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Journal
Aquatic Conservation Marine and Freshwater Ecosystems, 23(4)

ISSN
1052-7613

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Publication Date
2013-08-01

DOI
10.1002/aqc.2326

AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. (2013)

Stable isotope ratios of egg albumen of three waterbird species nesting in the Colorado River Delta indicate differences in foraging ground and isotopic niche breadth

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ABSTRACT

1. The Colorado River Delta is one of the most impacted wetland systems in the world and has experienced massive habitat loss owing to severe restrictions in freshwater inflow as a result of dam construction and diversion of water for irrigation. However, the delta still offers nesting and foraging habitats for waterbirds, although the habitats available are highly fragmented and limited.

2. Stable isotope ratio (SIR) analysis was used to assess quantitatively isotopic niche width of gull-billed terns (*Gelochelidon nilotica*), laughing gulls (*Leucophaeus atricilla*) and snowy egrets (*Egreta thula*) that nest at an inland and coastal location.

3. The variance in carbon and nitrogen SIR of egg albumen indicated that inland colonies have a much broader isotope niche width (range 2.9 to 23.9) than coastal colonies (<0.1 to 1.4).

4. Species-specific mean albumen $\delta^{13}C$ values from inland nests were significantly more depleted in ^{13}C than coastal colonies (−19.5 to −23.1‰ and −10.4 to −14.9‰, respectively). Comparison of albumen $\delta^{13}C$ values corrected for trophic fractionation with those of potential prey and primary producers collected at 10 potential foraging grounds indicates that females of the three species that nest in inland colonies did not feed in habitats located in the vicinity of their nesting site, while coastal colonies had distinct isotopic signatures reflecting marine primary production. Inland colonies probably forage in a variety of habitats and for different prey, relying on food webs based mostly on C3 terrestrial plants.

5. Differences in the isotopic composition of eggs from species nesting in the same area and between conspecifics nesting in different habitats indicate that foraging habitats vary substantially, suggesting that feeding varies as a function of local resource availability.

6. These results suggest that a variety of habitat types fulfill the foraging needs of this suite of nesting waterbird species, especially in inland colonies. Since the specific feeding areas of nesting females from the inland colonies have not been identified, protection of the remaining wetlands within the Colorado River Delta is warranted.

Received 12 June 2012; Revised 25 October 2012; Accepted 18 November 2012

KEY WORDS: estuary; brackish; habitat management; behaviour; birds

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INTRODUCTION

The Colorado River Delta is one of the most impacted wetland systems in the world. Since the early 1930s, the damming of the river for agricultural and urban purposes has led to a drastic and sustained reduction in freshwater inflow to the lower delta (Glenn *et al.*, 1996; see review in Zamora-Arroyo and Flessa, 2009). Except for years in which there is very high precipitation in the upper watershed, no fresh water reaches the river mouth in the upper Gulf of California, and it is well recognized that the main cause of wetland loss is the severe alteration of the river's hydrology (Carter, 1986). The extensive wetlands that once supported a rich wildlife and 200–400 species of vascular plants are now largely composed of mud and salt flats (Ezcurra *et al.*, 1988). There has been a 90% decrease in the areal wetland coverage during the last century; the remaining 10% is at risk due to the pressing water needs of urban and agricultural activities in the USA and Mexico, which could further reduce the already limited supply of water that feeds the delta's wetlands (Glenn *et al.*, 2001; Zamora-Arroyo and Flessa, 2009).

Historically, waterbirds nested in wetlands and riparian vegetation throughout the delta. Limited areas of freshwater, brackish and saltwater marshes remain, including those in the Río Hardy, the Ciénega El Doctor, the Ciénega de Santa Clara, the intertidal region of the river bank and Isla Montague at the mouth of the Colorado River, among others (Glenn *et al.*, 1996, 2001; Zamora-Arroyo *et al.*, 2005; Figure 1). However, the extensive loss of wetlands caused the loss of some nesting species, marked reduction in the population size of others, and changes in the species composition of the local bird fauna (Mellink and Ferreira-Bartrina, 2000; Patten *et al.*, 2001; Mellink, 2006). Nevertheless, there are still some waterbird colonies in the lower Colorado River Delta, most notably at Isla Montague at the mouth of the Colorado River, within the Ciénega de Santa Clara and within the Cerro Prieto Geothermal Evaporative Plant facility located 100 km from the coast.

Isla Montague currently supports the breeding, at least occasionally, of 11 species of waterbirds (Palacios and Mellink, 1992, 1993; Mellink and Palacios, 1993; Peresbarbosa-Rojas and Mellink, 1994, 2001; Patten *et al.*, 2001; Mellink *et al.*, 2002). Snowy egrets (*Egretta thula*), laughing gulls (*Leucophaeus atricilla*) and gull-billed terns (*Gelochelidon nilotica*) stand out because of their relatively large population size and nesting regularity. Islets in the Cerro Prieto evaporative

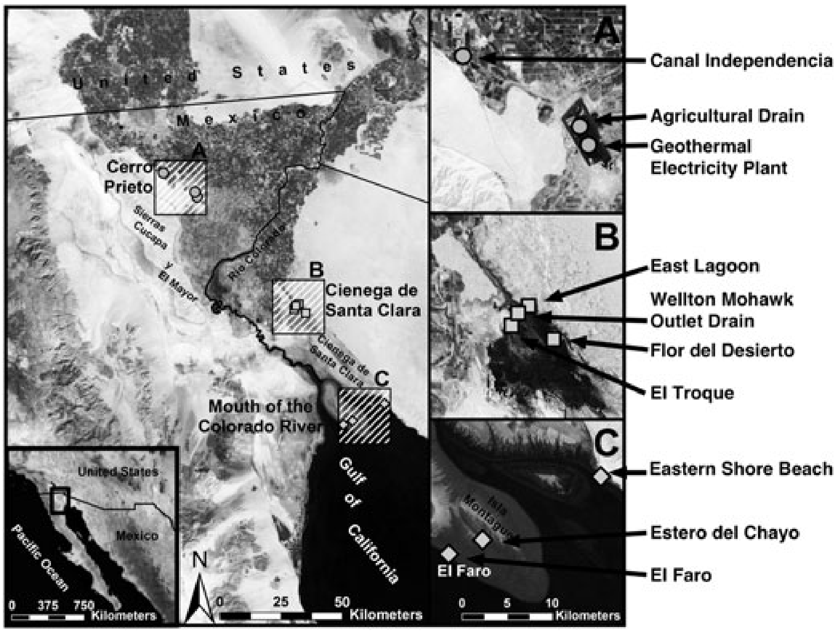

Figure 1. Map of the Colorado River Delta depicting areas where eggs of snowy egrets, gull-billed terns and laughing gulls were collected for stable isotope analysis. Nesting was found within the Cerro Prieto Geothermal Plant (CP) and at two sites on Montague Island at the mouth of the Colorado River (MCR). Primary producers and consumers were collected at 10 potential feeding habitats. Locations close to CP include an outlet drain, evaporative ponds within the geothermal plant and a water transport channel (Canal Independencia). Four sites were sampled in the Ciénenga de Santa Clara, an extensive marsh system: Wellton Mohawk Main Outlet Drain Extension, Wellton Mohawk East Lagoon, El Troque and Flor del Desierto. Three sites were sampled at MCR: El Chayo and El Faro on Montague Island and a nearby sandy beach.

ponds support eight nesting waterbird species, of which great egrets (*Egretta alba*), snowy egrets and gull-billed terns are the most common (Molina and Garrett, 2000; Patten *et al*., 2001).

The Cerro Prieto evaporative ponds and Isla Montague are important breeding areas for various waterbird species that nest in only a few colonies along the western coast of Mexico, a distance of over 2000 km. Very little is known about the ecology of these colonies. Basic information about colony size, breeding success, and the relationship between high water levels associated with spring tides and nesting failure has been documented (Molina and Garrett, 2000; Peresbarbosa-Rojas and Mellink, 2001), but dietary preferences, feeding habits and foraging areas remain unstudied. This paucity of information hinders our ability to manage and conserve the remaining habitats appropriately and to design effective restoration efforts (Hinojosa-Huerta *et al*., 2005).

Stable isotope ratios (SIR) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) serve as a powerful and rapid tool for identifying foraging grounds and inferring sources of primary production that support food webs in various habitat types in coastal areas (Rush *et al*., 2010; Brittain *et al*., 2012). This approach capitalizes on differences in the isotopic composition of the dominant types of primary producers and geochemical processes that are found in marine, brackish and freshwater systems (Fry and Sherr, 1984; Peterson and Fry, 1987; Deegan and Garritt, 1997). The SIR of a consumer's tissues provides an integrated measure of the prey assimilated through time (Hobson and Clark, 1992; Hobson, 2011). Because the isotopic signature of consumers reflects that of their foods, SIR serve as natural tracers with which to infer sources of primary production, nutrient sources and cycling, trophic level, and feeding grounds. This approach is particularly valuable in remote areas where it is difficult to perform direct observations of feeding behaviour or preferences and in the study of species that have the potential to forage over broad areas (Kelly, 2000; Inger and Bearhop, 2008).

In birds, SIR analysis of egg components, including yolk lipids and protein, albumen, membranes and shells has proven to be a powerful approach for inferring migration patterns, foraging grounds and the feeding preferences of nesting females (Forero *et al*., 2004; Rush *et al*., 2010). In income breeders that use exogenous nutrients to synthesize egg components, the SIR of the various egg fractions reflects the isotopic composition of a female's recent feeding and foraging grounds (Hobson, 1995, 2011). The variance in $\delta^{13}C$ and $\delta^{15}N$ values has recently been used as an indirect indicator of niche breadth in various taxa (Bearhop *et al*., 2004; Quevedo *et al*., 2009). The variance in isotopic ratios of a population does not directly reflect dietary niche, yet this approach is advantageous because it allows for the simple but quantitative comparison of the variability in isotopic composition among populations or species on a single scale (Bearhop *et al*., 2004; Martínez del Río *et al*., 2009).

The isotopic trophic niche breadth of three species of waterbirds that nest in the Colorado River Delta (gull-billed tern, laughing gull and snowy egrets) was assessed by quantifying the variance in the SIR of egg albumen from nests located at an inland and coastal habitat. The three species spend weeks foraging in the delta before nesting and egg-laying begins (Peresbarbosa-Rojas and Mellink, 2001; E. Palacios, CICESE, pers. comm.). Since the foraging strategies of gull-billed terns and snowy egrets differ substantially (egrets stand in shallow areas and reach for their prey and the terns fly and dive) focusing on different species allowed us to evaluate whether there were consistent patterns in isotopic trophic niche breadth within habitats or among species.

$\delta^{13}C$ and $\delta^{15}N$ values of albumen were compared with those of potential prey and primary producers collected at 10 potential feeding areas that lie along a coastal-terrestrial gradient to infer potential foraging grounds and to identify the dominant sources of primary production (terrestrial, marsh or marine) supporting their feeding. The hypothesis was that albumen from birds that nest inland would exhibit a broad isotopic niche breadth as a result of foraging in various habitat types throughout the delta, while that of populations that nest along the productive coast in the northernmost Gulf of California would exhibit less variation in their SIR.

METHODS

Sampling scheme and sites

Two reconnaissance trips were made to the delta in March 2002 and May 2002 to survey nesting grounds and select study sites. Gull-billed terns and snowy egrets were nesting at Isla Montague and on islets within the Cerro Prieto Geothermal Plant (CP, Figure 1). Laughing gulls regularly nest at the mouth of the Colorado River (MCR) and the species was chosen to allow comparison between a known marine feeder and the other two species. Sampling trips to collect eggs, potential prey and primary producers were conducted between April 2002 and July 2002 (Table 1).

Sample were taken in 10 potential feeding sites in three general areas within the delta: three sites were close to the CP nesting site, four were within the wetlands of the Ciénega de Santa Clara (CSC) that comprises extensive and diverse wetlands, and the other three sites were at the MCR in the upper Gulf of California (coordinates reported in Appendix A). Sampling spanned a distinct inland to coastal gradient. These sites were chosen based on previous knowledge of local nesting and feeding areas, observations taken during the reconnaissance trips, and for being representative of the wetland types found in the delta. The Cerro Prieto evaporative ponds, the Ciénega de Santa Clara, and the estuarine habitat of the upper Gulf of California have been listed as Conservation Priority areas (Zamora-Arroyo *et al*., 2005)

Cerro Prieto

The Cerro Prieto Geothermal Electricity Plant encompasses a series of evaporative cooling ponds (Figure 1). Waterbirds nest on small islets in one of the cooling ponds. Samples of primary producers and potential prey were collected for isotopic analysis (see Sampling for stable isotope analysis below) in the geothermal plant's evaporative cooling ponds, the Cerro Prieto Agricultural Drain, a <5 m wide shallow drain with vegetated banks located NE of the cooling ponds and Canal Independencia, a >10 m wide irrigation distribution channel with vegetated banks located a few kilometres from the geothermal plant.

Ciénega de Santa Clara

The ciénega is a large marsh created by the discharge of brackish water from the Wellton Mohawk Irrigation and Drainage District (Arizona, USA). It has dense stands of emergent vegetation (*Typha dominguensis, Phragmites communis*) as well as areas of open water. A gradient from lower to higher salinities occurs from the discharge point of the Wellton Mohawk main outlet drain, known as the Bypass Drain, southward. Sea water infrequently floods the southern section of the marsh during spring tides. The marsh holds the largest known population of the Yuma clapper rail (*Rallus longirostris yumanensis*) and supports other marsh birds (Hinojosa-Huerta *et al*., 2004). Several bird species nest on the mudflats of the southern ciénega and it is also an important wintering place for waterfowl (Mellink *et al*., 1996). A large and deep body of water at the discharge point of the Bypass Drain that is surrounded by aquatic emergent vegetation and trees was sampled (hereafter Wellton Mohawk outlet drain). In the ciénaga samples were obtained from a shallow lagoon of slow-running water separated from the Bypass Drain by a berm of soil (hereafter Wellton Mohawk East Lagoon), a large area of shallow open water located at the northernmost extent of the ciénega that supports dense stands of emergent vegetation (*Typha* and *Phragmites*) (Laguna El Troque), and a shallow water lagoon crisscrossed by *c*. 1.5 m deep channels in the southern ciénega (Flor del Desierto).

Mouth of the Colorado River

Isla Montague is a low-lying silt island located at the mouth of the Colorado River. The only

Table 1. Mean, standard deviation (SD), and variance of $\delta^{13}C$ and $\delta^{15}N$ values of albumen from freshly laid eggs of gull-billed terns, snowy egrets, and laughing gulls nesting in the Colorado River Delta. Eggs were collected in a coastal location at the mouth of the Colorado River (MCR) in the upper Gulf of California and in islets of the Cerro Prieto Geothermal Plant, an inland location (CP). All egg samples were collected within a 6-week period in 2002

			Mean ± SD		Mean ± SD	
Species	Nesting site	Egg collection date	$\delta^{13}C$ (‰)	Variance	$\delta^{15}N$ (‰)	Variance
Gull-billed tern	MCR	19 Apr (n = 11) 4 Jun (n = 10)	−10.4 ± 0.4	0.1[a]	17.1 ± 0.5	0.2[a]
Snowy egret	MCR	19 Apr (n = 10)	−12.1 ± 1.2	1.4[a]	19.0 ± 0.5	0.2[a]
Laughing gull	MCR	9 May (n = 10) 4 Jun (n = 2)	−14.9 ± 0.2	<0.1[a]	19.4 ± 0.2	<0.1[b]
Gull-billed tern	CP	30 Apr (n = 8) 1 May (n = 2)	−19.5 ± 4.9	23.9[b]	13.4 ± 3.4	11.3[c]
Snowy egret	CP	30 Apr (n = 10)	−23.1 ± 2.6	6.9[c]	14.2 ± 1.7	2.9[c]

n: number of eggs. Superscript letters indicate significant differences in the variance between colonies.

marshes are of Palmer's saltgrass (*Distichlis palmeri*). Saltgrass forms dense stands at the southeastern end of the island in an area known as Estero del Chayo, where one of two nesting areas found on the island was located. The other nesting area, El Faro, is located in a group of shell mounds (cheniers) 2 km south-east of Estero del Chayo. Food web components were sampled at both nesting sites. Samples were also taken at a beach about 15 km east of Estero del Chayo to characterize the isotopic composition of the food web of the upper Gulf of California.

Sampling for stable isotope analysis

Sampling for eggs was carried out throughout the breeding season within a 6-week period (Table 1). Only freshly laid eggs were collected (based on cleanliness and flotation; Hays and Lecroy, 1971) to avoid the potentially confounding effect of chick development on SIR. None of the eggs analysed exhibited more than the very initial stages of chick development. Only albumen was analysed for SIR since yolk has an isotopic composition depleted in ^{13}C because of its high lipid content (Hobson, 1995). Egg samples were analysed individually. Albumen was carefully separated from egg yolk and dried at 60°C for 48 h before grinding to a fine powder using an agate mortar and pestle.

Samples for isotopic analysis of food web components at each of the 10 potential feeding sites included terrestrial C3 plants, C4 marsh plants, micro and macroalgae, corixids (a ubiquitous herbivorous insect and a proxy for organic matter), particulate organic matter (POM), and sediment organic matter (SOM; see Appendix A for a detailed list of samples). For vascular C3 and C4 plants, the dominant species observed throughout each marsh were sampled. Macroalgal samples also consisted of individual plants collected from various locations within a marsh. Microalgal mats were collected from the sediment surface with a spatula and rinsed vigorously with distilled water to minimize the amount of sediment included in the samples. No other attempts were made to isolate algal cells. Water (1–2 L) was filtered through pre-combusted GFF filters to sample for POM. Potential prey for nesting waterbirds (fishes and aquatic invertebrates) were collected with cast nets, gill nets, a beach seine, and dip nets. All samples were kept on ice in the field and were frozen in the laboratory pending preparation for SIR analysis.

Muscle tissue from crab claws and crustacean tails, fish dorsal muscle, snail foot tissue, and clam adductor muscle were dissected in the laboratory. Primary producer samples were cleaned of epiphytes or adhered organic matter with a spatula. Samples for δ^{13}C analysis of SOM were fumed in 1 N HCL to eliminate carbonates and carbon and nitrogen isotopic ratios of sediments were analysed on separate subsamples (Harris *et al.*, 2001). Terrestrial plant species (including marsh plants), benthic microalgae (BMI), non-calcareous macroalgae and muscle tissue from potential prey were not acidified (Bosley and Wainright, 1999; Herzka *et al.*, 2002; Rush *et al.*, 2010; Brittain *et al.*, 2012). Although acidification of particulate organic matter samples is recommended, particularly for samples containing high carbonate content, acid treatment changes δ^{15}N values (Jacob *et al.*, 2005; Carabel *et al.*, 2006). Most of the samples analysed were from freshwater systems (irrigation and transport channels, freshwater marshes) and had a very high load of organic matter (pers. obs.). Because SIR from albumen was compared qualitatively with those of food web components and isotope-mixing models that are sensitive to small variations in SIR were not applied (Vander Zanden and Rasmussen, 2001), these results and interpretation are considered robust to small variations in δ^{13}C values of POM due to the presence of carbonates. All samples were rinsed in distilled water to remove carbonate ions from the water, dried at 60°C for 48 h and ground to a fine powder.

Three or more samples were analysed for each species or taxa and site when available. A concerted effort was made to sample different species of potential prey. The complete list of taxa, the number of samples collected, and isotopic results are presented in Appendix A. To facilitate the comparison of albumen SIR with those of potential sources of primary production and potential prey in what is a very complex isotopic landscape (see results), the isotopic values of food web components were separated into functional groups including C3 plants, C4 plants, aquatic vascular plants, macroalge, BMI, POM, SOM, corixids, fishes, shrimp, crabs, clams, snails and infauna. For each functional group, average δ^{13}C and δ^{15}N values and standard deviations (SD) were calculated. Each isotopic measurement was considered a replicate.

Dried samples were weighed and wrapped in tin capsules. Weights ranged from 500–1000 μg for albumen and potential prey samples, 1000–1500 μg for primary producers, and up to 5 mg for sediment samples. Samples were sent to the Stable Isotope Facility (SFU) at the University of California, Davis, USA for analysis of $\delta^{13}C$ and $\delta^{15}N$. Isotope ratios are reported using standard notation:

$$\delta_{sample} = \left(\left(R_{sample} - R_{standard}\right)/R_{standard}\right) * 1000$$

where δ_{sample} is the isotopic ratio of the sample and R is the ratio of the heavy to light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in the sample relative to V-PDB or atmospheric nitrogen, respectively. Internal, certified laboratory standards are routinely interspersed with target samples during analysis runs. Long-term standard deviations of internal standards used at SFU are 0.2‰ and 0.3‰ for carbon and nitrogen, respectively. To evaluate whether variations in lipid content skewed the $\delta^{13}C$ values of potential prey, C:N ratios were examined. The mean ± SD of the 139 samples of fish and invertebrate tissue sampled was 3.3 ± 0.6; only 5 $\delta^{13}C$ values ranged between 4.5 and 5.0. Post *et al.* (2007) showed that for C:N ratios < 5, the isotopic composition of the prey would be skewed by < 1.5 ‰ due to the presence of isotopically lighter lipids. Given the high variability in the $\delta^{13}C$ values of the potential prey collected (see results, Appendix A), the small proportion of potential prey that had C:N ratios between 4.5 and 5.0, and the qualitative nature of food web comparisons, it was decided not to correct $\delta^{13}C$ values for lipid content.

Data analysis

Statistical comparison of SIR from eggs from a given species and nesting area sampled on different dates was not conducted due to the very uneven sample sizes (Table 1). However, albumen isotope ratios from samples collected on different days overlapped and were pooled to calculate the mean, standard deviation, and variance for each species and colony. Levene's test for equality of variance was used to evaluate whether the isotopic niche width differed among colonies. Non-parametric Kruskall–Wallis tests (H statistic) were used to test for differences in albumen $\delta^{13}C$ and $\delta^{15}N$ values among eggs from different colonies. Multiple comparison *post hoc* tests were conducted with Bonferroni-adjusted Wilcoxon-Signed Ranks Test ($\alpha = 0.0025$; 20 comparisons). All statistical analyses were conducted using SYSTAT® version 11.

Owing to isotope discrimination associated with catabolic processes, consumers are usually more enriched in ^{13}C and ^{15}N than their diet (McCutchan *et al.*, 2003). Trophic discrimination (TD) also occurs between a female and egg components (Hobson, 1995). To facilitate the qualitative comparison of the SIR of albumen with the isotopic characteristics of the food web from each potential feeding site, albumen $\delta^{13}C$ and $\delta^{15}N$ values corrected for isotope trophic discrimination were calculated (Hobson *et al.*, 2000). The waterbird species we focused on have very broad carnivorous diets that include fresh, brackish and saltwater invertebrates and fishes (Kushlan, 1978; Burger, 1996; Molina *et al.*, 2009). Given that the specific trophic level at which females feed in the delta is not known, it was assumed that nesting females fed at TL of 3 or 4 (i.e. they preyed on tertiary or secondary consumers) and TD was calculated considering both scenarios (Table 2).

The TD factors reported by Hobson (1995) and Polito *et al.* (2009) were used for albumen (Table 2). Hobson (1995) conducted a controlled laboratory experiment on several bird species to estimate the isotope discrimination between a female's diet and various egg components. For three carnivorous species, the peregrine falcon

Table 2. Trophic discrimination (TD) factors used to estimate the difference in isotopic composition between egg albumen of waterbirds nesting in the Colorado River Delta and potential prey and carbon sources. The TD values from Hobson (1995) and Polito *et al.* (2009) are compared for nitrogen isotopes. The cumulative TD (sum) was calculated assuming nesting females fed at a trophic level (TL) of 3 or 4

	Carbon trophic discrimination (‰)		Nitrogen trophic discrimination (‰)			
			Hobson (1995)		Polito *et al.* (2009)	
	TL = 3	TL = 4	TL = 3	TL = 4	TL = 3	TL = 4
Egg albumen[b]	0.9	0.9	3.2	3.2	4.5	4.5
Tertiary consumer[a]	---	0.9	---	3.2	---	3.2
Secondary consumer[a]	0.9	0.9	3.2	3.2	3.2	3.2
Herbivore[a]	−0.4	−0.4	2.5	2.5	2.5	2.5
Sum	**1.4**	**2.3**	**8.9**	**12.1**	**10.3**	**13.5**

[a] Vander Zanden and Rasmussen (2001)
[b] Hobson (1995)
[c] Polito *et al.* (2009)

(*Falco peregrinus*), prairie falcon (*F. mexicanus*) and gyrfalcons (*F. rusticolis*), the mean TD was 0.9 ± 0.1‰ for δ^{13}C and 3.2 ± 0.1‰ for δ^{15}N. Polito *et al.* (2009) reported TD factors of 0.8‰ for carbon isotopes and of 4.5‰ for nitrogen for the egg albumen of Gentoo penguins (*Pygoscelis papua*) fed whole wild-caught herring in captivity. Because the TD factors reported by Hobson (1995) and Polito *et al.* (2009) for carbon isotopes were very similar, their average value was calculated. Given that the TD of nitrogen isotopes reported by Hobson (1995) and Polito *et al.* (2009) differed by 1.3‰, the albumen SIR was corrected considering both values. The mean trophic discrimination factors reported by Vander Zanden and Rasmussen (2001) were used for non-herbivorous aquatic consumers (0.9 ±1‰ and 3.2 ± 0.4‰, for carbon and nitrogen, respectively, mean ± SD) and aquatic herbivores (–0.4 ±1.4‰ and 2.5 ± 2.5‰ for carbon and nitrogen, respectively, mean ± SD; Table 2).

Trophic discrimination factors can vary substantially due to food quality and quantity, tissue, biochemical component analysed and species, among others (McCutchan *et al.*, 2003; Vanderklift and Ponsard, 2003). Thus these corrected δ^{13}C and δ^{15}N values were considered only a rough approximation of the mean isotopic composition of the diet consumed by the target species and were used in a qualitative fashion for comparison with isotopic values of primary producers.

Mean albumen SIR ± SD of each species and nesting area were plotted against functional group SIR from the 10 potential feeding sites. Frequency distributions of the carbon and nitrogen isotopic values of primary producers and consumers were generated for each of the three areas sampled (France, 1995). Frequency distributions were compared with mean ± 2 SD of TD-corrected SIR values of egg collected in CP or the MCR; we consider 2 SD represents the range of variability found in egg SIR. This approach allows for food web-level comparisons among habitats and can be used to infer the dominant sources of primary production and potential variability in carbon sources and nitrogen cycling at the base of a food web.

RESULTS

Egg albumen SIR

Overall, albumen δ^{13}C and δ^{15}N values exhibited a broad range of values (range: –27.7 to –9.8‰ and 6.8 to 19.8‰, respectively; Figure 2(a)). Snowy egret and gull-billed tern eggs from CP exhibited a high variance in carbon and nitrogen SIR (from 2.9 for δ^{15}N values of snowy egrets to 23.9 for δ^{15}N values of gull-billed terns). Carbon SIR of CP eggs spanned a range of 15 and 8‰ in the terns and egrets, respectively, while δ^{15}N also showed a large interval of values (11 and 6‰, respectively). In contrast, snowy egrets, gull-billed terns and laughing gulls nesting at MCR showed a much more limited range of isotopic ratios (< 1.1‰ and <1.9‰ for carbon and nitrogen, respectively, except for δ^{13}C values for snowy egret eggs that had a range of 4.3‰). Colonies from the MCR had a variance < 1.4 in all cases.

The variance in egg δ^{13}C and δ^{15}N values differed significantly among the five colonies (Levene's test F = 10.77, $P < 0.001$ and F = 11.31, $P < 0.001$,

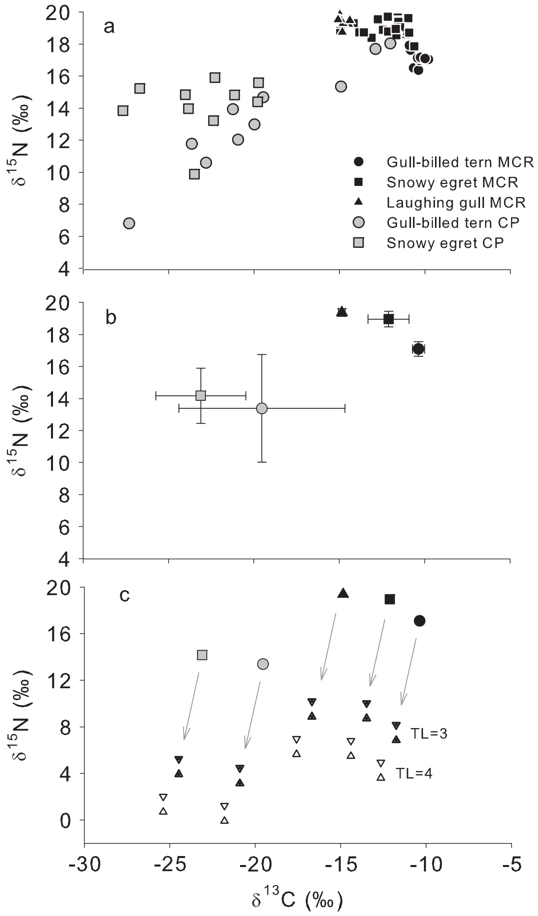

Figure 2. Albumen δ^{13}C and δ^{15}N values of (a) individual eggs collected in coastal (mouth of the Colorado River; MCR) and inland (Cerro Prieto; CP) colonies in the Colorado River Delta, (b) mean ± SD of species and colony-specific isotope ratios, and (c) trophic discrimination-corrected mean stable isotope values calculated considering females fed at a trophic level of 3 or 4 and the nitrogen isotope discrimination values reported by Hobson (1995; downward-pointing triangles) and Polito *et al.* (2009; upward-pointing triangles) and listed in Table 2.

respectively, Table 1), and was much higher in gull-billed tern and snowy egret eggs collected at CP for carbon and nitrogen SIR (range 2.9 to 23.9) than for the three species sampled at MCR (<1.4). The variance in egg SIR of gull-billed terns and snowy egrets nesting at CP differed significantly ($F = 9.14$, $P = 0.011$ and $F = 8.5$, $P = 0.001$ for carbon and nitrogen, respectively). In contrast, the variance in albumen $\delta^{13}C$ did not differ significantly between colonies of gull-billed terns, snowy egrets, and laughing gulls from MCR ($F = 2.2$, $P = 0.12$), although $\delta^{15}N$ values did differ significantly ($F = 7.1$, $P = 0.002$).

Carbon and nitrogen SIR of eggs from the colonies nesting at MCR were generally lighter than those from CP. There were significant differences between species-specific mean egg $\delta^{13}C$ (H statistic = 52.852, $P < 0.001$) and $\delta^{15}N$ values (H statistic = 51.057 $P < 0.001$) of the five colonies. Carbon and nitrogen SIR differed significantly in most pairwise comparisons (Table 3).

Corrections for food web TD varied as a function of the trophic level at which nesting females were assumed to feed (TL = 3 or 4) and whether the albumen TD factor reported by Polito *et al.* (2009) or Hobson (1995) for nitrogen isotopes was used (Table 2, Figure 2(b) and (c)). Trophic corrections for mean $\delta^{13}C$ values of egg albumen were 1.4‰ (TL = 3) and 2.3‰ (TL = 4). Corrections for mean $\delta^{15}N$ values varied between 8.9 and 13.5, depending on TL and the nitrogen isotope discrimination factor (Figure 2(b)).

Potential feeding grounds and food web structure

Food web components collected at the Cerro Prieto Geothermal Plant evaporative ponds and Agricultural Drain were substantially more enriched in ^{13}C and ^{15}N than the eggs from local colonies (Figure 3; Appendix A). In contrast, the SIR of potential prey (fish and shrimp) from Canal Independencia were similar to those of at least some eggs from local females. Carbon SIR of eggs from colonies from the MCR were 5–10‰ lighter than potential prey collected at the geothermal plant's evaporative ponds, and about 10‰ heavier than the prey from the other two CP locations.

The prey captured in two of the four habitats sampled within the Ciénega de Santa Clara had isotopic values consistent with the isotopic composition of egg albumen from CP (Figure 4). Carbon and nitrogen SIR of prey collected at the Wellton Mohawk Outlet Drain and Flor del Desierto had an isotopic composition similar to CP eggs, while those from Laguna El Troque and Wellton Mohawk East Lagoon differed substantially (Figure 4).

Potential prey collected at the three sites from the MCR had carbon and nitrogen SIR that overlapped with those of eggs collected in coastal colonies (−10 to −15‰ and 15 to 20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, Figure 5). Potential prey collected at MCR were substantially enriched in ^{13}C and ^{15}N relative to SIR of eggs from inland colonies.

The TD-corrected $\delta^{13}C$ values of most eggs collected at CP were < −19.6‰, which is consistent with feeding on prey that rely partially or solely on C3 terrestrial production. However, three gull-billed terns eggs had $\delta^{13}C$ values that were noticeably more enriched (TD-corrected values of −13.6 to −10.6‰). The $\delta^{13}C$ values of terrestrial C3 plants collected at the three sampling sites near CP were depleted in ^{13}C (mean = −25.8 ± 8‰, average of the mean value of 29 individual taxa) relative to aquatic vascular plants (−10.8 ± 4.5‰, n = 5), benthic microalgae (−8.4 ± 0.8‰, n = 2) and POM (−14.9 ± 1.7‰, n = 7, Figure 3). Similarly, the mean carbon isotope ratios of primary producer taxa collected at the Ciénega de Santa Clara exhibited a large range of mean values: –26.3 ± 1.9‰ for terrestrial C3 plants (n = 39), –19.9 ± 4.2‰ for POM (n = 24), –16.5 ± 1.8‰ for BMI (n = 7), –19.1 ± 3.2‰ for aquatic vascular plants (n = 2) and −14.0 ± 0.2‰ (n = 3) for the marsh grass *Distichlis palmeri*.

The TD-corrected $\delta^{13}C$ values of albumen of the three species nesting at MCR were similar to those

Table 3. Results of pairwise Wilcoxon-signed ranks (Z, *P* values) tests used to compare $\delta^{13}C$ (upper quadrant) and $\delta^{15}N$ (lower quadrant) values of egg albumen from colonies in an inland and coastal location of the Colorado River Delta. A Bonferroni correction was using to control for Type 1 errors ($\alpha = 0.005$; 10 comparisons). Statistical differences are indicated in bold. CP: Cerro Prieto, MRC: mouth of the Colorado River

Species	Gull-billed tern (MCR)	Snowy egret (MCR)	Laughing gull (MCR)	Gull-billed tern (CP)	Snowy egret (CP)
Gull-billed tern (MCR)	--	**0.005**	**0.005**	**0.005**	0.047
Snowy egret (MCR)	**0.005**	--	**0.002**	0.007	**0.005**
Laughing gull (MCR)	**0.005**	0.113	--	**0.005**	**0.005**
Gull-billed tern (CP)	0.013	**0.005**	**0.005**	--	0.028
Snowy egret (CP)	**0.005**	**0.005**	**0.005**	0.386	--

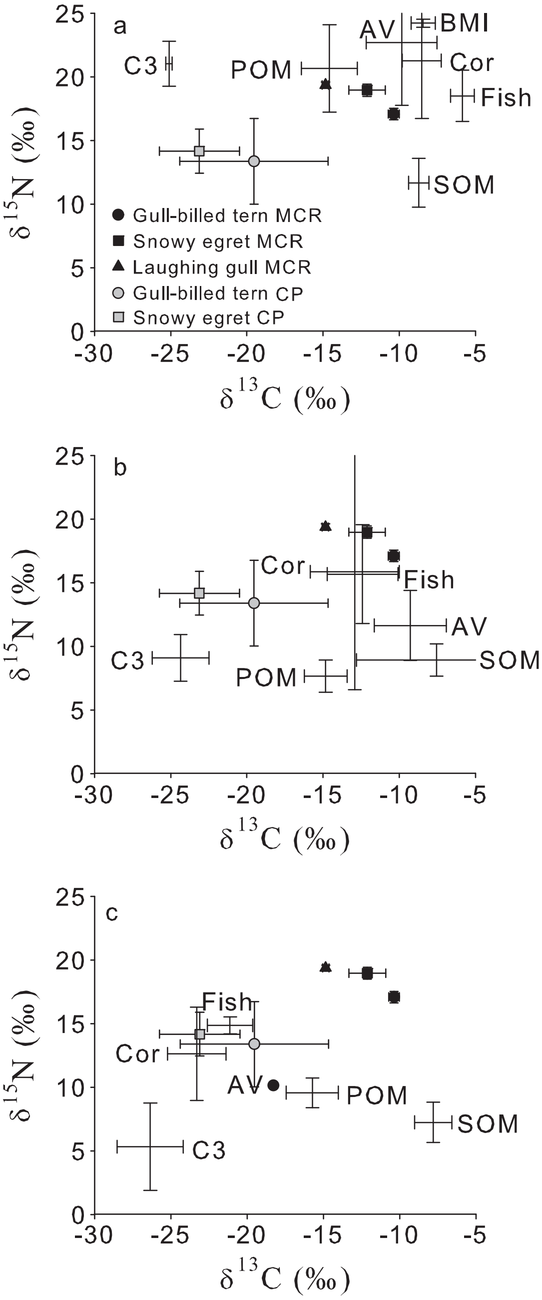

Figure 3. Mean ± SD δ^{13}C and δ^{15}N values of egg albumen of waterbirds that nest at the mouth of the Colorado River (MCR) and Cerro Prieto Geothermal Plant (CP) (larger symbols and dark error bars in all panels). Albumen isotope values are compared with those of primary producers and consumers collected at (a) the geothermal plant's evaporative ponds, (b) an agricultural drain, and (c) a water transport channel. Mean ± SD of δ^{13}C and δ^{15}N values of functional groups of primary producer and consumers are depicted with light gray error bars. Amph: amphiods; AV: aquatic vascular plants; BMI: benthic microalgae; C3: C3 terrestrial plants; Cor: corixids; POM: particulate organic matter; Shr: shrimp; Sna: snails; SOM: sediment organic matter.

of C4 (−13.6 ± 0.4‰, n = 6), POM (−14.5 ± 2.3‰, n = 15), macroalgae (−11.4 ± 1.9‰, n = 3) and BMI (−8.4 ± 1.0‰, n = 3) collected in the area. The range of mean nitrogen SIR of primary producers was high (5 to 13‰; Figures 3–5).

Frequency distributions of SIR

Frequency distributions of carbon and nitrogen SIR from the three CP sampling sites reflect the broad range of isotopic values documented for primary producers (Figure 6). The distribution of δ^{13}C values of primary producers was bimodal, with modes at −22 to −24‰ and −14 to −16‰. However, most consumers exhibited carbon isotope ratios within the more enriched range of values (≥ -14‰). The carbon SIR frequency distributions of producers and consumers from the Ciénega de Santa Clara and sites near the MCR nesting area exhibited a more restricted range of values than those collected at CP (Figure 6). They were, however, markedly different from each other. Most of the δ^{13}C values of primary producers from the Ciénega de Santa Clara were very depleted in ^{13}C (≤ -14‰) and consistent with that of C3 plants (Figure 4). In contrast, the SIR of all primary producers and consumers collected near the MCR nesting area were much more enriched in ^{13}C (Figure 6).

DISCUSSION

Relating the SIR of egg components to potential foraging grounds within the time scale of interest (in this case, the nesting period) requires ascertaining whether isotopic values reflect a female's recent feeding (as is the case in income breeders), or whether endogenous reserves also contribute to the synthesis of egg components (as occurs in capital breeders) (Hobson, 2006). It was assumed that the isotopic composition of egg albumen of our target species reflected the recent feeding of nesting females based on their temporal patterns of habitat utilization in the delta and time period over which egg albumen integrates the isotopic composition of prey. The target species arrive or are present in the Colorado River Delta weeks prior to nesting, and feed in the area before laying eggs (Patten *et al.*, 2001; Peresbarbosa-Rojas and Mellink, 2001). Snowy egrets are year-round residents in the area, while gull-billed terns and laughing gulls seem to be breeding visitors although they may remain in the northern gulf perennially. Hobson *et al.* (1997, 2000) used stable isotope analysis to determine whether the protein fraction of egg components of several species of Charadriformes, which includes terns and gulls, came from endogenous or exogenous sources. Their results clearly indicated that the SIR of the egg

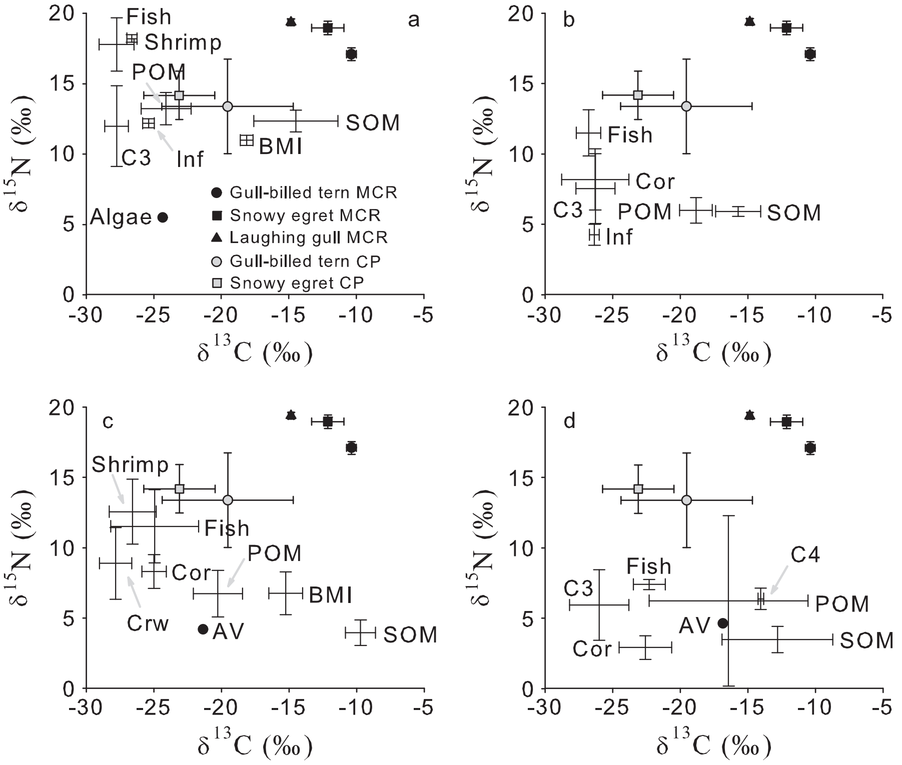

Figure 4. Mean ± SD δ^{13}C and δ^{15}N values of egg albumen of waterbirds that nest at the mouth of the Colorado River (MCR) and Cerro Prieto Geothermal Plant (CP) (larger symbols and dark error bars in all panels). Albumen isotope values are compared with those of primary producers and consumers collected at sites within a brackish marsh, including (a) El Troque, (b) Wellton Mohawk Outlet Drain, (c) Wellton Mohawk East Lagoon, and (d) Flor del Desierto. Means ± SD δ^{13}C and δ^{15}N values of primary producer and consumer functional grups are depicted with light gray error bars. Amph: ampipods; AV: aquatic vascular plants; BMI: benthic microalgae; C3: C3 terrestrial plants; C4: C4 terrestrial plants; Cor: corixids; Crw: crawfish; Inf: infaunal polychaetes; POM: particulate organic matter; Shr: shrimp; Sna: snails; SOM: sediment organic matter.

protein fraction reflected local feeding, although some species did use endogenous reserves for synthesis of the lipid fraction. Other studies have shown that the isotopic composition of egg protein of shorebirds reflect recently assimilated foods (Hobson and Jehl, 2010). Hence, the isotopic composition of egg albumen of waterbirds nesting in the delta reflects the recent feeding of females and represents a snapshot of their isotopic niche breadth during the summer.

Variance in egg SIR

The striking differences in the magnitude of the variance in carbon and nitrogen SIR of eggs collected in the Colorado River Delta indicates substantial differences in isotopic niche breadth among species nesting in the same area and between populations of the same species nesting at the inland and coastal location. In particular, a very high variance was calculated in the SIR of gull-billed terns nesting at CP, which is comparable in magnitude to only a few reports in the literature (Araujo *et al*., 2007; Newsome *et al*., 2007).

The isotopic composition of an individual consumer's tissues can vary as a function of spatial and temporal variation at the base of the food web and the absolute range of isotopic values exhibited by primary producers and prey (Newsome *et al*., 2007; Flaherty and Ben-David, 2010). The variance of the isotopic composition of eggs collected over 2 days was calculated (Table 1), and it is therefore unlikely that temporal variation at the base of the food web contributed to the high variance in δ^{13}C and δ^{15}N values of eggs collected from the CP nesting site. Bearhop *et al*. (2004) and Matthews and Mazumander (2004) rightly note that high intraspecific variation in consumer SIR can have several causes, and that the isotopic niche may not reflect individual specialization in feeding preferences. This present study was not designed to assess directly the relative importance of feeding on prey with distinct isotopic ratios (i.e. individual prey preferences). The high variance in the SIR of eggs from gull-billed terns and snowy egrets nesting at CP is, however, consistent with the level of variability in the isotopic signatures of food web components at the inland locations. The

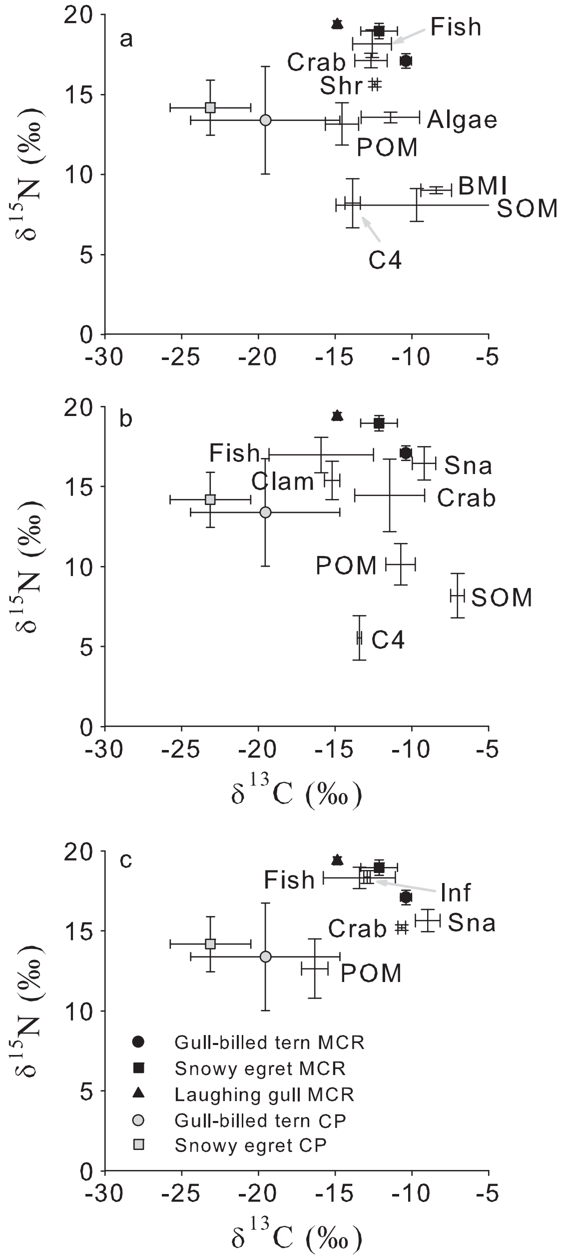

Figure 5. Mean ± SD δ^{13}C and δ^{15}N values of egg albumen of waterbirds that nest at the mouth of the Colorado River (MCR) and Cerro Prieto Geothermal Plant (CP) (larger symbols and dark error bars in all panels). Albumen isotope values are compared with those of primary producers and consumers collected at two sites in Montague Island sites (a) El Chayo and(b) El Faro and at (c) a nearby beach in the upper Gulf of California. Means ± SD of δ^{13}C and δ^{15}N of primary producer and consumer functional groups are depicted with light gray error bars. C4: C4 terrestrial plants; POM: particulate organic matter; SOM: sediment organic matter.

large variance observed in SIR for both species is likely to be attributed to feeding in various habitat types and isotopically variable prey.

The variance in carbon and nitrogen SIR of gull-billed terns from CP was approximately three times that of snowy egrets. Gull-billed terns may forage over a broader range of habitats and prey resources than snowy egrets. Differences in foraging were found between these two species, despite the fact that they share nesting grounds. In contrast to what we found at CP, the variance in carbon and nitrogen SIR of the eggs of gull-billed terns, snowy egrets and laughing gulls sampled at MCR was very low (< 0.1 to 1.4). At the intraspecific level, this suggests those females were more stereotyped in intraspecific prey use than those of CP.

Foraging habitats and food web structure

Trophic discrimination factors can vary substantially due to food quality and quantity, tissue, biochemical component analysed, and species, among others (McCutchan *et al.*, 2003; Vanderklift and Ponsard, 2003). Further, the number of studies reporting TD factors for egg albumen is limited, making it difficult to evaluate the consistency of these values between species of birds. Thus these corrected δ^{13}C and δ^{15}N values are considered only a rough approximation of the mean isotopic composition of the diet consumed by target species and are used in a qualitative fashion for comparison with isotopic values of primary producers.

The isotopic composition of albumen, primary producers, and potential prey items collected in the Colorado River Delta revealed a very heterogeneous isotopic landscape. Comparison of the isotopic composition of eggs with those from potential feeding sites indicates only some of the wetland habitats available in the Colorado River Delta may support feeding, and that birds from coastal and inland colonies forage in different areas and seem to rely on distinct carbon sources.

The lack of correspondence between albumen SIR of snowy egrets and gull-billed terns nesting at CP and the sources of primary production and potential prey that were collected in the vicinity of the nesting site clearly indicates those nearby wetlands do not play an important role supporting the feeding of local colonies. In contrast, the Ciénega de Santa Clara could provide the type of habitat in which these birds feed. The fact that the nesting habitat in Cerro Prieto provides physical habitat but not nutrition for snowy egret and gull-billed tern populations demonstrates that there can be strong decoupling between foraging and nesting habitats, at least over the spatial scale we considered. The present-day distribution of wetlands in the Colorado River Delta is very fragmented and limited in spatial extent (Glenn *et al.*, 1996; Zamora-Arroyo *et al.*, 2005;

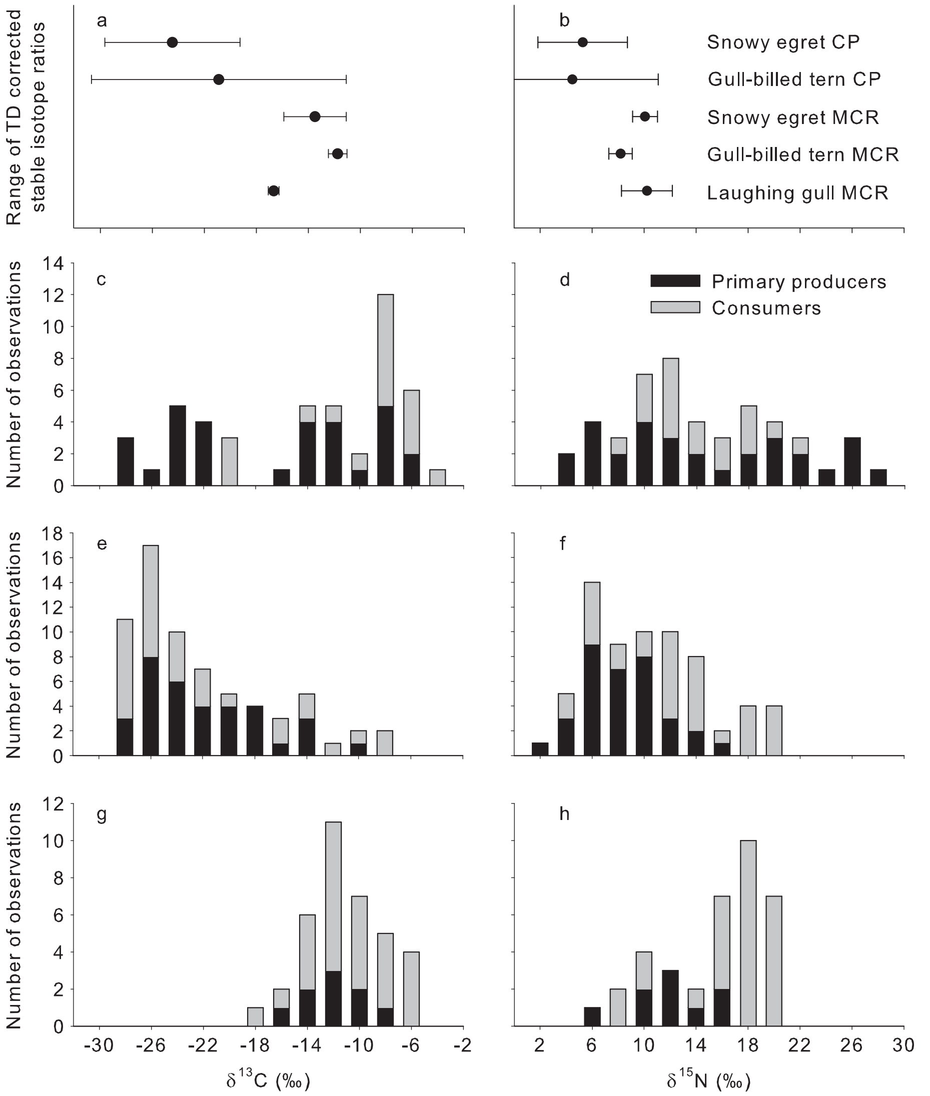

Figure 6. (a,b) Mean ± 2 SD of trophic discrimination-corrected $\delta^{13}C$ and $\delta^{15}N$ values of albumen from nesting waterbirds sampled at an inland (CP) and coastal (MRC) area in the Colorado River Delta. Frequency distributions of $\delta^{13}C$ and $\delta^{15}N$ of primary producer taxa (black bars) and consumer taxa (grey bars) collected at (c,d) Cerro Prieto (inland), (e,f) the Ciénega de Santa Clara (a brackish marsh), and (g,h) at the mouth of the Colorado River. Taxa and isotope ratios are listed in Appendix A.

Zamora-Arroyo and Flessa, 2009). It is possible that the individuals nesting at the inland location must forage in different areas (and consequently, on prey with differing isotopic composition) because of limited resources at any one potential feeding site or that they prefer prey found in different wetland types.

The sources of brackish or freshwater water that feed the delta are all intensively managed (Glenn *et al.*, 1996; Zamora-Arroyo *et al.*, 2005; Zamora-Arroyo and Flessa, 2009). Glenn *et al.* (2001) divided the Colorado River Delta's habitats into four terrestrial ecozones that include riparian, brackish and intertidal marshes, and a marine zone. They noted that the common threat to all ecozones is the lack of a dedicated source of freshwater inflow, although the more terrestrial ecozones seem to have a greater potential for recovery in response to the inflow of fresh water, even if its volume is limited or the flow sporadic, than the marine one (see also Zamora-Arroyo *et al.*, 2001). These results support the proposition that the remaining wetland habitats in the Colorado River Delta must be conserved through water management plans (Zamora-Arroyo and Flessa, 2009).

Food web structure

Comparison of TD-corrected isotopic values of CP eggs with those of primary producers collected at the inland locations (CP and CSC) indicates C3 terrestrial plants are the dominant source of production supporting feeding, especially for the individuals exhibiting the most depleted $\delta^{13}C$ values (Peterson and Fry, 1987). However, the broad range of SIR of CP eggs suggests that other primary producer taxa may also support local prey production. Owing to the broad range of isotope ratios of the other primary producer taxa, it was not possible to identify which specific carbon sources supported feeding of females nesting at CP. Nevertheless, C3 terrestrial plants have characteristic $\delta^{13}C$ values that are reflected in the isotopic composition of birds nesting inland.

The species nesting at the MCR clearly foraged in areas that are isotopically distinct from those used by the populations nesting inland at CP. Given that the SIR of those eggs were *c.* 15–20‰ more enriched in ^{13}C relative to potential prey from all CP and CSC sites, waterbirds from the coastal colonies do not forage inland. The enriched carbon and nitrogen isotopic ratios of eggs collected on Montague Island are consistent with the sources of coastal production sampled. The upper Gulf of California is located in an extremely arid region and is characterized by a 7–10 m tidal range during spring tides. Despite the persistent lack of freshwater inflow from the Colorado River, the area is considered productive owing to high rates of phytoplankton productivity that has been attributed to tidal mixing and upwelling (Millán-Nuñez *et al.*, 1999), and it supports important fisheries (Calderón-Aguilera and Flessa, 2009).

The isotopic signatures of albumen of eggs from MCR differed significantly among species. Snowy egrets, gull-billed terns and laughing gulls thus seem to feed on different prey. Regardless of the specific prey preferences and feeding behaviour of each species, the similarity in the isotopic composition of the eggs and the potential food sources collected in the area suggests that habitat appropriate for foraging habitat is available at or near the nesting area.

As was the case for carbon SIR, $\delta^{15}N$ values of producers and consumers collected throughout the delta were extremely variable, ranging from mean values of *c.* 4 to 28‰ for primary producer taxa and from *c.* 4 to 22‰ in consumers (excluding egg albumen; Figure 6). Although dramatic, such a broad range of $\delta^{15}N$ values is not unexpected. The habitats sampled include evaporative ponds associated with a geothermal plant, agricultural drains and channels, and an artificially maintained wetland that receives agricultural wastewater. The northernmost extent of the Gulf of California harbours high concentrations of inorganic nitrogen from marine origin and possibly limited groundwater inflow (Álvarez-Borrego, 2001). The Colorado River Delta is currently under intensive water management, and harbours the confluence of bodies of water having different origins (Glenn *et al.*, 1996; Zamora-Arroyo and Flessa, 2009) and within which different geochemical processes are likely to predominate and influence the isotopic composition of inorganic nitrogen (Bedard-Haughn *et al.*, 2003).

CONCLUSIONS

It was found that waterbirds nesting at the inland location in the Colorado River Delta exhibited a much broader isotopic niche width than those nesting at Montague Island at the mouth of the Colorado River. In contrast, the species nesting at the mouth of the Colorado River Delta exhibited a very narrow isotopic niche breadth, despite the fact that their foraging strategies differ. These findings highlight the need to better understand the full range of habitat features required to sustain populations of these species. Results support the proposition that careful study of foraging patterns and reproductive success are also required to adequately define critical habitat needs. Further, the diversity of habitats and foods that seem to be used by birds nesting in Cerro Prieto points to the need to protect and manage a variety of habitats, perhaps over a fairly broad spatial scale, in order to ensure the maintenance of target species.

ACKNOWLEDGEMENTS

UC-Mexus provided financial support through their Collaborative Grants programme. The IMADES research station allowed us to use their facilities. Samples were collected under permit SGPA/DGVS/2199 to E. Mellink. José Alfredo Castillo, Lya X. Avalos and Edith Suazo assisted during fieldwork. Silvia Avilés Torres helped with fish identification. We thank out two reviewers for their constructive feedback and comments.

CONFLICT OF INTEREST STATEMENT

The authors do not have a conflict of interest in submitting this manuscript for publication.

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APPENDIX A

Mean ± SD of food web components collected in three regions in the Colorado River Delta during the summer of 2002. For particulate organic matter (POM), sediment organic matter (SOM) and corixids (a ubiquitous herbivorous insect), replicate samples were sometimes collected at different locations within the same site but within hundreds of metres. In these cases, mean and error were calculated separately and values are differentiated using arabic numbers following the taxa. Taxa were classified into functional groups. C3: C3 terrestrial plants; C4: C4 terrestrial plants; BMI: benthic microalgae

Region	Site	Taxa	Functional group	δ^{13}C (‰)	SD	n	δ^{15}N (‰)	SD	n
Cerro Prieto	Agricultural Drain (32º 24.382 N, 115º16.324 W)	Aquat plant sp., unidentified	Aquatic vascular	−7.5			13.6		1
		Ruppia maritima	Aquatic vascular	−8.5		1	9.7		1
		Salicornia sp.	C3	−25.9	1.0	3	9.4	2.6	3
		Tamarix ramosissima leaves	C3	−22.8	0.9	3	8.8	1.0	3
		Corixids 1	Corixids	−12.4	1.2	2	18.5	11.6	2
		Corixids 2	Corixids	−13.4	4.8	2	13.2	9.6	2
		Cyprinodon macularis	Fish	−10.0	0.6	3	19.6	2.5	3
		Gambusia affinis	Fish	−14.5	1.6	3	11.4	1.0	3
		Poecilia latipinna	Fish	−12.8	1.8	3	16.0	1.5	3
		POM 1	POM	−14.2	1.7	3	6.5	0.3	3

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		POM 2	POM	−15.5	0.9	3	8.7	0.6	3
		SOM 1	SOM	−6.8	7.5	3	8.0	0.8	3
		SOM 2	SOM	−8.3	3.2	3	9.8	0.9	3
Cerro Prieto	Canal Independencia (32º 27.941 N 115º23.306 W)	Amphipod	Aquatic crustacean	−21.8	1.6	3	10.1	1.1	3
		Shrimp	Aquatic crustacean	−21.2	0.0	2	15.0	0.3	2
		Aquat plant sp., unidentified	Aquatic vascular	−22.2	3.5	3	11.7	3.4	3
		Compuesta noli	C3	−29.0	0.7	3	4.3	0.6	3
		Phragmites autralis	C3	−26.3	0.5	3	5.2	5.2	3
		Pluchea sericea	C3	−28.3		1	2.2		1
		Prosopis glandulosa	C3	−24.5	1.4	3	7.2	7.0	3
		Sonchus sp.	C3	−28.8	1.0	3	3.5	0.8	3
		Tamarix ramosissima-flowers	C3	−25.6	0.7	3	5.6	0.3	3
		Tamarix ramosissima-leaves	C3	−23.7	1.4	3	5.9	3.0	3
		Corixids 1	Corixids	−24.0	1.7	2	15.1	3.9	2
		Corixids 2	Corixids	−22.6	2.5	2	10.2	1.0	2
		Poecilia latipinna	Fish	−20.4	0.2	3	14.6	0.6	3
		POM	POM	−14.3	0.5	3	10.3	0.2	3
		SOM 1	SOM	−8.4	0.2	2	8.6	1.8	2
		SOM 2	SOM	−7.4	1.6	3	6.3	0.4	3
Cerro Prieto	Geothermal Plant (32º 23.455 N, 115º15.796 W)	Aquat plant sp., unidentified	Aquatic vascular	−11.5		1	26.2		1
		Ruppia maritima	Aquatic vascular	−8.2		1	19.2		1
		BMI	BMI	−8.4	0.8	2	24.2	0.3	2
		Allenrolfea sp.	C3	−25.1	0.2	3	21.0	1.8	3
		Corixids 1	Corixids	−9.9	1.2	2	23.5	0.2	2
		Corixids 2	Corixids	−7.4	0.6	2	16.1	4.7	2
		Corixids 3	Corixids	−8.2	0.2	2	24.3	0.1	2
		Cyprinodon macularius	Fish	−6.1	1.0	3	17.9	0.9	3
		Cyprinodon macularius	Fish	−5.6	0.9	4	17.7	0.6	4
		Cyprinodon macularius	Fish	−6.0	0.3	3	20.2	3.2	3
		POM 1	POM	−15.7	0.1	2	16.8	1.4	2
		POM 2	POM	−16.7	0.6	3	20.8	2.1	3
		POM 3	POM	−12.9	0.7	3	18.6	1.3	3
		POM 4	POM	−13.4	1.1	3	25.2	0.2	3
		SOM 1	SOM	−9.8	0.5	2	12.8	2.2	3
		SOM 2	SOM	−8.5	0.6	2	10.9	3.8	2
		SOM 3	SOM	−9.0	0.5	2	12.0	0.3	2
		SOM 4	SOM	−8.0	0.2	3	11.5	2.4	3
		SOM 5	SOM	−8.8	0.2	3	11.0	1.0	3
Ciénega de Santa Clara	WM East Lagoon	*Allenrolfea occidentalis*	C3	−27.1	0.7	3	6.3	1.0	3
		Salicornia sp.	C3	−28.3	3.2	3	3.8	3.8	3
		Scirpus maritimus	C3	−26.8	0.7	3	5.8	2.9	3
		Tamarix ramosissima flowers	C3	−23.9	0.2	3	7.8	3.1	3
		Tamarix ramosissima leaves	C3	−22.6	0.9	3	5.0	0.9	3
		Typha dominguensis dry leaves	C3	−26.6	0.6	3	8.3	1.4	3
		Typha dominguensis green leaves	C3	−26.6	0.7	3	4.5	1.2	3
		Distichlis palmeri	C4	−14.0	0.2	3	6.4	0.8	3
		Corixids 1	Corixids	−23.8	0.9	3	3.3	0.6	3
		Corixids 2	Corixids	−21.3	2.0	3	2.5	1.0	3
		Cyprinodon macularis	Fish	−21.3	0.4	3	7.7	0.2	3
		Gambusia affinis	Fish	−23.3	0.6	3	7.1	0.3	3
		POM 1	POM	−11.1	1.2	3	11.5	1.4	3
		POM 2	POM	−21.7	0.8	3	0.9	2.3	3
		SOM 1	SOM	−14.2	6.0	3	4.5	0.1	2
		SOM 2	SOM	−11.4	0.3	3	2.8	0.1	3
Ciénega de Santa Clara	El Troque (32º 02.467 N, 114º 54.417 W)	Spiny macroalgae	Algae	−24.3		1	5.5		1
		Shrimp	Aquatic crustacean	−26.6	0.4	3	18.2	0.3	3
		Microalgal mat	BMI	−18.1	0.5	3	11.0	0.4	3
		Decomposing *Typha*	C3	−17.1	1.7	3	10.8	1.0	3
		Typha dry leaves	C3	−27.3	0.7	3	14.0	0.9	3
		Typha green leaves	C3	−28.2	0.9	3	9.0	1.4	2
		Procambarus clarkii	Crawfish	−26.5			16.7		1
		Cyprinus sp.	Fish	−26.4	1.3	2	17.6	0.0	2
		Gillichthys mirabilis	Fish	−28.5	0.6	3	17.0	0.5	3
		Lepomis macrochirus	Fish	−28.3	1.1	3	19.4	0.5	3

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		Micropterus sp.	Fish	−28.3	0.7	3	19.6	0.7	3
		Mugil sp.	Fish	−28.4			13.0		1
		Oreochromisis sp.	Fish	−25.7	0.0	3	16.1	0.3	3
		Poecilia latipinna	Fish	−28.5	0.2	3	18.6	1.6	3
		Polychaetes	Infauna	−25.4	0.4	2	12.2	0.3	2
		POM 1	POM	−22.9	0.3	3	12.4	0.3	3
		POM 2	POM	−25.3	1.9	3	14.1	1.1	3
		SOM 1	SOM	−12.0	1.9	3	11.7	0.3	3
		SOM 2	SOM	−16.9	1.6	3	13.0	0.2	3
Ciénega de Santa Clara	Flor del Desierto (32º 01.777 N, 114º 51.918 W)	Grass shrimp	Aquatic crustacean	−28.2	1.0	3	11.2	0.3	3
		Shrimp	Aquatic crustacean	−26.3	0.6	3	14.8	2.3	3
		Shrimp	Aquatic crustacean	−25.2	1.8	3	11.6	2.1	3
		Ruppia maritima	Aquatic vascular	−14.3		1	5.1		1
		Aquat plant sp., unidentified	Aquatic vascular	−21.4		1	4.2		1
		Microalgal mat	BMI	−15.6	1.3	3	7.3	1.3	3
		Corixids 1	Corixids	−24.7	0.3	3	7.9	1.6	3
		Corixids 2	Corixids	−25.3	1.3	3	8.7	0.8	3
		Procambarus clarkii	Crawfish	−27.8	1.2	3	8.9	2.5	3
		Cyprinus sp.	Fish	−28.0	3.4	3	13.2	3.9	3
		Gambusia affinis	Fish	−23.7	3.0	3	11.6	1.7	3
		Gambusia affinis	Fish	−23.0	0.4	3	9.7	0.2	3
		POM 1	POM	−21.2	0.8	3	8.2	0.0	3
		POM 2	POM	−19.3	2.3	3	5.3	0.5	3
		SOM 1	SOM	−10.0	0.9	3	4.1	0.8	3
		SOM 2	SOM	−9.4	1.4	3	3.8	1.2	3
Ciénega de Santa Clara	WM Outlet Drain (32º 05.312 N, 114º 52.310 W)	*Pluchea sericea*	C3	−25.9	1.2	3	8.2	2.4	3
		Tamarix flowers	C3	−25.2	1.7	3	8.3	1.0	3
		Tamarix leaves	C3	−26.0	0.4	3	8.5	3.0	3
		Typha dominguensis	C3	−28.0	0.5	3	5.3	2.8	3
		Corixids 1	Corixids	−26.2	3.9	3	9.2	3.0	3
		Corixids 2	Corixids	−26.3	0.4	3	7.2	0.1	3
		Common carp	Fish	−26.7	0.1	3	10.2	0.8	3
		Gambusia affinis	Fish	−26.1	0.7	3	11.8	1.4	3
		Lepomis macrochirus	Fish	−26.0	0.8	3	12.9	2.4	3
		Micropterus sp.	Fish	−27.1	0.2	2	12.5	1.0	2
		Notropis shumardi	Fish	−28.1	0.2	3	10.5	0.3	3
		Capitella sp.	Infauna	−26.3	0.4	2	4.3	0.7	2
		POM 1	POM	−19.2	0.4	3	5.4	0.5	3
		POM 2	POM	−18.5	1.7	3	6.6	0.9	3
		SOM 1	SOM	−16.3	2.4	3	5.9	0.3	3
		SOM 2	SOM	−15.1	0.2	3	6.0	0.4	3
Colorado River mouth	Estero del Chayo (31º 41.529 N, 114º 41.529 W)	*Ulva* sp.	Algae	−11.4	1.9	3	13.6	0.3	3
		Shrimp	Aquatic crustacean	−12.4	0.2	3	15.6	0.2	3
		Microalgal mat	BMI	−8.4	1.0	3	9.0	0.2	3
		Distichlis palmerii	C4	−13.9	0.5	3	8.2	1.5	3
		Callinectes arcuatus	Crab	−13.3	0.8	3	17.2	0.5	3
		Eurytium albidigitum	Crab	−11.7	0.2	2	17.0	0.6	2
		Anchoa delicatissima	Fish	−14.5	1.2	2	18.9	0.7	2
		Atherinops affinis	Fish	−12.1	0.6	3	17.5	0.7	3
		Gillichthys mirabilis	Fish	−11.6	0.6	3	17.8	0.4	3
		Micropogonias megalops	Fish	−12.8	0.0	2	19.1	0.5	2
		POM 1	POM	−13.7	0.7	3	12.0	0.3	3
		POM 2	POM	−15.4	0.3	3	14.3	0.4	3
		SOM 1	SOM	−7.9	0.4	2	8.7	0.8	3
		SOM 2	SOM	−7.3	0.5	3	7.4	0.8	3
Colorado River mouth	El Faro (31º 40.813 N, 114º 43.546 W)	*Distichlis palmerii*	C4	−13.4	0.1	3	5.5	1.4	3
		Clam species A	Clam	−15.5	0.1	3	16.4	0.3	3
		Clam species B	Clam	−14.9	0.5	3	14.3	0.5	3
		Callinectes arcuatus	Crab	−13.3	1.7	3	16.5	0.3	3
		Uca princeps	Crab	−9.6	0.1	3	12.4	0.4	3
		Leptocephalus larvae	Fish	−18.2	1.6	3	16.3	1.0	3
		Micropogonias megalops	Fish	−12.4	0.6	2	17.9	0.3	2
		POM	POM	−10.7	1.0	3	10.1	1.3	3
		Snail species A	Snail	−9.9	0.2	3	17.4	0.1	3

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		Snail species B	Snail	−8.5	0.2	3	15.5	0.1	3
		SOM 1	SOM	−6.6	0.0	2	9.3	1.2	3
		SOM 2	SOM	−7.3	0.2	3	7.1	0.3	3
Colorado River mouth	Eastern Beach (31º 44.75 N, 114º 34.467 W)	*Callinectes arcuatus*	Crab	−10.7	0.2	3	15.2	0.2	3
		Anchoa sp.	Fish	−13.7	0.9	3	18.3	1.2	3
		Hyporhamphus unifasciatus	Fish	−14.7	0.6	2	17.7	0.7	2
		Mugil ondulatus	Fish	−11.5	0.4	3	18.1	0.2	3
		Quietula guaymasiae	Fish	−10.9	0.1	3	18.5	0.3	3
		Sciaenidae	Fish	−16.7	1.1	3	18.7	0.6	3
		Polychaetes	Infauna	−12.9	0.2	3	18.4	0.4	3
		POM 1	POM	−16.9	0.9	3	14.0	0.7	3
		POM 2	POM	−15.7	0.2	3	11.3	1.6	3
		Snail	Snail	−9.0	0.8	3	15.6	0.7	3