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Temporal changes to spatially stratified waterbird communities of the Coorong, South Australia: implications for the management of heterogenous wetlands

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Abstract

The Coorong, South Australia, is a globally significant wetland system, listed in the Ramsar Convention under a number of different criteria, including its importance to waterbird populations. Based on annual waterbird censuses conducted between 2000 and 2007, spatiotemporal analyses revealed that significant differences in waterbird community structure exist along the length of the Coorong. This spatial diversity in community structure was also found to be temporally consistent over this 8-year period. The abundance of the most numerically dominant bird species, such as red-necked stint *Calidris ruficollis* and grey teal *Anas gracilis*, explained much of this spatial variation. However, comparisons between data collected for the Coorong south lagoon in 1985 and 2000–2007 show that dramatic changes in these waterbird communities have occurred over longer periods of time, with 23 of the 27 most common species having declined in this period by at least 30%. The Coorong still regularly supports globally important populations (>1% of global population) of nine waterbird taxa, including three Palearctic shorebirds, confirming its Ramsar status. The functional links between the overutilized Murray-Darling basin river system and the Coorong are discussed.

Introduction

Coastal wetlands, including estuarine systems, are among the most productive biomes in the world (Alongi, 1998), and provide a range of important ecosystem services (Woodward & Wui, 2001). Such wetlands also provide important breeding and non-breeding habitats for a wide range of waterbird species, including long-distance migratory shorebirds. For example, 17 of the 29 Australian Ramsar sites that are listed for their importance to waterbirds (Criteria 5 and/or 6) are marine or coastal wetlands. However, due to increasing human pressure on estuaries in particular, Australian coastal wetlands have become increasingly threatened, such that their value as waterbird habitat is being eroded (Kingsford, 2000; Lee *et al.*, 2006).

Among the primary threats to the ecological health of estuaries are the regulation and extraction of water from the river systems that feed these estuaries (Kennish, 2002; Ravenscroft & Beardall, 2003). These threats are particularly important in low rainfall environments, where anthropogenic demands on water are highest relative to availability (Fox, Wilby & Moore, 2001; Sierra *et al.*, 2004). The relationship between human water extraction and threats to river estuaries are particularly evident in the Australian Murray-Darling Basin, where the extraction of water for human uses has resulted in only 27% of the median flow being discharged into the sea (Phillips & Muller, 2006).

Investigations regarding waterbird and wetland communities are often concerned with the nature of these communities at the spatial scale of individual wetlands (Halse *et al.*, 1993), with subsequent classifications of wetlands (e.g. Ramsar Status as important wetlands) being based at this spatial resolution (Environment Australia, 2001). These classifications do not account for spatial variation that occurs within wetlands. This is despite the fact that within single wetland systems, a wide range of habitats can exist that support distinctive waterbird communities (Ysebaert *et al.*, 2000). Such within-wetland diversity needs to be documented to appreciate and understand the true significance of wetland systems to avian communities, as it is this intra-wetland heterogeneity that supports diverse and robust communities. Understanding this diversity is particularly important in estuaries and reverse estuaries (such as the Coorong wetland system), which are defined by their salinity gradients and thus, by definition, possess inherent spatial heterogeneity (Kennish, 2002).

The Coorong wetland system of the Murray-Darling Basin (138°47′E, 35°30′S to 139°43′E, 36°17′S) provides an example of the importance of coastal wetlands to waterbird communities, as well as the ecological consequences of human impact on these wetlands. The Coorong supports regionally (Kingsford & Porter, 2008) and internationally significant populations of a range of waterbird species (Watkins, 1993; Gosbell & Grear, 2005), and primarily for this reason, has been listed as a Wetland of International Significance under the Ramsar Convention (Department for Environment and Heritage, 2000). These waterbird populations have traditionally been maintained through a combination of a highly productive, though relatively simple ecosystem, and the presence of extensive mudflats. Being located at the mouth of the Murray-Darling Basin, the ability for this system to maintain significant waterbird populations is dependent on adequate and suitably timed flows of water from the basin (Jensen *et al.*, 2000). This link between the Murray-Darling Basin and the Coorong makes the Coorong a sensitive indicator of whether the basin as a whole is being managed sustainably, in addition to the wetlands' own inherent biological significance. As a result, the 'Coorong, Lower Lakes and Murray Mouth' region is listed as one of six Significant Ecological Assets under the Living Murray program of the Murray-Darling Basin Commission (2006). However, there is now a general consensus (summarized in Phillips & Muller, 2006) that the Coorong's ecological values are in a state of drastic decline, largely in response to reductions in freshwater inflows from the Murray River. Understanding how the waterbird communities of the Coorong vary in space and time, and in response to different environmental scenarios, can thus give us insight into the sustainability of the entire Murray-Darling Basin.

Methods

Study site

The Coorong wetlands system is located in the south-east of South Australia, and is comprised of two long, narrow wetlands in series (total length: ~110 km; Fig. 1). The two lagoons are joined by a narrow channel <100 m in width (Parnka Point), which restricts (but does not exclude) water exchange between the lagoons. In total, the two lagoons are *c.* 110 km in length, with a maximum width of *c.* 5 km. The lagoons are typically shallow, with a maximum depth of 3 m. The mouth of the Murray River is located at the northern end of the Coorong, *c.* 55 km north of the junction between the two lagoons. Historically, the Coorong ecosystem has been defined by a salinity gradient that increases with distance from the Murray Mouth, such that salinities observed during this study varied between 29‰ total dissolved solids (TDS) in the north near the Mouth, to 124‰ TDS at the southern extremity (Fig. 2; Geddes & Hall, 1990).

Waterbird counts

Complete counts of all waterbirds were performed in the Coorong wetlands annually between 2000 and 2007. These counts began between 4 January and 24 January, and were completed between 12 January and 2 February. The census period was chosen to coincide with the peak in population size of transequatorial migratory shorebirds in southern

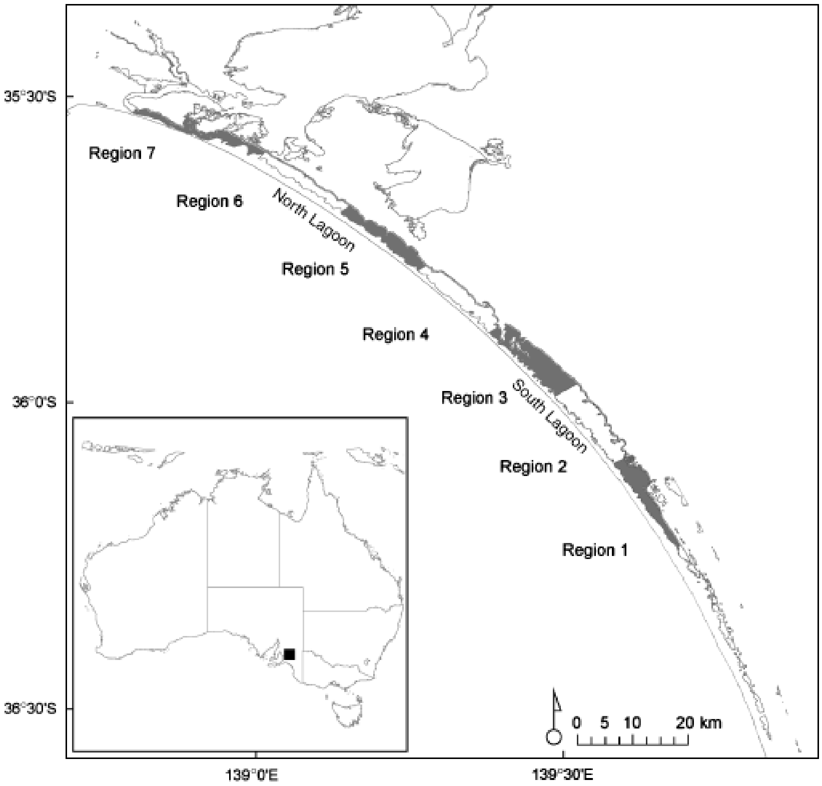

Figure 1 Maps showing the position of the Coorong wetland system in south-east South Australia. The main map shows the location of seven regions upon which the analyses presented here are based. The north lagoon and south lagoon of the Coorong are also marked. The inset shows the location of the Coorong in Australia (indicated by the black square).

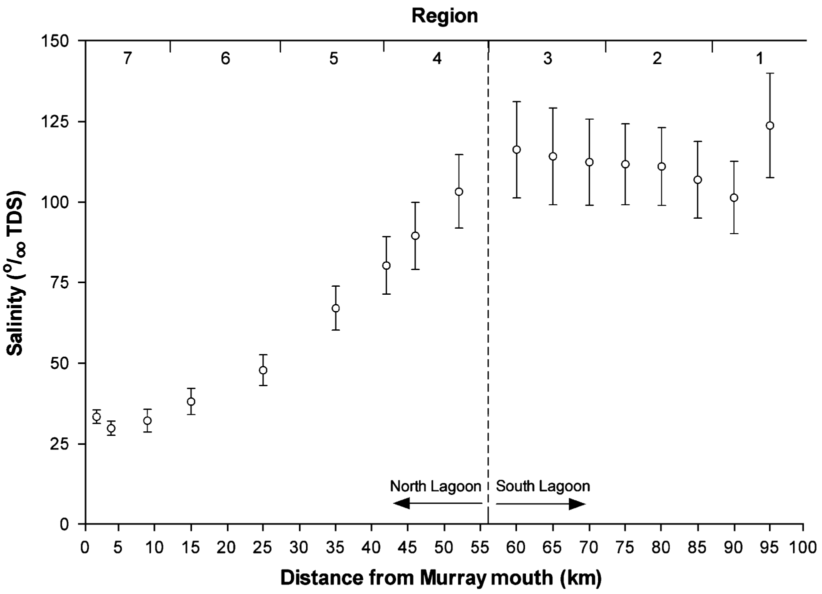

Figure 2 Mean (±SEM, $n=7$ years) salinity (in parts per thousand TDS) with distance from the mouth of the Murray River, along the Coorong. Each site was sampled once per year for 7 consecutive years (2001–2007). At each sampling site, a 1 L sample of water was collected, and salinity was subsequently measured in the laboratory using a Hanna H18220 conductivity meter (Hannah Instruments®, Padova, Italy), with samples being diluted in cases where the salinity of the sample was too high to be measured by the meter. Conductivity was converted to salinity (‰ TDS) using the equation developed by Williams (1986). The regions which the Coorong has been segregated for subsequent analyses are also presented at the top of the plot. TDS, total dissolved solids.

Australia (South Australian Department for Environment and Heritage, unpubl. data). The total census period ranged from 8 to 17 days.

Waterbird counts were performed on foot and by boat, by one to three observers trained in bird identification. Waterbird counts of the eastern and western shorelines of the Coorong were performed on foot, while waterbirds located in the centre of the lagoon were counted from a boat. Boats were also used to access and count birds on islands in the south lagoon, and other places inaccessible by foot. All waterbirds recorded were identified to species. The abundance of waterbirds was recorded within 1 km sections, with these locations being determined using printed topographical maps (1:50 000) of the Coorong. In addition, waterbird abundances were recorded within three components of each 1 km section, the land-side shoreline, sea-side shoreline and lagoon centre.

Analyses

For the community analyses presented in this paper, the Coorong wetlands were divided into seven regions, all *c.* 15 km in length (Fig. 1). With the exception of the boundary between regions 3 and 4 at Parnka Point, which corresponds to the junctions between the north and south lagoons of the Coorong, the boundaries between the regions were arbitrary, and corresponded to the seven regions sampled to determine spatiotemporal changes in the physical and biotic (aquatic plants and invertebrates) nature of the Coorong (Paton, 2005*b*). The community analyses presented here are thus grouped to these seven regions.

Community analyses were performed on the abundance of all waterbird species recorded at least once during the 8 survey years. A non-metric multidimensional scaling (NMS) analysis was performed on the fourth-root-transformed data for all waterbird data grouped by region and year, using Bray-Curtis dissimilarities. The ordinations presented in this paper show the relative distance between data points in multivariate space: data points that are closer together in the ordination reflect waterbird communities that are more similar than data points that are further apart (McCune & Grace, 2002). The grouping by region *and* year allowed both a determination of spatial variation in community structure (i.e. among regions), and temporal variation in community structure within a region, relative to spatial variation between regions. A blocked multiresponse permutation procedure (MRPP) was performed on the data, using Region as the grouping variable and Year as the block variable. MRPP compares intragroup distances (in this case, Bray-Curtis dissimilarities) with the average distances that result from all possible combinations in the data (i.e. across all groups). This test was used to determine whether the waterbird communities differed statistically among the regions.

In order to determine which species were important in structuring the waterbird community, indicator species analysis was performed (Dufrene & Legendre, 1997) for those species, where more than a total of 1000 individuals were recorded over the 8 sample years, with samples grouped by region. The statistical significance of these indicator species values was tested using Monte-Carlo techniques, within 1000 random permutations (McCune & Grace, 2002).

Longer-term changes

A complete count of waterbirds in the south lagoon of the Coorong was also conducted in January 1985 by three trained observers (including D. C. P.), and comparisons were also made between this count and those described above, to determine changes in the waterbird community over a longer time frame. This count was conducted between 10 January and 21 January 1985, using the same methods as described for the more recent counts. The data from this count were then compared with the seven annual counts described above. First, an NMS analysis was performed on fourth-root-transformed data using Bray-Curtis dissimilarities, with each sample representing the waterbird community of one of the three south lagoon regions, in each of the nine (1985 and 2000–2007) survey periods (total $n = 27$). Second, comparisons in the total abundance of species and functional guilds (see Table 2) between 1985 and 2000–2007 were performed between the values for the single count performed in 1985, and the mean values calculated across the eight counts performed between 2000 and 2007. Based on these mean values, the average change in abundance between the two survey periods was calculated, as the percentage increase or decrease relative to the values obtained in 1985 [i.e. % change = $((X_{2000\text{–}2007} - T_{1985})/T_{1985}) \times 100$, where $X_{2000\text{–}2007}$ is the mean value for the period 2000–2007, and T_{1985} is the total value obtained in 1985].

All multivariate analyses were performed using PC-ORD for Windows v5.0 (McCune & Mefford, 2006).

Global significance of Coorong waterbird populations

The global significance of the Coorong waterbird populations were assessed by comparing the total Coorong populations for each species, with flyway population estimates, acquired from Wetlands International's Waterbird Population Estimates (Wetlands International, 2006), for those species where global estimates exist. In particular, these comparisons were made in order to determine which species met Criterion 6 of the Ramsar Convention for wetlands of global significance, namely that a wetland 'regularly supports 1% of the individuals in a population of one species or subspecies of waterbird'. In this case, a species was found to *regularly* meet this criterion if 1% (or greater) of the estimated global population was recorded in the Coorong, in at least four of the eight surveys.

Results

Community analyses

A strong geographic gradients existed for the waterbird community structure of the Coorong wetlands, with the structure of the waterbird community changing consistently from north to south. Figure 3 presents the results of the NMS analysis of waterbird species abundance data (fourth-root-transformed), grouped by region, for the period 2000–2007. This analysis suggests that variation in community structure between regions is greater than variation in community structure between years within regions. Three distinct clusters were observed in the NMS ordination plot (Fig. 3). The waterbird community of region 7 (the region closest to the Murray Mouth, often referred to as the Murray Estuary; Phillips & Muller, 2006) is distinct from the communities of the remaining six regions. Regions 5 and 6 (comprising the bulk of the north lagoon) make up a second cluster, although overlap in community composition between these two regions was not absolute. A third distinct cluster was comprised of the waterbird communities of the south lagoon (regions 1–3), but also included the waterbird community of region 4, at the southern end of the north lagoon. Blocked MRPP confirmed that waterbird community structure differed significantly between these regions ($T = -18.56$, $A = 0.27$, $P < 0.0001$).

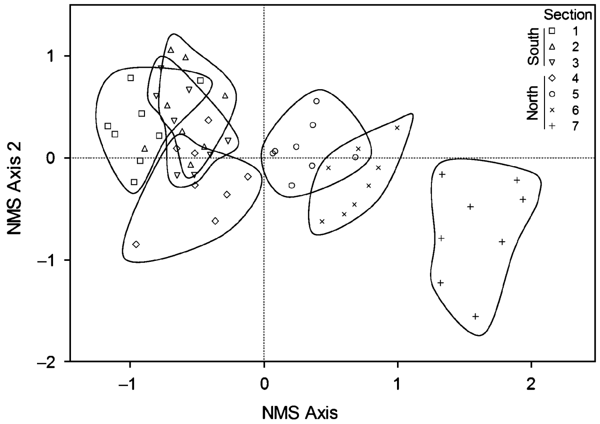

Figure 3 NMS plot of Bray-Curtis dissimilarities. This NMS analysis is based on fourth-root-transformed data for the total abundance of all species within each region in each year ($n = 56$ region-years). Stress for this two-dimensional solution = 0.135.

The results of the indicator species analysis are presented in Table 1. This analysis revealed that a large number of species acted as significant indicators for the waterbird community of region 7, confirming the distinct, species-rich nature of the Murray Estuary. Among these were species that are typically associated with freshwater and estuarine wetland systems, including black-winged stilt *Himantopus himantopus* and Australian white ibis *Threskiornis molucca*. The waterbird community of region 2 was best represented by three piscivorous species, Australian pelican *Pelecanus conspicillatus*, fairy tern *Sterna nereis* and crested tern *Sterna bergii*. All three species are known to nest within this region of the Coorong (see 'Discussion'). Red-necked stint *Calidris ruficollis*, the most common species recorded in the Coorong, was a significant indicator species for the community of region 4, immediately north of Parnka Point.

Longer-term changes in the Coorong south lagoon

Of the 27 most common waterbird species, 23 showed declines in abundance between 1985 and 2000–2007, based on the mean abundance value for each species over this latter period (Table 2). In addition, the maximum

Table 1 List of species for which a total of at least 1000 individuals were counted over the eight census periods, highlighting those species that were significant indicator species for the different regions of the Coorong

Species	Observed indicator value (IV)	P	Region
Fairy tern *Sterna nereis nereis*	**34.6**	**0.031**	**2**
Crested tern *Sterna bergii*	**67.5**	**0.001**	**2**
Australian pelican *Pelecanus conspicillatus*	**30.2**	**0.002**	**2**
Banded stilt *Cladorhynchus leucocephalus*	35.9	0.176	2
Red-necked avocet *Recurvirostra novaehollandiae*	29.9	0.196	3
Hoary-headed grebe *Poliocephalus poliocephalus*	30.7	0.508	3
Chestnut teal *Anas castanea*	**38.4**	**0.001**	**4**
Australian shelduck *Tadornis tadornoides*	**38.7**	**0.042**	**4**
Red-necked stint *Calidris ruficollis*	**38.3**	**0.003**	**4**
Red-capped plover *Charadrius ruficapillus*	**28.7**	**0.035**	**4**
Whiskered tern *Chlidonias hybridus fluviatilis*	36.9	0.479	4
Grey teal *Anas gracilis gracilis*	24.6	0.154	4
Little black cormorant *Phalacrocorax sulcirostris*	**52.0**	**0.007**	**5**
Pied cormorant *Phalacrocorax varius*	**48.6**	**0.001**	**6**
Great cormorant *Phalacrocorax carbo carboides*	**67.7**	**0.001**	**6**
Great crested grebe *Podiceps cristatus australis*	33.4	0.205	6
Little pied cormorant *Phalacrocorax melanoleucos*	**61.7**	**0.001**	**7**
Black swan *Cygnus atratus*	**66.8**	**0.001**	**7**
Pacific black duck *Anas superciliosa*	**76.4**	**0.001**	**7**
Musk duck *Biziura lobata*	**55.9**	**0.001**	**7**
White-faced heron *Egretta novaehollandiae*	**36.1**	**0.001**	**7**
Australian white ibis *Threskiornis molucca*	**83.9**	**0.001**	**7**
Common greenshank *Tringa nebularia*	**44.6**	**0.001**	**7**
Curlew sandpiper *Calidris ferruginea*	**45.0**	**0.002**	**7**
Pied oystercatcher *Haematopus longirostris*	**33.7**	**0.002**	**7**
Masked lapwing *Vanellus miles*	**25.1**	**0.019**	**7**
Black-winged stilt *Himantopus leucocephalus*	**38.2**	**0.015**	**7**
Caspian tern *Sterna caspia strenua*	**40.6**	**0.002**	**7**
Sharp-tailed sandpiper *Calidris acuminata*	**35.2**	**0.025**	**7**
Silver gull *Larus novaehollandiae*	24.5	0.096	7

The P value is the proportion of randomized trials in which the indicator value was equal to or greater than the observed indicator value; species with $P<0.05$ are marked in bold as significant indicator species. The region given for each species is the region for which the species acts as an indicator.

abundance for 19 of these species in the period 2000–2007 was lower than their abundance in 1985. Species showing dramatic declines in the south lagoon include the most common species in the Coorong, such as grey teal *Anas gracilis* (83.7% decline). The four migratory shorebirds commonly seen in the Coorong (common greenshank *Tringa nebularia*, sharp-tailed sandpiper *Calidris acuminata*, red-necked stint *C. ruficollis* and curlew sandpiper *Calidris ferruginea*) all declined in abundance between the two periods, with the mean abundance in 2000–2007 ranging from 6.5 to 34.4% of 1985 abundance. Of four species that showed increases in abundance between the two periods, banded stilt *Cladorhynchus leucocephalus* are strongly associated with ephemeral salt lakes, and became especially abundant in the Coorong following the arrival of Australian brine-shrimp *Parartemia zietziana* into the system in 2004–2005 (Fig. 4; Geddes, 2005). These patterns of decline are also reflected in analyses of foraging guilds (Fig. 4). The only guild that has not declined in abundance is large endemic waders; this can again be explained by the recent increases in banded stilt abundance (Fig. 4).

The NMS analysis revealed that the waterbird communities of the south lagoon in January 1985 were distinct from those in January 2000–January 2007 (Fig. 5), a distinction that was confirmed by MRPP ($T=-15.77$, $A=0.58$, $P=0.00002$). In addition, the waterbird communities of the south lagoon in 1985 appeared to have higher spatial diversity than those in the period 2000–2007, as reflected by the within-year distances between regions on the NMS plot.

Global significance of Coorong waterbird populations

Under the Ramsar Convention, a wetland is considered internationally important to waterbird populations if it 'regularly supports 20 000 or more waterbirds' (Criterion 5), or 'if it regularly supports 1% of the individuals in a population of one species or subspecies of waterbird' (Criterion 6). Based on the mean annual waterbird population estimated from the annual surveys, the Coorong certainly meets Criterion 5, with a minimum waterbird count of 111 723 individuals in 2000 (mean ± SE = 152 577 ± 18 224,

Table 2 Common (maximum count of >100 individuals in any 1 year) waterbird species recorded in the Coorong South Lagoon in 1985 and between 2000 and 2007

Species	1985	2000–2007 ($X\pm$ SE)	2000–2007 (range)	% Change
Australian pelican *Pelecanus conspicillatus* (P)	6045	1370.9 ± 320.4	394–2600	−77.3
Black-faced cormorant *Phalacrocorax fuscescens* (P)	84	49.9 ± 17.6	0–132	−40.6
Little black cormorant *Phalacrocorax sulcirostris* (P)	1190	72.3 ± 52.1	0–430	−93.9
Great crested grebe *Podiceps cristatus* (P)	263	19.4 ± 11.2	0–94	−92.6
Hoary-headed grebe *Poliocephalus poliocephalus* (P)	16 766	2517.9 ± 954.7	50–8141	−85.0
Black swan *Cygnus atratus* (D)	676	275.1 ± 58.3	68–526	−59.3
Australian shelduck *Tadorna tadornoides* (D)	6059	3290.4 ± 625.3	1339–6242	−45.7
Grey teal *Anas gracilis* (D)	59 113	8727.1 ± 2692.8	2446–24 460	−85.2
Chestnut teal *Anas castanea* (D)	660	4110.8 ± 989.1	430–10 147	+522.8
Pink-eared duck *Malacorhynchus membranaceus* (D)	–	98.2 ± 93.1	0–749	NA
White-faced heron *Ardea novaehollandiae* (P)	128	39.1 ± 8.4	15–75	−69.4
Straw-necked ibis *Threskiornis spinicollis* (L)	150	0.1 ± 0.1	0–1	−99.9
Common greenshank *Tringa nebularia* (M)	313	59.6 ± 10.6	16–103	−80.1
Sharp-tailed sandpiper *Calidris acuminata* (M)	6013	2218.4 ± 515.7	188–4202	−63.1
Red-necked stint *Calidris ruficollis* (M)	29 020	9197.9 ± 2298.0	1591–22 453	−68.3
Curlew sandpiper *Calidris ferruginea* (M)	9449	548.6 ± 394.7	7–3198	−94.2
Pied oystercatcher *Haematopus longirostris* (L)	142	59.6 ± 12.0	15–113	−58.0
Masked lapwing *Vanellus miles* (L)	323	162.0 ± 20.6	86–262	−49.8
Red-capped plover *Charadrius ruficapillus* (S)	2158	535.3 ± 121.6	206–1038	−75.2
Black-winged stilt *Himantopus himantopus* (L)	32	145.3 ± 75.3	14–505	+353.9
Banded stilt *Cladorhynchus leucocephalus* (L)	6208	22 257.4 ± 9284.9	1297–64 250	+258.5
Red-necked avocet *Recurvirostra novaehollandiae* (L)	7210	1819.8 ± 564.0	104–4864	−74.8
Silver gull *Larus novaehollandiae* (P)	4090	2830.4 ± 895.0	1077–8445	−30.8
Whiskered tern *Chlidonias hybridus* (P)	2656	1096.6 ± 273.5	334–2847	−58.7
Caspian tern *Sterna caspia* (P)	329	79.9 ± 42.1	0–345	−75.7
Fairy tern *Sterna nereis* (P)	1330	238.9 ± 74.7	6–586	−82.0
Crested tern *Sterna bergii* (P)	6687	3293.6 ± 864.3	877–8186	−50.7

The total abundance for each species is given for 1985, along with the mean (± SE) abundance, and abundance range, for the 8 years between 2000 and 2007. The % change is the percentage increase (positive) or decrease (negative) in abundance relative to the species' abundance in 1985 (calculated using the mean abundance for the period 2000–2007). The letter in parentheses following each species represents the guild that the species belongs to, for subsequent guild analyses: P, piscivores; D, ducks, swans and geese; M, migratory shorebirds; L, large non-migratory waders; S, small non-migratory shorebirds.

$n = 8$). For individual species of waterbird, global population estimates and 1% population levels, were acquired for 47 of the 68 species from Wetlands International (2006). Of these 47 species, the Coorong supported nine species whose population size was >1% of their estimated global population, in at least four of the eight surveys (Table 3), thus meeting the requirements of Criterion 6 of the Ramsar Convention. Furthermore, for four species, the Coorong supported >20% of the flyway population. For example, 36.2% of the estimated global population of banded stilt was recorded on the Coorong in 2006. These data also highlight the importance of the Coorong for transequatorial migratory shorebirds, with as much as 13.7% of the estimated global red-necked stint population, and 21.2% of the estimated global sharp-tailed sandpiper *C. acuminata* population, wintering on the Coorong wetlands (Table 3). The Coorong wetlands also support significant populations (up to 26.6% of the global population) of the south-eastern fairy tern *Sterna nereis nereis*, a taxa of conservation concern (e.g. listed as Vulnerable under the South Australian NPW Act 1972).

Discussion

The results presented here confirm the global significance of the Coorong wetlands as waterbird habitat. Nine species of waterbird regularly use the Coorong at levels of abundance that are deemed globally significant, and, for four species, often exceed 20% of the estimated global or flyway population. Among these species are both breeding and non-breeding endemic waterbirds, and three species of transequatorial migratory shorebird. In addition, spatial analyses of the waterbird community suggest that, within the Coorong, a range of wetland habitats exist, that subsequently support a diverse and spatially stratified waterbird community.

Over the 8-year time-frame of this study, the waterbird community of a particular region typically varied less through time, relative to the spatial variation in community structure. Over this time scale, this result probably reflects the relatively static distribution of some key resources, such as mudflats for shorebirds, or nesting sites for Australian pelican, and fairy and crested terns. However, the recent

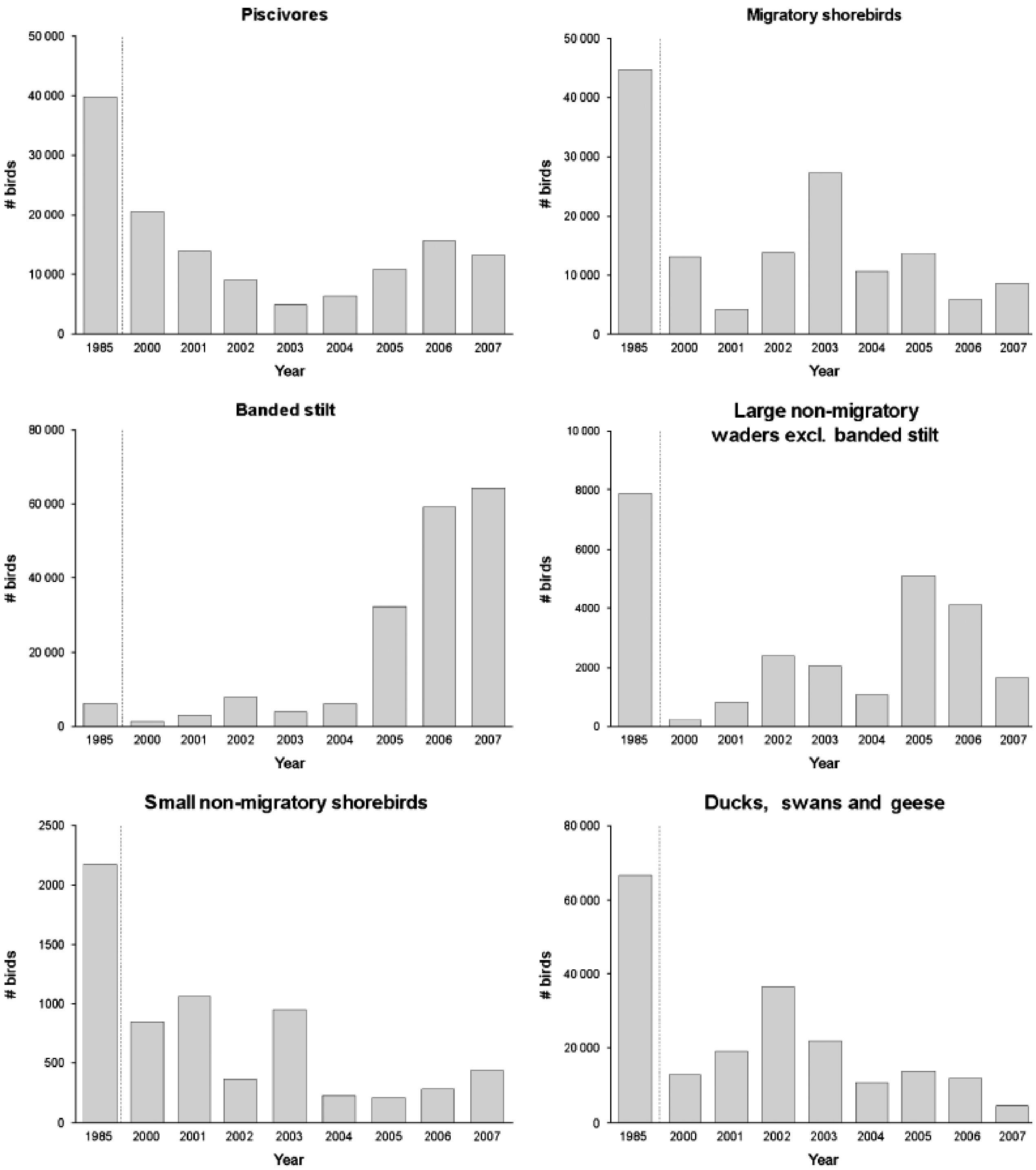

Figure 4 Changes in the abundance of five guilds of waterbird in the Coorong south lagoon, between 1985 and 2007. See Table 2 for the guild membership of each species.

temporal stability of the Coorong waterbird communities contrasts with the longer-term changes that have occurred to these waterbird communities (see also Kingsford & Norman, 2002; Chambers & Loyn, 2006). In the south lagoon of the Coorong, the majority of species, and particularly those that dominate the community, have declined in the period between 1985 and 2000–2007. Multivariate analysis also revealed that the community as a whole has changed, and became more spatially homogenous in the south lagoon, in this time-frame. Limiting this historical comparison to a single year (1985) subsequently limits the conclusions that can be drawn regarding changes in waterbird community composition, particularly given the stochastic nature of waterbird abundance in Australia (Kingsford & Norman, 2002). However, this comparison for the Coorong waterbirds is also supported by continuous datasets for migratory shorebirds in the Coorong, which also suggest an increasing constriction in the distribution of shorebirds in the Coorong, to the northern regions of the wetland system (Gosbell & Grear, 2005). Such shifts in distribution and abundance can be attributed to changes in the distribution of key food resources, such as benthic macroinvertebrates and aquatic vegetation; namely, increasing salinities in the south lagoon have dramatically restricted the distribution, and reduced the abundance of these resources (Phillips & Muller, 2006). Therefore, while the structural habitat (e.g. mudflats) required by some waterbird species (such as shorebirds) may be relatively stable through time, food resources appear to have shifted in distribution, resulting in concurrent changes in the distribution of some waterbird species.

The spatial distribution of key bird species listed generally reflects the distribution of food resource availability, both in relation to the abundance of food items, and ease of access to these food items by the birds. This is especially the case for the transequatorial and other non-breeding shorebirds, such as the *Calidris* shorebirds. However, the distribution of some species within the Coorong is not linked to food resources, as they either do not harvest prey within the Coorong wetland system (e.g. crested tern), or their foraging habitat is distributed differently to what their distribution suggests. Both fairy tern and Australian pelican nest within the Coorong wetlands, and their identification as indicator species for components of the Coorong south lagoon are primarily driven by the distribution of nest-site opportunities. However, even these piscivorous species have now largely vacated the south lagoon (see Fig. 4, Table 2), indicating that their presence in this part of the Coorong is as much related to changes in food supply as to the presence of suitable nesting opportunities. Identifying these different ecological factors is important for conservation, and is dependent on which factors are limiting for each species.

In the Coorong, salinity is seen as the principle driving factor for spatiotemporal variation in community structure, both for birds other components of the ecosystem (Geddes & Hall, 1990; Geddes, 2005). However, salinity is thought to indirectly impact on the distribution of waterbird habitat, through its influence on the distribution of food resources. Rather, the Coorong's water depth regime is crucial for the maintenance of waterbird habitat (Paton, 2000; Webster, 2005), through changes in the availability of suitably inundated mudflats. Significantly, the spatiotemporal dynamics of both salinity and water depth are closely linked to freshwater inflows and the maintenance of an open Murray Mouth (Webster, 2005). Future research will need to focus on the links between these important drivers, and how they influence both the structure of the waterbird communities,

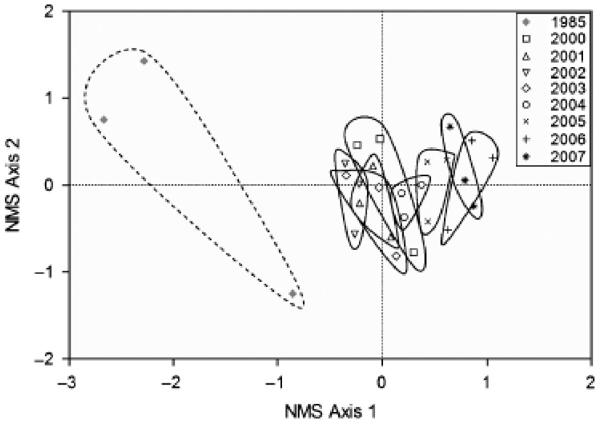

Figure 5 NMS plot based on the abundance of all waterbird species within the three regions of the Coorong south lagoon, across the eight surveys ($n=24$). NMS, non-metric multidimensional scaling.

Table 3 List of species whose Coorong populations were >1% of estimated flyway populations in at least four of the eight surveys performed, thus meeting the requirements of Criterion 6 of the Ramsar Convention

Species	Abundance (mean ± SEM)	Abundance (range)	Global population (estimated)	# Censuses >1%	Maximum % of global population
Chestnut teal *Anas castanea*	12 237 ± 2113	3037–21 302	100 000[a]	8	21.3
Sharp-tailed sandpiper *Calidris acuminata*	14 244 ± 3098	4399–33 897	160 000	8	21.2
Red-necked stint *Calidris ruficollis*	29 541 ± 2898	17 478–43 300	315 000	8	13.5
Curlew sandpiper *Calidris ferruginea*	3760 ± 754	1830–8157	180 000[b]	8	4.5
Pied oystercatcher *Haematopus longirostris*	164 ± 14	113–220	11 000	8	2.0
Red-capped plover *Charadrius ruficapillus*	1083 ± 151	474–1638	95 000	5	1.7
Banded stilt *Cladorhynchus leucocephalus*	27 150 ± 9849	2354–74 624	206 000	8	35.5
Red-necked avocet *Recurvirostra novaehollandiae*	3077 ± 750	163–6030	107 000	6	5.5
Fairy tern *Sterna nereis nereis*	389 ± 63	175–687	2580[a]	8	27.5

Flyway population estimates were taken from Wetlands International (2006). '# Censuses' refers to the number of surveys in which the 1% criterion was met between 2000 and 2007 (maximum = 8). Flyway populations are identical to the total global of the species, except for:

[a] South-east Australian subspecies.

[b] Australian wintering population.

and the availability of both physical (e.g. mudflats) and biotic (e.g. food availability) bird habitats.

The results presented here highlight the diversity of wetland ecosystems represented within the Coorong system, as suggested by the diversity of waterbird communities represented. Given that this ecological diversity is an important value of the Coorong (Department for Environment and Heritage, 2000; Phillips & Muller, 2006), future management strategies need to ensure that this diversity of wetland systems is maintained, rather than homogenizing the entire system to some 'ideal' state (such as estuarine or marine). This current study simply reinforces this notion, by demonstrating that such system diversity supports a range of distinct waterbird communities. More broadly, within-wetland habitat diversity is likely to be widespread, particularly in estuaries, but is also under-reported. This lack of knowledge will have important implications for the design of management strategies that aim to optimize biological diversity, and should be addressed in future studies of estuarine communities.

Recent evidence suggests that the Coorong system as a whole is in dramatic decline, particularly the hypermarine systems of the southern end (Paton, 2005*a*; Phillips & Muller, 2006). This decline is reflected in long-term changes to the waterbird community, with the abundance of many species for which the Coorong is globally important having declined over the past 20 years (Gosbell & Grear, 2005; this study). For some of these waterbird species (e.g. red-necked stint, sharp-tailed sandpiper), the Coorong has traditionally been the most important site in Australia (Watkins, 1993), and a local decline in habitat suitability (as has occurred) will thus have serious implications for these species globally. The maintenance of the Coorong ecosystems in general, and waterbird communities in particular, are inexorably linked to appropriate management of water regimes, both locally, and throughout the Murray-Darling Basin. Understanding the complex links between water regime, food availability, habitat availability and the performance of waterbirds represents the next big challenge in our understanding, but it is one that is critical if we are to manage the Coorong system appropriately for the maintenance of its waterbird populations.

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