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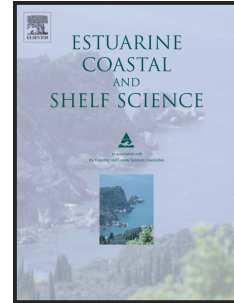
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**Comparisons between the characteristics of ichthyofaunas in
nearshore waters of five estuaries with varying degrees of
connectivity with the ocean**

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Abstract

The characteristics of the fish faunas in nearshore, shallow (< 1.2 m) waters of the basins of estuaries along the same coastline, but which were open to the ocean for varying periods, have been determined and compared. The fish faunas of the permanently-open Oyster Harbour, the seasonally-open Broke, Irwin and Wilson inlets and the normally-closed Wellstead Estuary on the south coast of Western Australia were sampled by seine net seasonally for two years. Irrespective of the frequency and duration that the estuary mouth was open, the ichthyofauna of each estuary was numerically dominated by three atherinid species and three gobiid species (92.9-99.7%), each of which completes its life cycle within these estuaries. The ichthyofaunal compositions of each estuary differed significantly, however, from that of each other estuary. These differences were largely attributable to the relative abundances of the above six species varying between estuaries, which, in turn, reflected differences in such factors as estuary mouth status, macrophyte cover and salinity. For example, *Favonigobius lateralis* and *Leptatherina presbyteroides*, which are also represented by marine populations, were most abundant in the permanently-open estuary (Oyster Harbour), which, in terms of substrate and salinity, most closely resembled the nearshore marine environment. In contrast, *Leptatherina wallacei* made its greatest contribution in the only estuary to exhibit a protracted period of greatly reduced salinities, which is consistent with its distribution in permanently-open estuaries on the lower west coast of Australia, while *Atherinosoma elongata* and *Pseudogobius olorum* were particularly numerous in estuaries containing dense stands of the seagrass *Ruppia megacarpa*. Marine species made the greatest contribution to species richness in the permanently-open estuary and least in the normally-closed estuary. Species richness was greatest in summer and least in winter in each estuary, but differed markedly between years only in Wilson Inlet. Density of fishes was greatest in the most eutrophic estuary (Wellstead Estuary) and least in the most oligotrophic estuary (Broke Inlet) and only underwent marked seasonal variations in Wilson Inlet and Wellstead Estuary, in which densities fell to their minima in winter. Ichthyofaunal composition varied between years in the Broke and Wilson inlets and Wellstead Estuary, in which there was little or no connection with the ocean in one of those years. Species composition underwent progressive seasonal changes throughout the year in Wellstead Estuary, due to the abundance of certain species peaking at different times of the year.

Keywords: microtidal estuaries; estuary mouth; ichthyofaunal composition, species richness and density; temporal variability; life-cycle guilds; Western Australia, south coast, 116.36-119.42 °E, 34.41-35.04 °S

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1. Introduction

The estuaries of south-western Australia were formed ca 7000 years ago by flooding during the Holocene marine transgression and, until about ca 3500 years ago, all had a free connection with the ocean and were tidally dominated (Hodgkin and Hesp, 1998). During more recent times, littoral drift and tidal action has led to sand accumulating at the narrow mouths that characterise these estuaries and, when that accumulation becomes sufficiently large, leads to the formation of a barrier between the estuary and the ocean (e.g. Lenanton and Hodgkin, 1985; Hodgkin and Hesp, 1998; Ranasinghe and Pattiaratchi, 2003).

Some estuaries in south-western Australia have retained a permanent free connection with the ocean, either through an insufficient amount of sand accumulating at their mouths or by artificial dredging, and are thus termed permanently-open estuaries (Lenanton and Hodgkin, 1985; Hodgkin and Hesp, 1998; Brearley, 2005). The majority of the estuaries in this region, however, are now closed to the ocean by a sand bar for variable periods. The bar at the mouth of some of these latter estuaries is typically breached for a period each year, either naturally or artificially, when the volume of water in the basin rises markedly during winter/early spring when rainfall and thus discharge increases substantially. Such systems are termed seasonally-open estuaries (e.g. Lenanton and Hodgkin, 1985; Hodgkin and Hesp, 1998). The mouths of other estuaries in south-western Australia can remain closed, however, for years at a time and their substantial bars are breached only following exceptional rainfall and thus also discharge and are consequently termed normally-closed estuaries (e.g. Lenanton and Hodgkin, 1985; Hodgkin, 1997; Hodgkin and Hesp, 1998).

There is thus a gradient in the duration and extent to which estuaries in south-western Australia are open to coastal marine waters, i.e. in their connectivity with the ocean. This situation parallels that found elsewhere along the coast of southern Australia (e.g. Hodgkin and Hesp, 1998; Roy et al., 2001; Ranasinghe and Pattiaratchi, 2003) and in southern Africa (Day, 1981; Whitfield, 1999). Furthermore, some estuaries in New Zealand (Hume et al., 2007) and on the west coast of North America (e.g. Kraus et al., 2008) also become barred from the ocean for periods. While the vast majority of biologists working in systems that correspond to those defined earlier as seasonally open and normally closed refer to them as estuaries, other workers elsewhere consider that the term estuary should be applied only to those

systems that have a permanent and free connection with the ocean (e.g. Pritchard, 1967) or to systems at those times when they have a free connection to the ocean (Perillo, 1995).

The estuaries in south-western Australia contain a large central basin region, the saline lower reaches of their tributaries and, when the estuary mouth is open to the ocean, a short and narrow entrance channel. The larger estuaries on the lower west coast are permanently open to the ocean, whereas those eastwards along the first 400 km of the south coast are mostly seasonally open and those along the next 800 km are normally closed (Lenanton and Hodgkin, 1985). During recent decades, some of these estuaries have become increasingly eutrophic and/or hypersaline as a result of anthropogenic activities, such as those associated with agriculture and urbanisation and the clearing of native vegetation (McComb and Lukatelich, 1995; Hodgkin and Hesp, 1998; Pen, 1999; Brearley, 2005; Young and Potter, 2002; Hoeksema et al., 2006).

Macrotidal estuaries in temperate regions of the northern hemisphere are dominated by marine species, the most abundant of which typically use estuaries as a nursery area, with diadromous species also being numerous at certain times during the year when they migrate through these systems (e.g. Kennish, 1990; Elliott and Dewailly, 1995; Potter et al., 1997a; Pihl et al., 2002; Able, 2005). Although estuaries along the microtidal coast of south-western Australia, and particularly those that remain permanently open, also constitute important nursery areas for many marine fish species, they also contain several fish species that are abundant and complete their whole life cycle within these systems (Lenanton and Potter, 1987; Potter et al., 1990; Potter and Hyndes, 1999). The latter species mainly spawn in the late spring to early autumn, when riverine discharge is negligible and environmental conditions are relatively stable and thus conducive to the survival of their eggs and larvae and the recruitment of their juveniles. The differences in the ways estuaries are used by fishes form the basis for their allocation to different functional use groups termed life-cycle guilds or categories (Potter and Hyndes, 1999; Elliott et al., 2007).

Previous studies on the characteristics of the fish faunas in nearshore, shallow waters of south-western Australian estuaries have focused largely on permanently open estuaries on the lower west coast, e.g. the Peel-Harvey Estuary (Potter et al., 1983; Loneragan et al., 1986; Young and Potter, 2003a, b), the Swan River Estuary (Loneragan et al., 1989; Loneragan and Potter, 1990; Hoeksema and Potter, 2006),

Leschenault Estuary (Potter et al., 1997b) and the Blackwood River Estuary (Valesini et al., 1997). These studies demonstrated that the ichthyofaunal compositions of these estuaries change seasonally due to time-staggered differences in the recruitment and immigration and emigration of the various fish species, and that they can differ markedly between years when environmental conditions in those years are conspicuously different. The ichthyofaunas of these estuaries mainly comprise the juveniles of species that spawn at sea and all life-cycle stages of the small and short-lived species that spend their entire life within the estuary. Quantitative data on the fish faunas of comparable waters on the south coast of Western Australia are restricted to those recorded for different years in the permanently-open Nornalup-Walpole Estuary (Potter and Hyndes, 1994), the seasonally-open Wilson Inlet (Potter et al., 1993) and the normally-closed Wellstead Estuary (Young and Potter, 2002). Those data showed that a number of small species that complete their life cycles within estuaries are particularly abundant in these systems.

The characteristics of fish faunas in nearshore, shallow waters of permanently-open, seasonally-open and normally-closed estuaries along the south-western coast of Africa were examined by Bennett (1989) over the course of a year. The results demonstrated that the species richness and number of individuals of marine species were greatest in the permanently-open estuary and least in the normally-closed estuary, and that the reverse was true of estuarine species. Such a trend in species richness has also recently been recorded for offshore, deeper waters in five estuaries on the south coast of Western Australia (Chuwen et al., 2009a).

This study is the first to have compared the characteristics of the fish faunas in nearshore, shallow waters of permanently-open, seasonally-open and normally-closed estuaries using data collected from seasonal sampling over the same two consecutive years. The five estuaries that were the focus of this study were the permanently-open Oyster Harbour, seasonally-open Broke, Irwin and Wilson inlets and the normally-closed Wellstead Estuary which are located on the southern coast of Western Australia. The data obtained from those estuaries were used to test the following hypotheses. 1) The contributions of estuarine species are greatest in estuaries that are normally closed or closed for protracted periods and least in those that are permanently open or open for protracted periods, while the reverse is true for marine species. 2) Species richness is greatest in estuaries that have permanent or protracted openings to the ocean and the densities of fishes are greatest in estuaries with the

highest primary productivity. 3) The species compositions of the fish faunas differ among the various estuaries in relation to factors such as salinity, duration of mouth opening and extent of macrophyte cover. 4) The ichthyofaunal composition in each estuary exhibits cyclical seasonal changes and, when environmental conditions differ conspicuously between years, also undergoes interannual changes.

2. Materials and methods

2.1. Sampling regime

Fishes at several sites in nearshore, shallow (< 1.2 m) waters of the basins of the seasonally-open Broke, Irwin and Wilson inlets, permanently-open Oyster Harbour and normally-closed Wellstead Estuary, which are located along a ca 400 km stretch of the south coast of Western Australia (Fig. 1), were sampled by seine net in each season between summer 2006 and spring 2007. The sample collected from each site in an estuary in each season of each year was considered a replicate for that estuary in that season and year.

The estuary basins ranged in area from 2.5 km² for Wellstead Estuary to 48 km² for the Broke and Wilson inlets. The characteristics of each of the above five estuaries and their catchments, e.g. estuary basin and catchment areas, percentage of cleared land within a catchment, volume of riverine discharge and duration of estuary mouth opening, are summarised in Chuwen et al. (2009b).

The seine net, which consisted of two 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m wide bunt made of 3 mm mesh, was laid parallel to the shore and then hauled on to the bank of the estuary. It fished to a maximum depth of 1.5 m and swept an area of 116 m². Salinity, water temperature and dissolved oxygen concentration were measured in the middle of the water column at each sampling site on each sampling occasion using a Yellow Springs International Model 85 oxygen, conductivity, salinity and temperature meter. The number of days that the estuary mouth had been open or closed prior to each sampling occasion and visual estimates of the percentage cover of macrophytes at each site on each sampling occasion were recorded.

Fishes were euthanised in an ice slurry immediately after capture and transported to the laboratory, where each individual was identified to species and measured to the nearest 1 mm. The total number and weight (to the nearest 0.01g) of each species in each sample was recorded, except when that number was particularly

large, in which case the number of individuals was estimated from the relationship between the weight (to the nearest 0.01g) of a random sub-sample of 50 individuals and the total weight of all individuals.

2.2. *Life-cycle guilds*

Each species of fish caught during the present study was allocated to a life-cycle guild (see Elliott et al., 2007), with the designation of the various species following those assigned by Potter and Hyndes (1999) on the basis of numerous studies in south-western Australia. Estuarine species, i.e. those that complete their entire life cycle within estuaries, consist of species that are typically restricted to estuaries (Estuarine Residents- ER) and those that are also represented by marine populations (Estuarine and Marine- E&M). Marine species comprise the Marine Estuarine-opportunists (MMO), which regularly enter estuaries in substantial numbers from the ocean and particularly as juveniles, and Marine Stragglers (MS), which enter estuaries infrequently and usually in low numbers. Freshwater Stragglers (FS) are those species which live in freshwater, but are occasionally found in estuaries and usually in their low salinity, upper reaches.

2.3. *Univariate analyses*

The species richness (number of species) and density of fishes (number of individuals 100 m⁻²) recorded for each replicate sample from each estuary in each season of 2006 and 2007 were subjected to three-way analysis of variance (ANOVA), to determine whether these two biotic variables differed significantly between estuaries, years and seasons. Each of these independent variables was considered a fixed factor. Prior to subjecting species richness and density of fishes to ANOVA, these data were square root and $\log_{10}(x + 1)$ transformed, respectively. These transformations were shown to be appropriate from the relationship between the \log_{10} of the standard deviation and \log_{10} of the mean of the values for each biotic variable in the replicate samples collected seasonally from each estuary in both years (see Clarke and Warwick, 2001). Following ANOVA, the resultant means and 95% confidence intervals for the significant main effects and interactions were back-transformed, i.e. the inverse of the above transformations, before being plotted. When there were significant interactions ($p < 0.05$), Scheffé's multiple comparison tests

were used to determine whether the differences in the means for each component of the interaction were significant.

2.4. *Multivariate analyses*

The mean abundances of each species in samples from each of the Broke, Irwin and Wilson inlets and Oyster Harbour and Wellstead Estuary in each season of the two years were dispersion weighted, square-root transformed and used to construct a Bray-Curtis resemblance matrix employing PRIMER v6.1.2 (Clarke and Gorley, 2006). The resultant matrix was subjected to non-metric Multidimensional Scaling (nMDS) ordination. When the data were broken down by factors, i.e. estuary, year and/or season, the resemblance matrices employed to produce the ordination plots were constructed using the abundances of each fish species in replicate samples.

Analyses of Similarity (ANOSIM) tests (Clarke, 1993) were used to determine whether the species compositions of the five estuaries were significantly different and whether the faunal composition of each estuary was significantly related to year and season. These tests, which employed Bray-Curtis similarity matrices, used the abundances of each species in replicate samples to ensure that the number of permutations at each level of each factor was adequate for each test. Two-way crossed ANOSIMs were used to elucidate the relative extents to which ichthyofaunal composition was influenced by each factor, i.e. estuary, year or season, after removing the confounding influence of the other two factors. This involved using, in turn, each factor vs a combination of the other two factors, by 'flattening' the two removed factors in each case to a single factor representing all combinations of the levels of those factors. Traditional two-way crossed and one-way ANOSIMs were employed when the influence of a pair of factors or a single factor were explored, respectively.

When pairwise comparisons in an ANOSIM test detected a significant difference between the ichthyofaunal compositions of the a priori levels of a factor, Similarity Percentages (SIMPER) were used to determine the species that best typified the ichthyofaunas of those a priori groups and those that best distinguished between the compositions of those groups (Clarke, 1993).

Biota and Environment matching (BIOENV) (Clarke and Warwick, 2001) was employed to elucidate which environmental variables, or combination of variables, provided the best correlation with the ichthyofaunal compositions in the various

replicate samples from the basin of each estuary and their associated rank orders of similarity. The environmental variables employed were salinity, water temperature, dissolved oxygen concentration, the number of days the mouth had been open or closed prior to each sampling occasion and the estimated percent cover of macrophytes. For this procedure, square root transformed and normalised data for the environmental variables in each replicate sample were used to construct a Euclidean resemblance matrix that was matched against the Bray-Curtis similarity matrix constructed using the dispersion weighted and square-root transformed abundance of each fish species in each of the corresponding samples.

3. Results

3.1. Environmental variables in nearshore, shallow waters

The salinity regimes in nearshore waters of the five estuaries varied markedly, reflecting, in part, variations in the size and duration of the connection of those estuaries with the ocean. Thus, mean seasonal salinities remained close to that of full-strength seawater in Oyster Harbour, whose mouth is deep and permanently open (Fig. 2). Although salinities in Wellstead Estuary were also often close to that of full-strength seawater, they increased conspicuously in two seasons (Fig. 2) as a result of the combined effects of the estuary mouth being closed for a protracted period, high evaporation and low discharge from its river. The bars at the mouths of the seasonally-open Broke, Irwin and Wilson inlets were breached for variable periods. The large and protracted openings of the mouths of Broke Inlet in 2007 and of Irwin Inlet in both 2006 and 2007, account for the salinities in nearshore waters of these systems undergoing very substantial seasonal changes in those years. Thus, their salinities ranged from minima of less than 10 to slightly above full-strength sea water (Fig. 2). The mouth of Wilson Inlet was small when open during 2006 and did not open in 2007 and, consequently, mean seasonal salinities remained below that of full strength seawater and ranged only from 19 to 26.

Mean water temperature in each of the five estuaries followed essentially the same seasonal trend, reaching a maximum of 23-27°C in summer or spring and declining to a minimum of 13-17°C in winter. The mean seasonal dissolved oxygen concentrations in the nearshore waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary showed no consistent and obvious trends throughout either year. Mean seasonal dissolved oxygen concentrations in the five estuaries

ranged between 4.0 and 9.6 mg l⁻¹, except in the basin of Oyster Harbour in summer 2006 when they were particularly low, i.e. 2.6 mg l⁻¹.

3.2. Contributions of species and life-cycle guilds in the five estuaries

The number of fishes caught in the five estuaries ranged from ca 9,700 in Broke Inlet to ca 78,000 in Wellstead Estuary, with the differences in total catch among estuaries not being directly related to the numbers of samples collected in each estuary (Table 1). Species richness ranged from 11 in Broke Inlet to between 17 and 20 in Irwin Inlet, Wilson Inlet and Wellstead Estuary, to 34 in Oyster Harbour, the only permanently-open estuary.

Atherinosoma elongata was the most abundant fish species in nearshore, shallow waters of the Broke, Irwin and Wilson inlets and Wellstead Estuary, contributing between 50 and 82% to the total numbers of fishes in those basins (Table 1). Although this atherinid was the second most abundant species in the basin of Oyster Harbour, it still contributed 30% to the total number of fishes caught in that estuary. Another atherinid, *Leptatherina wallacei*, was the second most abundant species in three of the estuaries and the third most abundant in the other two. The contributions of the above two atherinid species in the Broke, Irwin and Wilson inlets and Wellstead Estuary (78 to 90%) were far greater than in Oyster Harbour (45.4%). The ichthyofauna of the basin of Oyster Harbour differed from that of each of the other estuaries in that over a third of its numbers were attributable to the gobiid *Favonigobius lateralis* (Table 1).

The numbers of *A. elongata* and *L. wallacei* and of another atherinid *Leptatherina presbyteroides*, together with those of the gobiids *Pseudogobius olorum*, *F. lateralis* and *Afurcagobius suppositus*, collectively constituted $\geq 99.7\%$ of the total number of fishes caught in the Broke and Wilson inlets and Wellstead Estuary and 95.2% in Irwin Inlet and 92.9% in Oyster Harbour (Table 1). Each of the above species is represented by populations that complete their life cycles within estuaries. The only other species to contribute $\geq 1.5\%$ to the fish faunas of any estuary were the marine species *Aldrichetta forsteri* in Irwin Inlet and Oyster Harbour, the estuarine species *Engraulis australis* in the former estuary and the marine species *Haletta semifasciata* in the latter.

The number of species that complete their life cycles within estuaries was greater than that of marine species in the Broke, Irwin and Wilson inlets and

Wellstead Estuary, but not in Oyster Harbour. Indeed, the number of marine species (23) in the latter permanently-open estuary was more than twice that of estuarine species (11) and far greater than those in the other four estuaries (Table 1). In terms of number of individuals, the ichthyofauna of each estuary was overwhelmingly dominated by estuarine species (Table 1). The contributions made by Estuarine Residents in the Broke, Irwin and Wilson inlets and Wellstead Estuary (83 to 97%) were far greater, however, than the 50% recorded for this guild in Oyster Harbour, in which Estuarine and Marine species made a far higher contribution (Table 1). Collectively, marine species made a substantially greater contribution to the total number of fishes in the permanently-open Oyster Harbour than in the other four estuaries.

3.3. Species richness and density of fishes

Three-way ANOVA demonstrated that the species richness and density of fishes in the nearshore waters of the five estuaries differed significantly between estuaries and seasons but not between years, and that there was an interaction between estuary and year for species richness and density and also between estuary and season for density (Table 2). For species richness, the F-statistic for the two significant main effects and the interaction were similar, while for density the F-statistic was far greater for estuary than for season, which in turn was greater than that for each of the significant interactions (Table 2).

The mean species richness in each estuary declined significantly between summer and winter ($p < 0.01$) and then rose in spring (Fig. 3a). In 2006, mean species richness in Broke Inlet was less than that of each of the other estuaries and significantly so in the case of Irwin and Wilson inlets (both $p < 0.01$). While mean species richness in Broke Inlet and Oyster Harbour increased slightly in 2007, it decreased in Wellstead Estuary and particularly in Wilson Inlet ($p < 0.001$), which largely accounts for the estuary x year interaction (Fig. 3b). In 2007, mean species richness in Broke and Wilson inlets and Wellstead Estuary were each substantially lower than those in Irwin Inlet and Oyster Harbour and these differences were frequently significant ($p < 0.01-0.05$).

The mean densities of fishes in Broke Inlet and Oyster Harbour in 2006 and 2007 were significantly less (all $p < 0.001$) than those in Wellstead Estuary in both years (Fig. 3c). The mean densities in Irwin and Wilson inlets were intermediate, but

increased significantly between 2006 and 2007 in the former estuary and declined significantly in the latter (both $p < 0.05$), which largely accounts for the estuary x year interaction. In contrast to the situation in the Broke and Irwin inlets and Oyster Harbour, in which density did not differ significantly between seasons (all $p > 0.05$), the density in Wilson Inlet and particularly Wellstead Estuary declined from their maxima in summer to their minima in winter and then increased in spring (Fig. 3d). Thus, densities in winter were significantly less than those in summer in Wilson Inlet ($p < 0.05$) and than those in each of the other seasons in Wellstead Estuary ($p < 0.05$ -0.001). Furthermore, in winter, the densities of fishes in the basins of the various estuaries were not significantly different (all $p > 0.05$).

3.4. Comparisons between ichthyofaunal compositions in the five estuaries

The samples from Broke Inlet, Oyster Harbour and Wellstead Estuary exhibited no overlap on the ordination plot constructed using the mean abundances of the various fish species in each estuary in each season (Fig. 4a). The majority of points for Wilson Inlet lay between those for Broke Inlet and Wellstead Estuary and to the left or above those from Irwin Inlet, which in turn lay very largely to the left of those from Oyster Harbour (Fig. 4a).

The composition of the fish faunas differed significantly among estuaries and between years and seasons (all $p = 0.001$). The Global R-statistic was greater for estuary (0.442) than for year (0.238), which in turn was greater than for season (0.151). The composition of the fish fauna in each estuary was significantly different from that of each of the other estuaries (all $p = 0.001$). R-statistic values showed that the differences were greatest between Wellstead Estuary and both Broke Inlet (0.750) and Oyster Harbour (0.576) and between Oyster Harbour and Wilson Inlet (0.679), and were least between Wilson Inlet and both Wellstead Estuary (0.210) and Irwin Inlet (0.292).

Atherinosoma elongata was the main typifying species of the ichthyofaunas in the basins of Broke, Irwin and Wilson inlets and Wellstead Estuary and that *L. wallacei* and typically *P. olorum* were also important typifying species in these estuaries. Oyster Harbour was unique in that *F. lateralis* was the sole important typifying species for this estuary. Variations in the abundances of the above species often distinguished the fish faunas of the different estuaries (Table 3). Thus, for example, the fish fauna of Oyster Harbour was distinguished from that of each other

estuary by consistently large numbers of *F. lateralis*, while that of Wellstead Estuary was distinguished from those of all other estuaries by consistently greater abundances of *A. elongata*, *P. olorum* and typically also *L. wallacei*. Furthermore, the species that distinguished the fish fauna of Broke Inlet from that of each other estuary were almost invariably less abundant in that estuary (Table 3).

The ichthyofaunal compositions of the five estuaries, were shown by BIOENV, to be best correlated with a combination of the number of days the estuary mouth had been open or closed prior to each sampling occasion and percent macrophyte cover ($p = 0.010$, $\rho = 0.402$), followed by a combination of those two variables and salinity ($p = 0.010$, $\rho = 0.350$).

3.5. Compositions of the ichthyofaunas of the five estuaries

Broke Inlet

The composition of the fish fauna of Broke Inlet was significantly related to both year ($p = 0.005$; $R = 0.181$) and season ($p = 0.007$; $R = 0.125$). On the ordination plot, constructed using the composition data for replicate samples from Broke Inlet, the samples for 2006 tended to lie to the left of those for 2007 (Fig. 4b). The composition of the fish fauna of Broke Inlet in 2006 was distinguished from that in 2007 by consistently greater abundances of *A. elongata* and lower abundances of *A. suppositus* and particularly *F. lateralis*.

When the data for 2006 and 2007 were considered separately, the composition of the fish fauna was significantly related to season in 2006 ($p = 0.007$; $R = 0.231$), but not in 2007 ($p = 0.338$). In Broke Inlet in 2006, the ichthyofaunal composition in summer differed significantly from that in each other season, with the samples for summer on the ordination plot showing virtually no overlap with those for autumn, winter and spring of that year (Fig. 4c). The ichthyofaunal composition of Broke Inlet in summer 2006 was consistently distinguished from that in each other season of that year by consistently greater abundances of *L. presbyteroides*. While greater abundances of *A. suppositus* and lower abundances of *A. elongata* and *L. wallacei* further distinguished the composition of the fish fauna in summer from that in both autumn and winter, greater abundances of the latter two species distinguished that of spring from summer.

Irwin Inlet

The composition of the fish fauna of Irwin Inlet was significantly related neither to year ($p = 0.094$; $R = 0.085$) nor season ($p = 0.165$; $R = 0.052$).

Wilson Inlet

The composition of the fish fauna in Wilson Inlet was significantly related to both year and season (both $p = 0.001$), with the R-statistic being greater for the former (0.259) than latter (0.127). On the ordination plot, the points for 2006 lay largely to the left of those for 2007 (Fig. 5a). This interannual difference was attributable to consistently greater abundances of *P. olorum*, *L. wallacei*, *F. lateralis* and *A. suppositus* and lower abundances of *A. elongata* in 2006.

Ichthyofaunal composition in Wilson Inlet was significantly related to season in 2006 ($p = 0.001$; $R = 0.260$) but not 2007 ($p = 0.425$), with the seasonal effect in 2006 due predominantly to the composition in winter differing from that in each other season ($p = 0.001$ -0.015) and, in particular, from that in summer ($R = 0.693$). The latter seasonal difference is reflected in the lack of overlap between the summer and winter samples on the ordination plot (Fig. 5b) and is largely attributable to consistently greater abundances of *P. olorum*, *L. wallacei*, *F. lateralis*, *A. elongata*, *A. suppositus* and also of *Urocampus carinirostris* in summer.

Oyster Harbour

Ichthyofaunal composition in Oyster Harbour was significantly related to season ($p = 0.006$; $R = 0.129$), but not year ($p = 0.067$). This was due primarily to differences between the compositions in summer and winter ($p = 0.006$; $R = 0.244$) (data not shown), which were largely attributable to consistently greater abundances of *F. lateralis* in summer and of *L. wallacei* and *A. elongata* in winter. When each season was considered separately, one-way ANOSIM demonstrated that the composition of the ichthyofauna was related to year in summer ($p = 0.037$; $R = 0.253$), but not in any other season ($p = 0.123$ -0.567). On the ordination plot of the data for summer, the samples for 2006 showed virtually no overlap with those of 2007 (Fig. 5c). This interannual difference in composition was largely attributable to consistently greater abundances of *F. lateralis* in 2006 and of *Pseudorhombus jenynsii* in 2007.

Wellstead Estuary

The composition of the fish fauna of Wellstead Estuary was significantly related to year and season (both $p = 0.001$), with the effect of year ($R = 0.500$) being greater than that of season ($R = 0.307$). The significant interannual difference in ichthyofaunal composition was due largely to a decrease in the abundances of the gobiids *P. olorum* and *F. lateralis* and an increase in those of the atherinids *A. elongata* and *L. wallacei* in 2007 and was reflected on the ordination plot by the samples for 2006 laying largely to the left of those for 2007 (Fig. 6a).

When the data for 2006 (Fig. 6b) and 2007 (Fig. 6c) were each subjected to ordination, the samples for summer, autumn and winter showed a marked tendency to progress sequentially from left to right on the plot, with those for spring largely lying between those for autumn and winter. The composition of the fish fauna was significantly related to season in 2006 ($p = 0.001$; $R = 0.355$) and 2007 ($p = 0.001$; $R = 0.265$), with seasonal differences being greatest between summer and winter in both years (2006: $p = 0.010$, $R = 0.714$; 2007: $p = 0.002$, $R = 0.633$). These latter differences were due to consistently higher summer abundances of *P. olorum*, *A. elongata* and *F. lateralis* in both years and of *A. butcheri* in 2006 and *L. wallacei* in 2007.

4. Discussion

4.1. Dominance of estuarine species and contributions of marine species

Analyses of catches obtained by seasonal sampling over two consecutive years demonstrated that the ichthyofaunas of nearshore, shallow waters in the basins of Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary were dominated to a remarkable extent by the atherinids *Atherinosoma elongata*, *Leptatherina wallacei* and *Leptatherina presbyteroides*, and the gobiids *Favonigobius lateralis*, *Pseudogobius olorum* and *Afurcagobius suppositus*. These species thus collectively contributed as much as 99.7 or 99.8% to the total catches in the Broke and Wilson inlets and Wellstead Estuary, 95.2% in Irwin Inlet and even as high as 92.9% in Oyster Harbour, the sole permanently-open estuary.

The above atherinid and gobiid species, which are small and have a life cycle of only one or two years, are represented in estuaries by populations whose individuals complete their life cycles within those systems (e.g. Prince and Potter, 1983; Gill et al., 1996). Thus, unlike marine species, the individuals in these estuarine populations do not need to migrate from the estuary to the marine environment in

order to reproduce. The high abundances of each of the three atherinid and three gobiid species in a range of estuary types, i.e. permanently open, seasonally open and normally closed, and thus also of salinity regimes, demonstrate that these species must be highly euryhaline and therefore well adapted for life in a wide variety of estuarine environments. Atherinid and gobiid species, including *L. presbyteroides*, *F. lateralis* and *P. olorum*, are also abundant in eastern Australian estuaries (e.g. Potter et al., 1986; Pollard, 1994; Potter and Hyndes, 1999; Griffiths, 2001) and can presumably likewise complete their life cycles within those systems. Indeed, Pollard (1994) has drawn attention to the marked similarity of the ichthyofaunal compositions of estuaries in south-western and south-eastern Australia.

The extreme dominance of the ichthyofaunas of nearshore waters of south coast estuaries by species that complete their life cycles within those systems, which include not only the above three atherinid and three gobiid species but also, in some estuaries, species such as *Acanthopagrus butcheri*, *Urocampus carinirostris* and *Engraulis australis*, contrasts markedly with the situation in the vast majority of macrotidal estuaries of temperate regions in the northern hemisphere (e.g. Haedrich, 1983; Claridge et al., 1986; Elliott and Dewailly, 1995). As most estuaries on the south coast are closed to the ocean for various and sometimes substantial periods, selection pressures would have favoured those species that are able to spawn successfully within these systems and whose larvae and juveniles could survive in that environment. It is therefore particularly relevant that, in comparison with macrotidal estuaries, the estuaries on the south coast of Western Australia provide a far more benign environment in late spring to early autumn, when the fish species in these systems typically spawn and their larvae are hatched (Potter and Hyndes, 1999). Thus, during this period, discharge into the basin is usually negligible, salinities are not depressed and food is abundant and, as at all times, tidal water movement is limited, thereby providing an environment ideal for the survival and development of fish during the larval and early juvenile phases of their life.

Although the contributions made by marine species to the total numbers of fishes caught in nearshore waters of the permanently and seasonally-open estuaries were far lower than those of the abundant atherinid and gobiid species, 398 *Aldrichetta forsteri*, 138 *Sillaginoides punctata* and 127 *Mugil cephalus* were collected from these waters in those estuaries. As these species were represented predominantly by individuals < 100 mm in length, the nearshore waters of south coast

estuaries act as a nursery area for at least some individuals of these species. However, the densities of particularly the mugilids in nearshore waters are low compared with those recorded in comparable waters in permanently-open estuaries along the lower west coast (Chubb et al., 1981; Loneragan et al., 1986). Furthermore, *S. punctata* were caught and *A. forsteri* and *M. cephalus* were very abundant in offshore waters of two or more of the south coast estuaries when sampled concurrently with the present study (Chuwen et al., 2009a).

The above comparisons suggest that the numbers of *A. forsteri*, *M. cephalus* and *S. punctata* in nearshore waters of south coast estuaries are lower than might have been expected. It is thus relevant that the mouths of the seasonally-open estuaries were typically closed for much of the protracted period when these species, in particular the mugilids, spawn at sea (Chubb et al., 1981; Hyndes et al., 1998) and thus many of the juveniles are already of a substantial size, i.e. > 100 mm, when they enter the estuary and as a consequence tend to occupy more offshore, deeper waters (Chuwen et al., 2009a). Such a view is consistent with the fact that the catches of small *A. forsteri* were greatest in the permanently-open Oyster Harbour and in the seasonally-open Irwin Inlet whose mouth opened earlier each year, i.e. in winter, and remained open in total for a far longer period than that of each of the other seasonally-open estuaries, i.e. Broke and Wilson inlets, which opened to the ocean in spring in those years when the estuary mouth was breached.

The catches of *Arripis georgianus*, another marine-estuarine opportunist, were negligible in nearshore waters but substantial in offshore waters (Chuwen et al., 2009a) where they were represented predominantly by individuals > 150 mm and > two years of age (I.C. Potter, unpublished data). This reflects the fact that the individuals of this species take a substantial period to migrate from their nursery areas in South Australia to the south coast of Western Australia where they occupy coastal marine waters and estuaries (Fairclough et al., 2000).

4.2. Comparisons of the ichthyofaunas of the five estuaries

Although the ichthyofaunas of the nearshore waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary were all overwhelmingly dominated by the collective contribution of three atherinid and three gobiid species, the species compositions of the fish faunas of the basins of these five estuaries were significantly different. This largely reflected differences in the relative abundances of

those species in each estuary. For example, *F. lateralis* and *L. presbyteroides* were relatively far more abundant in the basin of the permanently-open Oyster Harbour, in which salinities were always close to that of full-strength sea water, than in each of the other estuaries, in which salinities were far more variable. Furthermore, *F. lateralis* made only a small contribution to the fish fauna of the Wellstead Estuary and *L. presbyteroides* was not caught in that normally-closed system. It is further relevant that *L. presbyteroides* and *F. lateralis* were the most abundant fish species during a study in 1989-90 of nearshore waters of the Nornalup-Walpole Estuary, the only other large and permanently open estuary on the south coast of Western Australia (Potter and Hyndes, 1994). Detailed ecological studies of *F. lateralis* and *L. presbyteroides* in the large and permanently-open Swan River Estuary on the lower west coast of Australia showed that these two species were most abundant in the lower estuary (Prince et al., 1982; Gill and Potter, 1993), where salinities are close to that of full-strength seawater for most of the year and the substrate is sandy and thus resembles the nearshore marine environment. The above patterns of distribution of estuarine populations of *F. lateralis* and *L. presbyteroides* strongly suggest that the individuals of these populations have a strong affinity for a marine-like environment. This conclusion is consistent with the fact that, unlike the other abundant atherinid and gobiid species, *F. lateralis* and *L. presbyteroides* are also represented by populations in similar habitats in nearshore marine waters (Potter and Hyndes, 1999; Valesini et al., 2004). As south-western Australian estuaries are of relatively recent origin, having been formed during the Holocene marine transgression (Hodgkin and Hesp, 1998), the estuarine populations of *F. lateralis* and *L. presbyteroides* may have been derived from marine populations of these species. In this context, it is relevant that genetic studies on a number of fish species, including *L. presbyteroides*, indicate that estuaries in south-western Australia have offered special opportunities for increasing the genetic subdivision of inshore species (Watts and Johnson, 2004).

In contrast to the above example, *L. wallacei* made its greatest contribution to the ichthyofauna of Broke Inlet, the only estuary to exhibit a protracted period of greatly reduced salinities. This is consistent with *L. wallacei* typically being most abundant in the upper reaches of permanently-open estuaries on the lower west coast of Australia where salinities become greatly reduced during periods of heavy discharge (Prince et al., 1982; Loneragan et al., 1986; Loneragan and Potter, 1990).

The difference between the ichthyofaunal compositions of the highly eutrophic Wellstead Estuary and near pristine Broke Inlet, which represented the greatest such difference between any two south coast estuaries, largely reflected the far greater abundances of *A. elongata*, *P. olorum* and *L. wallacei* in the former system. The high densities of the above three species in Wellstead Estuary are presumably related to the presence of very substantial growths of *Ruppia megacarpa* (Brearley, 2005), which have been shown to provide an important habitat and source of prey for the above three species (Humphries et al., 1992; Humphries and Potter, 1993; Pollard, 1994). It would thus follow that the particularly low densities of those species and of all fishes collectively in Broke Inlet, represent, in particular, the paucity of macrophytes and thus limited densities of the associated invertebrates on which these fish species prey (Humphries and Potter, 1993). In the context of the putative role of macrophytes, it is relevant that, although the compositions of the fish faunas of Wilson and Irwin inlets and Wellstead Estuary were significantly different, each estuary contained substantial growths of *R. megacarpa* (Brearley, 2005) and their major typifying fish species were *A. elongata*, *P. olorum* and *L. wallacei*. The paucity of species and low density of fishes in the nearshore, shallow waters of Broke Inlet parallels the situation in offshore, deeper waters (Chuwen et al., 2009a) of this oligotrophic system (Brearley, 2005).

While variations in the relative abundances of estuarine species in the various estuaries made the greatest contribution to the differences in species composition among those systems, those differences were still influenced, to some degree, by variations in the relative abundances of marine species, i.e. marine stragglers and marine estuarine-opportunists. As hypothesised, the number and densities of marine species were the greatest by far in Oyster Harbour, which, through possessing a substantial and permanently-open mouth, provides access to these species at all times. The ichthyofaunas of South African estuaries with a permanent connection to the ocean likewise contain a greater number of marine species than seasonally-open and normally-closed estuaries and thus overall a relatively greater species richness (Bennett, 1989; Whitfield and Kok, 1992; Harrison and Whitfield, 2006). The influence on ichthyofaunal composition of connectivity to the ocean is further illustrated by the greater contribution made by marine species to the fish fauna of Irwin Inlet than to those in the Broke and Wilson inlets, the other two seasonally-open estuaries, which were not open to the ocean for the same overall length of time.

The poor representation of marine species in Wilson Inlet and particularly in 2007 can be attributed to its mouth being atypically closed for the majority of the study (Chuwen et al., 2009b), and to the fact that, when briefly open, the channel scoured through the sand bar at the mouth was narrow and shallow. This paralleled the situation in an eastern Australian estuary in which the very brief and restricted opening of its mouth provided limited opportunities for marine fishes to enter (Griffiths, 2001). The sand bar at the mouth of Wilson Inlet remained open overall for a longer period between 1987 and 1989 than in the current study, which accounts for a greater prevalence of marine species in that earlier period, but even then their contribution was very small compared with that of estuarine species (Potter et al., 1993).

The capture of marine species such as *A. forsteri*, *M. cephalus* and *S. punctata* in nearshore and offshore waters of Wellstead Estuary during the present and past studies (Young and Potter, 2002; Chuwen et al., 2009a) emphasise that mugilids, in particular, are able to capitalise on any breaching of the bar of a normally-closed estuary to enter such systems.

Although the results of BIOENV, derived from the data collected from all five estuaries, showed that, overall, the ichthyofaunal composition in these different types of estuaries was related to a combination of the duration of mouth opening and macrophyte cover and, to a lesser extent, a combination of the above two variables and salinity, the p values were not particularly high, i.e. 0.402 and 0.350, respectively. BIOENV showed that, overall, the strength of the relationship between the ichthyofaunal composition of selected South African estuaries and the status of the estuary mouth was greater than in the south coast estuaries (Vorwerk et al., 2003), a difference that is attributable to the immigrations of larger numbers of the juveniles of certain marine species into the former estuaries. Moreover, differences among the ichthyofaunal composition in nearshore waters of a permanently-open, seasonally-open and normally-closed estuary in the south western cape region of South Africa were shown to be strongly related to the duration of the connection between the estuary and the ocean (Bennett, 1989).

The fact that overall ichthyofaunal composition in the estuaries on the south coast of Western Australia is not as strongly related to whether or not the estuary mouth is open, as is the case in southern Africa, is not surprising in view of the overwhelming numerical domination of the estuarine fish faunas of this region by

species which complete their life cycle without having to leave the estuary. Thus, while an estuary mouth that is either permanently open (Oyster Harbour) or open annually for protracted periods (Irwin Inlet) provides an avenue for the immigration and emigration of marine species, they are also responsible for producing the marine-like conditions, and in particular of salinity and a sandy substrate, that are apparently favoured by estuarine species with strong marine affinities, such as *F. lateralis* and *L. presbyteroides* (see above). The identification that overall the ichthyofaunal composition of south coast estuaries is related to the extent of macrophyte cover is consistent with the strong tendency for certain species to occupy stands of such macrophyte species as *R. megacarpa* (see above; Humphries et al., 1992, Humphries and Potter, 1993).

A collation of records of estuarine and marine fish species emphasised that the distribution of some fish species that are abundant in estuaries on the lower west coast of Australia do not extend to estuaries on the south coast (Potter et al., 1990). However, the same suite of fish species was recorded in estuaries along the southern coast between Broke Inlet and Wellstead Estuary and thus differences in the number of species recorded in the five estuaries is unlikely to be related to geographical location.

4.3. Temporal characteristics of the fish faunas

As the ichthyofaunas of the basins of Wilson Inlet and Wellstead Estuary were the only estuaries to undergo both a significant decrease in species richness and shift in ichthyofaunal composition between 2006 and 2007, it is relevant that they were also the only estuaries to remain closed throughout the second of those years. The decrease in species richness in both estuaries was due, in part, to a decline in the number of marine species. This reflected a lack of access to these estuaries for the new recruits of marine estuarine-opportunist species and for marine stragglers in the second year, and to the individuals of some of those marine species, which had previously recruited to the estuary, having increased in size and moved to more offshore and deeper waters (Chuwen et al., 2009a). The contribution of these marine species, however, was low and thus the shift in composition between 2006 and 2007 was largely attributable to changes in the abundances of certain estuarine species and in particular, to a decrease in *F. lateralis* and *P. olorum*.

While the compositions of the ichthyofaunas in nearshore waters of the Broke and Wilson inlets, Oyster Harbour and Wellstead Estuary underwent seasonal changes, these were not as pronounced as those exhibited in permanently-open estuaries on the lower west coast of Australia (e.g. Young and Potter, 2003a; Hoeksema and Potter, 2006) and in macrotidal systems in temperate regions of the northern hemisphere (e.g. Potter et al., 1997a; Theil and Potter, 2001; Maes et al., 2005). The weak cyclicity in south coast estuaries can be attributed to the overwhelming dominance of species that complete their life cycles within the estuary and which are thus typically present at a given location throughout the year. In contrast, the ichthyofaunas of estuaries on the lower west coast contained a greater number of marine species whose peak abundances varied throughout the year (Young and Potter, 2003a) and, in their upper reaches, also to a small number of euryhaline freshwater species (Hoeksema and Potter, 2006).

In summary, the ichthyofaunas of nearshore, shallow waters of estuaries along the southern coast of Western Australia differ markedly from those of the vast majority of macrotidal estuaries in the northern hemisphere in that they are dominated, to a remarkable extent, by species that complete their life cycles within estuaries, rather than by the juveniles of marine species. The dominance of such species occurs in all types of estuaries and thus irrespective of whether the estuary is permanently open, seasonally open or normally closed to the ocean. Indeed, three species of atherinid and three species of gobiid, all of which complete their life cycles without leaving the estuary, contributed between 95.2 and 99.8% to the total numbers of fish caught in the three seasonally-open and one normally-closed estuary, and even as much as 92.9% in the permanently-open estuary. The ichthyofaunal composition of each of these estuaries was significantly different, however, from that of each of the other estuaries, due in particular to variations in the relative abundances of those atherinid and gobiid species among the five estuaries. Our data suggest that such variations reflect differences in the affinities of those species for certain habitat characteristics and the fact that the extent to which these characteristics are present vary among estuaries. Thus, for example, *L. presbyteroides* and especially *F. lateralis*, which are also represented by marine populations, made their greatest contributions in the permanently-open estuary where salinities remained close to that of full strength sea water and the substrate was similar to that of nearshore coastal waters. In addition, the compositions and densities of fishes were related to whether

or not macrophytes were abundant. Species composition did not undergo the pronounced cyclical seasonal changes that are exhibited by nearshore fish faunas in the macrotidal estuaries of the northern hemisphere, reflecting the far lower numbers of marine species and thus a lack of time-staggered immigrations and emigrations by such species.

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List of figures

Fig. 1. Maps showing the location of Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary on the south coast of Western Australia and the sampling sites (circles) within those estuaries. The bar in the map of each estuary represents 2 km. The location of the sampling region in Western Australia is shown as a rectangle in the top left corner.

Fig. 2. Mean seasonal salinities \pm 1SE in nearshore waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. White and grey bars at the base of the plot for each estuary denote when the mouth of that estuary was open and closed, respectively.

Fig. 3. Mean species richness \pm 95% CI of a) all estuaries collectively in each season and of b) each estuary in 2006 (black symbols) and 2007 (white symbols) and the mean densities of fishes \pm 95% CI of c) each estuary in 2006 and 2007 and of d) Broke (\circ), Irwin (\blacktriangle) and Wilson (\blacklozenge) inlets, Oyster Harbour (∇) and Wellstead Estuary (\blacksquare) in each season (overall mean \pm 95% CI for each estuary presented).

Fig. 4. Non-metric multidimensional scaling ordination plot, derived from the matrix constructed using the mean seasonal abundance of each species in the nearshore waters of a) Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary. nMDS ordination plots, derived from the matrix constructed employing the abundance of each species in replicate samples of Broke Inlet in a) 2006 and 2007 and c) in each season of 2006.

Fig. 5. Non-metric multidimensional scaling ordination plots derived from the matrices constructed using the abundance of each species in replicate samples of the nearshore waters of Wilson Inlet in a) 2006 and 2007 and b) in each season of 2006, and from Oyster Harbour in c) the summers of 2006 and 2007.

Fig. 6. Non-metric multidimensional scaling ordination plots derived from the matrices constructed using the abundance of each species in replicate samples of the nearshore waters of Wellstead Estuary in a) 2006 and 2007 and in each season of b) 2006 and c) 2007.

Table 1. Life-cycle guilds (LCG), rank and percentage contributions of each fish species to the total catch from nearshore waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary and the numbers of species and individuals (N) and the percentage contributions (%) of the different life-cycle guilds to the total catch of those estuaries. MS = marine straggler, MMO = marine estuarine-opportunist, E&M = estuarine & marine, ER = estuarine resident, FS = freshwater straggler.

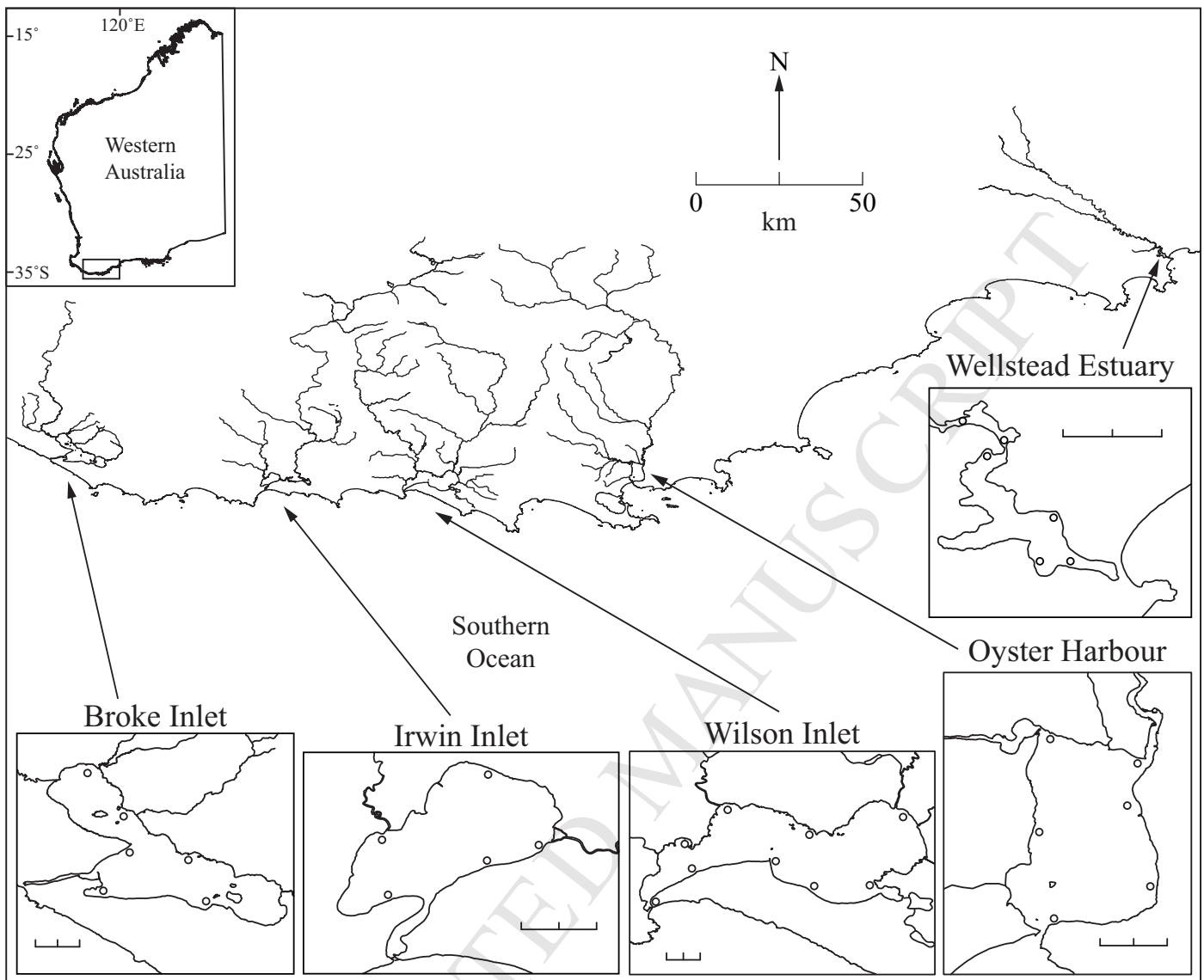
Species	LCG	Broke		Irwin		Wilson		Oyster		Wellstead	
		R	%	R	%	R	%	R	%	R	%
<i>Atherinosoma elongata</i>	ER	1	50.2	1	57.6	1	65.2	2	29.7	1	82.3
<i>Leptatherina wallacei</i>	ER	2	39.7	2	20.3	2	20.5	3	15.7	3	5.8
<i>Favonigobius lateralis</i>	EM	4	2.3	4	5.9	4	2.5	1	34.8	4	5.3
<i>Pseudogobius olorum</i>	ER	5	1.7	5	4.4	3	10.0	10	0.4	2	6.1
<i>Leptatherina presbyteroides</i>	EM	3	4.2	3	6.3	6	0.7	4	8.4		
<i>Afurcagobius suppositus</i>	ER	6	1.6	8	0.7	5	0.9	5	3.9	5	0.2
<i>Aldrichetta forsteri</i>	MMO	9	<0.1	6	2.1			6	2.3	11	<0.1
<i>Engraulis australis</i>	EM			7	1.8					11	<0.1
<i>Sillaginodes punctata</i>	MMO			10	0.3	7	<0.1	14	0.1	7	0.1
<i>Acanthopagrus butcheri</i>	ER			14	<0.1	15	<0.1	13	0.2	6	0.2
<i>Haletta semifasciata</i>	MS							7	1.5		<0.1
<i>Urocampus carinirostris</i>	EM			9	0.5	9	<0.1		<0.1		
<i>Arripis truttaceus</i>	MMO	9	<0.1	12	<0.1			8	0.6		
<i>Stigmatopora argus</i>	MS					11	<0.1	9	0.4		
<i>Mugil cephalus</i>	MMO			12	<0.1	13	<0.1	11	0.3	10	<0.1
<i>Neoodax balteatus</i>	MS							9	0.4		
<i>Pelates sexlineatus</i>	MMO			11	<0.1			15	0.1		
<i>Acanthaluteres spilomelanurus</i>	MS							12	0.2		
<i>Galaxias maculatus</i>	FS			13	<0.1					8	<0.1
<i>Ammotretis rostratus</i>	MMO	7	<0.1	13	<0.1	14	<0.1	19	<0.1	11	<0.1
<i>Cnidogobius macrocephalus</i>	EM			14	<0.1	8	<0.1			11	<0.1
<i>Pugnaso curtirostris</i>	MS					10	<0.1	18	<0.1		
<i>Apogon rueppellii</i>	EM							15	0.1		
<i>Pseudorhombus jenynsii</i>	MMO					15	<0.1	16	<0.1		
<i>Gymnapistes marmoratus</i>	MMO									9	<0.1
<i>Cristiceps australis</i>	MS							17	<0.1		
<i>Acanthaluteres brownii</i>	MS							17	<0.1		
<i>Parablennius postoculomaculatus</i>	MMO					12	<0.1				
<i>Siphamia cephalotes</i>	EM							18	<0.1		
<i>Rhabdosargus sarba</i>	MMO	8	<0.1			14	<0.1			10	<0.1
<i>Spratelloides robustus</i>	MS			15	<0.1			20	<0.1		
<i>Arripis georgianus</i>	MMO							19	<0.1		
<i>Ammotretis elongates</i>	MS							20	<0.1		
<i>Hyporhamphus melanochir</i>	EM	9	<0.1	14	<0.1						
<i>Nesogobius pulchellus</i>	EM							21	<0.1		
<i>Arenigobius bifrenatus</i>	EM									9	<0.1
<i>Meuschenia freycineti</i>	MMO			15	<0.1			22	<0.1		
<i>Posidonichthys hutchinsi</i>	MS							22	<0.1		
<i>Platycephalus laevigatus</i>	MMO					15	<0.1				
<i>Platycephalus speculator</i>	EM					15	<0.1				
<i>Cristiceps aurantiacus</i>	MS										
<i>Heteroclinus roseus</i>	MS							22	<0.1		
<i>Brachaluteres jacksonianus</i>	MS							22	<0.1		
<i>Enoplosus armatus</i>	MS							22	<0.1		
<i>Notolabrus parilus</i>	MS										
<i>Halichoeres brownfieldi</i>	MS										
<i>Paraplagiusa bilineata</i>	MS										
Species		N	%	N	%	N	%	N	%	N	%
Marine stragglers	MS	-	-	1	5.0	2	10.5	13	38.2	1	5.9
Marine estuarine-opportunists	MMO	4	36.4	7	35.0	7	36.8	10	29.4	6	35.3
Estuarine & marine	EM	3	27.3	6	30.0	5	26.3	6	17.6	4	23.5
Estuarine residents	ER	4	36.4	5	25.0	5	28.3	5	14.7	5	29.4
Freshwater	F	-	-	1	5.0	-	-	-	-	1	5.9
Individuals											
Marine stragglers	MS	-	-	1	<0.1	18	<0.1	329	2.9	1	<0.1
Marine estuarine-opportunists	MMO	13	0.1	473	2.5	55	0.1	429	3.8	96	0.1
Estuarine & marine	EM	637	6.6	2773	14.6	1409	3.2	4954	43.5	4159	5.4
Estuarine residents	ER	9068	93.3	15806	82.9	42424	96.6	5670	49.8	73514	94.5
Freshwater	F	-	-	4	<0.1	-	-	-	-	20	<0.1
Number of samples		48		40		71		48		46	
Number of species		11		20		19		34		17	
Total number		9718		19057		43906		11382		77790	

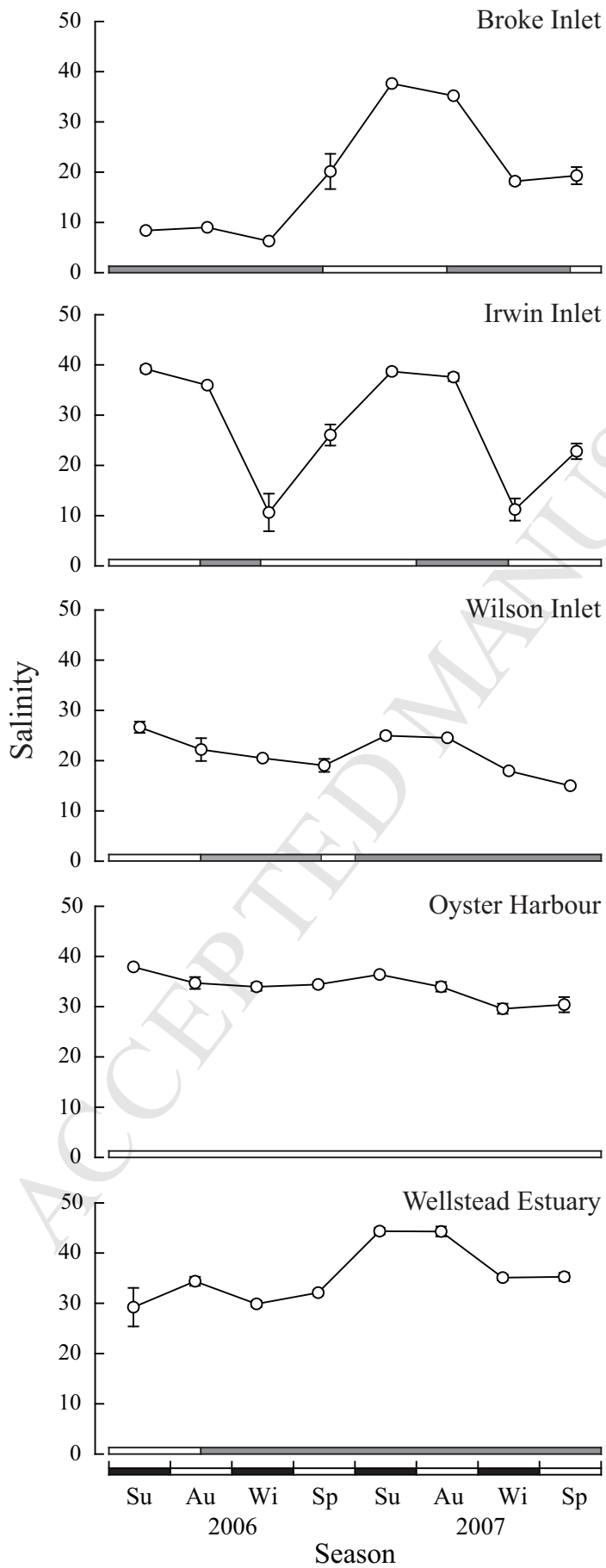
Table 2. F-statistics, mean squares (given in parentheses) and significance levels for three-way ANOVAs of the number of species and density of fishes recorded in nearshore waters of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary in each season of 2006 and 2007. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

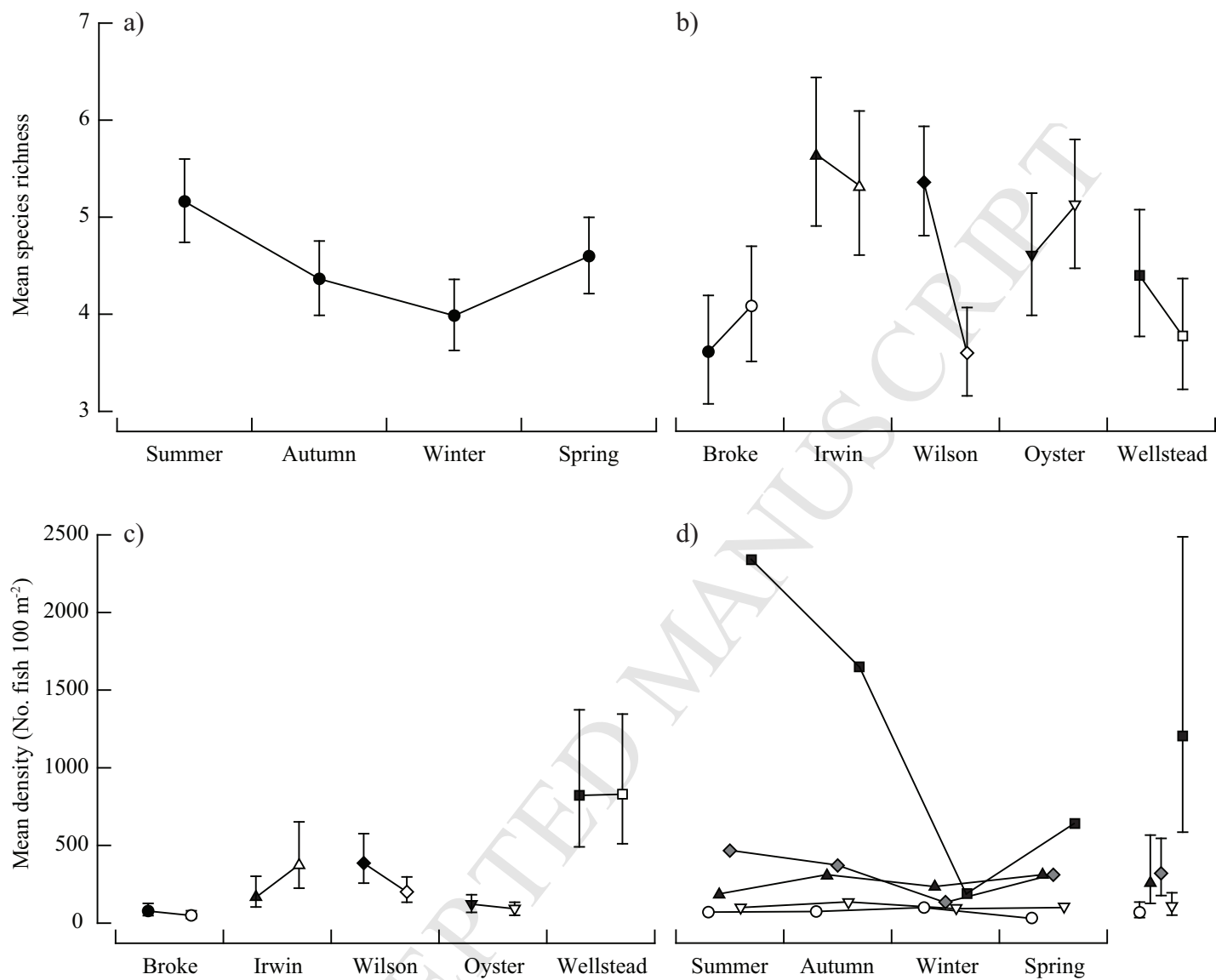
Main effects				
	Estuary (E)	Year (Y)	Season (Se)	Residual
<i>df</i>	4	1	3	213
Number of species	7.471*** (0.996)	2.967 (0.395)	5.949** (0.793)	(0.133)
Density	33.063*** (9.032)	0.708 (0.193)	4.772** (1.304)	(0.273)
Interactions				
	E x Y	E x S	Y x S	E x Y x S
<i>df</i>	4	12	3	12
Number of species	5.583*** (0.744)	1.195 (0.159)	2.083 (0.278)	1.400 (0.187)
Density	2.502* (0.683)	2.747** (0.750)	1.260 (0.344)	0.945 (0.258)

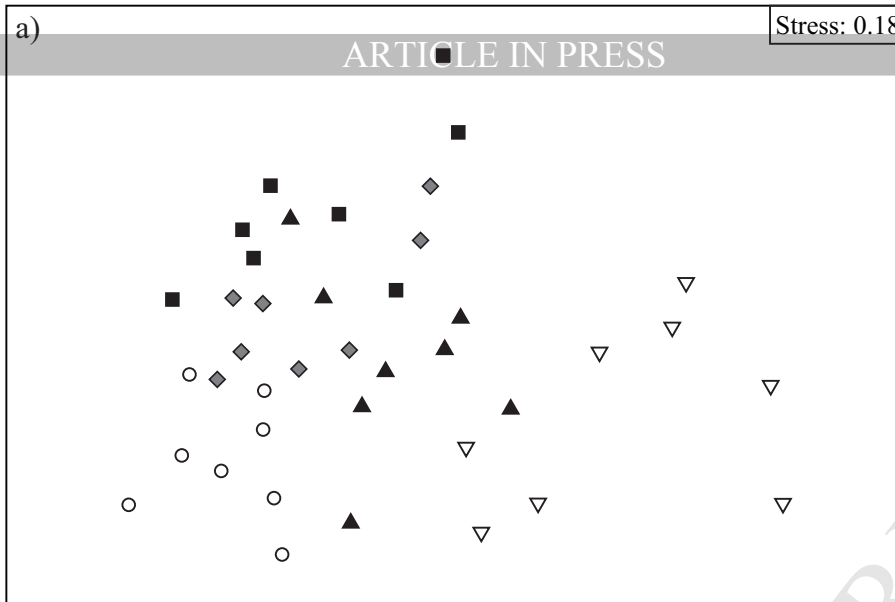
Table 3. R-statistic values and significance levels (light shaded boxes) for pairwise ANOSIMs of the ichthyofaunal compositions of the Broke, Irwin and Wilson inlets, Oyster Harbour and Wellstead Estuary derived from the matrix constructed using the abundance of the various fish species in each replicate sample. The species determined by SIMPER as most responsible for typifying the ichthyofaunal composition of the basin of individual estuaries (dark shaded boxes) and for distinguishing between the ichthyofaunal compositions in each pairing of those five estuaries (unshaded boxes). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ^B = Broke Inlet, ^I = Irwin Inlet, ^W = Wilson Inlet, ^O = Oyster Harbour and ^{We} = Wellstead Estuary denote the estuary in which the species made the greater contribution to ichthyofaunal composition.

	Broke	Irwin	Wilson	Oyster	Wellstead
Broke	<i>A. elongata</i> <i>L. wallacei</i>	0.467***	0.445***	0.434***	0.750***
Irwin	<i>P. olorum</i> ^I <i>A. elongata</i> ^I <i>L. wallacei</i> ^I <i>F. lateralis</i> ^I	<i>A. elongata</i> <i>L. wallacei</i> <i>P. olorum</i>	0.292***	0.369***	0.425***
Wilson	<i>P. olorum</i> ^W <i>A. elongata</i> ^W <i>L. wallacei</i> ^W <i>A. suppositus</i> ^W	<i>P. olorum</i> ^W <i>A. elongata</i> ^W <i>L. wallacei</i> ^I <i>F. lateralis</i> ^I <i>A. suppositus</i> ^W	<i>A. elongata</i> <i>P. olorum</i> <i>L. wallacei</i>	0.679***	0.210***
Oyster	<i>F. lateralis</i> ^O <i>A. elongata</i> ^B	<i>F. lateralis</i> ^O <i>A. elongata</i> ^I <i>P. olorum</i> ^I <i>L. wallacei</i> ^I	<i>P. olorum</i> ^W <i>F. lateralis</i> ^O <i>A. elongata</i> ^W <i>L. wallacei</i> ^W	<i>F. lateralis</i>	0.576***
Wellstead	<i>A. elongata</i> ^{We} <i>P. olorum</i> ^{We} <i>L. wallacei</i> ^{We}	<i>A. elongata</i> ^{We} <i>P. olorum</i> ^{We} <i>L. wallacei</i> ^{We}	<i>A. elongata</i> ^{We} <i>P. olorum</i> ^{We} <i>L. wallacei</i> ^{W/We}	<i>A. elongata</i> ^{We} <i>P. olorum</i> ^{We} <i>F. lateralis</i> ^O <i>L. wallacei</i> ^{We}	<i>A. elongata</i> <i>P. olorum</i> <i>L. wallacei</i>

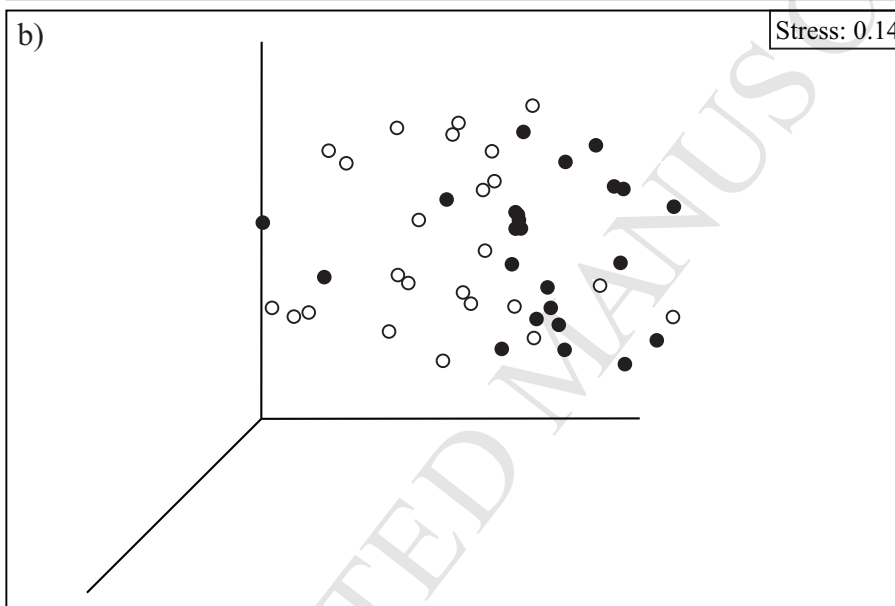




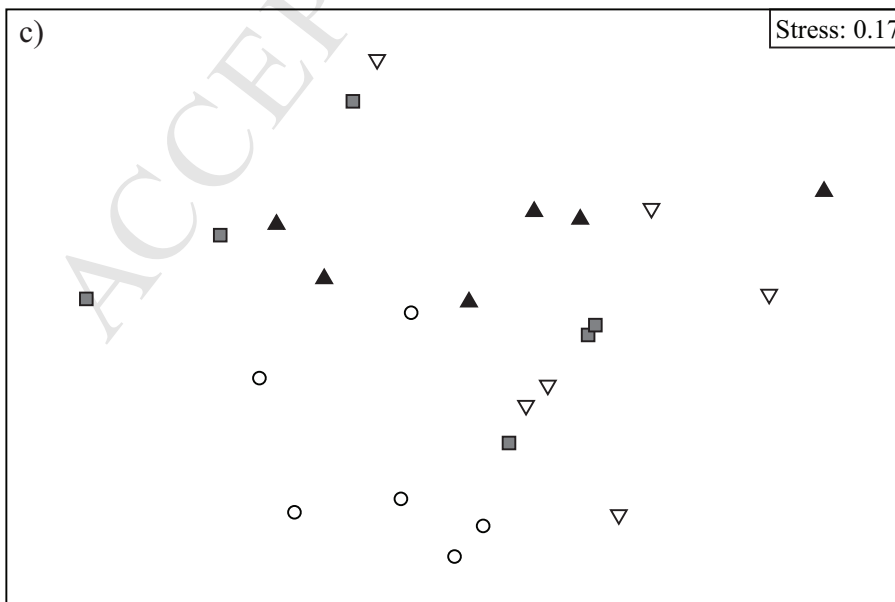




Legend: Broke Inlet ○ Irwin Inlet ▲ Wilson Inlet ◆ Oyster Harbour ▽ Wellstead Estuary ■



Legend: 2006 ○ 2007 ●



Legend: Summer ○ Autumn ▲ Winter ■ Spring ▽

