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DAM AND GEOMORPHOLOGICAL INFLUENCES ON COLORADO RIVER WATERBIRD DISTRIBUTION, GRAND CANYON, ARIZONA, USA

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ABSTRACT

Impoundment effects override natural, reach-based channel geomorphology influences on seasonal waterbird distribution in Grand Canyon along the Colorado River downstream from Glen Canyon Dam. Large winter waterbird populations were rare or non-existent prior to completion of Glen Canyon Dam in 1963, and pre-dam summer breeding was rare. Post-dam river corridor surveys of 13 geomorphological reaches from 1973 to 1994 detected 58 species of waterfowl, waders, shorebirds and piscivorous raptors, with a grand mean of 138·2 waterbirds/reach (SE = 31·0, $n = 727$ reach surveys), and a mean area-adjusted rate of encounter (AARE) of 372·8 waterbirds km^{-1} h^{-1} of observation per reach (SE = 69·1). The post-dam assemblage has been dominated by Anseriformes (13 diving and 12 dabbling species) and includes regionally significant populations of wintering waterfowl and bald eagle, and breeding mallard. Most wading birds and shorebirds occur primarily as migrants or summer vagrants.

Total waterbird AARE was greatest in the productive clear water (CW) and variably turbid (VT) segments upstream from the Little Colorado River (LCR) (km 98), decreasing downstream on the usually turbid (UT) lower Grand Canyon segment. Mean total winter waterfowl AARE was 1076·8, and decreased by three orders of magnitude from the CW to the UT segments ($p = 0{\cdot}0001$). Mean total summer AARE was 2·7, and also decreased across the turbidity segments ($p = 0{\cdot}066$). In contrast, AARE varied little between wide and narrow geomorphological reaches. Total AARE was only 1·4 and 1·3-fold greater in wide versus narrow reaches within the VT and UT turbidity segments, respectively ($p < 0{\cdot}0002$). Winter AARE was threefold greater ($p = 0{\cdot}0002$), while summer AARE was equivalent between wide and narrow reaches. These tributary-related turbidity and geomorphological reach width factors contributed to a non-linear, circuitous shift in the waterbird assemblage over distance downstream from the dam, differentially affecting the seasonal distribution of waterbird feeding guilds. We discuss flow regulation and habitat management implications. ©1997 by John Wiley & Sons, Ltd.

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INTRODUCTION

Flow regulation is an ubiquitous modification of fluvial ecosystems (Ward and Stanford, 1979; Lillehammer and Saltveit, 1984; Gore and Petts, 1989) that can influence the distribution of riverine waterbirds (aquatic and semi-aquatic avifauna) through modification of habitats and food resources. The natural channel geometry of large, complex rivers also affects waterbird food and habitat availability (Hupp 1988; Stevens *et al*., 1995, 1997), but the influences of flow regulation versus natural channel geomorphology on river waterbird distribution have not been differentiated. Such information is important for evaluating the extent to which flow regulation alters the trophic structure of river ecosystems.

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River regulation effects on waterbird distribution are of ecological interest because of the changing status of some economically important species owing to recreational hunting and land development (Caithamer *et al*., 1994), legal and conservation biology issues (e.g. endangered species management), effects on ecosystem nutrient dynamics (Andrikovics and Andrikovics, 1992), human health issues (i.e. transmission of parasites; Blair and Finlayson, 1981), and habitat relationships (Dahl, 1990; Gregory *et al*., 1991; Rushton *et al*., 1994). Long-term monitoring from 1955 to 1994 in the United States shows that Canada goose (*Branta canadensis*), gadwall (*Anas strepera*) and northern shoveler (*A. clypeata*) populations increased, while green-winged teal (*Anas crecca*) and canvasback (*Aythya valisineria*) populations remained unchanged, northern pintail (*Anas acuta*) populations decreased and American wigeon (*Anas americana*) and blue-winged teal (*Anas discors*) populations fluctuated in abundance (Flather and Hoekstra, 1989; Caithamer *et al*., 1994). Bald eagle (*Haliaeetus leucocephalus*) populations have decreased (Spencer *et al*., 1991) or increased (Brown *et al*., 1989; Hunt *et al*., 1992; Brown and Stevens, in press) in regulated river ecosystems, depending on management practices. Several wading and shorebird populations have declined along regulated rivers (Repking and Ohmart, 1977; Books, 1985; Ziewitze *et al*., 1992). Few data are available on population trends of some passerine river waterbirds, such as American dippers (*Cinclus mexicanus*) and pipits (*Anthus* spp.), or other terrestrial vertebrates, in regulated river ecosystems (Nilsson and Dynesius, 1994).

Flow regulation alters large river ecosystems through complex changes in hydrology and flood frequency; sediment transport; water chemistry, temperature and clarity; organic drift; and wetland and riparian vegetation cover (Miller *et al*., 1983; Armitage, 1984; Nilsson, 1984; Hupp, 1988; Ohmart *et al*,. 1988; Lieberman and Burke, 1993). Short-term flow variation may erode streamside habitats and change reach-based and microsite resource availability (Schmidt *et al*., 1995; Stevens *et al*., 1995), resulting in species-specific changes in waterbird distribution (Rickard *et al*., 1982; Ziewitze *et al*., 1992). In addition, flow regulation may increase predation pressure, including human hunting (Books, 1985; Anderson and Ohmart, 1988). Tributary contributions of flow and sediment increase turbidity and natural flow variability downstream, depending on tributary size and location (Ward and Stanford, 1983; Minshall *et al*., 1992; Roos and Pierterse, 1994). Thus, flow regulation resets key physical parameters, particularly in large, geologically constrained rivers. These changes are overlaid on pre-existing channel conditions which were previously governed by natural geomorphological processes. Therefore, flow regulation may affect waterbird distribution by altering resource availability.

Waterbird assemblages respond strongly to dam-induced habitat changes, and are indicators of ecosystem change. Waterbird populations often increase on reservoirs in response to development of new habitats and food resources (Wiebe, 1946; Anderson and Ohmart, 1988; Grubaugh and Anderson, 1988; Breininger and Smith, 1990; Fruget, 1992), and vary according to season, migration routes (Pandey, 1993) and lake surface area (Weller and Batt, 1988; Elmberg *et al*., 1994). Although waterbirds are generally regarded as rare in fluvial ecosystems (Steele and Vander Wall, 1985), the few studies conducted on waterbirds on impounded rivers indicate that significant population changes have occurred following flow regulation (Rickard *et al*., 1982; Anderson and Ohmart, 1988). Therefore, changes in waterbird populations on dammed rivers may help distinguish between the effects of flow regulation and the influences of natural channel geomorphology on river ecosystems.

We examined the influences of Glen Canyon Dam and natural channel geometry on the seasonal distribution of five Colorado River waterbird feeding guilds: dabbling waterfowl, diving waterfowl, wading birds, shorebirds and piscivorous raptors. First, we present a synopsis of historical information to evaluate pre-dam and post-dam waterbird distribution. Next, we present a reach-based analysis of post-dam waterbird distribution to distinguish between the influences of seasonality, flow regulation (distance-related turbidity) and geomorphology. We discuss the mechanisms responsible for these patterns and changes, and the implications for waterbird management in large regulated river ecosystems.

METHODS

Study site and background

The Colorado River flows 472 km and drops from 957 m to 370 m elevation (a total of 590 m) between Glen Canyon Dam and Lake Mead, Arizona. The river traverses the deserts of lower Glen Canyon and all of Grand

Canyon (Figure 1). Glen Canyon Dam lies 24·6 km upstream from Lees Ferry, from which distances along the river are measured. Hunting was permitted on the uppermost 24 km of the river in Glen Canyon National Recreation Area (except near Glen Canyon Dam and at Lees Ferry) during this study, but not in Grand Canyon. Additional climate and geographical information, and the history of flow regulation are discussed in Sellers and Hill (1974), Howard and Dolan (1981), Schmidt and Graf (1990), Marzolf (1991), and Stevens *et al.* (1995, 1997).

The Colorado River between Glen Canyon Dam and Lake Mead includes 13 bedrock-defined reaches (Howard and Dolan, 1981; modified from Schmidt and Graf, 1990; Table I). Reduced flood frequency and sediment transport (turbidity) has altered some geomorphological characteristics of the Colorado River, including extent of channel bed armouring and the geometry of riffles and rapids (Kieffer, 1985), thereby affecting substrate-dependent production of benthic and riparian vegetation. These resources comprise the autochthonous lower trophic levels and potential food and habitat of waterbirds. Water clarity and benthic production in the upper 123 km has been associated with increased densities of rainbow trout (*Oncorhynchus mykiss*), wintering bald eagle and breeding mallard (*Anas platyrhynchos*) (Brown *et al.*, 1987, 1989; Blinn and Cole, 1991; Blinn *et al.*, 1995; Stevens *et al.* 1997). Riparian and low velocity aquatic habitat and food resource availability are positively correlated with reach width (Stevens *et al.*, 1995), and increased post-dam shoreline and wetland and riparian vegetation are correlated with river avifauna density (Turner and Karpiscak, 1980; Brown and Trosset, 1989; Johnson, 1991).

Water clarity decreases over distance from Glen Canyon Dam as tributaries contribute seasonally varying suspended sediment loads (Andrews, 1991; Table I; Figure 1). This creates three major turbidity segments within

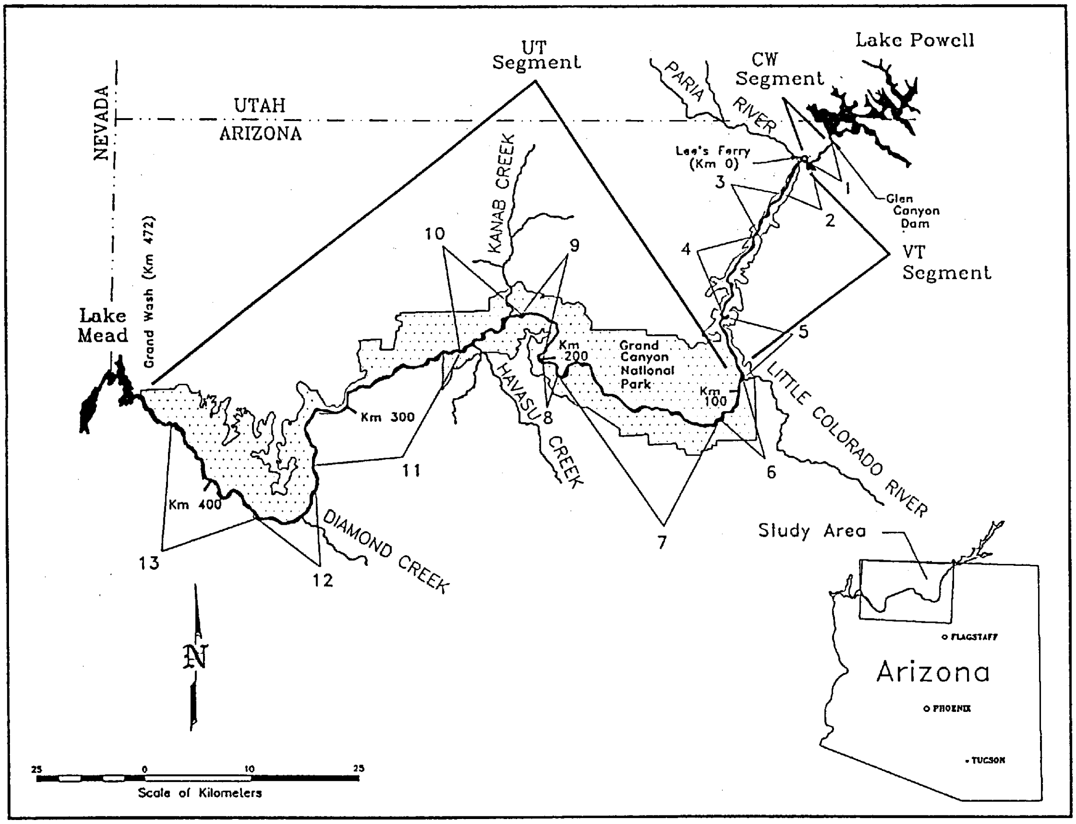

Figure 1. Map of the Colorado River between Lake Powell and Lake Mead, Arizona, including major tributaries. Turbidity segments include the clear water (CW, the geomorphologically wide reach 1), variably turbid (VT, wide reaches 2 and 5, and narrow reaches 3 and 4) and usually turbid (UT, wide reaches 6 and 11, and narrow reaches 7–10 and 12) segments. Reach names are listed in Table I

Table I. Geomorphological reaches (Figure 1), selected reach characteristics and duration of waterbird censuses/reach between Glen Canyon Dam and Lake Mead, Arizona, 1973–1994

Distance from Lees Ferry (km)[a]	Reach name (number)[a]	Mean reach width (m)[b]	Water surface area (km^2)[b]	Mean Secchi depth (m)[c]	Mean 1991 AFD algal mass (m)[c]	Mean 1991 AFD invert mass (m)[c]	Total 1991 marsh cover (ha)[d]	Number of surveys per reach	Mean census duration (h, 1SD)	Total census duration (h)
−24·6–1·0	Glen Canyon (1)	158 W	4·04	5·4 ±1·01	7·00 ±19·96	1·34 ±4·03	—	49	0·52 (0·306)	25·38
1·0–17·7	Permian Gorge (2)	94 W	1·57	4·3 ±2·12	0·38 ±1·46	0·21 ±0·78	0·77	65	2·32 (0·821)	150·64
17·7–36·2	Supai Gorge (3)	52 N	0·96	—	—	—	0·31	59	1·97 (0·938)	116·08
36·2–64·4	Redwall Gorge (4)	62 N	1·75	1·0 ±1·01	0·08 ±0·28	0·02 ±0·05	0·74	65	3·47 (1·699)	225·83
64·4–98·6	Marble Cyn (5)	88 W	3·01	1·1 ±1·10	0·76 ±3·10	0·10 ±0·29	5·14	69	5·48 (2·679)	378·38
98·6–124·5	Furnace Flats (6)	96 W	2·49	0·9 ±1·36	0·99 ±2·36	0·04 ±0·21	1·46	64	2·94 (1·705)	188·30
124·5–189·5	Upper Granite (7)	51 N	3·32	0·9 ±1·80	0·32 ±2·33	0·02 ±0·08	0·49	65	7·49 (3·239)	487·08
189·5–201·9	The Isles (8)	56 N	0·69	—	—	—	0·64	51	1·82 (0·900)	92·62
201·9–225·3	Mid. Granite (9)	52 N	1·22	—	—	—	0·45	57	3·41 (1·676)	194·28
225·3–257·4	Muav Gorge (10)	48 N	1·54	0·3 ±0·42	0·07 ±0·17	0·03 ±0·10	0·40	55	3·76 (1·638)	206·61
257·4–344·1	Lower Canyon (11)	80 W	6·94	0·6 ±0·40	0·43 ±0·84	0·02 ±0·09	12·58	59	9·95 (2·712)	587·03
344·1–386·2	Lower Granite (12)	68 N	2·86	0·6 ±0·10	0·52 ±1·75	0·02 ±0·15	4·46	56	3·03 (1·667)	169·80
386·2–448·9	Upper L. Mead (13)	235 W	14·73	—	—	—	—	13	4·94 (1·513)	64·22

[a] Modified from Schmidt and Graf (1990); N, narrow reach, W, wide reach.

[b] Derived from Randle and Pemberton's (1988) flow routing data at a discharge of 425 $m^3 s^{-1}$.

[c] Stevens *et al*. (1997) ash-free dry (AFD) standing biomass data from 1991.

[d] Stevens *et al*. (1995).

the river, as described by Stevens *et al*. (1997): the clear water (CW, km −24·6 to 1·0) segment between the dam and the Paria River confluence (km 1·0) contains the wide, cold-stenothermic Glen Canyon reach, with elevated water clarity and benthic algal and invertebrate standing mass (Angradi and Kubly, 1994; Blinn *et al*., 1995). The variably turbid (VT, km 1·0 to 98) segment between the Paria River and the Little Colorado River (LCR) contains two narrow and two wide reaches, with sediment concentrations as great as 780 000 g/l contributed by the Paria River (Graf *et al*., 1991). The usually turbid (UT, km 98 to 386) segment receives suspended sediment from upstream reaches, the LCR, Kanab Creek and other tributaries, and contains five narrow and two wide reaches, including the wide upper Lake Mead reach.

Historic waterbird distribution

Behle (1948), Behle and Higgins (1959) and Woodbury (1959) conducted limited avifaunal studies in Glen Canyon prior to impoundment; however, no detailed avian studies were performed on the pre-dam river in Grand Canyon. To determine pre-dam waterbird distribution, we interviewed two pre-dam residents, two dam construction workers and 10 pre-dam river runners, and compiled information from 31 published and unpublished journals and reports on $\geqslant 29$ partial or full pre-dam river trips during all months except April (Table II and Appendix).

Journal information may be unreliable in that (i) durations of observations within any reach were typically brief and therefore may not have been representative, (ii) expedition members may have been poor observers, or (iii) observers simply may not have recorded waterbirds they saw. However, many early river explorers were professional hunters and trappers who were aware of the significance of their expeditions, and were sufficiently inspired to document their expeditions carefully, including the wildlife they encountered. We have been careful not to over-extend conclusions based on these historical data.

Field data

We surveyed waterbird abundance during 42 full and 62 partial river trips ($\geqslant 2886$ hours of observation) from 1973 to 1994 (Table I). Waterbirds were enumerated and identified by one to three observers from motorized or oar-powered rafts. The river is generally narrow (23 to 150 m wide) and contains few islands; therefore, we were able to view virtually the entire expanse of the river during these surveys. Only waterbirds that were passed by the boat or flew upstream were counted, providing conservative estimates of abundance. Additional data were collected from 1990 to 1994 at Lees Ferry by surveying a 0·75-km reach of the river visible from km 0. Data were compiled by reach and feeding guild (Table II). Barrow's goldeneye (*Bucephalus islandica*) probably occurs rarely in large winter flocks of common goldeneye (*B. clangula*), but none were detected by us.

Analyses

We standardized waterbird abundance data for species/area effects and the duration of observation. The geomorphological reaches vary in width and water surface area, so we calculated the water surface area of each reach at 425 m^3/s (near the grand mean post-dam flow) using Randle and Pemberton's (1988) flow routing data. Daily kinematic wave movement through these relatively long reaches confounds precise calculation of water surface area, and we did not attempt calculation of surface area under unsteady flows. Also, the duration of waterbird observation periods varied between motorized versus oar-powered river trips. We standardized our data by dividing raw waterbird counts on each reach by the water surface area and the duration of observation, creating an area-adjusted rate of encounter (AARE):

$$\mathrm{AARE} = (\text{Number of birds})/(\text{Reach area})/(\text{Duration of observation})$$

with units of birds $\mathrm{km}^{-2}\,\mathrm{h}^{-1}$. Inter-observer effects were not significant ($p = 0{\cdot}059$); therefore, we pooled all AARE data, but conservatively evaluated our results (Verner and Milne, 1989).

We contrasted effects of distance from Glen Canyon Dam (across the three turbidity segments) with reach width and seasonal waterbird distribution. We conducted separate serial Bonferroni-adjusted (Rice, 1989) Friedman analyses on guild AARE data by reach, using trip as a blocking factor (Wilkinson, 1990). These analyses and Mann–Whitney tests were conducted separately by season for 33 winter, 12 spring (April), 38

Table II. Raw abundance (SE) and AARE (SE) by season, of all waterbird species observed on the Colorado River between Glen Canyon Dam and Lake Mead, Arizona, 1973–1994. Asterices indicate species that were observed prior to impoundment in 1963. Other rare species reported by other observers are included below (from Brown *et al*., 1994)

			April ($n = 98$)				Summer ($n = 390$)				October ($n = 33$)				Winter ($n = 206$)			
Common name	Scientific name	Guild	Mean number	Mean SE	Mean AARE	AARE SE	Mean number	Mean SE	Mean AARE	AARE SE	Mean number	Mean SE	Mean AARE	AARE SE	Mean number	Mean SE	Mean AARE	AARE SE
Common Loon	*Gavia immer*	DAB	0	0	0	0	0·003	0·003	0·001	0·001	0·03	0·03	0·001	0·001	0	0	0	0
Pied Billed Grebe	*Podilymbus podiceps*	DIV	0	0	0	0	0·003	0·003	t	t	0	0	0	0	0·068	0·054	0·18	0·135
Horned Grebe	*Podiceps auritus*	DIV	0	0	0	0	0	0	0	0	0·03	0·03	0·006	0·006	0	0	0	0
Eared Grebe	*Podiceps nigricollis*	DIV	0·02	0·014	0·262	0·259	0·003	0·003	0·001	0·001	0	0	0	0	0·005	0·005	t	t
Western Grebe*	*Aechmophorus oxidentalis*	DIV	0·041	0·025	0·093	0·09	0·021	0·016	t	t	0·061	0·042	0·517	0·508	0·01	0·007	0·238	0·168
American White Pelican	*Pelecanus erythrorynchos*	DAB	0·112	0·112	0·092	0·092	0·003	0·003	0·001	0·001	0	0	0	0	0	0	0	0
Double-crested Commorant	*Phalacrocorax auritus*	DIV	0·01	0·01	0·002	0·002	0·005	0·004	0·001	0·001	0·091	0·05	0·018	0·01	0·005	0·005	t	t
Great Blue Heron*	*Ardea herodias*	WAD	0·316	0·069	0·063	0·021	0·413	0·052	0·276	0·154	0·758	0·161	1·672	1·52	0·981	0·101	1·14	0·351
Snowy Egret*	*Egretta thula*	WAD	0·5	0·176	0·182	0·092	0·085	0·024	0·016	0·005	0·333	0·299	0·044	0·035	0	0	0	0
Cattle Egret	*Bubulcus ibis*	WAD	0·02	0·02	0·015	0·015	0·021	0·012	0·003	0·002	0	0	0	0	0	0	0	0
Green-backed Heron	*Butorides striatus*	WAD	0	0	0	0	0·008	0·004	0·001	0·001	0	0	0	0	0	0	0	0
Black-crowned Night Heron*	*Nycticorax nycticorax*	WAD	0·051	0·033	0·018	0·017	0·021	0·008	0·005	0·003	0	0	0	0	0·005	0·005	t	t
White-faced Ibis*	*Plegadis chihi*	WAD	0	0	0	0	0·015	0·007	0·002	0·001	0	0	0	0	0	0	0	0
Tundra Swan	*Cygnus columbianus*	DAB	0	0	0	0	0	0	0	0	0	0	0	0	t	t	t	t
Snow Goose*	*Chen caerulescens*	DAB	0	0	0	0	0	0	0	0	0	0	0	0	t	t	t	t
Canada Goose*	*Branta canadensis*	DAB	0·01	0·01	0·002	0·002	0·013	0·008	0·002	0·001	0	0	0	0	11·417	2·102	10·058	3·591
Wood Duck	*Aix sponsa*	DAB	0	0	0	0	0	0	0	0	0	0	0	0	0·005	0·005	0·001	0·001
Green-winged Teal*	*Anas crecca*	DAB	0·726	0·382	2·752	2·592	0·469	0·146	0·087	0·034	0·788	0·404	0·123	0·093	1·316	0·363	3·016	0·943
Mallard*	*Anas platyrhynchos*	DAB	3·735	1·24	2·421	1·822	2·682	0·383	1·069	0·51	5·848	2·157	31·141	19·856	2·432	1·761	32·342	7·588
Northern Pintail*	*Anas acuta*	DAB	0	0	0	0	0	0	0	0	0	0	0	0	0·859	0·652	0·811	0·464
Blue-winged Teal*	*Anas discors*	DAB	0·337	0·146	0·078	0·042	0·441	0·157	0·059	0·021	0·667	0·598	0·116	0·097	0·218	0·194	0·288	0·224
Cinnamon Teal*	*Anas cyanoptera*	DAB	1·316	0·31	1·564	1·296	0·254	0·064	0·064	0·028	0	0	0	0	0·374	0·265	0·391	0·331
Northern Shoveler	*Anas clypeata*	DAB	0·173	0·138	1·044	1·036	0·023	0·016	0·016	0·012	0	0	0	0	0·024	0·014	0·128	0·125
Gadwall*	*Anas strepera*	DAB	1·316	1·179	2·542	1·579	0·031	0·017	0·083	0·079	0·333	0·213	6·216	6·092	22·233	4·585	255·076	54·683
American Wigeon	*Anas americana*	DAB	0·235	0·132	0·888	0·864	0·008	0·006	0·002	0·002	0·03	0·03	1·547	1·523	17·277	3·239	149·547	29·616
Canvasback	*Aythya valisineria*	DIV	0	0	0	0	0	0	0	0	0	0	0	0	0·369	0·197	1·473	0·698
Redhead	*Aythya americana*	DIV	0·01	0·01	2·17	1·915	0	0	0	0	0·152	0·076	3·617	2·158	4·35	1·175	43·132	12·006
Ring-necked Duck	*Aythya collaris*	DIV	t	t	0·347	0·345	0	0	0	0	0	0	0	0	3·345	1·152	40·272	17·782
Lesser Scaup	*Aythya affinis*	DIV	0	0	0	0	0·008	0·004	0·001	0·001	0·03	0·03	1·547	1·523	9·471	2·797	147·218	42·659
Oldsquaw	*Clangula hyemalis*	DIV	0	0	0	0	0	0	0	0	0	0	0	0	0·019	0·01	0·282	0·14
Surf Scoter	*Melanitta perspicillata*	DIV	0	0	0	0	0·005	0·004	t	t	0·03	0·03	1·547	1·523	0·058	0·023	1·019	0·41
White-winged Scoter	*Melanitta fusca*	DIV	0	0	0	0	0	0	0	0	0	0	0	0	0·029	0·022	0·28	0·235
Common Goldeneye	*Bucephala clangula*	DIV	1·316	0·572	0·874	0·548	0·005	0·004	0·001	0	0·212	0·181	9·293	9·139	32·607	5·294	72·597	26·439
Bufflehead*	*Bucephala albeola*	DIV	1·051	0·856	12·742	12·264	0·003	0·003	0·001	0·001	0·879	0·675	38·684	33·68	2·398	1·956	190·611	43·905
Hooded Merganser*	*Lophodytes cucullatus*	DIV	0	0	0	0	0	0	0	0	0	0	0	0	0·184	0·057	3·126	1·088

Red-breasted Merganser*	*Mergus serrator*	DIV	t	t	t	t	0	0	0	0	0	0	0	0	0	0	0	0
Common Merganser	*Mergus merganser*	DIV	0·459	0·112	0·106	0·046	0·372	0·078	0·071	0·019	0·545	0·321	0·097	0·059	4·956	0·815	12·898	3·597
Ruddy Duck	*Oxyura jamaicensis*	DIV	0	0	0	0	0	0	0	0	0	0	0	0	0·18	0·072	2·532	1·184
Osprey	*Pandion haliaetus*	RAP	0·051	0·027	0·009	0·008	0·044	0·012	0·007	0·002	0·273	0·107	0·574	0·507	0·01	0·007	t	t
Bald Eagle*	*Haliaeetus leucocephalus*	RAP	0	0	0	0	0	0	0	0	0·061	0·042	0·01	0·007	0·481	0·089	0·129	0·03
Virginia Rail	*Rallus limicola*	SHOR	t	t	0·174	0·173	0	0	0	0	0	0	0	0	0	0	0	0
American Coot*	*Fulica americana*	DIV	0·031	0·023	0·001	0·001	0·049	0·019	0·002	0·001	0·061	0·042	0·003	0·002	0·816	0·22	5·139	2·01
Snowy Plover	*Charadrius alexandrinus*	SHOR	0	0	0	0	0	0	0	0	t	t	t	t	0	0	0	0
Semipalmated Plover	*Charadrius semipalmatus*	SHOR	0	0	0	0	0·003	0·003	t	t	0	0	0	0	0	0	0	0
Killdeer	*Charadrius vociferus*	SHOR	0·031	0·017	0·261	0·259	0·005	0·004	0·001	0·001	0	0	0	0	0·019	0·012	0·007	0·004
Black-necked Stilt	*Himantopus mexicanus*	SHOR	0	0	0	0	0·464	0·222	0·025	0·011	0	0	0	0	0	0	0	0
American Avocet*	*Recurvirostra americana*	SHOR	0·153	0·152	0·009	0·009	0·203	0·097	0·041	0·03	0	0	0	0	0	0	0	0
Solitary Sandpiper	*Tringa solitaria*	SHOR	0	0	0	0	0	0	0	0	0	0	0	0	0·005	0·005	t	t
Willet	*Catoptrophorus semipalmatus*	SHOR	1·867	0·946	0·086	0·046	0·013	0·009	0·001	0·001	0	0	0	0	0	0	0	0
Spotted Sandpiper	*Actitis macularia*	SHOR	0·551	0·203	0·092	0·031	1·718	0·159	0·589	0·263	0·303	0·109	0·047	0·022	0·073	0·041	0·012	0·008
Common Snipe*	*Gallinago gallinago*	SHOR	0	0	0	0	0	0	0	0	0	0	0	0	0·005	0·005	0·047	0·047
Wilson’s Phalarope	*Phalaropus galllinago*	SHOR	0	0	0	0	0	0	0	0	0	0	0	0	0·005	0·005	0·007	0·007
Red-necked? Phalarope	*Phalaropus lobatus*	SHOR	0	0	0	0	0·405	0·329	0·074	0·072	0	0	0	0	0	0	0	0
Ring-billed Gull	*Larus delawarensis*	SHOR	0·204	0·154	7·318	7·255	0·049	0·03	0·016	0·014	0	0	0	0	0·01	0·007	0·001	0·001
California Gull	*Larus californicus*	SHOR	0·306	0·294	0·07	0·069	0·021	0·018	t	t	0	0	0	0	0·063	0·048	0·028	0·026
Belted Kingfisher	*Ceryle alcyon*	DIV	0·51	0·084	0·153	0·052	0·062	0·018	0·008	0·003	0·03	0·03	0·016	0·016	0	0	0	0
American Dipper*	*Cinclus mexicanus*	SHOR	0·051	0·027	0·009	0·006	0·021	0·013	0·004	0·002	0·091	0·05	0·016	0·011	0·218	0·047	0·074	0·025
American Pipit	*Anthus spinoletta*	SHOR	0	0	0	0	0·005	0·004	t	t	0	0	0	0	0·005	0·005	0·001	0·001
Unid. Waders		WAD	0·041	0·02	0·007	0·004	0·051	0·033	0·009	0·006	0	0	0	0	0·044	0·044	0·007	0·007
Unid. Dabblers		DAB	1·469	1·061	0·259	0·239	0·444	0·114	0·079	0·028	1·121	0·531	1·632	1·522	11·646	4·87	38·421	17·551
Unid. Divers		DIV	1·02	0·935	0·231	0·214	0·028	0·015	0·002	0·001	0·03	0·03	0·001	0·001	3·354	0·882	13·431	11·018
Unid. Ducks			4·531	1·156	2·923	1·378	0·177	0·05	0·041	0·013	0·212	0·119	0·036	0·025	16·427	5·393	50·737	26·204
Unid. Shorebirds		SHOR	0·796	0·401	0·165	0·103	0·451	0·158	0·031	0·007	0·121	0·071	1·552	1·523	0·087	0·044	0·057	0·05
Divers		DIV	5·337	1·639	16·98	14·527	0·562	0·086	0·088	0·019	2·152	0·953	55·346	47·391	72·223	8·001	534·431	112·214
Dabblers		DAB	9·532	2·713	11·641	8·203	4·369	0·493	1·462	0·519	8·818	2·333	40·775	26·57	77·801	10·511	490·08	91·267
Waders		WAD	0·929	0·199	0·284	0·101	0·613	0·073	0·313	0·154	1·091	0·349	1·717	1·519	1·029	0·12	1·147	0·351
Raptors		RAP	0·051	0·027	0·009	0·008	0·044	0·012	0·007	0·002	0·333	0·119	0·584	0·507	0·49	0·09	0·129	0·03
Shorebirds		SHOR	4·388	1·254	8·183	7·253	3·356	0·475	0·781	0·275	0·515	0·129	1·615	1·521	0·49	0·089	0·234	0·077
Other		Other	4·531	1·156	2·923	1·378	0·177	0·05	0·041	0·013	0·212	0·119	0·036	0·025	16·427	5·393	50·737	26·204
Total		ALL	24·767	4·534	40·02	25·321	9·121	0·767	2·692	0·707	13·121	2·71	100·073	72·949	168·461	18·648	1076·758	203·956

Other waterbird species reported from Grand Canyon, but not observed by us during the study period: Pacific loon (*Gavia pacifica*), brown pelican* (*Pelicanus occidentalis*), magnificent frigatebird (*Fregata magnificens*), American bittern (*Botaurus lentiginosus*), great egret (*Casmerodius albus*), wood stork (*Mycteria americana*), Eurasian wigeon (*Anas penelope*), Barrow’s goldeneye (*Bucephala islandica*), sora (*Porzana carolina*), common moorhen (*Gallinula chloropus*), sandhill crane (*Grus canadensis*), greater yellowlegs (*Tringa melanoleuca*), lesser yellowlegs (*Tringa flavipes*), long-billed curlew (*Numenius americana*), marbled godwit (*Limosa fedoa*), semipalmated sandpiper (*Calidris pusilla*), western sandpiper (*Calidris mauri*), least sandpiper (*Calidris minutilla*), pectoral sandpiper (*Calidris melanotos*), dunlin (*Calidris alpina*), long-billed dowitcher (*Limnodromus scolopaceus*), Bonaparte’s gull (*Larus philadelphia*), herring gull (*Larus argentatus*), Sabine’s gull (*Xema sabini*), common tern (*Sterna hirundo),* Forster’s tern (*Sterna forsteri*), black tern (*Chlidonias niger*) summer, and 4 autumn (October) trips. We present only descriptive data for the UT Upper Lake Mead reach (13), on which few surveys were conducted.

We described reach-based and temporal waterbird distribution using canonical community ordination (CANOCO; Ter Braak, 1992). This modified canonical correlation analysis seeks to describe patterns of assemblage composition in relation to patterns among environmental variables. CANOCO also eliminates undesirable correlations between multivariate axes, which may confound principal components analyses (Palmer, 1993). CANOCO assumes a Gaussian distribution of species in relation to each environmental gradient, and calculates correlation coefficients between samples and environmental predictor variables. We reduced variance by $\log_e$ transforming the AARE data, and used season, year, distance of reach mid-point from Glen Canyon Dam and mean reach width as environmental predictors.

RESULTS AND DISCUSSION

Waterbird diversity

A total of 85 waterbird species have been detected in the study area, in 10 orders and 19 families (Brown *et al*., 1994), representing 68% of the 125 waterbird species detected in the northern Arizona/southern Utah region (Woodbury and Russell, 1945; Phillips *et al*., 1964; Carothers and Sharber, 1976; Blake, 1978; Pinnock and Spence 1993; Brown *et al*., 1994; Table II; Appendix). Eight waterbird species breed in the study area (Brown *et al*., 1987, 1994): black-crowned night heron (*Nycticorax nycticorax*), great blue heron (*Ardea herodias*; four nests at km 417 in 1991, LES), mallard, blue-winged teal (*Anas discors*; a single brood at km 78 in 1987, LES), common merganser (*Mergus merganser*; on the Glen Canyon reach in 1994, J. Grahame, personal communication), American coot, spotted sandpiper (*Actitis macularia*, km 89 in 1989 and 1990) and American dipper (*Cinclus mexicanus*, only along tributaries).

Historical studies

Although a relatively diverse waterbird fauna existed on the pre-dam Colorado River, substantial wintering and summer breeding populations were not reported there, nor were distinctive differences between reaches identified. McKee (1930, 1937a), Bailey (1939), Woodbury (1959, in lower Glen Canyon) and other pre-dam observers documented 23 species (Table II). Pre-dam Lees Ferry residents, dam workers and river runners reported a general paucity of waterbirds (Appendix). Spencer Johnson and Hal Nelson lived at Lees Ferry from 1923 to 1931 and 1931 to 1940, respectively. As children, they hunted and fished along the river, and reported that large winter waterbird populations did not occur there. Their observations are particularly relevant because they walked to school past our Lees Ferry observation point each day during winter, where post-dam winter waterfowl are now abundant. Johnson reported 'greenhead' (mallard) and 'mudhen' (probably American coot, *Fulica americana*) breeding at the Paria River confluence as it ponded during late spring mainstream floods. Martin Litton, who floated the river in the 1950s and early 1960s, reported a single Canada goose nest near km 220 (Brown *et al*., 1987), but we encountered no other reports of mainstream waterbird breeding.

River runner's diaries likewise suggested little to no breeding or substantial winter populations prior to the dam (Appendix). Early river runners commonly observed, reported and shot waterfowl that concentrated along the middle reaches of the Green River (e.g. Edwards, unpublished 1941; Kolb, 1963) and downstream from Grand Canyon (e.g. Stone, 1932; Sumner, in Marston, 1969), but not in lower Glen Canyon or Grand Canyon (e.g. Flavell, in Carmony and Brown, 1987). Buzz Holmstrom's (unpublished) report on his 7–21 November 1937 trip through Grand Canyon was representative of these journals: the butterfly he observed near km 48 was '. . . the first living thing . . . seen since entering Marble Canyon.' Few reports of shooting waterfowl exist in these journals, despite food shortages on many trips. M.K. Baker (1940, unpublished) reported the expected and observed avifauna she encountered on a summer river trip in 1940, documenting low densities of 10 waterbird species.

Three statements appear to contradict the general pattern of pre-dam waterbird rarity (Appendix). (1) Of the 83 days spent in Grand Canyon on Stanton's 1889–1890 expedition, W.H. Edwards (1941, unpublished) reported '. . . lots of ducks . . .' on 28 February 1890 near km 320. Although winter waterfowl pass through this reach sporadically, it does not presently support a large post-dam wintering population. We consider this observation to be consonant with the post-dam pattern of sporadic waterbird presence there. (2) Prospectors Harry Simpson and Martin Spencer traversed the variably turbid (VT) segment in October 1936, and reported '...many unusual waterfowl...' (Anonymous, 1934). The post-dam winter population on that segment does not arrive until mid-November, and they may have observed white pelican (*Pelecanus erythrorhynchos*), shorebirds [e.g. black-necked stilt (*Himantopus mexicanus*) or American avocet (*Recurvirostra americana*)] or other morphologically distinctive migratory species. (3) On 19 August 1940, during his first traverse of the Colorado River, Barry Goldwater reported '...ducks and geese...constantly rising from the water in front of us...' on the Lower Granite Gorge reach (Reach 12; B. Goldwater, 1940 and personal communication). High summer densities on this reach on that trip were not corroborated by M.K. Baker (1940, unpublished), and the reach presently supports few summer waterbirds. Mr Goldwater's boat may have been repeatedly flushing the same flock of waterfowl. From these historic reports, we conclude that if any substantial waterbird populations occurred in the unregulated river corridor, they were rare, sporadic and occurred on different segments and seasons than those of the post-dam era.

Most pre-dam waterbird species probably occurred on a wandering or accidental basis. At least 23 (26·7%) of the species in this system occurred before impoundment, and all reported pre-dam species except brown pelican (*Pelecanus occidentalis*) and curlew (*Numenius* sp.) are presently relatively common. Fifty (58·8%) of the species in the system are presently rare or accidental (Brown *et al*., 1994), and rare species were unlikely to have been detected during pre-dam time. Therefore, many additional waterbird species may have occurred on the pre-dam river, and flow regulation may not have substantially increased waterbird diversity. Also, we found no evidence that flow regulation resulted in the loss or decline of any river waterbird species.

Post-dam waterbirds

We detected a total of 58 waterbird species during reach-based surveys from 1973 to 1994 (Table II), with a grand mean of 138·2 waterbirds/reach (SE = 31·0, $n = 727$ surveys of individual reaches) and a grand mean AARE of 372·8 birds km^{-1} h^{-1} of observation per reach (SE = 69·05). Our post-dam assemblage data included 68·2% of the species known to occur in the study area, and 46·4% of the species reported in the region. Anseriformes (25 species) dominated the assemblage. Diving (13 species) and dabbling (12 species) waterfowl guilds were most common, with gadwall > bufflehead (*Bucephala albeola*) > American wigeon > lesser scaup (*Aythya affinis*) > common goldeneye (total annual mean AARE > 40); consistent occurrence of redhead (*Aythya americana*) > mallard > ring-necked duck (*Athya collaris*) with a total mean AARE 10 to 40; and mean annual AARE of common merganser and Canada goose of 3·71 and 2·85, respectively. The shorebird guild (16 species) was dominated by spotted sandpiper (0·33), with ring-billed gull (*Larus delawarensis*) and California gull (*L. californicus*) (AARE $\leqslant$ 0·03). The wader guild (six species) was dominated by great blue heron (0·57). Raptors included bald eagle (0·04) and osprey (0·03). We observed substantial winter waterbird populations in upper Grand Canyon since 1975.

Seasonality

Definition of seasons. Analysis of AARE data and multivariate analyses (below) allowed a clear definition between winter and summer seasons, but spring (April) and autumn (October) migratory seasons were only weakly distinguishable. Total mean waterbird AARE was 89-fold greater in winter than in spring, summer or autumn ($p_{\text{Mann–Whitney}} < 0{\cdot}00001$), and spring AARE was greater than summer ($p_{\text{Mann–Whitney}} < 0{\cdot}0001$); but autumn AARE was equivalent to that in spring and summer ($p_{\text{Mann–Whitney}} = 0{\cdot}098$ and $> 0{\cdot}1$, respectively; Table II; Figures 2A, 5B).

Winter season. Mean total AARE values increased in mid-November, remained consistently high through February and declined in March (Figure 2A). Winter waterfowl dominated the overall composition (Figure 2A–C), but non-Anseriformes AARE values were more variable (Figure 2D–F). Piscivorous raptors comprised 0·012% of the entire winter waterbird assemblage (Figure 2F).

Table III. Mean total mallard adult and duckling abundance, brood size from Lees Ferry (km 0) to the Little Colorado River confluence (km 98) by month during the summers of 1991–1994

Month	Mean adult abundance ±1SD (*n*)	Mean duckling abundance ±1SD	Mean number of broods ±1SD	Mean brood size ±1SD
May	51·5 ±23·216 (4)	8·3 ±3·948	2·0 ±1·414	5·4 ±1·493
June	51·3 ±15·308 (3)	12·7 ±5·686	4·7 ±3·055	3·0 ±0·851
July	47·0 — (1)	21·0 —	8·0 ± —	2·0 —
August	4·0 ±4·243 (2)	1·5 ±2·121	1·0 ±1·414	0·8 ±1·061
September	36·4 ±24·936 (5)	0·2 ±0·447	0·2 ±0·447	0·2 ±0·447

Winter AARE varied monthly between species within guilds (Table II). On the CW segment, dabbling gadwall and American wigeon AARE were highest in December and January, while green-winged teal AARE peaked in February and March. Diving *Bucephala* spp. and common merganser mean AARE were relatively constant from November to March, but *Aythya* spp. AARE peaked in mid-winter. Canada goose AARE peaked early and declined in mid-winter, a pattern opposite to that of green-winged teal and bald eagle.

Migration. Mean April and October AARE were intermediate for most waterbird species (Table II, Figure 2), and several common winter waterfowl (e.g. *Bucephala* spp., gadwall and American wigeon) were relatively abundant during migration. However, snowy egret (*Egretta thula*), great blue heron, osprey, *Larus* spp., killdeer (*Charadrius vociferus*) and belted kingfisher (*Ceryle alcyon*) primarily occurred as spring and/or autumn migrants.

Summer season. Summer waterbird populations and AARE were low compared with those in winter, with dominance by mallard and common merganser (mean AARE =1·07 and 0·07, respectively; Table II, Figure 2). Spotted sandpiper and great blue heron were relatively common (0·59 and 0·28, respectively), and wandering flocks of American avocet and *Phalaropus* spp. also occurred.

Intensive observation of summer bird populations since 1973 revealed that post-dam mallard breeding along the mainstream did not begin until 1982 (Brown *et al*., 1987). Although mallard AARE decreased 30-fold from winter to summer, virtually every large eddy on the CW and VT segments supported a mallard pair during summer from 1990 to 1994 (Table III). We observed no successful mainstream breeding of mallard during the high flows of 1983–1986, but mallard broods have been regularly observed since 1987 on the wide CW and VT segments, to a lesser extent on narrow VT reaches, rarely on the UT Furnace Flats reach, and not downstream

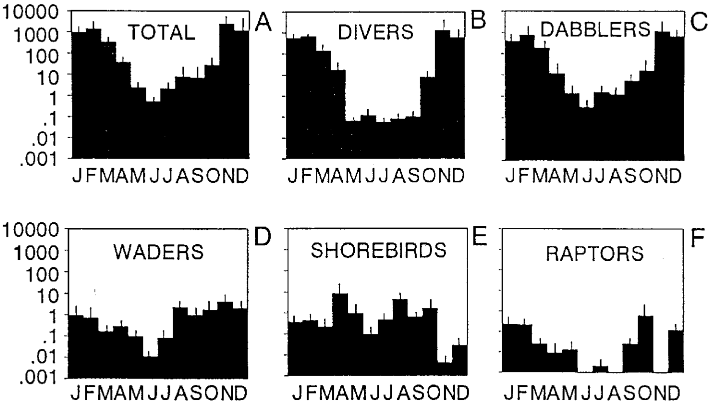

Figure 2. Mean waterbird guild AARE (birds $\mathrm{km}^{-2}\,\mathrm{hr}^{-1}$) by month: (A) total waterbird assemblage; (B) diving waterbirds; (C) dabbling waterfowl; (D) wading birds; (E) shorebirds; (F) piscivorous raptors. Error bars are 1 SE

from km 122. We located mallard nests at km −0·1R, 4·2L, 54·0R, 89·0R and 114·2L. All nests lay between the 800 and 950 m^3/s stages in dense horsetail (*Equisetum laevigatum* × *hyemale*) stands, where they were susceptible to inundation by high discharges.

Despite the many mallard pairs observed, mean monthly duckling abundance between Lees Ferry and km 122 remained low (<21) from 1991 to 1994 (Table III). Broods were observed from May until September, and mean brood size decreased from 5·4 ± 1·49 in May to 0·2 ± 0·45 ducklings/brood in September. Decreasing mean brood size was partially attributable to observed predation by peregrine falcon (*Falco peregrinus*), common raven (*Corvus corax*) and mammalian predators, species that appear to have increased in abundance following flow regulation.

Distance (turbidity) and reach width effects

Seasonal waterbird AARE varied strongly between turbidity segments (Figures 3A–F and 4A–F). Mean total AARE decreased from 4548 on the CW segment to 24·7 on the VT segment (a 184-fold decrease), and further decreased to 2·1 on the UT segment (a 12-fold decrease; Figure 3A). Mean diving and dabbling guild AARE decreased over distance during winter ($p_{\mathrm{Friedman}} < 0{\cdot}0001$), and decreased non-linearly during summer ($p_{\mathrm{Friedman}} = 0{\cdot}066$ for summer dabbling waterbirds), but not during migration ($p_{\mathrm{Friedman}} > 0{\cdot}1$ for both spring and autumn; Figures 3B–C, 4B–C). Mean winter diving guild AARE was 54-fold higher on the CW segment than on the first VT reach, decreased across distance to the LCR confluence, but was <1·0 among the reaches downstream from km 123 (Figure 3B). Similarly, mean winter dabbling guild AARE decreased 38-fold from the CW segment to the uppermost VT reach (Figure 3C), while mean AARE of other guilds decreased non-significantly between turbidity segments. These general patterns also occurred during summer, but AARE values were much lower (Figure 4C). The higher ratio of dabbling (herbivorous) to diving (predatory) waterfowl on upper reaches further indicates the extent to which flow regulation has altered the trophic structure in this system.

In contrast to strong relationships with turbidity (flow regulation), seasonal waterbird AARE was slightly, but significantly, greater on wide versus narrow geomorphological reaches (Figures 3A–F and 4A–F). Mean total AARE decreased from 28·45 to 20·91 on wide versus narrow VT reaches (a 1·4-fold decrease), and from 2·5 to 1·9 on wide versus narrow UT reaches (a 1·3-fold decrease) and from 2·5 to 1·9 on wide versus narrow UT reaches (a 1·3-fold decrease; $p_{\mathrm{Friedman}} = 0{\cdot}0002$). This difference was the result of two- to three-fold higher mean winter dabbling guild AARE between wide versus narrow reaches within VT and UT segments (multiple comparisons $p_{\mathrm{Friedman}} < 0{\cdot}05$; Figure 3C). The abundance of other winter guilds did not differ between wide and narrow reaches ($p_{\mathrm{Friedman}} > 0{\cdot}05$; Figure 3B, D–F). Summer total AARE of all guilds was not significantly greater between wide and narrow VT and UT segments (multiple comparisons $p_{\mathrm{Friedman}} > 0{\cdot}05$; Figure 4A–F).

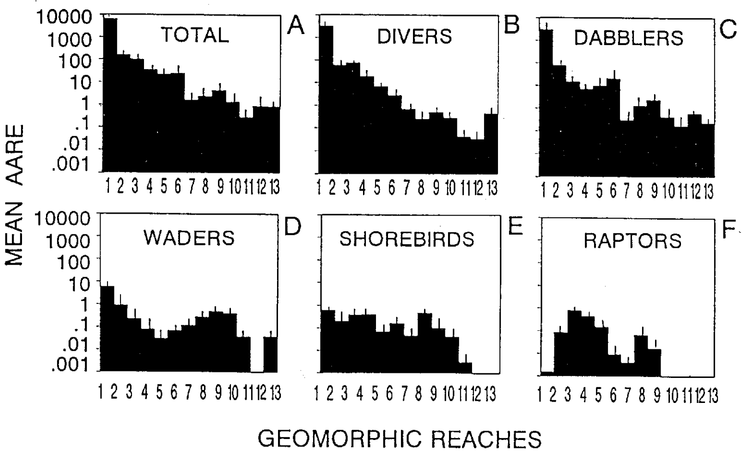

Figure 3. Mean winter waterbird guild AARE (birds $km^{-2} hr^{-1}$) on the 13 Colorado River reaches: (A) total waterbird assemblage; (B) diving waterbirds; (C) dabbling waterfowl; (D) wading birds; (E) shorebirds; F) piscivorous raptors. Error bars are 1 SE

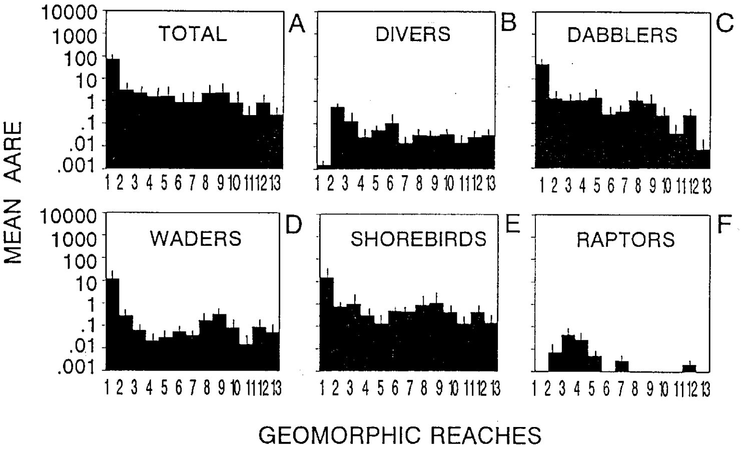

Figure 4. Mean summer waterbird guild AARE (birds km^{-2} hr^{-1}) on the 13 Colorado River reaches: (A) total waterbird assemblage; (B) diving waterbirds; C) dabbling waterfowl; (D) wading birds; (E) shorebirds; (F) picivorous raptors. Error bars are 1 SE

Wide VT segment reaches contain equivalent numbers of low velocity eddies, but five to ten-fold higher standing mass of benthic algae and invertebrates, and 1·6- to 2·8-fold higher total area of fluvial marshes, compared with narrow reaches (Schmidt and Graf, 1990; Stevens *et al.*, 1995, in press; Table I). Despite these large biological differences between wide and narrow reaches, waterbird AARE was only slightly greater on wide versus narrow reaches, compared with the large decrease in waterbird AARE over distance downstream and between turbidity segments.

Ordination

Interactions between species and environmental variables were clarified through ordination analyses. The first three CANOCO axes described 89·7% of the waterbird species-to-environment (S–E) relationship (Figure 5A). CANOCO axis 1 (eigenvalue = 0·451, 55·4% of the S–E relationship) was positively correlated with seasonality and distance downstream from Glen Canyon Dam, and negatively correlated with reach width and year. Axis 2 (eigenvalue = 0·174, 21·4% of the S–E relationship) was positively correlated with reach width, the primary geomorphological variable. Axis 3 (eigenvalue = 0·105, 12·9% of the overall S–E relationship) was weakly negatively correlated with seasonality and year. Thus, seasonality exerted the strongest influence over guild distribution, with strong differences between winter and summer composition, and transitional differences during April and October migration (Figure 5B). Distance from the dam (turbidity) and geomorphic reach width influenced composition in a non-linear, circuitous fashion (Figure 5C). Lower axis 1 values occurred on the clear water and wider reaches, and higher values on the more turbid and narrower reaches. The upper Lake Mead reach (13) exhibited greater similarity to the upstream turbidity segments and wide reaches, although overall mean AARE there was low (Figure 3A). Differences between years in this system were largely driven by increased *Bucephala* spp. abundance over post-dam time, and development of post-1982 breeding mallard and winter bald eagle populations.

Mechanisms

The serial discontinuity concept (Ward and Stanford, 1983) proposes that river ecosystems ‘recover’ from the effects of flow regulation over distance downstream in relation to river size, and tributary size and location. The post-dam, downstream reduction in waterbird abundance constitutes ‘recovery’ of this assemblage to a state resembling the natural, depauperate condition of the river. Like the benthos in this system, downstream ‘recovery’ is not uni-directional (Stevens *et al.*, in press); rather, it is a circuitous, guild-specific assemblage shift,

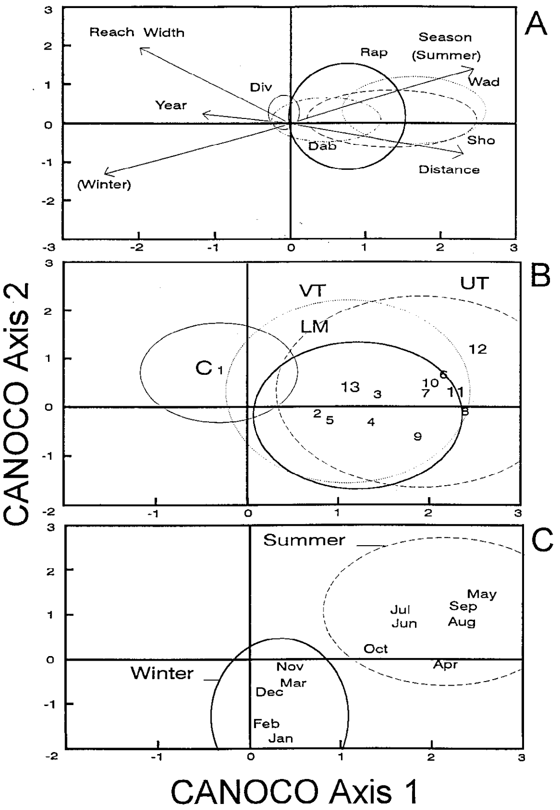

Figure 5. Ordination of the first two CANOCO axes for post-dam Colorado River waterbird distribution. Circles represent 1 SD around the centroid mean. (A) Centroids of species in samples space of the mean waterbird AARE for each guild, and environmental variables. (B) Centroids of samples in species space of months and seasons. (C) Centroids of samples in species space of geomorphological reaches (numbers) and distance downstream (turbidity segments CW, VT and UT)

influenced by abrupt changes in turbidity and benthic production (tributary effects), and reach-controlled aquatic and wetland habitat distribution.

Waterfowl and piscivorous raptors are strongly influenced by resource availability, as documented for waterfowl downstream from Grand Canyon by Anderson and Ohmart (1988). In contrast, most wading and shorebird species used the study area as stopover habitat during migration or wandering, and were only indirectly affected by flow regulation. We conclude that flow regulation effects have overridden the influences of natural channel geomorphology on river waterbird distribution, a pattern that has not been quantified previously. The dramatic decrease in AARE from the CW to the UT segments matches the pattern of decreased water clarity and decreased standing biomass of benthic algae and invertebrates across that distance, but does not follow strongly the pattern of increased wetland habitat along wide versus narrow reaches (Table I). Organic drift from the CW segment (Shannon *et al.*, 1996) may contribute directly (as waterfowl forage) or indirectly (by increasing fish abundance) to the maintenance of higher waterbird density between the dam and the LCR. However, the minor decrease in water clarity downstream from the LCR confluence further reduced benthic standing biomass (Stevens *et al.*, 1997), overriding the benefits of increased drift. Increased turbidity on the UT segment limits the waterbird assemblage there primarily to migrant or vagrant species, despite abundant wetland vegetation on wide reaches.

Our results are regionally consistent with those of Anderson and Ohmart (1988) who reported increased *Bucephala* populations following flow regulation, and substantial post-dam winter populations of *Bucephala*, *Anas*, *Aythya* and *Mergus* species along the lower Colorado River. In contrast, Steele and Vander Wall (1985) observed that White River, Utah, waterfowl populations increased during spring. Although numerous reports exist of substantial wintering waterfowl populations on wide reaches of the Green River (Appendix), the absence of a large population on the White River may be related to its small stream size, geomorphological constraints, ice formation or migratory staging behaviour.

An alternative hypothesis may explain our results: as a large body of water, Lake Powell may attract waterbirds, resulting in the observed negative correlation between waterbird density and distance downstream from the dam. We reject this hypothesis because: (i) the winter assemblage on Lake Powell differs greatly in comparison with that on downstream reaches; (ii) wintering and summer breeding populations were largest at Lees Ferry and on the Marble Canyon reach, respectively, and not immediately downstream from the dam; and (iii) with surface area effects controlled, waterfowl and picivorous raptor densities were still significantly greater on wide reaches, where food and nesting habitat resources are more available.

Management implications

River management practices can influence waterbird distribution. For example, mallard nesting was limited by high flows from 1983 to 1986. The relatively large wintering waterbird population at Lees Ferry may be partially attributed to its management as a ‘no wake’ boating zone in which hunting is not permitted. Other non-hunting recreational activities, such as motor boat traffic, also influence distribution (Brown and Stevens, in press). We observed that virtually all waterbird species, except mallard, repeatedly flushed from their resting or foraging areas in response to passing river boats, often flying many kilometres downstream. Reduction of winter boat traffic during the morning foraging hours at Nankoweap Creek could improve the quality of stopover habitat for wintering bald eagles. Increased post-dam aquatic and riparian production has also increased predator populations [e.g. bald eagle, peregrine falcon, common raven and coyote (*Canis latrans*)], thereby increasing predator pressure on waterbirds (Brown *et al*., 1989; L.E.S., personal observations).

Development of discharge management strategies that optimize waterbird diversity, benthic and riparian production and access to those resources for waterbirds, requires: (i) clear definition of management goals and objectives; (ii) understanding relationships between historical, existing and potential waterbird and other avifaunal distributions, as well as understanding seasonal shifts in food and habitat availability under normal and exceptional flow regimes; and (iii) active incorporation of monitoring and research data into an adaptive management programme.

Flow regulation will not offset all waterbird habitat and population losses in impounded upstream reaches, and is unlikely to mitigate those losses in all river systems. Waterbird species requiring open, sparsely vegetated lower riparian zone foraging and nesting habitats (e.g. spotted sandpiper and other shorebird species, and Neotropical migrant passerines) may decrease on regulated rivers with large daily varying flows and little annual flooding (Repking and Ohmart, 1977; Books, 1985; Ziewitze *et al*., 1992).

CONCLUSIONS

Historical sources indicate that flow regulation increased winter and breeding Colorado River waterbird populations in lower Glen Canyon and upper Grand Canyon. Post-dam seasonal waterfowl population densities vary more strongly in relation to distance (turbidity) downstream from the dam than to reach width (natural channel geomorphology), but seasonal distribution varies between feeding guilds. Mean winter waterbird AARE decrease by three orders of magnitude from the clear water segment to the usually turbid segment, while wide reaches on those segments support $\leqslant 1{\cdot}4$-fold greater mean AARE compared with narrow reaches. In contrast to dabbling and diving waterfowl, most wading bird, shorebird and some piscivorous raptor (e.g. osprey) species occur as migrants or wanderers, and the effects of flow regulation and natural channel geomorphology on these taxa are indirect. Summer-breeding mallard are distributed in relation to both dam-related water clarity on upper turbidity segments and increased shoreline vegetation on wide geomorphological reaches. Flow regulation may, to some extent, offset upstream waterbird population and habitat losses on regulated rivers, but effective flow and avifaunal management requires application of scientific information on waterbird distribution and ecology to achieve clearly defined management objectives.

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Observer	Year	Comments
J. W. Powell	1869, 1872	He reported killing ‘a fine lot of ducks’ (Powell, 1895, p. 147) on the middle Green River, but neither Powell nor Dellenbaugh (1908) mentioned waterfowl in the Grand Canyon, despite precariously low food supplies in 1869 (5–29 August), or in 1872 (17 August to 8 September; Fowler and Fowler, 1968).
J. C. Sumner	1869	On the first Powell expedition, Sumner documented diverse and abundant waterfowl on Green River (Marston, 1969), but Grand Canyon data were not recorded.
J. D. Lee	1871–1876	Lee established Lees Ferry in 1871. In his detailed journal (Cleland and Brooks, 1983) he made no mention of waterbirds at the ferry site.
R. B. Stanton	1889	During an extended two-part expedition, Stanton mentioned snipe in upper Glen Canyon (Smith and Crampton, 1987, p. 107); and reported that his party shot one duck near km 30·5 on 12 July 1889 (p. 78), and another near km 325 on 28 February 1890 (p 232).
W. H. Edwards	1889–1890	He participated in Stanton’s second expedition from 28 November 1889 to 23 March 1890 (28 December to 17 March in Grand Canyon; Edwards, 1941), reporting that a crew member shot one duck near km 160 on 1 February 1890. On 28 February 1890 near km 325 he reported ‘ . . . lots of ducks today.’
G. F. Flavell	1897	During a beaver trapping expedition from 27 August, 1896 to 8 January 1897 (17–30 October in Grand Canyon), Flavell reported a paucity of wildfowl and wildlife in Cataract, Glen and Grand canyons (Carmony and Brown, 1987, p. 74).
J. D. Stone	1909	During a hunting and trapping expedition from Green River, Wyoming to Needles, California from 12 September to 19 November 1909 (28 October to 15 November in Grand Canyon), Stone (1932) reported shooting many waterfowl on the Green River and upper Glen Canyon (1932: e.g. pp. 62,71,80,81), and in Black Canyon downstream from the Grand Canyon, including ‘ . . . an enormous flock of snow geese . . . ’ (p. 106) upstream from Fort Mojave), but no waterbirds were recorded in Grand Canyon.
E. and E. Kolb	1911–1912	During their motion picture filming expedition from Green River,Wyoming to the lower Colorado River basin (11 September 1911 to 18 January 1912, and in Grand Canyon from early November 1911 to 12 January 1912), the Kolb brothers reported waterfowl on the Green and upper Colorado rivers (Kolb, 1963, pp. 46, 132), but recorded no waterbird observations in Grand Canyon.

U.S.G.S.	1923	R. H. Webb (US Geological Survey, Tucson, written communication) reported that the US Geological Survey staff shot or reported ducks at Kanab Creek (1), near km 328 (‘ . . . a few, the first for several days’), and at km 447 (4), as well as a great blue heron at km 319 during their 1 August to 13 October 1923 mapping expedition. Neither F. B. Dodge (1944, unpublished) nor C.H. Birdseye (1923, unpublished) commented on waterbirds in their diaries.
S. Johnson	1923–1931	Johnson lived at Lees Ferry from 1923 and 1931 and described his childhood of hunting and fishing activities along the Colorado River there during an interview with Stevens and Buck in 1993. He described limited waterfowl breeding, and occasional other species, but stated that no significant waterfowl populations occurred there.
H. Simpson	1936	H. Simpson and M. Spencer, prospectors, boated from Lees Ferry to Phantom Ranch in October 1936 and reported ‘ . . . many unusual waterfowl . . . ’ to E. D. McKee (Anonymous, 1934).
B. Holmstrom	1937	On his solo river trip from 4 October to 21 November 1937 (7–21 November in Grand Canyon) Holmstrom (1937, unpublished) reported numerous waterfowl on the upper and middle Green River (e.g. pp. 3, 4), but commented on the dearth of life in Marble Canyon (p. 15). He reported ‘water ouzels’ (*Cinclus mexicanus*) at km 219.
A. Burg	1938	R. H. Webb (US Geological Survey, Tucson, written communication) reported that Burg shot a single duck on 16 October 1938 near km 15.
E. D. McKee	1937	On a river expedition in November, 1937 McKee (1937b, unpublished data) reported great blue heron at km 242 (2) and 315 (1), 11 mallard at km 336, one gadwall at km 185, one northern pintail at km 319, and seven bufflehead at km 356.
R. Grater	1937	Like E. D. McKee, Grater compiled observations on Grand Canyon avifauna, which were included in Bailey (1939).
F. M. Bailey	1930s	Bailey (1939) summarized waterbird species observations from Grand Canyon, but had few data on river corridor waterbirds.
H. Nelson	1931–1940	In an interview with Stevens in 1994, Nelson related his childhood hunting expeditions at Lees Ferry from 1931 to 1940, reporting no significant wintering waterfowl populations at Lees Ferry during that time.
M. K. Baker	1940	On her summer trip with Nevills, Baker (1940, unpublished) listed the bird species she expected and actually observed (10 species in Grand Canyon in low densities) between Green River, Wyoming and Lake Mead, Arizona. No observations of breeding waterfowl were recorded.
B. Goldwater	1940	On the same trip with M. Baker (above), Goldwater (1940, and written communication) reported numerous waterfowl on 14 August, 1940 near Diamond Creek (km 362).
N. Nevills	1938–1948	He made no mention of waterbirds in his diaries of six summer trips (Nelson, 1991).
Others	1938–1962	In addition, the following pre-dam river runners reported during interviews with Stevens in 1994 that waterbirds were generally rare on the pre-dam Colorado River, and they did not observe waterfowl breeding during their summer trips in Grand Canyon: L. (Jotter) Cutter (1938, 1 trip), F. Wright (1940s, several trips), K. Frost (1940s–1950s, several trips), T. Nichols (1950s and 1960s, several trips), K. Sleight (1950s and 1960s, several trips), J. Cross, Sr. (1950s and 1960s, several trips) and J. Cross, Jr. (late 1950s and 1960s).

P. T. Reilly	1950s	As reported by R. H. Webb (US Geological Survey, Tucson, written communication), Reilly reported the following summer waterbirds in his diaries: 1949 and 1953 (no comments on waterbirds); early July 1955 (teal at km 250 and 386, a great blue heron at km 330 and 350); 27 June 1956 (two mallard at km 215); 1957 (no comments on waterbirds); mid-May 1959 (three ducks on the Permian Reach, one duck at km 23, six ducks at km 113); 9 July 1962 (two ducks at km 245). In contrast to these pre-dam trips, Reilly recorded 22 waterbirds (at least four species) during an early May 1964 trip.
M. Litton	1950s	In interviews with Brown (Brown *et al*., 1987) and Stevens in 1994, Litton reported a Canada goose nest near km 219 during summer in the late 1950s.
W. L. Rusho	1959	Rusho worked for the Bureau of Reclamation during the construction of Glen Canyon Dam. In an interview with Stevens in 1994, he reported that he motored from the dam site to km 12 in mid-winter, 1959, and recalled only a few waterfowl, but he saw 'one or two great blue heron'.
R. McCallum	1962	McCallum repeatedly ran from Lees Ferry to km 12·8 during January and February, and reported '...almost no waterfowl.'

Behle and Higgins (1959) compiled data by Woodbury (1939), Woodbury and Russell (1945) and Behle (1948), reporting a limited, seasonal presence of waterbirds in Glen Canyon prior to completion of Glen Canyon Dam.

S. W. Carothers, R. R. Johnson and N.J. Sharber documented a substantial post-dam wintering waterbird population in upper Marble Canyon in January 1975 (Carothers and Sharber, 1976, unpublished).

Brown *et al*. (1987) summarized all available literature on Grand Canyon avifauna.

Pinnock and Spence (1993, unpublished) reported on the avifauna of the Glen Canyon reach during 1992–1993.

Brown *et al*. (1994) compiled the most recent checklist of Grand Canyon avifauna.

APPENDIX

Historical journals, reports, publications and interview data pertaining to pre-dam and post-dam Colorado River waterbirds between Glen Canyon Dam and Lake Mead, Arizona.

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