were essentially the same as those in the 102.5 m seine samples in 1980-81, 1996-97 and 2008-10, reflecting the restricted and largely common range of species that represent this guild.

As with marine estuarine-opportunists in the 102.5 m seine samples, the number of species comprising the estuarine & marine, estuarine & freshwater and solely estuarine guilds, which collectively represent the species that complete their life cycles within the Peel-Harvey Estuary and thus constitute the estuarine category (Potter et al., 2015a), were similar in each period. Furthermore, 12 of the 18 species comprising the estuarine category, subsequently referred to as estuarine residents, were found in each of the three periods and four in two of those periods and thus only two species were restricted to one period. Irrespective of period, the number of species representing each guild in the estuarine category in the 21.5 m seine samples is the same or differs by only one from that recorded using the 102.5 m seine. The finding that the number of species in the various guilds comprising the estuarine category remained essentially the same between 1980-81 and 2008-10 was not surprising as there appears to be no a priori reason why the presence of such species should be markedly influenced by increased tidal exchange with the ocean or higher salinities.

In terms of the number of individuals, the samples obtained by the 102.5 m seine in each period, and particularly in 1980-81 and 1996-97, were dominated by marine estuarine-opportunists and the same was true for those using the 21.5 m seine in 1996-97. The finding that, in the 21.5 m seine samples, the contribution of this guild in 2008-10 was approximately half that in 1996-97 was due to a pronounced decline in the abundance of a single species, the clupeid *H. vittatus*, whose density in nearby coastal marine waters also declined between those periods (Smith et al., 2008; Valesini and Tweedley, 2015).

The estuarine & marine guild was the second most important guild in terms of abundance in the 102.5 m seine samples in each period and markedly so in 1980-81 (23%) and 2008-10 (32%) and the same was marginally true for those taken by the 21.5 m seine in 1996-97 (16%). Although the contribution made by individuals of species in this guild to the 21.5 m seine samples in 2008-10 was as high as 24%, this value was far less than the corresponding contribution of 38% by the solely estuarine guild in that period, which was due to exceptionally large numbers of the atherinid *C. mugiloides*.

It is relevant that the contributions of the solely estuarine guild to the number of individuals caught by the 21.5 m seine in 1996-97 and 2008-10 were greater than those with the 102.5 m seine in those two periods and in 1980-81. This trend is attributable, in particular, to differences in the abundances of the main species caught by the smaller seine, which samples along the shoreline, and those taken by the larger seine, which samples much further outwards from the shore and includes some deeper water. Among the estuarine category, the most abundant species along the shoreline comprised predominantly small-bodied atherinids, such as *A. elongata* and *C. mugiloides*, which are confined to estuaries. The most abundant estuarine-resident species in waters extending further offshore include species such as the deep-bodied *O. rueppellii*.

Although the number of species in each guild, except marine stragglers, was very similar in 1980-81, 1996-97 and 2008-10, the abundance of certain species in particularly the marine estuarine-opportunist, solely estuarine and estuarine & marine guilds, which dominated the catches, varied. These differences, rather than variations in the number of species in those guilds, are thus responsible for the differences in species composition.

Although the number of marine stragglers increased progressively with period, the abundances of these adventitious species were low and thus had minimal influence on the variations in ichthyofaunal composition in different periods.

Ichthyofaunal composition

The distinctness of the groups of points on nMDS ordination plots for samples, collected from the five regions in the Peel-Harvey Estuary using the 102.5 m seine, demonstrate that ichthyofaunal composition changed markedly between 1980-81, 1996-97 and 2008-10, and that, on the basis of the plots derived from data for the 21.5 m seine samples, the same is true for the samples obtained in the last two periods. The strong Period effect is further emphasized by the results of ANOSIM tests, which, for the 102.5 and also 21.5 m seine samples, yielded far greater \bar{R} values for Period than for either Region or Season, with the value for Year particularly low. The differences in ichthyofaunal composition between periods is further illustrated by the finding that, from data for the 102.5 m seine samples, the composition in the Mandurah Channel and three of the four basin regions, i.e. Eastern Peel, Northern Harvey and Southern Harvey, each differed significantly between periods. The changes that occurred in the composition of the fish fauna of the Peel-Harvey Estuary, after the opening of the Dawesville Channel and a consequent reduction in eutrophication, provide some parallels with those brought about in the Mondego Estuary in Portugal by structural changes that facilitated greater flow and thus a reduction in residence time and eutrophication (Castro et al., 2016).

The trends exhibited by the relative abundance of species in the shade plot (Fig. 6) highlight the species that made important contributions to inter-period differences in the 102.5 m seine samples. For a number of species, such differences can be related to changes in the environment, which were associated with the increases in tidal and salinity regimes produced by the construction of the Dawesville Channel, and to subsequent changes in macrophytes biomass. These species include the tetrapontid *P. octolineatus* and apogonid *O. rueppellii* and, to a lesser extent, the odacid *H. semifasciata* and scorpaenid *G. marmoratus*, which were all relatively more numerous in 1980-81 and 2008-10 than in

1996-97. As macrophytes were most abundant in 1980-81 and 2008-10 (Wilson et al., 1999; Pedretti et al., 2011), it is relevant that these four species are typically associated with aquatic vegetation (Travers and Potter, 2002; Valesini et al., 2004; Gomon et al., 2008; Veale et al., 2014; 2015). Thus, for example, *P. octolineatus* lives predominantly and is abundant in seagrass, both along the lower west coast of Australia, into which the Peel-Harvey Estuary discharges (Valesini et al., 2004; Veale et al., 2015), and in the large marine embayment of Shark Bay ~ 800 km further north (Burkholder et al., 2012), where this tetrapontid feeds mainly on seagrass and algae (Bessey and Heithaus, 2015). Furthermore, *O. rueppellii* was found almost exclusively over seagrass during extensive trawling of shallow, inshore vegetated and unvegetated areas in Shark Bay, in which it was the second most abundant species sampled overall (Travers and Potter, 2002). The impact that a reduction and subsequent increase in macroalgae and seagrass can have on the abundance of a species is particularly well illustrated by the decline and then rise that occurred in the catches of the Tiger Prawn *Penaeus esculentus*, when such changes in macrophytes took place in a large embayment in north-western Australia (Loneragan et al., 2013).

The above trends exhibited by species on the shade plot are consistent with those for the untransformed overall densities and percentage contributions (Table 1). Thus, the densities and percentage contributions of *P. octolineatus* were greatest in 1980-81 and less in 1996-97 than in 2008-10, with this tetrapontid ranking first in terms of density in 1980-81, when it contributed a remarkable 37% to the total catch in that period and thus when macrophyte biomass was greatest. Furthermore, this species ranked higher in terms of abundance (7) and contributed more to the total catch (2.5%) in 2008-10 than in 1996-97, when it ranked 10 and contributed only 1% and therefore when the extent of macrophyte growth was not as extensive as in 1980-81, but still greater than in 1996-97. As with *P. octolineatus*, the ranking by abundance and contribution to the total catch of *O. rueppellii* were substantially greater in both 1980-81 and 2008-10 than in 1996-97.

In contrast to the trends exhibited by the above macrophyte-associated species, the tetraodontid *T. pleurogramma* was relatively far less abundant in 1980-81 than in 2008-10 and even more particularly in 1996-97, and thus when the area covered by macrophytes was

least. This converse trend strongly suggests that *T. pleurogramma* ‘prefers’ unvegetated substrata. Such a view is consistent with the high abundances of this species over sand in the Swan River Estuary, just to the north of the Peel-Harvey (Potter et al., 1988), and in the Noosa River Estuary in eastern Australia (Miller and Skilleter, 2006). Furthermore, this species was almost invariably caught over sand rather than seagrass during trawling over those two habitats in Shark Bay (Travers and Potter, 2002) and is known to bury in sand and to feed on polychaetes, amphipods and molluscs in and on the sediment (Potter et al., 1988; Miller and Skilleter, 2006). Although *T. pleurogramma* was scarcely caught in the basin of the Peel-Harvey Estuary in 1980-81, it was so abundant in the Mandurah Channel in that period that it was a diagnostic species for the ichthyofauna of that region (Loneragan et al., 1986). It is thus relevant that, in marked contrast to the large basin areas, the Mandurah Channel did not house massive macroalgal growths in 1980-81 and thus contained substantial areas of unvegetated substrata (McComb and Lukatelich, 1995). The negative relationship between the abundance of *T. pleurogramma* and extent of macroalgal growths and the positive relationship between the abundance of this species and salinity (Potter et al., 1988), allied with the maintenance of higher salinities throughout the basin in 1996-97 and 2008-10, account for the densities of this tetraodontid being far greater in these latter two periods.

As *F. lateralis* also has a strong preference for a sandy substrate and its densities are likewise positively related to salinity (Gill and Potter, 1993), the basis for this gobiid becoming more widespread in the estuary in 1996-97 and 2008-10 than in 1980-81 is apparently the same as for *T. pleurogramma*, i.e. a preference for unvegetated soft substrata and high salinities. Furthermore, as with *T. pleurogramma*, *F. lateralis* was very abundant in the Mandurah Channel in 1980-81, paralleling the situation in the Swan River Estuary, in which this species is largely confined to the high salinities and sandy substrata of its entrance channel (Gill and Potter, 1993).

In contrast to *T. pleurogramma* and *F. lateralis*, the hemiramphid *H. regularis* was never caught in the Mandurah Channel in any of the three periods and its abundance in the basins was less in 1996-97 and 2008-10 than in 1980-81. These trends are consistent with this

so called “river garfish” typically occurring in reduced salinities and in association with macrophytes, which house their food source (Gomon, 2011).

The data derived from the 102.5 and 21.5 m seine samples provided strong evidence that the atherinid *C. mugiloides* was relatively more abundant in 2008-10 than in earlier periods, thereby paralleling the trend in the Swan River Estuary (Loneragan et al., 1989; Valesini et al., 2009; 2014). Furthermore, while this species was not recorded in 1994 in the Leschenault Estuary, ~75 km to the south of the Peel-Harvey, it was very abundant in this system in 2008-10 (Veale et al., 2014). This suggests that increases in the abundance of *C. mugiloides* in the Swan River and Peel-Harvey estuaries in the most recent period and the southwards extension of this tropical species into the Leschenault Estuary are related to increases in water temperature associated with climate change in south-western Australia (Lough et al., 2012).

The results of this study emphasise the value of acquiring data at key intervals over time to be able to predict, in the future, the ways in which extreme structural modifications and climate change will influence the fish faunas of particularly microtidal estuaries.

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994 69

995 List of Figures

996 **Figure 1.** Map showing the five regions of the Peel-Harvey Estuary, *i.e.* the Mandurah
997 Channel, Eastern Peel, Western Peel, Northern Harvey and Southern Harvey, that were
998 sampled seasonally using a 102.5 m in 1980-81, 1996-97 and 2008-10 and a 21.5 m seine in
999 the last two of those periods.

1000

1001 **Figure 2.** Mean seasonal salinities in each of the five regions of the Peel-Harvey Estuary
1002 between (a) summer 1980 and spring 1981, (b) summer 1996 and spring 1997, and (c) winter
1003 2008 and autumn 2010. In this and subsequent figures, regions are abbreviated as Mandurah
1004 Channel, MC; Eastern Peel, EP; Western Peel, WP; Northern Harvey, NH; and Southern
1005 Harvey, SH.

1006

1007 **Figure 3.** Species-accumulation curve for the number of all species, number of all species
1008 excluding marine stragglers and number of marine straggler species vs number of samples for
1009 (a-c) the 102.5 m seine in 1980-81, 1996-97 and 2008-10 and (d-f) 21.5 m seine in the last
1010 two of those periods.

1011

1012 **Figure 4.** Centroid non-metric MDS ordination of fish community data for the five regions
1013 (MC, EP, WP, NH, SH, as in Fig. 2) of the Peel-Harvey Estuary, derived from (a) 102.5 m
1014 seine samples collected during 1980-81 (1); 1996-7 (2) and 2008-10 (3), and for (b) 21.5 m
1015 seine samples in the last two of those periods.

1016

1017 **Figure 5.** nMDS ordination plots constructed from Bray-Curtis similarity matrices, derived
1018 from the mean abundances of fish species sampled in four seasons over two years in the three
1019 periods in: Mandurah Channel (a, f); Eastern Peel (b, g); Western Peel (c, h); Northern
1020 Harvey (d, i); Southern Harvey (e, j) of the Peel-Harvey Estuary, using the 102.5 m (a, b, c, d,
1021 e) in 1980-81, 1996-97 and 2008-10 and the 21.5 m (f, g, h, i, j) in the last two periods. Points
1022 coded for years (1-6) and seasons: S, summer; A, autumn; W, winter; Sp, spring.

Figure 6. Shade plot of the abundance for 41 fish species (those occurring in more than 4 replicates) derived from 102.5 m seine samples from the four seasons (Su: Summer, A: Autumn, W: Winter, Sp: Spring) and five regions (MC, EP, WP, NH, SH, as in Fig. 1) in each of the three periods (1980-81, 1996-97, 2008-10). Density of each species has been divided by the dispersion weighting factor shown after the species name, square root transformed and averaged over replicates and the two years in each Season \times Region \times Period combination, and the result represented by the colour shading shown in the key.

Figure 7. Shade plot of the abundance for 30 fish species (those occurring in more than four replicates) derived from 21.5 m seine samples in each of the two periods (1996-97, 2008-10). Construction as in legend to Fig. 6.

Figure 8. Centroid nMDS as in Fig. 4 but (for greater clarity) for only three of the five regions, spanning the regional conditions. Superimposed is a segmented bubble plot where segment size reflects the dispersion weighted then root-transformed abundances, averaged over years and seasons, for six species (selected from the shade plot of Fig. 6, as important in distinguishing these regions and/or the period changes). The segment sizes in the key correspond to a value of 1 on this weighted, transformed scale, the same for all species.

Table 1. Life cycle guilds (LC), rankings by ordered density (*Rk*), mean densities (*N*; numbers of fish 100 m⁻²) and percentage contributions to the total catch (%) of the fish species caught in the Peel-Harvey Estuary using a 102.5 m seine seasonally during two consecutive years, i.e. 1980-81, 1996-97 and 2008-10. In this and subsequent Tables, life cycle guilds are abbreviated as follows. MS, marine straggler; MEO, marine estuarine-opportunist; E&M, estuarine & marine; E, solely estuarine; E&F, estuarine & freshwater and SA, semi-anadromous.

Species	LC	1980-1981			1996-1997			2008-2010		
		<i>Rk</i>	<i>N</i>	%	<i>Rk</i>	<i>N</i>	%	<i>Rk</i>	<i>N</i>	%
<i>Torquigener pleurogramma</i>	MEO	6	2.6	5.7	1	5.6	41.8	1	13.3	30.7
<i>Ostorhinchus rueppellii</i>	E&M	2	6.4	14.3	7	0.5	3.3	2	10.7	24.6
<i>Hyperlophus vittatus</i>	MEO	4	3.1	6.8	2	2.3	16.9	3	7.2	16.5
<i>Atherinosoma elongata</i>	E	10	1.0	2.2	4	1.3	9.3	4	2.8	6.5
<i>Leptatherina presbyteroides</i>	E&M	11	1.0	2.2	3	1.3	9.4	5	2.2	5.1
<i>Atherinomorus vaigiensis</i>	MEO	8	1.4	3.1	15	<0.1	0.5	6	1.1	2.5
<i>Pelates octolineatus</i>	MEO	1	16.4	36.6	10	0.1	1.0	7	1.1	2.5
<i>Favonigobius lateralis</i>	E&M	5	2.6	5.8	8	0.3	2.5	8	1.1	2.5
<i>Craterocephalus mugiloides</i>	E	22	0.1	0.3	30	<0.1	<0.1	9	0.8	1.9
<i>Aldrichetta forsteri</i>	MEO	7	2.2	5.0	5	0.6	4.2	10	0.6	1.5
<i>Gymnapistes marmoratus</i>	MEO	13	0.4	0.9	12	0.1	0.9	11	0.6	1.5
<i>Haletta semifasciata</i>	MEO	23	0.1	0.2	31	<0.1	<0.1	12	0.3	0.8
<i>Gerres subfasciatus</i>	MEO	3	3.9	8.8	6	0.6	4.1	13	0.3	0.7
<i>Sillaginodes punctatus</i>	MEO	20	0.1	0.3	16	<0.1	0.4	14	0.3	0.6
<i>Hyporhamphus melanochir</i>	E&M	24	0.1	0.2	21	<0.1	0.1	15	0.2	0.5
<i>Pseudogobius olorum</i>	E&F	15	0.3	0.6	20	<0.1	0.2	16	0.2	0.4
<i>Spratelloides robustus</i>	MS				35	<0.1	<0.1	17	0.1	0.3
<i>Rhabdosargus sarba</i>	MEO	26	<0.1	0.1	9	0.2	1.2	18	<0.1	0.2
<i>Callogobius depressus</i>	E&M	31	<0.1	<0.1	32	<0.1	<0.1	19	<0.1	0.2
<i>Sillago vittata</i>	MS				29	<0.1	<0.1	20	<0.1	<0.1
<i>Pseudorhombus jenynsii</i>	MEO	21	0.1	0.3	17	<0.1	0.4	21	<0.1	<0.1
<i>Sillago schomburgkii</i>	MEO	12	0.5	1.2	18	<0.1	0.3	22	<0.1	<0.1
<i>Scobinichthys granulatus</i>	MS	36	<0.1	<0.1	32	<0.1	<0.1	23	<0.1	<0.1
<i>Sillago burrus</i>	MEO	34	<0.1	<0.1	13	<0.1	0.7	24	<0.1	<0.1
<i>Arenigobius bifrenatus</i>	E&M	18	0.1	0.3	26	<0.1	<0.1	25	<0.1	<0.1
<i>Acanthaluteres brownii</i>	MS							26	<0.1	<0.1
<i>Stigmatophora argus</i>	MS							27	<0.1	<0.1
<i>Cnidogobius macrocephalus</i>	E&M	29	<0.1	<0.1	35	<0.1	<0.1	28	<0.1	<0.1
<i>Leptatherina wallacei</i>	E&F	17	0.2	0.3	28	<0.1	<0.1	29	<0.1	<0.1
<i>Arripis georgianus</i>	MEO				23	<0.1	0.1	30	<0.1	<0.1
<i>Hyporhamphus regularis</i>	E	19	0.1	0.3	27	<0.1	<0.1	31	<0.1	<0.1
<i>Monacanthus chinensis</i>	MS							32	<0.1	<0.1
<i>Mugil cephalus</i>	MEO	14	0.3	0.8	23	<0.1	0.1	33	<0.1	<0.1
<i>Meuschenia freycineti</i>	MS				39	<0.1	<0.1	34	<0.1	<0.1
<i>Sillago bassensis</i>	MS	9	1.1	2.5	14	<0.1	0.6	35	<0.1	<0.1
<i>Engraulis australis</i>	MS	30	<0.1	<0.1	11	0.1	0.9	36	<0.1	<0.1
<i>Acanthopagrus butcheri</i>	E							36	<0.1	<0.1
<i>Ammotretis elongatus</i>	MS	32	<0.1	<0.1	22	<0.1	0.1	36	<0.1	<0.1
<i>Callogobius mucosus</i>	E&M							39	<0.1	<0.1
<i>Pseudocaranx wrighti</i>	MS							40	<0.1	<0.1
<i>Platycephalus laevigatus</i>	MS							41	<0.1	<0.1
<i>Lesueurina platycephala</i>	MS							41	<0.1	<0.1
<i>Myliobatis australis</i>	MS							43	<0.1	<0.1
<i>Siphamia cephalotes</i>	E&M				39	<0.1	<0.1	43	<0.1	<0.1
<i>Arripis truttaceus</i>	MEO	37	<0.1	<0.1				43	<0.1	<0.1
<i>Favonigobius punctatus</i>	MS							43	<0.1	<0.1
<i>Contusus brevicaudus</i>	MEO	25	0.1	0.2	23	<0.1	0.1	43	<0.1	<0.1
<i>Filicampus tigris</i>	MS							48	<0.1	<0.1
<i>Pomatomus saltatrix</i>	MEO	27	0.1	0.1	19	<0.1	0.2	48	<0.1	<0.1
<i>Notolabrus parilus</i>	MS							48	<0.1	<0.1
<i>Brachaluteres jacksonianus</i>	MS	37	<0.1	<0.1	43	<0.1	<0.1	48	<0.1	<0.1
<i>Iso rhotophilus</i>	MS							52	<0.1	<0.1
<i>Pentapodus vitta</i>	MS							52	<0.1	<0.1
<i>Neatypus obliquus</i>	MS							52	<0.1	<0.1
<i>Enoplosus armatus</i>	MS				39	<0.1	<0.1	52	<0.1	<0.1
<i>Diodon nichthemerus</i>	MS							52	<0.1	<0.1
<i>Heterodontus portusjacksoni</i>	MS				43	<0.1	<0.1			
<i>Sardinops neopilchardus</i>	MS	32	<0.1	0.0						
<i>Nematalosa vlaminghi</i>	SA	35	<0.1	0.0	35	<0.1	<0.1			
<i>Urocampus carinirostris</i>	E&M	37	<0.1	<0.1	43	<0.1	<0.1			
<i>Platycephalus speculator</i>	MS				35	<0.1	<0.1			
<i>Amniataba caudavittata</i>	E	16	0.2	0.5	32	<0.1	<0.1			
<i>Pseudocaranx dentex</i>	MS				39	<0.1	<0.1			
<i>Upeneus tragula</i>	MS				43	<0.1	<0.1			
<i>Afurcagobius suppositus</i>	E&F	28	<0.1	0.1	43	<0.1	<0.1			
Number of samples			62			120			155	
Number of species			39			47			56	
Number of fish			44,386			25,792			107,670	
Mean number of fish 100 m ⁻²			44			13			44	

Table 2. Life cycle guilds (LC), rankings by density (*Rk*), mean densities (*N*, number of fish 100 m⁻²) and percentage contributions to the total catch (%) of the fish species caught in the Peel-Harvey Estuary using a 21.5 m seine over two consecutive years, i.e. 1996-97 and 2008-10.

Species	LC	1996-1997			2008-2010		
		<i>Rk</i>	<i>N</i>	%	<i>Rk</i>	<i>N</i>	%
<i>Atherinosoma elongata</i>	E	2	27.2	12.1	1	76.5	27.1
<i>Hyperlophus vittatus</i>	MEO	1	130.9	58.4	2	62.6	22.2
<i>Leptatherina presbyteroides</i>	E&M	3	24.4	10.9	3	37.2	13.1
<i>Craterocephalus mugiloides</i>	E	22	0.1	<0.1	4	31.9	11.3
<i>Ostorhinchus rueppellii</i>	E&M	7	3.8	1.7	5	19.8	7.0
<i>Torquigener pleurogramma</i>	MEO	4	12.2	5.4	6	13.9	4.9
<i>Aldrichetta forsteri</i>	MEO	5	9.9	4.4	7	13.7	4.8
<i>Favonigobius lateralis</i>	E&M	6	7.0	3.1	8	9.7	3.4
<i>Atherinomorus vaigiensis</i>	MEO	8	2.6	1.2	9	7.8	2.7
<i>Gymnapistes marmoratus</i>	MEO	10	0.6	0.3	10	2.2	0.8
<i>Haletta semifasciata</i>	MEO	18	0.1	<0.1	11	1.2	0.4
<i>Pelates octolineatus</i>	MEO	15	0.2	0.1	12	1.2	0.4
<i>Leptatherina wallacei</i>	E&F	9	2.6	1.1	13	1.1	0.4
<i>Sillaginodes punctatus</i>	MEO	13	0.2	0.1	14	1.0	0.3
<i>Pseudogobius olorum</i>	E&F	11	0.5	0.2	15	0.8	0.3
<i>Mugil cephalus</i>	MEO	16	0.2	0.1	16	0.4	0.1
<i>Stigmatophora argus</i>	MS	37	<0.1	<0.1	17	0.3	0.1
<i>Hyporhamphus melanochir</i>	E&M	19	0.1	<0.1	18	0.2	0.1
<i>Sillago burrus</i>	MEO	20	<0.1	<0.1	19	0.1	<0.1
<i>Sillago vittata</i>	MEO	14	0.2	0.1	20	0.1	<0.1
<i>Callogobius mucosus</i>	E&M				20	0.1	<0.1
<i>Rhabdosargus sarba</i>	MEO	21	<0.1	<0.1	22	0.1	<0.1
<i>Ammotretis elongatus</i>	MS	17	0.2	0.1	23	<0.1	<0.1
<i>Cnidoglanis macrocephalus</i>	E&M	34	<0.1	<0.1	24	<0.1	<0.1
<i>Arenigobius bifrenatus</i>	E&M	26	<0.1	<0.1	24	<0.1	<0.1
<i>Arripis truttaceus</i>	MEO				26	<0.1	<0.1
<i>Engraulis australis</i>	MS				27	<0.1	<0.1
<i>Scobinichthys granulatus</i>	MS	34	<0.1	<0.1	28	<0.1	<0.1
<i>Pseudorhombus jenynsii</i>	MEO	12	0.4	0.2	29	<0.1	<0.1
<i>Hyporhamphus regularis</i>	E	30	<0.1	<0.1	29	<0.1	<0.1
<i>Gerres subfasciatus</i>	MEO	22	<0.1	<0.1	29	<0.1	<0.1
<i>Sillago schomburgkii</i>	MEO	24	<0.1	<0.1	32	<0.1	<0.1
<i>Spratelloides robustus</i>	MS	39	<0.1	<0.1	33	<0.1	<0.1
<i>Omobranchus germaini</i>	MS				34	<0.1	<0.1
<i>Contusus breviceaudus</i>	MEO	31	<0.1	<0.1	35	<0.1	<0.1
<i>Urocampus carinirostris</i>	E&M	27	<0.1	<0.1	36	<0.1	<0.1
<i>Pugnaso curtirostris</i>	E				36	<0.1	<0.1
<i>Lesueurina platycephala</i>	MS				36	<0.1	<0.1
<i>Meuschenia freycineti</i>	MS				36	<0.1	<0.1
<i>Acanthaluteres brownii</i>	MS				36	<0.1	<0.1
<i>Monacanthus chinensis</i>	MS				36	<0.1	<0.1
<i>Siphamia cephalotes</i>	E&M				42	<0.1	<0.1
<i>Platycephalus laevigatus</i>	MS	37	<0.1	<0.1	43	<0.1	<0.1
<i>Acanthopagrus butcheri</i>	E				43	<0.1	<0.1
<i>Enoplosus armatus</i>	MS				43	<0.1	<0.1
<i>Acanthaluteres vittiger</i>	MS				43	<0.1	<0.1
<i>Arripis georgianus</i>	MEO	31	<0.1	<0.1			
<i>Brachaluteres jacksonianus</i>	MS	39	<0.1	<0.1			
<i>Callogobius depressus</i>	E&M	34	<0.1	<0.1			
<i>Afurcagobius suppositus</i>	E	28	<0.1	<0.1			
<i>Gonorynchus greyi</i>	MEO	31	<0.1	<0.1			
<i>Nematalosa vlaminghi</i>	SA	39	<0.1	<0.1			
<i>Petroscirtes breviceps</i>	MS	39	<0.1	<0.1			
<i>Pomatomus saltatrix</i>	MEO	28	<0.1	<0.1			
<i>Sillago bassensis</i>	MS	25	<0.1	<0.1			
<i>Sardinops neopilchardus</i>	MS	39	<0.1	<0.1			
Number of samples			240			155	
Number of species			43			46	
Number of fish			62,350			50,845	
Mean number of fish 100 m⁻²			224			283	

Table 3. Number of species and number of individuals of each life cycle guild in samples collected from the Peel-Harvey Estuary using a 102.5 m seine in 1980-81, 1996-97 and 2008-10 and a 21.5 m seine in the last two periods.

LC Guild	(a) 102.5 m seine						(b) 21.5 m seine			
	1980-81		1996-97		2008-10		1996-97		2008-10	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
<i>Species</i>										
MS	6	15.4	13	27.7	23	39.3	9	20.9	13	28.3
MEO	17	43.6	17	36.2	18	33.9	19	44.2	17	37.0
E&M	8	20.5	9	19.1	9	16.1	8	18.6	9	19.6
E	4	12.8	4	10.6	4	7.1	4	9.3	5	10.9
E&F	3	5.1	3	4.3	2	3.6	2	4.7	2	4.3
A	1	2.6	1	2.1	0	0	1	2.3	0	0
Total	39		47		56		43		46	
LC Guild	<i>D</i>	%	<i>D</i>	%	<i>D</i>	%	<i>D</i>	%	<i>D</i>	%
<i>Individuals</i>										
MS	1.4	3.0	0.7	4.7	1.2	2.6	0.6	0.3	0.9	0.3
MEO	31.5	69.7	10.0	67.8	25.3	56.4	158.0	70.3	104.6	36.9
E&M	10.4	22.9	2.4	16.3	14.5	32.2	35.5	15.8	67.2	23.7
E	1.5	3.2	1.5	10.2	3.7	8.2	27.4	12.2	108.6	38.3
E&F	0.5	1.1	0.1	0.7	0.3	0.6	3.1	1.4	1.9	0.7
SA	0.1	0.1	0.1	0.3	0	0	<0.1	<0.1	0	0
Total	45.4		14.8		45.0		225		283.1	

Table 4. Mean squares (MS), Pseudo-F (*pF*) values, components of variation (COV) and significance levels (*P*) for the four-factor PERMANOVA tests on the Bray-Curtis similarity matrices constructed from fish abundances for the five regions of the Peel-Harvey Estuary using (a) 102.5 m seine seasonally over two consecutive years in three periods, i.e. 1980-81, 1996-97 and 2008-10, and (b) 21.5 m seine seasonally in 1996-97 and 2008-10. *df* = degrees of freedom. Clearly significant results (at the *P* < 0.005 level) are highlighted in bold. *P* values marked with an asterisk are from tests on low numbers of *df*, so are generated by the Monte Carlo method, which involves an extra degree of approximation.

Main effects	(a) 102.5 m seine					(b) 21.5 m seine				
	<i>df</i>	MS	<i>pF</i>	COV	<i>P</i>	<i>df</i>	MS	<i>pF</i>	COV	<i>P</i>
Period	2	53409	8.8	447	0.001*	1	21526	3.7	116	0.003*
Season	3	15920	2.8	123	0.002	3	13112	3.2	132	0.004
Region	4	13568	3.8	152	0.001	4	14110	5.4	209	0.001
Year (Period)	3	6241	2.9	74	0.001	2	5912	2.8	55	0.001
Interactions										
Period × Season	6	5811	1.2	30	0.238	3	6381	1.6	72	0.094
Period × Region	8	9501	3.0	301	0.001	4	6877	2.7	159	0.002
Season × Region	12	3098	1.3	43	0.032	12	3674	1.4	78	0.010
Year (Period) × Season	9	5096	2.4	214	0.001	6	3974	1.9	107	0.001
Year (Period) × Region	12	3168	1.5	91	0.001	8	2581	1.2	32	0.085
Period × Season × Region	24	2808	1.2	89	0.038	12	2895	1.1	46	0.219
Year (Period) × Season × Region	35	2354	1.1	71	0.082	24	2592	1.2	133	0.008
Residuals	218	2154		2154		195	2136		2136	

Table 5. \bar{R} and significance level (P) values, derived from two-way crossed ANOSIM tests of the abundances of the various fish species caught in the Peel-Harvey Estuary using (a) 102.5 m seine in 1980-81, 1996-97 and 2008-10 and (b) 21.5 m seine 1996-97 and 2008-10. Significant results for region and season are highlighted in grey.

(a)	1980-81	1996-97	2008-10
Region	0.405	0.028	0.523
Season	0.076	0.129	0.417

(b)	1996-97	2008-10
Region	0.403	0.283
Season	0.363	0.425

Table 6. Average and pairwise \bar{R} statistic and significance level (P) values, derived from two-way crossed ANOSIM tests for Period and Season, separately for each region, based on abundances of the various fish species caught using a 102.5 m seine in 1980-81, 1996-97 and 2008-10, with the values for pairwise period and seasonal comparisons given below.

Mandurah Channel					
Period	$\bar{R} = 0.833$	$P = 0.1\%$	Season	$\bar{R} = 0.479$	$P = 0.2\%$
			Su	A	W
	1980-81	1996-97	A	0.750	
1996-97	0.938		W	0.500	0.417
2008-10	1.000	0.500	Sp	0.667	0.500 0.250
Eastern Peel					
Period	$\bar{R} = 0.883$	$P = 0.1\%$	Season	$\bar{R} = 0.486$	$P = 0.4\%$
			Su	A	W
	1980-81	1996-97	A	0.417	
1996-97	0.813		W	0.667	0.583
2008-10	1.000	0.750	Sp	0.500	0.583 0.167
Western Peel					
Period	$\bar{R} = 0.153$	$P = 9.5\%$	Season	$\bar{R} = 0.076$	$P = 31.3\%$
			Su	A	W
	1980-81	1996-97	A	-0.167	
1996-97	0.313		W	0.167	0.250
2008-10	0.188	0.000	Sp	-0.167	0.417 0.000
Northern Harvey					
Period	$\bar{R} = 0.583$	$P = 0.1\%$	Season	$\bar{R} = 0.111$	$P = 22.8\%$
			Su	A	W
	1980-81	1996-97	A	-0.083	
1996-97	0.625		W	0.583	0.083
2008-10	0.563	0.750	Sp	-0.083	-0.167 0.083
Southern Harvey					
Region	$\bar{R} = 0.508$	$P = 0.1\%$	Season	$\bar{R} = 0.144$	$P = 15.8\%$
			Su	A	W
	1980-81	1996-97	A	-0.333	
1996-97	0.540		W	0.208	0.167
2008-10	0.611	0.563	Sp	0.605	0.507 -0.395

Table 7. Average and pairwise \bar{R} statistic and significance level (P) values, derived from two-way crossed ANOSIM tests for Period and Season, separately for each region, based on abundances of the various fish species caught using a 21.5 m seine in 1996-97 and 2008-10, with the values for pairwise seasonal comparisons given below.

Mandurah Channel			
Period	$\bar{R} = 0.938$	$P = 1.2\%$	
Season	$\bar{R} = 0.792$	$P = 0.2\%$	
	Su	A	W
A	0.875		
W	1.000	0.625	
Sp	0.750	0.875	0.500
Eastern Peel			
Period	$\bar{R} = 0.375$	$P = 1.2\%$	
Season	$\bar{R} = 0.188$	$P = 15.3\%$	
	Su	A	W
A	0.625		
W	0.250	0.250	
Sp	-0.375	0.500	-0.250
Western Peel			
Period	$\bar{R} = 0.313$	$P = 16\%$	
Season	$\bar{R} = 0.208$	$P = 11.3\%$	
	Su	A	W
A	0.500		
W	0.375	0.125	
Sp	0.250	0.250	0.000
Northern Harvey			
Period	$\bar{R} = 0.563$	$P = 6.2\%$	
Season	$\bar{R} = 0.094$	$P = 32.2\%$	
	Su	A	W
A	-0.375		
W	0.625	-0.250	
Sp	0.125	-0.250	0.500
Southern Harvey			
Period	$\bar{R} = 0.750$	$P = 1.2\%$	
Season	$\bar{R} = 0.448$	$P = 0.3\%$	
	Su	A	W
A	0.375		
W	0.625	0.000	
Sp	0.250	0.500	0.500

Figure 1

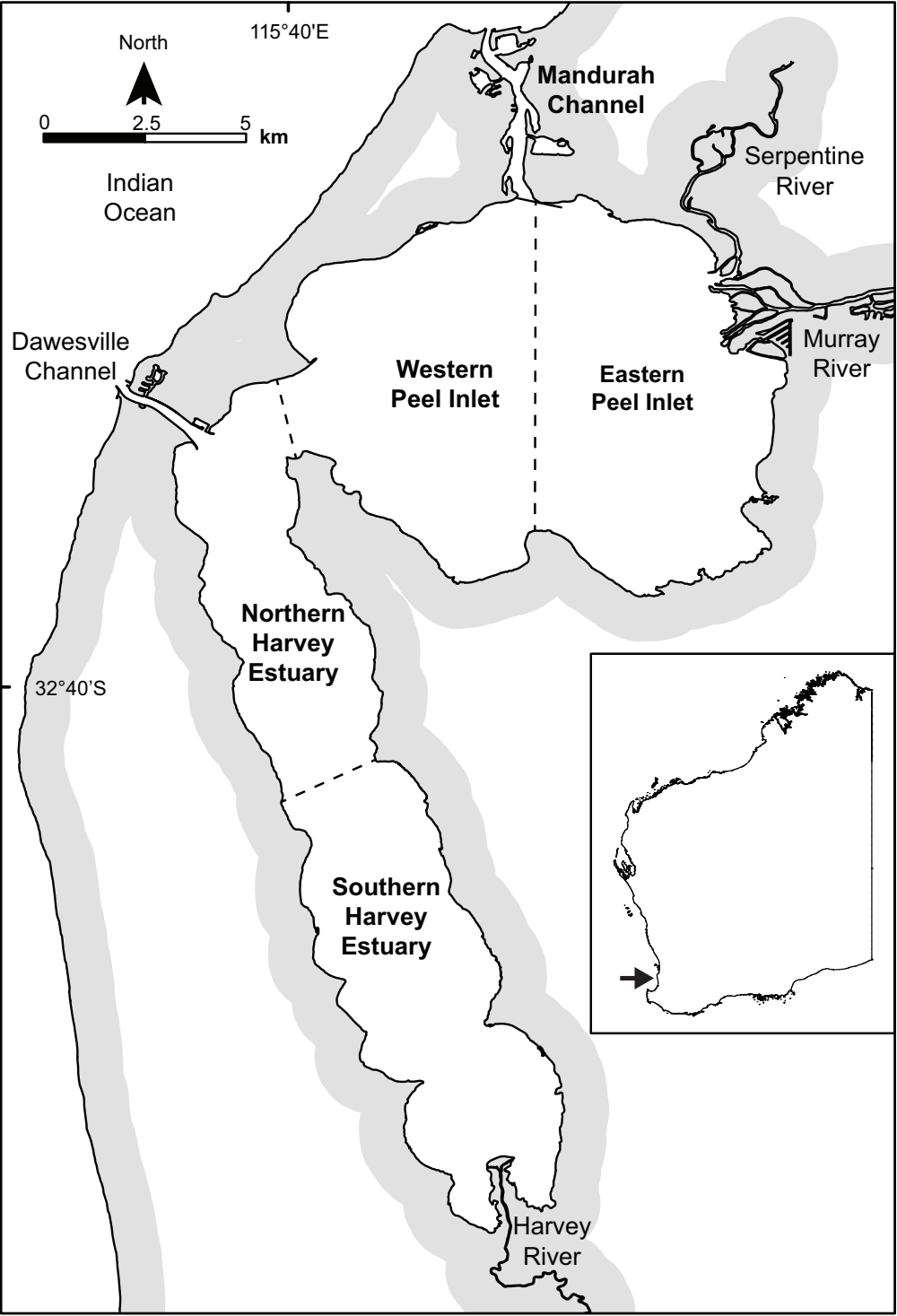


Figure. 1

Figure 2_Colour

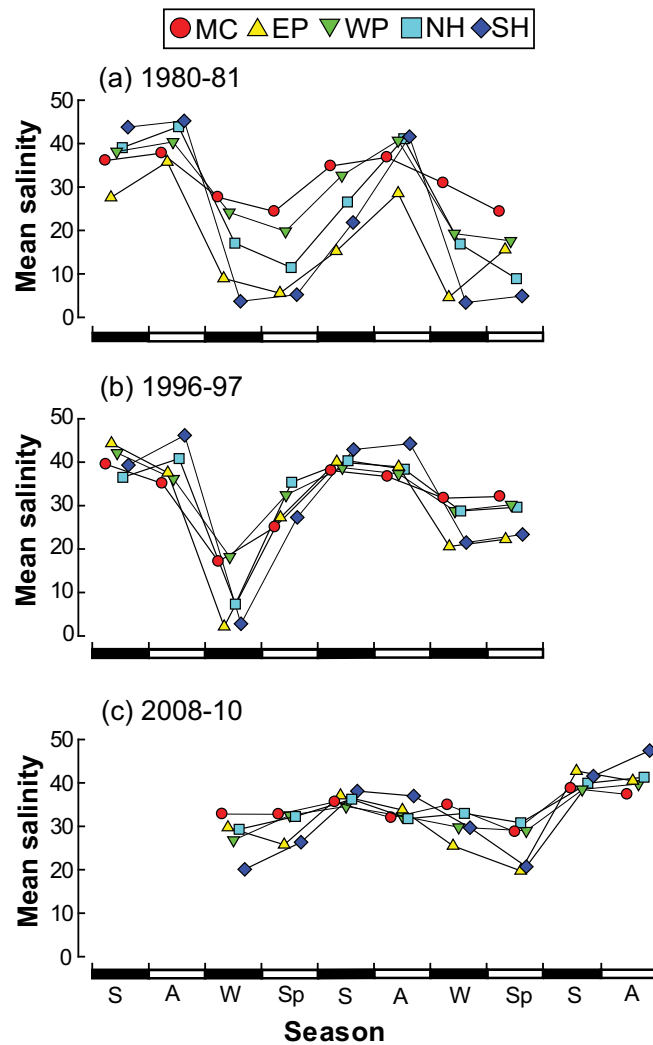


Figure. 2

Figure 2_Black & White

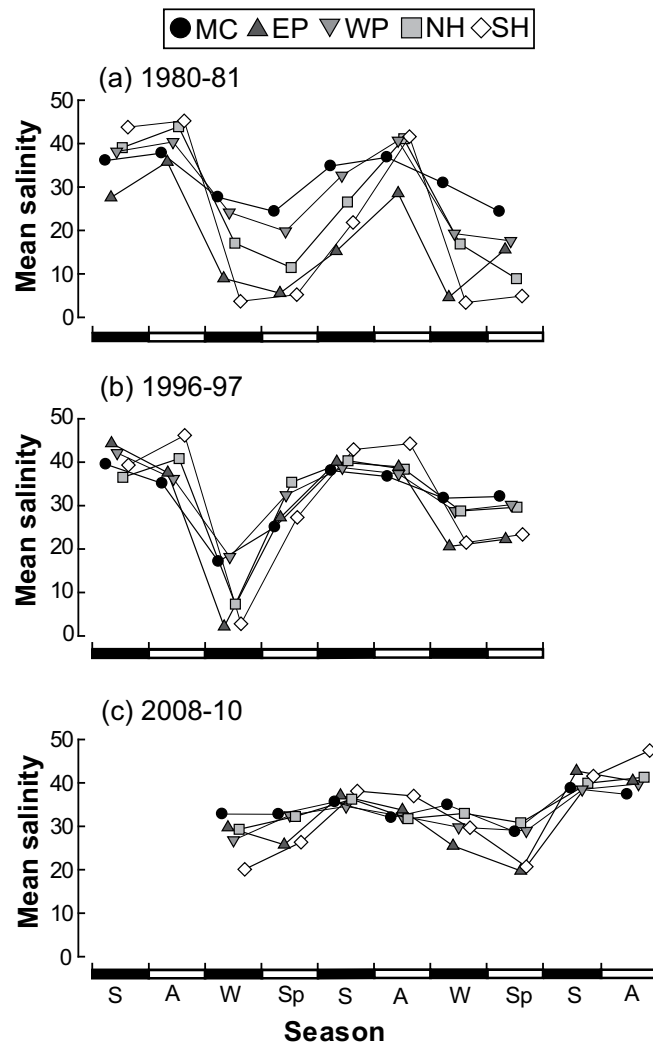


Figure. 2

Figure 3

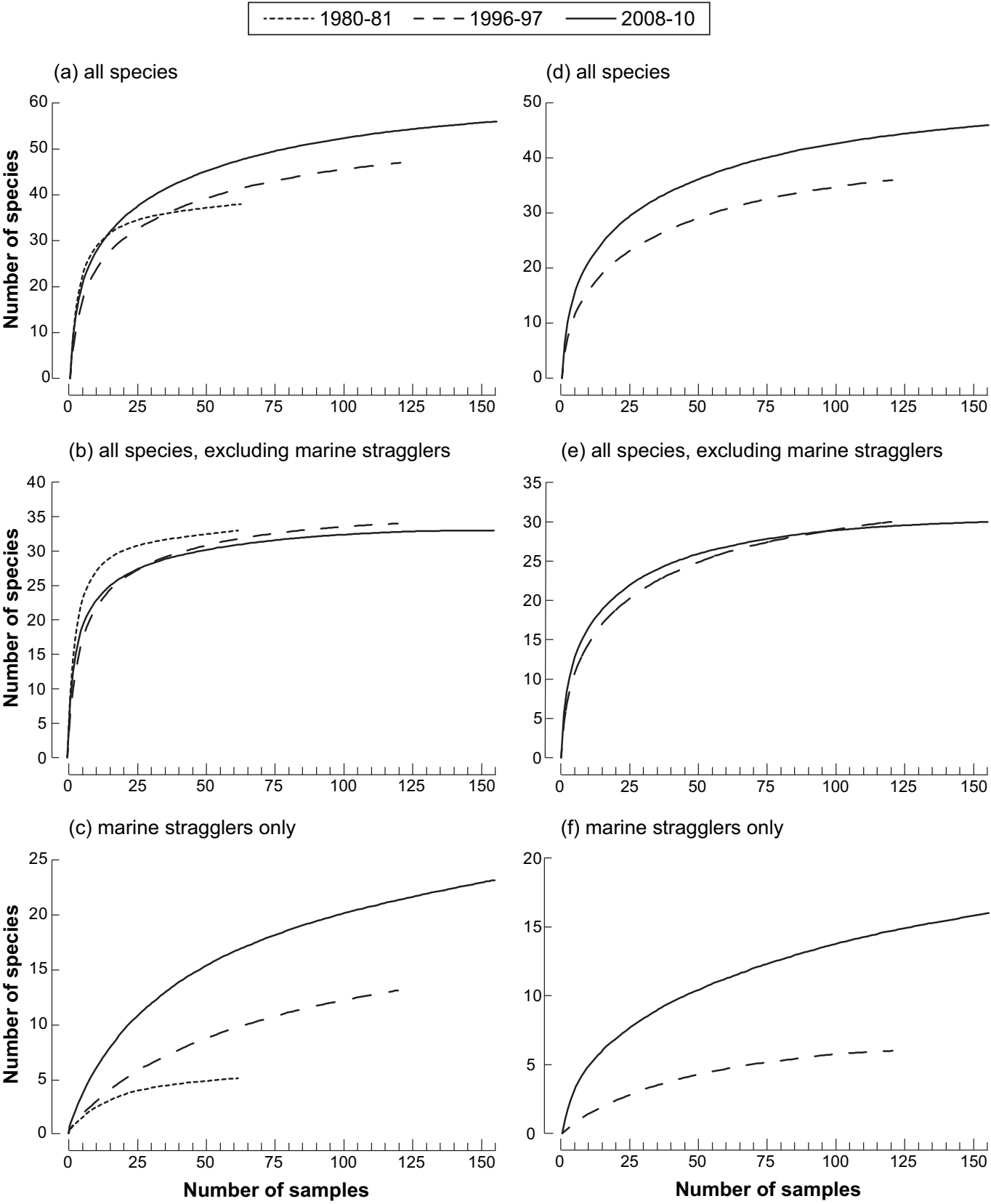


Figure 3

Figure 4_Colour

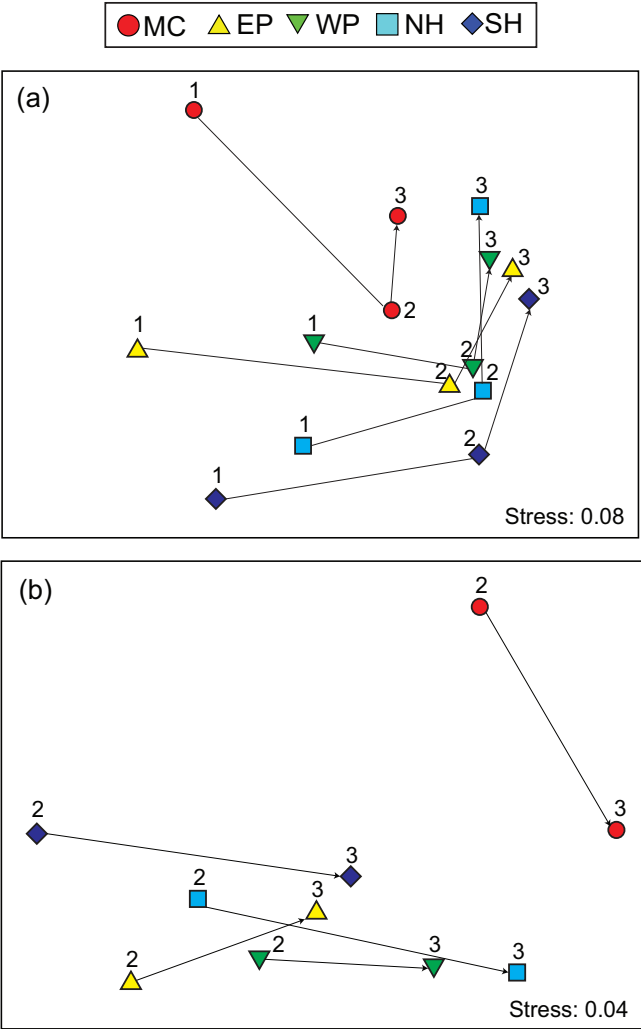


Figure. 4

Figure 4_Black & White

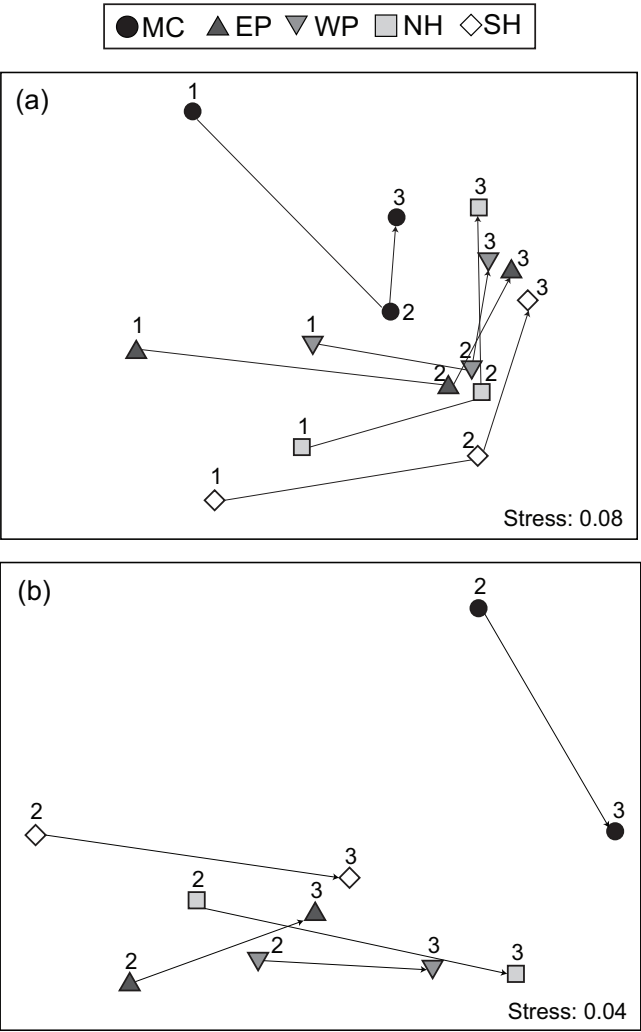


Figure. 4

Figure 5

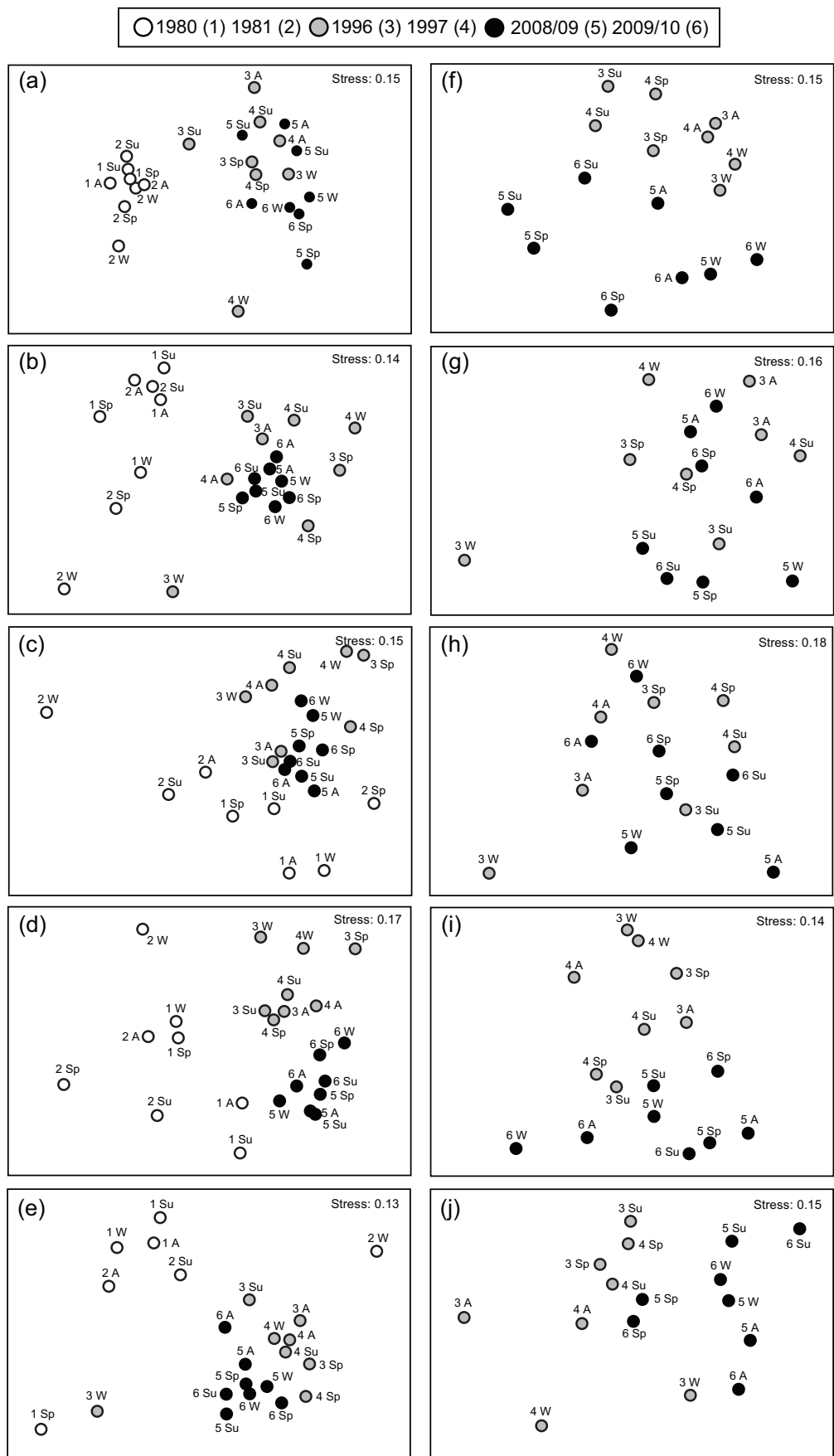


Figure 5

Figure 6

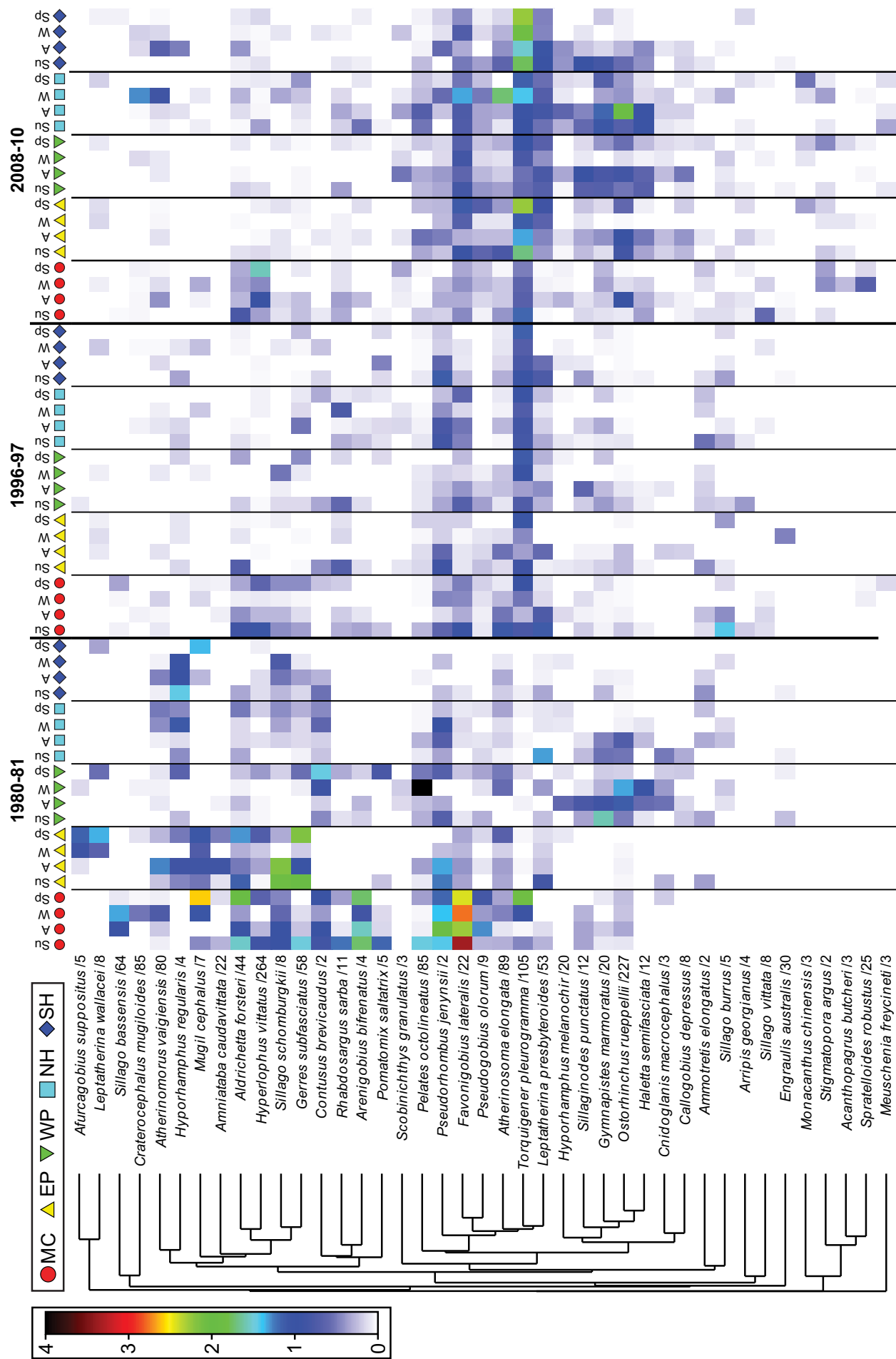


Figure 6

Figure 7

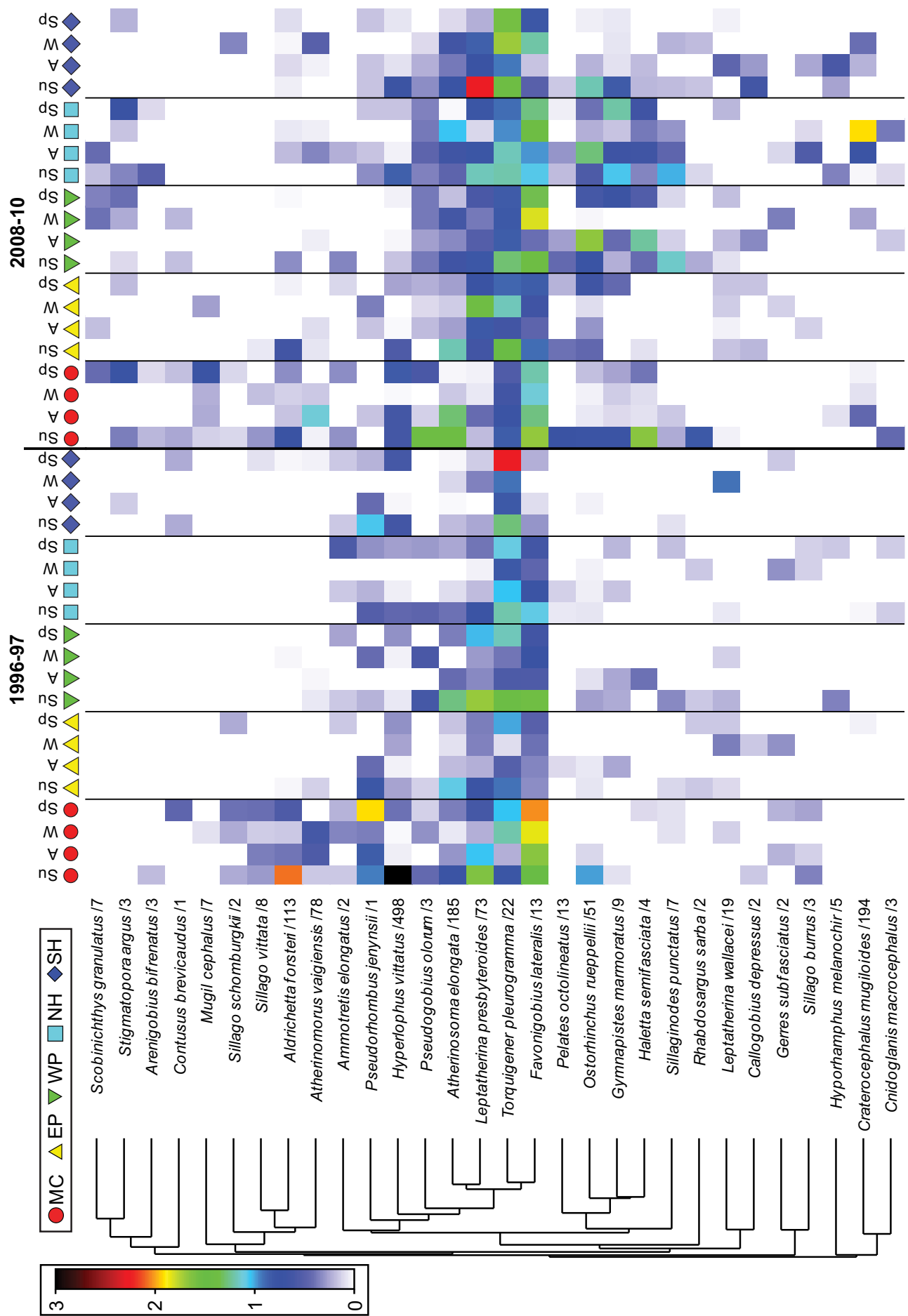


Figure 7

Figure 8

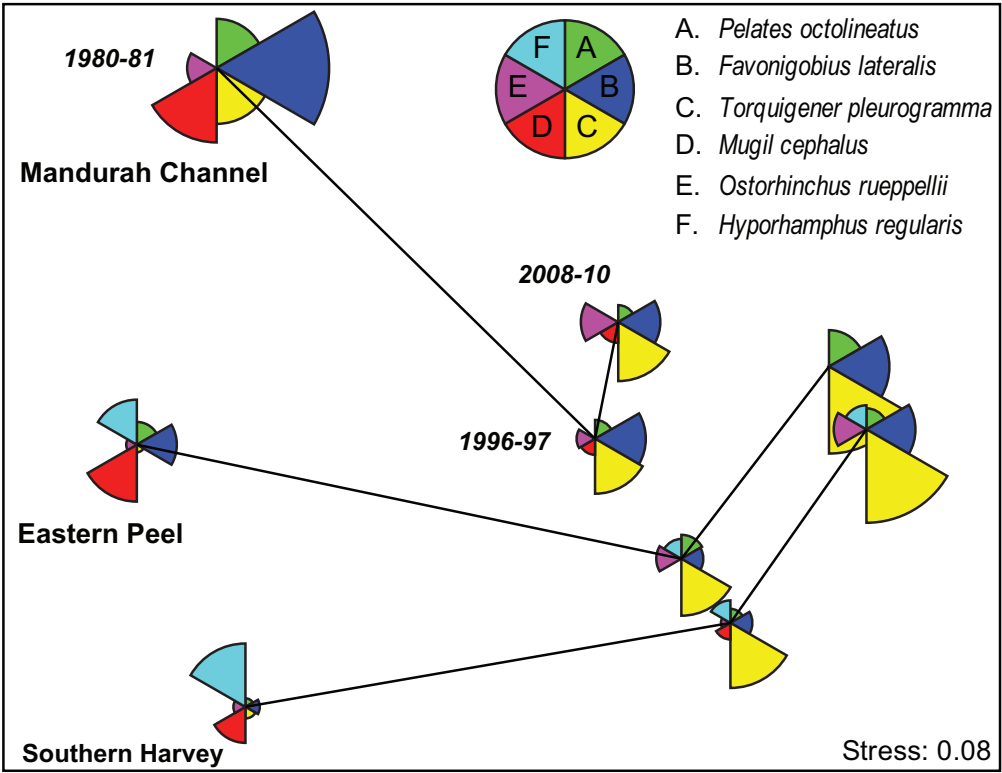


Figure. 8