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Interdecadal changes in the community, population and individual levels of the fish fauna of an extensively modified estuary

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This study examined inter-period changes over two to three decades in the fish fauna of an urbanized estuary experiencing rapid population growth and a drying climate (Swan–Canning Estuary, Western Australia). Responses were compared at the fish community level (species composition; 1978–2009 in the shallows and 1993–2009 in deeper waters) and at the population and individual levels of an estuarine indicator species, black bream Acanthopagrus butcheri (biomass–abundance and per capita mass at age, respectively; 1993–2009). All three levels showed distinct shifts from earlier to later periods, but their patterns, sensitivity and breadth differed. Community composition changed markedly in the shallows of the lower-middle estuary between the late 1970s and all later periods and moderately between more disparate periods from 1995 to 2009. Several species trends could be linked to the increasing salinity of the estuary or declining dissolved oxygen levels in its middle–upper reaches. Community changes were, however, small or insignificant in the shallow and deeper waters of the upper estuary and deeper waters of the middle estuary, where environmental perturbations are often most pronounced. This may reflect the resilience of the limited suite of species that typify those reaches and thus their lack of sensitivity in reflecting longer-term change at the coarser level of mean abundance. One such species, the selected indicator, A. butcheri, did, however, show marked temporal changes at both the population and individual levels. Biomass decreased markedly in deeper waters while increasing in the shallows from earlier to later periods, presumably reflecting an onshore movement of fish, and per capita body mass in the 2+, 3+ and 4+ year classes fell steadily over time. Such changes probably indicate deteriorating habitat quality in the deeper waters. The study outcomes provide support for a multifaceted approach to the biomonitoring of estuaries using fishes and highlight the need for complementary monitoring of relevant stressors to better disentangle cause–effect pathways.

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Key words: bio-indicators; biological organization; estuary condition; long-term change; monitoring.

INTRODUCTION

The extreme and growing stressors on urbanized estuaries resulting from high population growth in the coastal zone (Kennish, 2002; Elliott & Whitfield, 2011; Jennerjahn & Mitchell, 2013), as well as climate change effects (Scavia et al., 2002; Statham, 2012; Wetz & Yoskowitz, 2013), are well documented worldwide. Copious examples of the

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ecosystem services threatened or lost through the degradation of these highly productive environments are also provided throughout the ecological literature (Lotze et al., 2006; Davis & Kidd, 2012; Mayer-Pinto et al., 2015).

It is now well accepted that approaches to understanding and monitoring the status of estuarine ecosystem health must extend beyond simple environmental facets such as water quality, to include aspects of estuarine ecology that not only reflect ecosystem structure, function and processes, but that the public can readily relate to (Karr & Dudley, 1981; Ribeiro et al., 2008; Sheaves et al., 2012; Hallett et al., 2016b). On this basis, fishes have received considerable attention for providing useful indicators and their various advantages are well summarized by Whitfield & Elliott (2002) and Harrison & Whitfield (2004).

The ecological effects of stressors on estuaries, or indeed any ecosystem, can be expressed at various levels of biological organization, i.e. molecular, cellular, individual, population, community or ecosystem. Unsurprisingly, considerable debate surrounds which of these levels and which of their attributes provide the most sensitive, practical and meaningful indicators of ecosystem condition (Dale & Beyeler, 2001). While lower levels respond more quickly to stressors and enable better understanding of cause-and-effect pathways, the broader ecological implications of these responses can be unclear. Conversely, while the ecological relevance of higher-level responses is often more apparent, they can be complex, insensitive to sub-lethal effects and lack a well-defined mechanistic explanation. Variability at each organizational level and particularly higher ones, can also make detection of change difficult (Adams et al., 2000, 2005; Clements, 2000; Whitfield & Elliott, 2002; Niemi & McDonald, 2004; Richardson et al., 2011).

At the broader fish community level in estuaries, some workers have found that high stochastic variability across the assemblage precludes detection of any response to changing environmental quality (Ellis & Bell, 2013), while others have shown they provide reliable indicators of ecosystem health, especially when such variability is minimized (Sheaves & Johnston, 2010; Sheaves et al., 2012). In particular, many workers have demonstrated the effectiveness of fish assemblages in reflecting longer-term changes in estuarine condition, including: Henderson (2007) and Ferguson et al. (2013) using 25 year fish data sets in the Severn Estuary (U.K.) and Murray River Estuary (Australia), respectively; Nyitrai et al. (2012) over a 7 year period in the Mondego Estuary (Portugal); Ribeiro et al. (2008) from 1980–1986 to 2001–2002 in the Ria Formosa system (Portugal); Ecoutin et al. (2010) over a 10 year period in the Sine Saloum Estuary (Senegal).

With respect to indicator fish species, or those considered representative of particular environmental conditions, numerous approaches have been adopted worldwide at the population, individual or finer (e.g. molecular) levels for reflecting changes in estuarine condition. Measures of fish production, or rate of change in mass, provide useful approaches at both the population level (e.g. changes in abundance or biomass; Pihl et al., 1992; Randall & Minns, 2000; Eby & Crowder, 2002; Campbell & Rice, 2014) and individual level (e.g. body mass at age, typically reported as growth rates or mass–length relationships; Eby et al., 2005; Campbell & Rice, 2014; Cottingham et al., 2014). Because body mass at age reflects accumulation of mass over time and often several years depending on the age at capture, it is particularly useful for reflecting longer-term changes in ecosystem condition. Some authors, however, have cautioned about the confounding influences of other factors such as natural variability in fish
recruitment, changes in fishing pressure and prey availability (Lorenzen & Enberg, 2002; Selleslagh & Amara, 2015). Molecular responses of estuarine fishes to stressors such as pollutants have been examined by many workers (Elliott et al., 2003; Forrester et al., 2003; Minier & Amara, 2009; Denslow & Sabo-Attwood, 2015), but the ecological significance of these effects is often unknown (Clements, 2000).

Given the different perspectives, advantages and challenges of fish-based indicators derived from different biological levels, several workers have moved towards the use of multiple indices spanning two or more levels to provide a more complete understanding of estuarine condition, identify those indices with the greatest response to stressors, and help determine the causes of observed effects (Yeom & Adams, 2007; Richardson et al., 2011; Borja et al., 2016). The current study contributes to this knowledge by examining and comparing fish faunal changes at three levels of biological organization (community, population and individual) over a 15–30 year period in an urbanized estuary, the Swan-Canning, in south-western Australia. This hypereutrophic system (Cloern et al., 2013) has shown multiple signs of decline over the past few decades (Office of the Auditor General Western Australia, 2014), including more prevalent phytoplankton blooms (Twomey & John, 2001; Robson & Hamilton, 2003; Kristiana et al., 2012), extensive bottom-water hypoxia (Kurup & Hamilton, 2002; Hipsey et al., 2014; Tweedley et al., 2016) and fish-kill events in most years since 2000 (Smith, 2006; Place et al., 2012). Many of these issues, often most severe in the upper estuary (Hallett et al., 2016a), are linked not only with the effects of increasing catchment development to support a rapidly growing population (doubled over the past 30 years; Australian Bureau of Statistics, www.abs.gov.au), but also with climate change effects, including marked reductions in rainfall (16%) and thus stream flows (>50%) in the region since the mid-1970s (Silberstein et al., 2012).

The overarching objective of this study was to use multi-decadal fish data sets for the Swan–Canning Estuary to assess any inter-period shifts in the fish community in the shallows (1978–2009) and deeper waters (1993–2009), and the population and individual levels of an abundant estuarine fish species [black bream Acanthopagrus butcheri (Munro 1949)] (1993–2009), which has many suitable attributes as a bio-indicator (Cottingham et al., 2014). Any such ichthyofaunal changes were then considered in the context of those reflecting aspects of the estuarine environment. More specifically, the main aims were: to explore the different signals and sensitivities of fish community (species composition), population (overall biomass and abundance of A. butcheri) and individual (per capita body mass at age of A. butcheri) levels of biological organization in reflecting longer-term change in the Swan–Canning Estuary; to examine whether any such temporal trends in the ichthyofauna were correlated with those in a suite of biologically-important water-quality variables that provide an independent basis for understanding estuarine condition.

**MATERIALS AND METHODS**

**STUDY AREA**

The Swan–Canning Estuary on the lower west coast of Australia (32°055' S; 115°735' E) experiences a temperate climate and diurnal tides with a spring range of c. 0.5 m. It is a permanently open drowned river valley system (Hodgkin & Hesp, 1998) that is c. 50 km long, 55 km² and mostly < 5 m deep. It comprises a narrow entrance channel, a large central lagoonal
basin, a smaller second basin and the tidal portions of the Swan and Canning Rivers (Fig. 1). Estuary managers have divided the system into several ecological management zones (hereafter zones), the estuarine components of which include the lower Swan–Canning Estuary (LSCE), Canning Estuary (CE), middle Swan Estuary (MSE) and upper Swan Estuary (USE) (Fig. 1; Swan River Trust, 2009). The 126 000 km$^2$ estuary catchment contains c.1.7 million people (c.75% of Western Australia’s population; Australian Bureau of Statistics, www.abs.gov.au) and is mostly cleared for urban, industrial and agricultural activity (Swan River Trust, 2009; Petrone, 2010). The estuary has also been extensively modified since European settlement in the early–mid 1800s (National Land and Water Resources Audit, 2002a, b), including major shoreline alterations, diversion or damming of river flow, wetland reclamation, substantial in-stream constructions and the widening and deepening of its mouth to accommodate an international shipping port (Chan et al., 2002; Brearley, 2005).

FISH SAMPLING

Fish community

Samples of the fish community in the Swan–Canning Estuary have been collected by various workers from the shallow nearshore waters (<2 m deep) during the day and from the deeper offshore waters (>2 m deep) at night during several inter-annual periods from 1978 to 2009 and
1993 to 2009, respectively. The sampling periods, along with other key aspects of the sampling regimes in each study, are summarized in Tables I and II for the nearshore and offshore waters, respectively, with further details given in the cited references. In each sample, all fishes were identified to species and their total numbers counted.

Sampling methodology in the shallows varied markedly among several studies, reflecting differences in their original aims. The following approaches were used to harmonize the nearshore data sets as far as practicable and thus maximize their comparability.

Standardization for seine type: equivalence factors derived from a generalized linear modelling approach to minimize seine bias effects (Hallett & Hall, 2012) were applied to all samples collected using the larger nets (41.5–133 m long) to standardize fish species counts to those most likely recorded if the smallest net (21.5 m long) was used consistently. Data to support this approach were derived from a net-comparison study by the above workers that employed the 21.5, 41.5 and 133 m long seines in the estuary basin and rivers.

Corrections for spatio-temporal sampling intensity: all data sets were standardized such that sites represented replicates of the zones (i.e. no replication within sites) and sampling frequency was seasonal (i.e. no replication within seasons). Where samples were collected at finer scales, a single replicate of a site was randomly selected in the first of these cases and one from the middle month of each season was selected in the second case. Data from eight of the 12 LSCE sites sampled by Valesini et al. (2009), which were not sampled in other studies, were also excluded to reduce sampling imbalance in that zone (Table I).

The only standardization required for the offshore data sets included correcting all studies to a sampling frequency of seasonal as described above and a sampling duration of fishes h−1. Data recorded at several offshore sites by Hallett et al. (2012), mainly in the LSCE and CE, were also excluded since they were not sampled in any other period, as was that for a single site in the USE collected by Kanandjembo et al. (2001) (Table II).

Acanthopagrus butcheri

Samples of A. butcheri were retained from the above fish community studies in 2003–2004 and 2007–2009. A sampling regime targeting only this species was also undertaken in 1993–1995 (Sarre & Potter, 2000), in which samples were collected monthly at sites 18–23 in the nearshore waters using the 41.5 m seine and at sites 18–26 in the offshore waters using gillnets (Tables I and II, and Fig. 1). Samples of A. butcheri were also obtained from those sites during smaller opportunistic surveys in 2004–2005 and 2006–2007 (Valesini et al., 2009). For parity across data sets, only those A. butcheri collected in the middle month of each season were used in the following data analyses for this species. Any A. butcheri caught during winter were not included given the increased likelihood of this species, which typically occupies the middle–upper estuary, being flushed downstream in this season. Each individual retained was measured to the nearest 1 mm (total length, \( L_T \)), weighed to the nearest 0.1 g, sexed and aged [see Cottingham et al. (2014) for full details].

Water quality measurements

The Western Australian Department of Water (DoW) has undertaken weekly measurements of various water-quality variables at routine monitoring sites throughout the estuary since 1994 (Fig. 1). Data for those variables considered likely to influence fishes, either directly or indirectly, were derived from DoW records for those years and months in which fishes were sampled from 1994 to 2009 and from those sites closest to fish sampling sites. Selected variables included salinity, water temperature (°C), dissolved oxygen concentration (mg l−1) and chlorophyll \( a \) concentration (mg l−1). Measurements in the top 0.5 m of the water column were selected to represent surface waters and those within 0.5 m of the substratum represented bottom waters. Other variables such as turbidity were also of interest, but were excluded given inconsistencies in their records, as was chlorophyll \( a \) concentration in the bottom waters.

For fish sampling periods prior to 1994, the only available water-quality data were measurements of salinity and temperature taken concurrently with fish collection. Measurements were made at the water surface at nearshore sites and at the surface and bottom at offshore sites.
Table I. Summary of the nearshore fish sampling regimes in the Swan–Canning Estuary in each study period from 1978 to 2009. Estuary zones include the lower Swan–Canning Estuary (LSCE), middle Swan Estuary (MSE), upper Swan Estuary (USE) and Canning Estuary (CE); see Fig. 1 for their locations and replicate sites. All fishes were collected using beach seines, the dimensions of which are given below.

<table>
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<td>CE 36</td>
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| Net length (m)      | Biweekly–bimonthly 66.5, 102.5 or 133 | Seasonally 41.5 | Monthly 21.5 | Seasonally 41.5 | Seasonally 21.5 | Seasonally 21.5 or 41.5 |
| Net depth (m)       | 2 Wings; 25, bunt; 16 | 2 Wings; 25, bunt; 9 | 1.5 Wings; 3–9, bunt; 3 | 2 Wings; 25, bunt; 9 | 1.5 Wings; 3–9, bunt; 3 | 1.5 or 2 Wings; 3–9 or 25, bunt; 3 or 9 |
| Net mesh (mm)       | 704, 1670 or 2815 | 274 | 116 | 274 | 116 | 116 or 274 |

*F. J. Valesini, S. D. Hoeksema, K. A. Smith, N. G. Hall, R. C. J. Lenanton, & I. C. Potter, unpub. data. • fish sampling site and data used in analyses; ◆ fish sampling site, but data not used in analyses (see Materials and Methods).
Table II. Summary of the offshore fish sampling regimes in the Swan–Canning Estuary in each study period from 1993 to 2009. Estuary zones include the lower Swan–Canning Estuary (LSCE), middle Swan Estuary (MSE), upper Swan Estuary (USE) and Canning Estuary (CE); see Fig. 1 for their locations and replicate sites. All fishes were collected using bottom-set, multi-mesh gillnets with six–eight 20 m long x 2 m high panels with stretched mesh sizes ranging from 35–127 mm in increments of 12–16 mm.

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●, fish sampling site and data used in analyses; ●, fish sampling site, but data not used in analyses (see Materials and Methods).

STATISTICAL ANALYSES

Fish community

Fish species abundance data were subjected to a range of multivariate analyses to determine the extent and cause of any significant differences in composition among study periods from 1978 to 2009 in the shallows and 1993 to 2009 in the deeper waters. Other relevant factors such as estuary zone and season were included to account for any confounding influences on period, but any significant trends in these other factors were not explored. All analyses were carried out using the PRIMER 7 multivariate statistics package (Clarke & Gorley, 2015) with the PERMANOV A+ add-on module (Anderson et al., 2008).

The nearshore and offshore fish data sets were each initially dispersion-weighted to down-weight those species with large variability among replicates (Clarke et al., 2006), then square-root transformed to balance contributions of abundant and less abundant species (Clarke et al., 2014a). These pre-treated data were then used to construct Bray-Curtis similarity matrices.

Both fish data sets and particularly that for the nearshore waters had considerable imbalance among studies in the number of sites per zone and, in some cases, particular zones were not sampled (Tables I and II). The effect of the first of these issues on the following PERMANOVA
[permutational ANOVA and MANOVA; Anderson (2001)] tests was small, as demonstrated by comparing results obtained using a type III sums of squares (recommended for unbalanced designs) with those obtained using a type I sums of squares with different orderings of model terms (Anderson et al., 2008). This issue was further minimized in the offshore analyses by excluding data from the three additional USE sites sampled only in 2003–2009 from analyses of the 1993–2009 data, then undertaking a separate analysis for all USE sites sampled from 2003 to 2009. The second of the above issues was ameliorated for the nearshore waters by analysing data from the LSCE zone separately from that for the CE, MSE and USE given it was only sampled in four of the six periods (Table I) and for the offshore waters by analysing data for the MSE and USE separately.

The nearshore Bray-Curtis matrix, with only samples from the CE, MSE and USE selected, was initially subjected to a preliminary four-factor PERMANOVA analysis using period, year, zone and season as factors to determine if years within a period were best pooled or treated as a separate factor in the test design. All factors were fixed and crossed with each other, except year which was random and nested in period, henceforth year (period). This four-factor design is conventionally denoted as zone × season × year (period). Given the significant year (period) differences (P < 0.001), this factor was retained in the model. To both minimize unwanted variability among sites within zones and ensure years (rather than sites) provided the replicates of periods, the pre-treated fish data were then averaged for each combination of year, zone and season and used to construct another Bray-Curtis matrix, which was then subjected to the same PERMANOVA test as above, but using the highest-level interaction as the residual. The same approach was adopted for the LSCE samples, except excluding zone from the model. In these and all other PERMANOVA tests, the null hypothesis of no significant group differences was rejected if P < 0.05 and the components of variation (COV) values were used to ascertain the relative importance of each significant term.

The offshore Bray-Curtis matrix, with either MSE or USE samples selected, was firstly subjected to a preliminary four-factor PERMANOVA analysis using period, year, zone and season as factors to determine if years within a period were best pooled or treated as a separate factor in the test design. All factors were fixed and crossed with each other, except year which was random and nested in period, henceforth year (period). Period and season were fixed and year (period) and site were treated as random. Site was included in this design because the same set of locations was sampled in each period. Given that year (period) effects were either insignificant or very small, years within periods were pooled and the data subjected to a three-factor crossed period × season × site PERMANOVA.

When PERMANOVA detected significant period differences, either as a main effect or interaction, appropriate sub-sets of the relevant Bray-Curtis matrix were then subjected to a one-way or two-way crossed analysis of similarities test (ANOSIM; Clarke & Green, 1988) to more fully examine inter-period differences. The particular sub-matrices and factors for each of these tests are given in the Results. The criterion for rejecting the null hypothesis was the same as above and the extent of any significant differences was determined by the R-statistic (Clarke & Green, 1988).

To illustrate any significant inter-period trends, distances among the centroids of groups of replicate samples in each period were calculated (within each level of any other influential factor) and the resultant matrix subjected to either non-metric or metric multidimensional scaling ordination (nMDS and mMDS, respectively). The latter was used when the 2-d stress level was <0-2, which is relatively low for mMDS (Clarke et al., 2014b). The species mainly responsible for any such trends were ascertained by subjecting the pre-treated abundance matrices (averaged for period within any other important factor) to a shade plot analysis (Clarke et al., 2014a). This produced a visual display of species (y-axis) against samples (x-axis) where the intensity of grey-scale shading was linearly proportional to fish abundance (dispersion-weighted and square-root transformed counts). Only those species contributing ≥5% of the total abundance in at least one averaged sample were included. Species were displayed according to a group-average hierarchical agglomerative cluster analysis of a resemblance matrix defined between species as Whittaker’s index of association (Legendre & Legendre, 1998). A similarity profiles test [SIMPROF type 3; Somerfield & Clarke (2013)] was also applied to determine those points in the clustering procedure at which no significant (P > 0.05) structure could be detected, thus identifying species with similar abundance patterns. The species dendrogram was then rotated to optimize conformity to a serial pattern of species similarities (Clarke et al., 2014b), with these rotations preserving the entire clustering structure.
Fish community and water–quality relationships

To test whether any longer-term patterns in the fish community were significantly correlated with those in any combination of water-quality variables (and if so, which was the best sub-set), both the distance-based linear modelling routine [DISTLM; McArdle & Anderson (2001)] and the biota and environment matching routine [BIOENV; Clarke & Ainsworth (1993)] were used, given their differing advantages and perspectives (Anderson et al., 2008). In all of these analyses, Bray-Curtis matrices constructed from the pre-treated fish data were used as the response matrix, while the water-quality data comprised the predictor matrix. Surface-water measurements were correlated with the nearshore fish data, while both surface and bottom-water measurements were correlated with the offshore fish data.

Prior to analysis, the water-quality data were subjected to Draftsman plots to guide appropriate transformation choices for minimizing any notable skew, demonstrating that surface chlorophyll a and dissolved oxygen concentrations required ln and square-root transformations, respectively. All water-quality data were then normalized to place variables on the same (dimensionless) scale and averaged appropriately to achieve complementarity with the fish data. Note that, rather than correlating period averages between the fish and water-quality data, yearly averages were instead used to maximize the number of samples relative to predictor variables. This is particularly pertinent for DISTLM (Anderson et al., 2008), which could not be used reliably in some cases given insufficient sample to variable ratios. Moreover, as the number of samples was still relatively low for the offshore data sets, an alternative DISTLM approach was employed to bolster numbers, whereby samples from all years and seasons were employed, but with any seasonal effects removed by forcing inclusion of four naïve season variables, i.e. a summer variable where all summer samples were coded as 1 and the remainder coded as 0 and repeating this for autumn, winter and spring. This approach fitted and removed any seasonal variation, leaving any remaining interannual variability on which to regress the true predictor (water-quality) variables.

For the nearshore waters, interannual relationships between the fish and water-quality data were tested not only for the corresponding years in which they were collected, but also after a 1 year lag was introduced into the latter to explore any delayed environmental effects. These lag analyses were not undertaken for the offshore data due to a lack of samples, particularly as they often led to the loss of a year due to mismatches between the fish and water sampling regimes.

For all DISTLM tests, a step-wise selection procedure was employed and a modified version of the Akaike (1973) information criterion (AICc) used as the selection criterion. The proportion of fish faunal variability explained by the best water-quality model was reflected by the $R^2$ value. For BIOENV, the Spearman rank correlation coefficient ($\rho$) was used as the matching coefficient and Euclidean distance was used to define sample resemblances for the water-quality data. For both tests, the null hypothesis of no significant interannual relationships was rejected if $P < 0.05$. When DISTLM detected significant results, a distance-based redundancy analysis (DBRDA) was used to illustrate the modelled relationships between the fish and selected water-quality data. Significant matches detected by BIOENV were illustrated by subjecting the relevant Bray-Curtis matrices derived from the fish data to nMDS ordination, then overlaying the selected water-quality data as circles of proportionate sizes (i.e. bubble plots).

Acanthopagrus butcheri

To provide measures of A. butcheri production at the population level, mean abundance (and 95% c.i.) and total biomass of all fish caught in the nearshore waters (fish 116 m$^{-2}$ and kg 116 m$^{-2}$, respectively) and offshore waters (fish h$^{-1}$ and kg h$^{-1}$, respectively) were calculated for each sampling year. The abundance data were subjected to ANOVA to determine if there were any significant ($P < 0.05$) annual differences, with year treated as a fixed factor. Prior to undertaking these tests, the data were ln($x + 1$) transformed to approximate test assumptions of normality and homogeneous dispersions among groups. If ANOVA detected any significant differences, Scheffe’s test was used to identify their main sources.

To provide a measure of A. butcheri production at the individual or per-capita level, mean body mass (and 95% c.i.) of individual fish (kg) was calculated separately for females and males in the 2+, 3+ and 4+ age classes in each year. This measure was used rather than growth or body condition (mass-length relationship), as it integrates both of the latter measures and is thus considered to better reflect fish physiological response to environmental conditions.
RESULTS

INTER-PERIOD TRENDS IN THE NEARSHORE FISH COMMUNITY AND RELATIONSHIPS WITH WATER QUALITY

The mean density of each fish species caught in the shallows of the Swan–Canning Estuary in each sampling period from 1978 to 2009, following practicable data standardization, is provided in Table S1, Supporting Information. Note however, that direct comparability among some studies remains hindered by the fact that not all workers sampled all estuary zones (see Table I). The most conspicuous difference was the marked drop in abundance of the semi-anadromous Perth herring *Nematalosa vlam- inghi* (Munro 1956) from the late 1970s (c. 500 fish 116 m\(^{-2}\), comprising c. 47% of the catch) to 1995–1997 (55 fish 116 m\(^{-2}\)) then all subsequent periods (<20 fish 116 m\(^{-2}\), <3.7% of the catch). This was particularly marked in each of the three sampling periods from 1999 to 2006, the last two of which comprised the same zones as in 1978–1981 (Table I). Other species that declined notably from the earliest to all later periods included the marine species western striped grunter *Helotes octolineatus* Jenyns 1840, southern longfin goby *Favonigobius lateralis* (Macleay 1881), sea mullet *Mugil cephalus* (L. 1758) and yelloweye mullet *Aldrichetta forsteri* (Valenciennes 1836). In contrast, the opposite was generally true for species such as the estuarine and freshwater western hardyhead *Leptatherina pallacei* (Prince, Ivantsoff & Potter 1982) and the estuarine spotted hardyhead *Craterocephalus mugiloides* (McCulloch 1912) and *A. butcheri* (Table S1).

The high abundance of several other species in particular periods may have more strongly reflected the particular zones sampled and the schooling behaviour of those species, rather than notable inter-period trends. For example, silver fish *Leptatherina presbyteroides* (Richardson 1843), a highly schooling atherinid with marine affinities, ranked in the top five in all periods except 1995–1997 and 1999–2001 when the LSCE was not sampled. Similarly, the far higher abundances of the bluespot goby *Pseudogobius olorum* (Sauvage 1880) and southwestern goby *Afurcagobius suppositus* (Sauvage 1880) in 1999–2001 than all other periods probably reflects, at least in part, the sampling focus in the MSE–USE where these estuarine and freshwater species typically occur (Table S1).

The overall mean density of fish was considerably higher in 1978–1981, 1995–1997 and 2003–2004 (c. 1060–1500 fish 116 m\(^{-2}\)) than in 1999–2001, 2005–2006 and to a lesser extent 2007–2009 (c.260–540 fish 116 m\(^{-2}\)), the last two periods of which comprised the same sampling zones as in 1978–1981 and 2003–2004. The comparatively high densities in 1995–1997 and 2003–2004 were driven mainly by large catches of the schooling Australian anchovy *Engraulis australis* (Shaw 1790) and *C. mugiloides*, respectively. The mean number of species ranged from 7.5 to 7.9 in the two earliest periods and 5.0 to 6.8 in all other periods (Table S1).

PERMANOVA showed that the species composition of the shallow-water fish assemblages in the CE, MSE and USE zones and also the LSCE zone (Table III) differed significantly among periods (*P* < 0.01) and, in the former test, also among the period × zone interaction (*P* < 0.001). In both cases, the period main effect was notably more influential than any other term and the latter period × zone effect was the most important interaction (see COV values in Table III). Further exploration of inter-period differences using ANOSIM was thus undertaken separately for each zone, but pooled over seasons. One-way ANOSIM found significant overall period
Table III. Mean squares (MS), pseudo $F$-ratios, significance levels ($P$) and components of variation values (COV) for a four-factor zone $\times$ season $\times$ year (period) PERMANOVA on the nearshore fish species composition recorded in each period from 1978 to 2009 in the Canning Estuary (CE), middle Swan Estuary (MSE) and upper Swan Estuary (USE) zones, and for a three-factor season $\times$ year (period) PERMANOVA over the same time frame in the lower Swan–Canning Estuary (LSCE) zone. Significant effects involving period are in bold text.

<table>
<thead>
<tr>
<th>Four-factor PERMANOVA</th>
<th>Three-factor PERMANOVA</th>
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<tr>
<td></td>
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Differences in each zone ($P < 0.001$) except the USE ($P > 0.05$), with the extent of those significant differences being moderately high and ranging from global $R = 0.660$ in the LSCE to 0.546 in the MSE (Table IV). The greatest or close to the greatest differences occurred between 1978–1981 and one or more later periods (pair-wise $R$ often > 0.75), particularly in the CE and LSCE. Similarly high differences occurred between 2003–2004 and periods from 2005 to 2009 in the LSCE and 1995–1997 v. 2005–2006 in the CE. Moderate differences ($R > 0.4$) were also found between most remaining periods in the MSE and CE, except those within the 2003–2009 timeframe, which were often insignificant. The smallest differences also occurred between the two most recent periods in the LSCE (Table IV).

The nMDS ordination of the sample centroids in each period and zone clearly illustrated the relatively large inter-period differences in fish composition in the LSCE, CE and MSE (longer trajectories) and the far smaller differences in the USE (short trajectories; Fig. 2). In all zones, the longest trajectories occurred between 1978–1981 and the following period, with smaller but often still reasonable differences between several periods in the 1995–2009 timeframe.

A shade plot of the pre-treated species abundances revealed that, in all zones, one of the main drivers of the pronounced differences between the earliest and all later periods was a marked drop in *N. vlamighi* and *M. cephalus*. This was also true, to a slightly lesser extent, of *A. forsteri* and tailor Pomatomus saltatrix (L. 1766) (Fig. 3). In contrast, *A. butcheri* consistently increased in abundance over time, particularly in the middle–upper estuary, as did the marine estuarine-opportunist weeping toadfish Torquigener pleurogramma (Regan 1903) in the lower–middle reaches. The estuarine and marine bridled goby Arenigobius bifrenatus (Kner 1865) and estuarine and freshwater *P. olorum* both generally declined from earlier to later periods in the LSCE, CE
and MSE, as did another estuarine and freshwater gobiid *A. suppositus* in the CE and MSE. These last two species conversely tended to increase in abundance over time in the USE. Several other species also showed notable inter-period trends in specific zones, e.g. the prominent declines in *H. octolineatus*, western gobbeguts *Ostorhinchus rueppelli* (Günther 1859) and *F. lateralis*, along with increases in yellowsotted sandgoby *Favonigobius punctatus* (Gill & Miller 1990), spotted pipefish *Stigmatopora argus* (Richardson 1840) and soldier *Gymnapistes marmoratus* (Cuvier 1829) over time in the LSCE. Other species, such as several belonging to the Atherinidae, exhibited less consistent temporal change, e.g. *L. wallacei*, elongate hardyhead *Atherinosoma elongata* (Klunzinger 1879) and *C. mugiloides* in the CE and MSE (Fig. 3).

Interannual trends in the nearshore fish fauna in each zone were occasionally significantly correlated with those in sub-sets of the water-quality variables, but the extent of those relationships was small to moderate. Thus, from 1978 to 2009, when only salinity and temperature data were consistently recorded, DISTLM did not detect any significant relationships between the fish and water-quality data, while BIOENV found a small to moderate match in the CE for water temperature (*P* < 0·01; *ρ* = 0·347). From 1995 to 2009, when data for a wider range of water-quality attributes were available, significant matches were found between the CE fish fauna and dissolved oxygen concentration by DISTLM (*P* < 0·05; *R*² = 0·477) and salinity, dissolved oxygen and temperature by BIOENV (*P* < 0·05; *ρ* = 0·711). Examination of the respective DBRDA and bubble plots, however, showed that these correlations were driven more by intrathan inter-period variation. Note that matches between the fish and water-quality data in the LSCE from 1995 to 2009 could not be explored owing to a lack of samples.

After a 1 year lag was introduced into the water-quality data, both DISTLM and BIOENV found a significant match between the fish fauna and temperature from 1978 to 2009 in the MSE ($P < 0.05$, $R^2 = 0.234$ and $P < 0.01$, $r = 0.465$, respectively) and DISTLM also found the same in the USE ($P < 0.05$, $R^2 = 0.305$). Again, however, the associated plots did not reveal clear inter-period trends. No significant relationships were found for the 1995–2009 data sets under the 1-year lag scenario, noting also that they could not be explored in the LSCE using either test, nor in the CE using DISTLM, owing to a lack of samples.

**INTER-PERIOD TRENDS IN THE OFFSHORE FISH COMMUNITY AND RELATIONSHIPS WITH WATER QUALITY**

Mean catch rates of each species caught in the deeper waters of the MSE–USE in each period from 1993 to 2009 are given in Table S2. Note, however, that comparability between 1995–1997 and the remaining periods is hindered by the fact that only the MSE was sampled in the former (Table II).

One of the most prominent inter-period shifts in the deeper waters was the declining mean catch rate of *A. butcheri*, which fell from 2.3 fish h$^{-1}$ in the early to later 1990s (14–22% of the catch) to 0.3 fish h$^{-1}$ in the late 2000s (3.5% of the catch; Table S2). In contrast, catches of another estuarine species, yellowtail grunter *Ammiataba caudavittata* (Richardson 1845), increased progressively from 1993–1994 to 2003–2004 (1.6–4.1 fish h$^{-1}$), then declined in 2007–2009. *Nematalosa vlaminghi* was the most abundant species in all periods, comprising 46–60% of the overall catch, with mean catch rates peaking in 1995–1997. Although not abundant, catches of several other species declined from earlier periods to 2007–2009, e.g. yellowtail flathead *Platycephalus westraliae* (Whitley 1938), mulloway *Argyrosomus japonicus* (Temminck &
Schlegel 1843) and estuary cobbler *Cnidoglanis macrocephalus* (Valenciennes 1840). The overall mean number of species and catch rate in 2007–2009 was also the lowest of any period, *i.e.* 2.5 v. 3.2–3.5 species and 9.8 v. 10.2–16.1 fish h⁻¹, respectively (Table S2).

Species composition of the offshore fish fauna differed significantly among periods in both the MSE and USE (*P* < 0.01; Table V). A significant period × season effect was also found in the latter zone (*P* < 0.01), with this interaction verging on significance in the former zone (*P* > 0.05). Unlike in the shallows, however, the relative importance of period or the above interaction was less than that of season, particularly in the USE (compare COV values in Tables III and V). Given the above, period × season ANOSIM tests were then used to further examine period differences in each zone. The period component of these tests showed that while such differences were significant overall (*P* < 0.01), their extent was small (Global *R* = 0.164–0.178) and several consecutive periods were not significantly different (*i.e.* 1993–1994 v. 1995–1997 and 1995–1997 v. 2003–2004 in the MSE and 1993–1994 v. 2003–2004 in the USE). The greatest significant pair-wise differences were between 1995–1997 and 2007–2009 in the MSE (*P* < 0.001, *R* = 0.282) and 1993–1994 and 2007–2009 in the USE (*P* < 0.001, *R* = 0.269). A further period × season ANOSIM test on the full suite of USE sites sampled only in 2003–2004 and 2007–2009 also revealed significant, but small inter-period differences (*P* < 0.01, *R* = 0.206).

Inter-period trends in the offshore fish composition in each season are illustrated for the MSE and USE in the mMDS ordination plots of sample centroids in Fig. 4(a).
Table V. Mean squares (MS), pseudo F-ratios, significance levels (P) and components of variation values (COV) for a three-factor period × season × site PERMANOVA on the offshore fish species composition recorded in each period from 1993 to 2009 in the middle Swan Estuary (MSE) and upper Swan Estuary (USE). Significant effects involving period are in bold text.

<table>
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</tr>
<tr>
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<td>1003.9</td>
</tr>
<tr>
<td>P × S × Si × Si</td>
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<td>957.33</td>
</tr>
<tr>
<td>Residual</td>
<td>40</td>
<td>919.42</td>
</tr>
</tbody>
</table>

and (b), respectively. In the MSE, the greatest or near greatest differences occurred between one of the two earliest periods and 2007–2009 in all seasons except autumn, when differences between 2003–2004 and 2007–2009 were clearly largest [Fig. 4(a)]. In the USE, similar differences occurred between all periods in summer, the earliest and latest periods were most distinct in winter and spring, while 2003–2004 v. 2007–2009 showed the greatest differences in autumn [Fig. 4(b)].

A shade plot of the pre-treated catches of the most prevalent species in each period, zone and season revealed that, in the MSE, the above inter-period shifts were mainly driven in at least three seasons by declines of *A. butcheri*, *M. cephalus* and *P. westraliae* (Fig. 5). In autumn and spring, the major temporal shifts were further influenced by falling catches of *A. caudavittata*, as well as those of *N. vlaminghi*, *H. octolineatus* and common silverbiddy *Gerres subfasciatus* Cuvier 1830 in the former season, and increased catches of *E. australis* in the latter. Declining catches of *A. japonicus* and *C. macrocephalus* further contributed to the main inter-period shifts in summer. In the USE, the above inter-period trends were likewise driven mainly by declines in *A. butcheri* in autumn, winter and spring and also by declines in *M. cephalus* and *A. caudavittata* in winter and increases in the latter species and *N. vlaminghi* in spring. Conversely, the sequential temporal shifts in summer mainly reflected peaks in abundance of several species in 2003–2004 compared with earlier and especially later periods, e.g. *A. butcheri*, *N. vlaminghi* and *A. caudavittata* (Fig. 5). A further shade plot of data from all USE sites sampled only from 2003 to 2009 generally revealed falling catches of *A. butcheri*, *M. cephalus* and *N. vlaminghi* over time.

No significant interannual relationships were found by either DISTLM or BIOENV between the offshore fish fauna and any combination of the available water quality variables in either zone.

**INTER-PERIOD TRENDS IN A. BUTCHERI PRODUCTION AT THE POPULATION AND INDIVIDUAL LEVELS**

The mean density of *A. butcheri* in the shallows differed significantly among years (*P < 0.001*), with values in 1993–1995 (0.8–1.1 fish 116 m$^{-2}$) being significantly...
Fig. 4. Centroid metric multidimensional scaling (mMDS) ordination plots produced from Bray-Curtis similarities of the offshore fish assemblages in each period and season in the (a) middle Swan Estuary and (b) upper Swan Estuary. , summer; , autumn; , winter; , spring; , 1993–1994; , 1995–1997; , 2003–2004; , 2007–2009.

lower \( (P < 0.001) \) than those in all years from 2003 to 2009 \( [5.3–9.8 \text{ fish m}^{-2}] \); Fig. 6(a)]. Catches of \textit{A. butcheri} in the deeper waters also differed significantly among years \( (P < 0.01) \), but in contrast to the nearshore waters, were significantly greater in 1993–1994 and 2003–2004 \( (2.3–2.6 \text{ fish h}^{-1}) \) than in 2007–2008 \( (0.3 \text{ fish h}^{-1}; P < 0.05; \) Fig. 6(b)]. Catches in 2008–2009 were also low \( (0.6 \text{ fish h}^{-1}) \), although not significantly different from those in previous years \( (P > 0.05) \). The trends in total
Biomass of *A. butcheri* followed those of abundance, with values in the shallows increasing from c. 0.10 to 0.66 kg m\(^{-2}\) from 1993–1994 to 2008–2009, while those in the deeper waters declined from a peak of 2.30 kg h\(^{-1}\) in 1994–1995 to <0.04 kg h\(^{-1}\) in 2007–2009 (Fig. 6).

At the individual level, the mean body mass of both female and male *A. butcheri* in any given age class declined markedly and progressively from earlier to later years (Fig. 7). For example, the average mass of 2+ year old females fell from a maximum of 263 g in 1993–1994 to a minimum of 44 g in 2007–2008, while the mass of 4+ year old females fell from 701 to 141 g over the same period.

**DISCUSSION**

**INTER-PERIOD TRENDS IN THE FISH COMMUNITY**

Fish community composition in the shallows of the lower to middle estuary (LSCE, CE and MSE) differed markedly among sampling periods from 1978 to 2009. While the most pronounced shifts were typically between the earliest and subsequent periods, moderate differences also occurred between most other periods from 1995 to 2009, except the most recent ones. In contrast, no significant inter-period changes were found in the nearshore fish fauna of the USE. Moreover, while significant ichthyofaunal shifts were detected in the deeper waters of this zone and the MSE from 1993 to 2009, their extent was small.
Fig. 6. (a) Total biomass (histogram bars) and mean density ± 95% c.l. (lines) of Acanthopagrus butcheri in the shallows and (b) total biomass and mean catch rate ± 95% c.l. of A. butcheri in the deeper waters of the middle to upper Swan Estuary in each sampling year from 1993 to 2009.

The above significant temporal changes in the fish community were not, however, statistically well matched with those in the available suite of water-quality variables, some potential reasons for which are explored in the following sub-section. Yet, when mean annual values of these environmental attributes are examined over the full study period (Fig. 8), as opposed to only the intermittent years able to be matched statistically, clear trends in both salinity and dissolved oxygen levels become apparent, reflecting a progressive marinization of the whole estuary and increasing hypoxia in the MSE and USE (Fig. 8). Such trends are undoubtedly related to the major reductions in rainfall (16%) and stream discharge (50%) across south-western Australia since the 1970s (Silberstein et al., 2012), resulting in reduced flushing, greater penetration of the salt-wedge upstream and more persistent stratification of the water column (Kurup & Hamilton, 2002; Hipsey et al., 2014). In addition to these climate change effects, the declines in dissolved oxygen levels may further reflect the effects of increased nutrient
and organic matter loading from substantial population growth (Australian Bureau of Statistics; www.abs.gov.au) and thus catchment development since the 1970s.

In view of the clear marinization of the estuary, it is relevant that several of the fish species that showed notable abundance shifts from earlier to later periods have affinities with fresh or marine conditions, either during particular life-cycle phases or throughout life. These include *M. cephalus*, which showed a conspicuous decline in both the shallow and deeper waters and whose juveniles reportedly have a preference for fresh or
Fig. 8. Mean annual (a) salinity in the surface waters of each estuary zone in 1978–1981 and 1995–2009 and (b) salinity and (c) dissolved oxygen concentration in the bottom waters of the MSE and USE in 1993–2009. Trend with time is indicated by straight lines (---). LSCE, lower Swan–Canning Estuary; CE, Canning Estuary; MSE, middle Swan Estuary; USE, upper Swan Estuary.
oligohaline conditions (Thomson, 1955; Chubb et al., 1981; Nordlie et al., 1982; Cardona, 2000; Whitfield et al., 2012). Chubb et al. (1981) also suggested that M. cephalus recruits, which migrate from the sea to the upper estuary in the austral winter-spring, use estuarine stimuli as a cue to enter these systems and it thus follows that the major reductions in stream flows have weakened that signal. Other species with freshwater affinities, including the estuarine and freshwater gobies P. olorum and A. suppositus (Gill & Potter, 1993), declined in the shallows of the lower-middle estuary, but increased in the upper estuary, possibly reflecting their contraction into those fresher reaches. Some marine species in the nearshore waters either increased in abundance and penetrated further upstream over time, such as the marine estuarine-opportunist T. pleurogramma, or became more prevalent just in the lower reaches, e.g. the marine stragglers S. argus and G. marmoratus. Others with marine affinities, however, declined over time in the shallows of the lower estuary (e.g. H. octolineatus, O. rueppellii and F. lateralis), which may alternatively reflect detrimental changes in other habitat attributes or, for the first of these species which spends part of its life in marine waters, effects in that environment.

The most marked inter-period shift in the fish community, however, was the decline of N. vlaminghi in the shallows, with mean densities falling from c. 500 fish 116 m$^{-2}$ in 1978–1981 to c. 55 fish 116 m$^{-2}$ in 1995–1997 then c. <1 to 20 fish 116 m$^{-2}$ in all later periods, representing a drop from c. 47 to <4% of the total catch. This endemic, semi-anadromous species migrates from coastal waters to the upper estuary in late spring–summer to spawn (Chubb & Potter, 1984), producing pelagic eggs in demersal waters (Malanczak, 2015). Egg and larval abundance has been shown by the latter worker to be negatively linked with water-column stratification in the middle–upper estuary and the distribution of these early life stages has shifted from c. 31–40 km from the estuary mouth in the 1980s (Neira et al., 1992) to c. 38–46 km in 2013 (Malanczak, 2015). Given reduced river flows since the 1970s and thus greater stratification and bottom water hypoxia in the middle–upper estuary (Kurup & Hamilton, 2002; Hipsey et al., 2014; Fig. 8), the declines in N. vlaminghi could feasibly reflect poorer environmental conditions for its early life stages, particularly as its spawning time and location coincide with the most severe of the above perturbations, as well as algal blooms (Hallett et al., 2016a). Such conditions could also affect the upstream migration of N. vlaminghi, as shown for other anadromous species (Maes et al., 2007), and its relatively slow growth (Chubb & Potter, 1986) and reliance of the stock on self-replenishment (Smith, 2006) may compound these influences.

The increasing abundance of A. butcheri over time in the shallows of the middle to upper estuary, but decreasing prevalence in the adjacent offshore waters, probably reflects its onshore movement away from deeper habitats. This apparent habitat compression in the nearshore waters is likely to be related to the increasing bottom water hypoxia in the deeper areas, as also proposed by Cottingham et al. (2014). Further sub-lethal effects on the growth, condition and maturity of this species have been examined by the latter authors, while the effects on its production are discussed below. Declines in P. westraliae in the deeper waters of the MSE since the early 1990s may also reflect the direct or indirect effects of a less hospitable benthic environment, particularly as this species lives on the substratum (Coulson et al., 2015).

It must be recognized that, as well as the above potential explanations for the temporal shifts in the fish community, other confounding factors could be implicated. These
include the different sampling approaches between periods, particularly in the shallows where sampling locations and net type sometimes differed considerably. While both were harmonized as far as practicable, some legacy effects invariably remain. For example, it was not possible to overcome biases due to not all zones being sampled in all periods. Additionally, despite the sophistication of the generalized linear modelling technique used to standardize all seine catches to those in a common net type (Hallett & Hall, 2012), it is impossible to model the abundance of a species not caught in a sample or determine if its absence was genuine or due to gear bias. Several of the larger species which declined notably in the shallows after 1978–1981 (e.g. *N. vlaminghi* and *M. cephalus*), which was the only period in which the largest (133 m) seine was used, are probably more prone to capture in this net than the smaller (21.5–41.5 m) seines used in all other studies, given its ability to sample further from shore. Yet, comparison of the nearshore mean densities of *N. vlaminghi* between 1995–1997, 2003–2004 and 2007–2009 in the MSE, when the same net was used (41.5 m seine) and similar sites were sampled (Table I), still shows an appreciable decline from earlier to later periods (c. 89, 3 and 31 fish 116 m$^{-2}$, respectively). Moreover, the annual commercial catch-per-unit-effort (CPUE) of this species in the estuary, which was targeted heavily since at least the 1960s, peaked in 1967–1968 before falling steadily after the mid-1970s (Smith, 2006). While reduced market demand may have affected more recent trends, Chubb & Potter (1984) also reported declines in CPUE from 1977 to 1983 and attributed them to large commercial catches. In the case of *M. cephalus*, the concurrent declines in the shallow and deeper waters, the latter of which were sampled relatively consistently over time, suggest a more pervading ecological trend rather than simply a sampling artefact. Moreover, as some of the above species spend part of their life at sea or in rivers and are targeted by fishers, other such environmental or human-use effects on the observed inter-period trends cannot be discounted.

Finally, the small or insignificant longer-term changes in the fish faunas of the upper estuary and deeper waters of the middle estuary may seem anomalous, given these areas typically experience the most severe perturbations such as hypoxia and phytoplankton blooms. Yet, they probably partly reflect the ‘estuarine quality paradox’ (Elliott & Quintino, 2007), which recognizes that since estuarine fishes are adapted to naturally variable and thus stressful environments, assemblage structure will resemble that in anthropogenically stressed areas. Natural stressors are far higher in the upper than lower Swan–Canning Estuary, as reflected, for example, by the seasonal ranges in mean surface salinity, *i.e.* 5–20 v. 25–36, respectively (based on data from the lower- and upper-most DoW monitoring sites in 2007–2009; Fig. 1). The suite of typifying species in the USE was far more restricted than in the LSCE (Fig. 3) and dominated by robust taxa that are, for example, highly euryhaline [e.g. *A. butcheri* and *L. wallacei*; (Hoeksema et al., 2006; Rashnavadi et al., 2014)] or have adaptations such as aquatic surface respiration [e.g. *P. orlorum*; (Gee & Gee, 1991)]. It is thus unsurprising that these communities have been relatively unresponsive to inter-period changes, a feature of this level of biological organization that is discussed further below. Moreover, for the offshore fish fauna, the shorter time frame over which temporal changes could be examined is likely to have contributed to the smaller effects observed than in the shallows.
STATISTICAL RELATIONSHIPS BETWEEN INTER-PERIOD TRENDS IN THE FISH FAUNA AND WATER QUALITY

Despite the feasible correspondence between inter-period shifts in several species comprising the fish community and continuous annual trends in salinity and dissolved oxygen described above, few significant and clear statistical relationships were found for any combination of the available water-quality variables. This was the case both when complementary sampling years were matched between the fish and water-quality data and when a 1 year lag was introduced into the latter to explore any delayed environmental effects.

While such findings might genuinely indicate a lack of or an unmatched response by the fish fauna to these water-quality variables, it should be recognized that the potential to detect any correlation was compromised for several reasons. The first of these related to the discontinuous and irregular nature of both the fish and water-quality data over the timeframe of interest. This resulted in the ability to explore relationships only for patches of complementary years and for two of the four water-quality variables (salinity and temperature) over all years in which fishes were collected, given the others were not recorded prior to 1994. Secondly, a lack of statistical power was an issue in some cases, particularly for the offshore data set which had relatively few sampling years, as well as for analyses involving DISTLM which require substantially more samples than predictor variables to yield reliable results (Anderson et al., 2008). Finally, the high replicate-to-replicate variability in some fish species abundances and water-quality variables such as chlorophyll $a$ concentration may have further compromised detection of any relationships, even though this variability was ameliorated through several data pre-treatment approaches.

INTER-PERIOD TRENDS IN A. BUTCHERI PRODUCTION AT THE POPULATION AND INDIVIDUAL LEVELS

Measures of fish production often integrate growth, body condition, relative abundance and age structure and are thus regarded as comprehensive biotic indicators of ecosystem condition, particularly at the individual level of biological organization (Randall & Minns, 2000; Searcy et al., 2007). In estuaries, this is especially true of species confined to their natal system throughout life, which not only circumvents any confounding effects of the adjacent marine or freshwater environments (Potter et al., 1986; Thiel & Potter, 2001; Able & Fahay, 2010), but reduces sources of error arising from large seasonal variation in fish abundance when estimating production (Cowley & Whitfield, 2002; Pombo et al., 2007; Dolbeth et al., 2008). Acanthopagrus butcheri has many attributes that make it highly suitable as a single species indicator of estuarine condition, including not only that it is an estuarine resident, but also that it is long-lived (c. 30 years; Morison et al., 1998; Potter et al., 2008), is often abundant, shows high physiological (as opposed to genetic) plasticity in response to environmental conditions (Partridge et al., 2004; Cottingham et al., 2014; 2016), is targeted by fishers and so is socio-economically important and a detailed historical database on its biology exists over a wide area (Sarre & Potter, 2000; Nicholson et al., 2008; Williams et al., 2012; Cottingham et al., 2015; Doubleday et al., 2015).

The trends in A. butcheri production at the population level from 1993 to 2009 in the MSE and USE, namely notable increases in abundance and biomass in the shallows and corresponding declines in the deeper waters, suggest an onshore movement of fish over
time. As identified earlier, these trends probably reflect the seeking of shallow-water refugia due to reduced habitat quality in the deeper bottom waters, as indicated, for example, by the declines in dissolved oxygen over the same time frame (Fig. 8; Cottingham et al., 2014). Such findings are consistent with those for fish in other microtidal estuaries following the development of hypoxia in deeper waters (Howell & Simpson, 1994; Thiel et al., 1995; Eby & Crowder, 2002; Tuckey & Fabrizio, 2016). Moreover, the smooth declining trends in A. butcheri production at the individual level over time (and so consistently for each of the 2+, 3+ and 4+ year classes), provide further evidence of negative effects on this species and suggest a more sustained habitat degradation [i.e. a press perturbation (Underwood, 1989)] rather than a discrete event (or pulse perturbation) such as an algal bloom.

As well as the direct negative effects of hypoxia on fishes at both the population and individual levels, including mortality through suffocation and sub-lethal effects such as compromised growth and protracted time to reach maturity (Pichavant et al., 2001; Wu, 2002; Hassell et al., 2008), it can also have negative effects via indirect pathways. These include density-dependent effects on growth in over-populated refuge areas (Breitburg, 2002; Eby & Crowder, 2002; Campbell & Rice, 2014; Cottingham et al., 2014) and reduced dietary quality through declines in key prey such as benthic macroinvertebrates (Pihl et al., 1992; Powers et al., 2005). The latter fauna are major prey for A. butcheri (Sarre et al., 2000) and are known to undergo mass mortality following persistent hypoxia in the Swan–Canning Estuary (Tweedley et al., 2016) and many other estuaries worldwide (Pihl et al., 1992; Peterson et al., 2000; Powers et al., 2005). Although A. butcheri is an opportunistic omnivore, it is relevant that the declines in per capita production observed in this study were accompanied by marked changes in diet. Thus, gut volume comprising benthic macroinvertebrates, a high-calorie food, declined from 64 to 19% between 1993–1995 and 2007, whereas that of low-calorie food, such as macrophytes and detritus, increased from 15 to 30% (Sarre et al., 2000; Linke, 2011).

FISH COMMUNITY V. SINGLE SPECIES INDICATORS OF ESTUARINE CONDITION

It is clear from the above findings that the fish community, population and individual levels of biological organization have shown significant inter-period shifts over the past two to three decades in the Swan–Canning Estuary, which are likely to reflect changes in the environmental condition of that system. The temporal patterns, sensitivity and perspectives of those levels, however, differed considerably.

The major advantage of examining change at the fish community level is the ability to capture signals from all species spanning different estuarine use, feeding and habitat guilds, thus providing a far more holistic representation than that achievable by a single species alone. This has allowed, for example, detection of multiple species responses to effects such as the marinization of the estuary in recent decades, which was not reflected at either the population or individual levels of A. butcheri, which is highly robust, euryhaline and largely confined to the middle–upper estuary. Conversely, the reliance of community-level assessments on species abundances across the whole assemblage can reduce the ability to detect clear responses due to factors such as high stochastic variability (particularly for schooling species), confounding influences of the adjacent marine and freshwater environments for non-resident species, as well as the relative
insensitivity (at this level) of highly resilient species. The latter point was probably implicated in the weak temporal shifts in the fish fauna of the upper estuary, the region with the most pronounced declines in water quality, yet which is typified by a restricted suite of highly tolerant resident species that are less inclined to reflect longer-term change at the coarser level of mean abundance. Resilient estuarine residents, however, and specifically those that are long-lived, larger and abundant like *A. butcheri*, do provide clear signals of sub-lethal, longer-term environmental stress through changes in their growth, body condition and length and age at maturity. Population-level indicators integrate information across the whole stock, while those at the individual level provide a finer assessment of how growth, in particular, is affected by environmental stressors. The latter was clearly shown in this study by the major declines in per capita body mass at age of *A. butcheri* since the 1990s, providing a real-time reflection of changes in the physiological costs of living within the estuary. It is worth noting, however, that while *A. butcheri* has various attributes that make it a reliable bio-indicator of estuarine condition, species with most of these features may be absent in many estuaries.

In conclusion, this study has demonstrated that fish community, population and individual levels of biological organization provide informative indicators of longer-term change in the Swan–Canning Estuary, but that their patterns, sensitivity and breadth differed. These outcomes provide support for a multifaceted approach to the biomonitoring of estuaries using fishes, including community-level assessments to encompass the diversity of species responses and single indicator species (particularly at the individual level) to understand sub-lethal, physiological changes that are not captured at the broader assemblage scale.

It is further recommended that assessments at each of the above organizational levels are extended to develop robust indices that encompass appropriate benchmarks or reference points. Many fish-based multimetric indices have been developed in recent decades (Harrison & Whitfield, 2004; Birk *et al.*, 2012; Hallett *et al.*, 2012; Pérez-Domínguez *et al.*, 2012), at the community level at least, which compare observed responses with pristine, least impacted or best available reference conditions (Stoddard *et al.*, 2006; Borja *et al.*, 2012) to quantify and track estuarine health.

The difficulties encountered in this study of attempting to standardize fish data sets collected using different methods also underscores the need for consistent monitoring regimes to avoid compromising detection of true biotic signals. This need has been widely recognized, including recently by Hallett *et al.* (2016c) and Testa *et al.* (2016), the latter of which identified it as the foremost challenge worldwide for the advancement of estuarine ecosystem science. These regimes must also be undertaken at the appropriate scale, both spatially to represent environmental heterogeneity and regularly (e.g. annually to biannually) to better characterize trajectories over time. Lastly, to better disentangle the drivers of any such biotic trends and thus establish the cause–effect pathways on which sound estuarine management depends, it is imperative that monitoring of relevant environmental and socio-economic stressors is undertaken at complementary scales to the fauna. Ideally, groups of similar stressors (e.g. water-quality and benthic habitat-quality metrics) should be integrated into environmental health indices, thereby providing an independent and reliable basis against which biotic signals can be interpreted (Hallett *et al.*, 2016c).

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Supporting Information

Supporting Information may be found in the online version of this paper:

**Table S1.** Mean density ($M$; fish 116 m$^{-2}$), standard error (s.e., superscript), percentage contribution to the overall catch (%) and rank by density ($R$) of each fish species recorded in the shallow nearshore waters of the Swan–Canning Estuary in each study period from 1978 to 2009. All data are untransformed, but have been standardized for net type and spatio-temporal sampling intensity (see Materials and Methods). Abundant species (those contributing > 5% to the catch) are highlighted in grey. The estuarine usage functional guild for each species (*sensu* Potter *et al.*, 2013) is also provided in superscript, *i.e.* MS, marine straggler; MEO, marine estuarine–opportunist; E, solely estuarine; EM, estuarine & marine; EF, estuarine & freshwater; SA, semi–anadromous; FS, freshwater straggler; FEO, freshwater estuarine–opportunist.

**Table S2.** Mean catch rate ($M$; fish h$^{-1}$), standard error (s.e., superscript), percentage contribution to the overall catch (%) and rank by density ($R$) of each fish species recorded in the deeper offshore waters of the Swan-Canning Estuary in each study period from 1993 to 2009. All data are untransformed and abundant species (those contributing > 5% to the catch) are highlighted in grey. The estuarine usage functional guild for each species (*sensu* Potter *et al.*, 2013) is also provided in superscript, *i.e.* MS, marine straggler; MEO, marine estuarine-opportunist; E, solely estuarine; EM, estuarine & marine; EF, estuarine & freshwater; SA, semi–anadromous; FS, freshwater straggler; FEO, freshwater estuarine-opportunist.

References


Electronic References


