

# POPULATION STATUS, FOODS AND FORAGING OF LAYSAN ALBATROSSES *PHOEBASTRIA IMMUTABILIS* NESTING ON GUADALUPE ISLAND, MEXICO

ROBERT L. PITMAN,<sup>1</sup> WILLIAM A. WALKER,<sup>2</sup> WILLIAM T. EVERETT<sup>3</sup> & JUAN PABLO GALLO-REYNOSO<sup>4</sup>

<sup>1</sup>*Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California 92037, USA  
(Robert.Pitman@noaa.gov)*

<sup>2</sup>*National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, NE, Seattle, Washington 98115, USA*

<sup>3</sup>*Endangered Species Recovery Council, P.O. Box 1085, La Jolla, California 92038, USA*

<sup>4</sup>*CIAD, A.C., Unidad Guaymas, Apdo. Postal 284, Guaymas, Sonora 85480, Mexico*

*Received 4 March 2004, accepted 9 November 2004*

## SUMMARY

PITMAN, R.L., WALKER, W.A., EVERETT, W.T. & GALLO-REYNOSO, J.P. 2004. Population status, foods and foraging of Laysan Albatross *Phoebastria immutabilis* nesting on Guadalupe Island, Mexico. *Marine Ornithology* 32: 159-165.

During the 1983/84 winter breeding season, Laysan Albatrosses *Phoebastria immutabilis* bred in the eastern Pacific for the first time in recorded history, on Guadalupe Island, Mexico. By 1991/92, the last reported census, the population had grown to 45 pairs. We conducted censuses during 1999/2000 and 2000/01 and found that, in addition to nesting at the only previously known colony (on the main island), albatrosses were breeding at another site on the main island and on two offshore islets. We estimated the entire population to be a minimum of 119 and 193 pairs for each of the two seasons respectively. Although the colonies on the main island are threatened by predation pressure from introduced mammals, the offshore islets remain predator-free. During June 2000, we also collected 27 chick regurgitation pellets (comprised only of indigestible hard parts) for analysis of diet. The pellets included beaks from a minimum of 964 individual cephalopods representing a minimum of 12 families and 22 species. The most common species were squids: *Histioteuthis hoylei* (20.4% of identified beaks), *Taonius borealis* (13.8%), *Gonatus pyros* (11.2%), and *Galiteuthis?* sp. A (11.0%). A previous study from colonies in Hawaii identified ommastrephid squids as the most important prey, but we did not find any in our sample. The reason(s) for this discrepancy are not clear. It has been suggested that Laysan Albatrosses catch squid at night, taking them alive when they migrate to the surface. Most of the squids that we identified were species that live only in deep water, but after mating the females die and float to the surface. That knowledge, coupled with recently published results indicating that foraging Laysan Albatrosses regularly feed during the daytime, leads us to conclude that Laysan Albatrosses probably take most of their squid prey by diurnal scavenging.

## RESUMEN

Durante la temporada invernal de reproducción de 1983/84 los Albatros de Laysan *Phoebastria immutabilis* se reprodujeron en el Pacífico oriental por primera vez en la actualidad en la Isla de Guadalupe, México. Para 1991/92, en el último censo reportado, la población cerció hasta alcanzar las 45 parejas. Durante 1999/2000 y 2000/01, realizamos censos y encontramos que además de anidar en la colonia previamente conocida (en la isla principal), los albatros se estaban reproduciendo en otro sitio en la isla principal y en otras dos islas. Se estimó que el mínimo poblacional es de 119 y 193 parejas, respectivamente para cada una de las estaciones de anidación. A pesar de que las colonias en la isla principal se encuentran amenazadas por la presión de los mamíferos depredadores introducidos, los islotes de costa afuera permanecen libres de predadores. Durante Junio del 2000 también colectamos regurgitaciones de los pollos (compuestas por partes duras indigeribles) para analizar la dieta. Estas incluyen picos de un mínimo de 964 individuos de cefalópodos, representando un mínimo de 12 familias y 22 especies. Las especies más comunes fueron los calamares: *Histioteuthis hoylei* (20.4% de los picos identificados), *Taonius borealis* (13.8%), *Gonatus pyros* (11.2%), y *Galiteuthis?* sp. A (11.0%), respectivamente. Un estudio previo sobre la alimentación de colonias en Hawaii, identificó que los calamares ommastrephidos son la presa más importante, nosotros no encontramos ninguno en nuestra muestra; las razón(es) para esta discrepancia no son claras. Se ha sugerido que los Albatros de Laysan capturan el calamar durante la noche, capturándolos vivos cuando migran hacia la superficie. Aún así, la mayoría de los calamares que identificamos eran especies que solamente viven en aguas profundas, pero después de aparearse las hembras mueren y flotan hacia la superficie. Aunado con los resultados recién publicados que indican que los Albatros de Laysan durante su búsqueda de comida se alimentan regularmente durante el día, concluimos que los Albatros de Laysan probablemente capturan la mayoría de su presa de calamares como carroña durante el día..

Key words: Laysan Albatross, *Phoebastria immutabilis*, Guadalupe Island, population status, foods, foraging, scavenging, squid

## INTRODUCTION

Laysan Albatrosses *Phoebastria immutabilis* nest almost exclusively within the Hawaiian Archipelago, where an estimated 623,500 breeding pairs comprise 99.9% of the world population (Gales 1998, E. Flint pers. comm.). However, before they were eliminated by feather hunters in the 1800s, several other large colonies existed in the central and western Pacific (Tickell 2000). Around the mid 1970s, Laysans began scouting new nesting colonies in the eastern Pacific (Pitman 1985), and the first nests were discovered during the 1983/84 breeding season (they nest during the boreal winter), at Guadalupe Island, Mexico (29°00'N, 118°15'W), 240 km off the Pacific coast of Baja California (Gallo-Reynoso & Figueroa-Carranza 1996; Fig. 1). This report was the first recorded nesting of the species east of the Hawaiian Islands and a range extension of more than 4000 km. Subsequently, breeding birds were discovered on the islands of San Benedicto and Clarion in the Revillagigedo Islands, Mexico (Howell & Webb 1992) and Alijos Rocks (see Fig. 1).

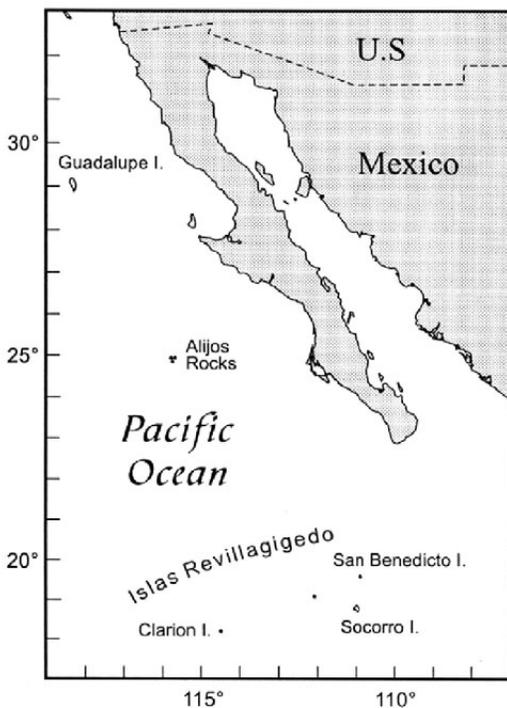
Laysan Albatross colonies in the eastern Pacific are still small, but continue to grow. The pinnacles at Alijos Rocks will never support more than a few nesting pairs (Pitman 1985) and three to four pairs were confirmed nesting in December 2003 (RLP pers. obs.). San Benedicto Island is substantially larger (20 km<sup>2</sup>), uninhabited and predator-free, and the colony there is growing slowly, with 12 nesting pairs in 2000 (Pitman & Ballance 2002) and 17 pairs in 2003 (RLP pers. obs.). At Clarion Island, military personnel continue to add feral animals (including pigs and rabbits) that threaten the existence of all of the island's indigenous fauna (Everett 1988, Howell & Webb 1989, Santaella & Sada 1991). The last published population estimate of Laysan Albatrosses at Clarion Island was from the 1987/88 season, when 30 birds were present at minimum, including two on eggs (Howell & Webb 1992). Guadalupe Island

still has the largest population in the eastern Pacific, despite harassment by military personnel and introduced animals. The most recent census (1991/92) reported 131 birds, including 45 nesting pairs (Gallo-Reynoso & Figueroa-Carranza 1996).

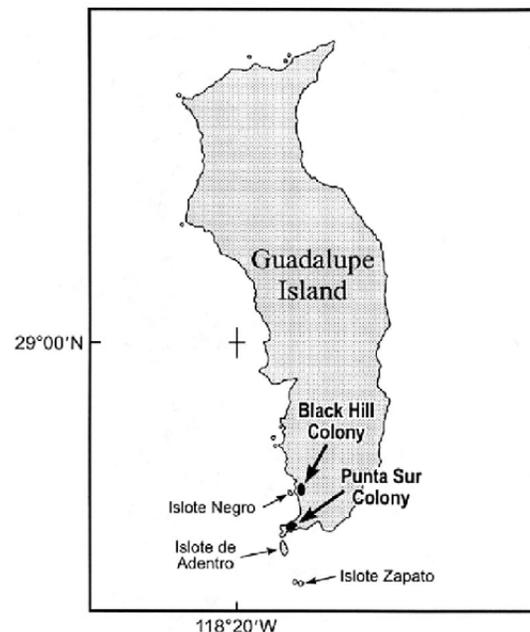
The prey preferences of Laysan Albatrosses in the central Pacific have been studied both at breeding colonies (Harrison *et al.* 1983) and at sea during the non-breeding season (Gould *et al.* 1997a, 1997b), but no data from eastern Pacific populations are available. Here, we update information on the number of Laysan Albatrosses breeding at Guadalupe Island, provide data on their food habits based on squid beaks found in chick regurgitation pellets, and comment on their foraging habits relative to how and when they feed.

## METHODS

We visited Guadalupe Island three times, during two breeding seasons: January and June 2000 (the 1999/2000 breeding season) and December 2000 (2000/01 season). On 5 January 2000, JPG counted the Punta Sur breeding colony, located on the hill behind the military garrison at the south end of the island (Fig. 2). That colony is the only previously reported nesting colony on Guadalupe Island. RLP and WTE visited the island during 4–9 June 2000 as part of the Guadalupe 2000 Bi-national Biocomplexity Survey Expedition. During that time, they landed a helicopter on the three main offshore islets at the south end of the island, surveying Isote Zapato (= Afuera), Isote de Adentro (= El Toro) and Isote Negro. Although they did not visit the Punta Sur colony at that time, they interviewed military personnel stationed on the island about the status of albatrosses nesting there. On 7 December 2000, RLP visited Isote Negro for 1.5 hours, conducted a helicopter survey of Isote Zapato, Isote de Adentro and Isote Negro, and surveyed the Punta Sur colony on foot.



**Fig. 1.** Laysan Albatross breeding sites in the eastern Pacific Ocean (see text).



**Fig. 2.** Locations of Laysan Albatross breeding colonies at Guadalupe Island, Mexico. The island is 37 km long.

Nest counts from land at the beginning of the season were based on the number of nests (with and without eggs present) attended by adults; from the helicopter we counted territorial spaced individuals or pairs. Late in the nesting season, chick counts provided a minimum estimate of the number of nesting pairs for the previous season.

To investigate food habits, we collected approximately 27 regurgitation pellets from Isote Zapato and Isote Negro during the June 2000 expedition. Some of the pellets were very fresh, others were weeks—possibly months—old, but all appeared to be from the current (1999/2000) breeding season. All of the samples were composed of indigestible hard parts (mostly squid beaks and plastic bits); no undigested whole prey items were found. When we collected the pellets, many large chicks were present at both of the colonies, and only three adults were present (see “Results”). In December 2000, many adults and no chicks were present at the Isote Negro colony, and we found no pellets. Similarly, when JPG visited the Punta Sur colony in January 2000, he found numerous

adults, but no chicks or pellets. We assume, therefore, that the pellets were regurgitated by chicks (see also Harrison 1990:117).

Because these samples represent prey provided to chicks, they may differ from prey that adults consume for themselves (Cherel & Klages 1997, Hodum & Hobson 2000). Also, albatross regurgitation samples consist of two basic types: boluses that include recently ingested (and therefore largely undigested) prey, and pellets that include only indigestible hard parts from many previous meals. The latter (the type we collected) generally provide information only on larger cephalopods in the diet, because other prey with less durable hard parts (e.g. fish, small squid, other invertebrates) are underrepresented because of differential digestion and retention in the stomach (Furness *et al.* 1984). Nevertheless, the pellet samples are informative because dietary studies at colonies (Harrison *et al.* 1983) and at sea (Gould *et al.* 1997a, 1997b) have found that squid constitute the predominant prey of Laysan Albatrosses.

TABLE 1

Number and frequency of occurrence of cephalopod prey items identified from Laysan Albatross regurgitation pellets, Guadalupe Island, Mexico, June 2000. Also shown are beak measurements and calculated dorsal mantle lengths (DMLs) for selected species

Family	Species	Number	% Total	(N)	Beak measurements (LRL)		Mean of Estimated DML (mm)
					Range (mm)	Mean (mm)	
Ancistrocheiridae	<i>Ancistrocheirus lesueuri</i>	8	0.8	7	5.9–8.3	6.6	227.7
Octopoteuthidae	<i>Octopoteuthis deletron</i>	80	8.3	65	5.2–8.9	7.6	131.3
Onychoteuthidae	<i>Onychoteuthis borealijaponica</i>	23	2.4	22	2.2–7.1	4.3	233.4
	<i>Moroteuthis</i> sp.	3	0.3	3	6.2–10.0	7.9	—
	All Onychoteuthidae	26	2.7				
Gonatidae	<i>Gonatopsis borealis</i>	7	0.7	7	2.5–8.7	5.4	198.3
	<i>Gonatus berryi</i>	50	5.2	45	3.0–6.3	5.2	179.5
	<i>Gonatus pyros</i>	108	11.2	96	3.4–5.0	4.2	136.7
	<i>Gonatus onyx</i>	8	0.8	8	3.1–4.2	3.6	81.3
	<i>Gonatus</i> sp(p). (damaged)	18	1.9	0	—	—	—
	All Gonatidae	191	19.8				
Lepidoteuthidae	<i>Pholidoteuthis boschmai</i>	3	0.3	3	3.7–3.9	3.8	167.4
Histioteuthidae	<i>Histioteuthis hoylei</i>	197	20.4	128	1.8–8.5	6.0	107.8
	<i>Histioteuthis heteropsis</i>	58	6.0	50	2.2–4.8	3.4	72.0
	All Histioteuthidae	255	26.4				
Chroteuthidae	<i>Chroteuthis calyx</i>	7	0.7	6	2.5–4.7	3.3	92.1
Mastigoteuthidae	<i>Mastigoteuthis pyrodes</i>	24	2.5	23	2.4–5.1	3.4	97.1
	Unident. mastigoteuthid sp. A	10	1.0	8	4.0–4.7	4.3	123.2
	All Mastigoteuthidae	34	3.5				
Cranchiidae	<i>Taonius borealis</i>	133	13.8	108	5.0–9.5	6.8	405.4
	<i>Liocranchia reinhardti</i>	23	2.4	23	1.9–4.7	3.5	281.4
	<i>Galiteuthis phyllura</i>	2	0.2	2	3.3–4.8	—	—
	<i>Galiteuthis?</i> sp. A	106	11.0	93	5.7–10.4	9.2	552.6
	<i>Leachia dislocata</i>	44	4.6	44	1.3–2.0	1.5	120.1
	All Cranchiidae	308	32.0				
	Unident. oegopsid lower beaks (damaged)	24	2.5	0	—	—	—
Bolitaenidae	<i>Japatella heathi</i>	6	0.6	0	—	—	—
Ocythoidae	<i>Ocythoe tuberculata</i>	2	0.2	2	3.9–5.5	—	—
Alloposidae	<i>Haliphron atlanticus</i>	20	2.1	14	6.5–23.3	16.0	—

LRL = lower rostral length (for pelagic octopods, we measured lower hood length).

Cephalopod lower beaks were identified using reference specimens housed in the collections of the National Marine Mammal Laboratory, Seattle, Washington, and the Santa Barbara Museum of Natural History, Santa Barbara, California. For future reference, a series of voucher beaks from each of the major taxa represented in the present study were archived with both of those institutions.

To estimate the original size of the ingested cephalopods when they were alive, we measured lower-beak rostral length (LRL) to the nearest 0.05 mm using Vernier calipers or an optical micrometer. Measurements were converted into estimates of dorsal mantle length (DML) using regression equations provided by Clarke (1980, 1986) and Wolff (1982).

## RESULTS

### Population status

We found albatrosses breeding at four locations on Guadalupe Island, including three previously unrecorded sites. In January 2000, 50 pairs were beginning to nest at the Punta Sur colony and an additional 17 pairs occupied a newly discovered colony on a small black lava hill on the cliff adjacent to Isote Negro (the "Black Hill colony," Fig. 2). In June 2000, we recorded albatrosses breeding on the offshore islets for the first time. There were 30 chicks and two adults on the higher part of Isote Zapato, and 22 chicks (including one that had recently died) and one adult on Isote Negro. All of the chicks were adult-sized and fully feathered, but with large patches of down still adherent. In June 2000, we also surveyed Isote de Adentro, on foot and by helicopter. Although plenty of suitable habitat was available, no albatrosses were present. We were unable to check the main island at that time, but military personnel told us that the Punta Sur colony was completely abandoned during the previous month because of harassment by cats and packs of feral dogs. From those observations and reports, we estimate that a minimum of 119 pairs of albatrosses nested at Guadalupe Island in 1999/2000.

In December 2000, 51 nests and 70 adults were present on Isote Negro. Many birds were on eggs, but there were some empty nests also. Several adults not associated with nests were still displaying, and it appeared that a few more pairs might yet start to breed. At Isote Zapato, we counted 93 albatrosses from the helicopter, including singles and pairs, and we estimated that 70 active nests were present. On the main island during the same day, we counted 55 nests at the Punta Sur colony. We were not able to visit the Black Hill colony; but, assuming that the same number of pairs was present as during the previous season (17), our estimate of the total number of nesting albatrosses was 193 pairs at a minimum.

### Food habits

Guadalupe albatrosses fed their chicks a diverse array of cephalopods (Table 1). The 27 pellets that we collected contained remains of 967 individual prey items, including 964 cephalopods (99.7% of the prey items) and three fish. We identified 940 cephalopod beaks (97.5% of total) to species (or species group); the rest were too damaged to identify. The identified cephalopods represented a minimum of 12 families and 22 species.

The most numerous cephalopod families were squids, including Cranchiidae (32.1% of identified beaks), Histioteuthidae (27.1%) and Gonatidae (20.3%). Of these, *Histioteuthis hoylei* made up

20.4% of the identified individuals; *Taonius borealis*, 13.8%; *Gonatus pyros*, 11.2%; and *Galiteuthis?* sp. A, 11.0%. The fish remains included teeth from two hagfish (*Eptatretus* sp.) and cranial bones of an unidentified teleost.

A wide range of squid size classes were found (Table 1, Fig. 3). We were able to measure 758 (81%) of the identified beaks and to calculate mean DMLs for 17 species. The DMLs ranged from 21.2 mm to 626.6 mm, except for one outlier (not included in Fig. 3) at 1853.6 mm. Mean DMLs for individual species ranged from 72.0 mm (*Histioteuthis heteropsis*) to 552.6 mm (*Galiteuthis?* sp. A). Frequency distributions of DMLs for individual species were, in most cases, strongly unimodal and clustered around the maximum size classes reported for the individual species (Fig. 3).

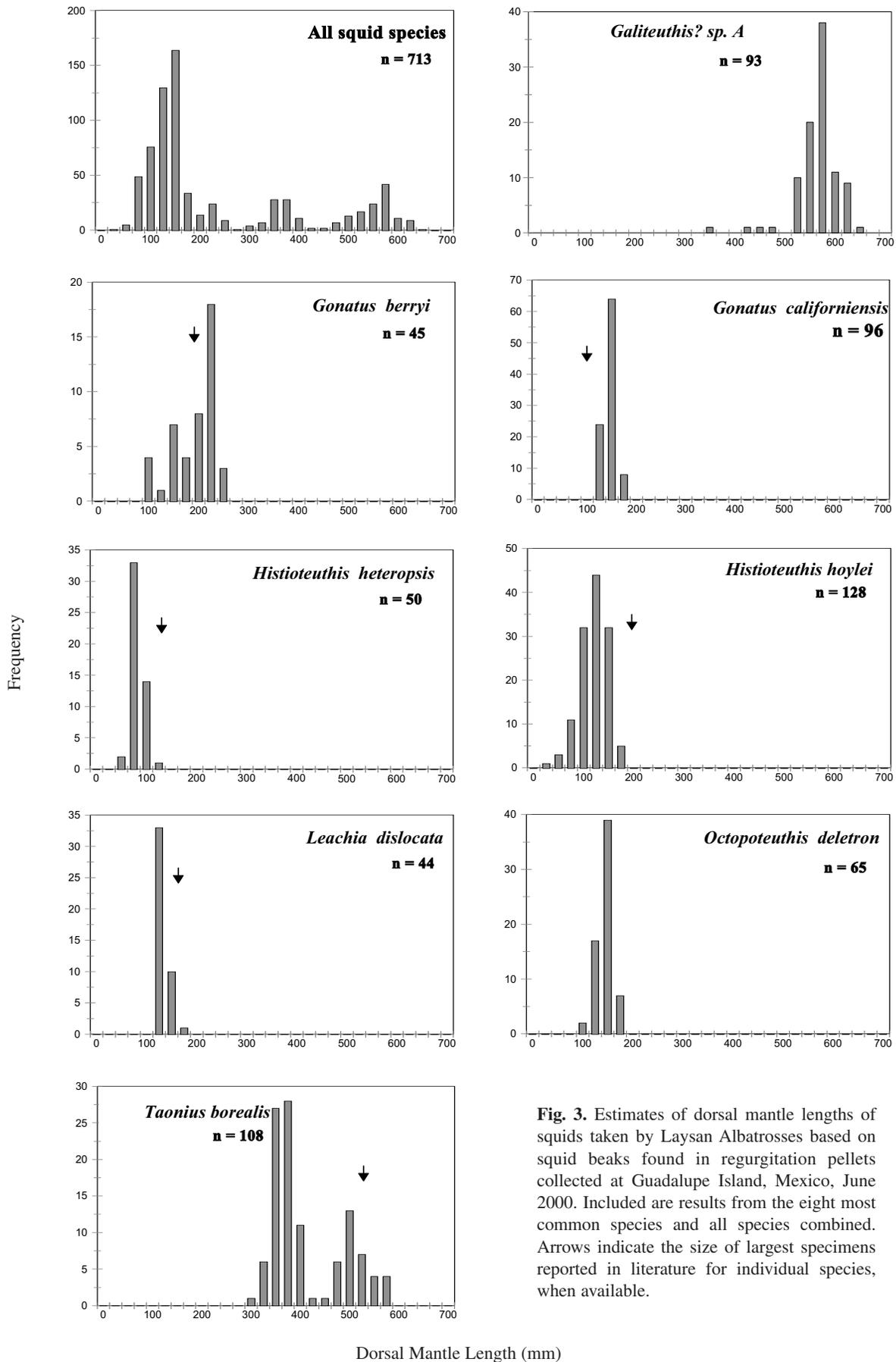
## DISCUSSION

### Population status

Since they first began breeding in 1983, Laysan Albatrosses at Guadalupe Island have continued to increase in number despite continuing harassment and predation on the main island. We do not know when albatrosses started nesting on the offshore islets, although the birds were showing an interest in Isote Zapato as early as January 1988 and could have been nesting at that time (Howell & Webb 1992). Earlier censuses of breeding albatrosses did not include the Black Hill colony or the offshore islets, and so direct comparisons are not possible. However, it is possible to examine the trend at the Punta Sur colony. The previous highest count there was 45 nests in 1992 (Gallo-Reynoso & Figueroa-Carranza 1996). We counted 50 nests in January 2000 and 55 in December 2000 (i.e. two separate breeding seasons). However, the apparent growth of this colony does not appear to be attributable to successful reproduction, because few or no chicks fledge there each year. For example, Sweet *et al.* (2001) observed only six chicks at the colony in May–June 1996, and, according to military personnel, the colony did not fledge a single chick during the 1999/2000 season, apparently because of predation by cats and dogs. Gallo-Reynoso & Figueroa-Carranza (1996) also concluded that the growth of this colony was probably attributable, at least in part, to immigration. It is likely that the colonies on the main island will continue to struggle with introduced predators and could become extirpated, but offshore islets should continue to provide a refuge for nesting albatrosses as long as those islets remain predator-free and undisturbed by humans.

### Foods and foraging

How and when albatrosses, including Laysans, catch the squid that often make up a significant portion of their diet has been the subject of ongoing debate: Do the birds feed primarily at night or during the daytime? Do they take live prey or mainly scavenge them? (e.g. Croxall & Prince 1994, Cherel & Klages 1997). In particular, the issue of live versus dead prey can have important implications. For example, in the North Pacific, Black-footed and Laysan Albatrosses together consume an estimated 167,000 tonnes of squid annually (Harrison & Seki 1987). The birds' role in the pelagic food web depends in large part on whether they function mainly as predators or scavengers. Although our prey analyses were limited almost entirely to the cephalopod portion of the diet, our results suggest that Laysan Albatrosses obtain squid primarily by scavenging during the day.



**Fig. 3.** Estimates of dorsal mantle lengths of squids taken by Laysan Albatrosses based on squid beaks found in regurgitation pellets collected at Guadalupe Island, Mexico, June 2000. Included are results from the eight most common species and all species combined. Arrows indicate the size of largest specimens reported in literature for individual species, when available.

The most comprehensive study to date on the diet of breeding Laysan Albatrosses was from Hawaii: Harrison *et al.* (1983) analyzed regurgitation samples (>95% from chicks) and reported that squid constituted most of the diet (65% by volume). However, the cephalopods that they identified were all from partially intact remains and did not include any isolated squid beaks. As a result, of the 3434 individual cephalopods represented in their sample, 94% could not be identified even to family; 6% were ommastrephids and <1% were from five other cephalopod families. From this largely incomplete data set, it has consistently been stated that ommastrephid squids are the most important prey of Laysan Albatrosses (e.g. Harrison and Seki 1987, Harrison 1990, Whittow 1993).

In contrast, we identified nearly all of the 964 squid beaks in our sample and did not find a single ommastrephid species. The reason for this discrepancy is not clear.

The samples Harrison *et al.* (1983) analyzed were collected during the years when the North Pacific driftnet fishery was operating (1978–1992) and albatrosses were scavenging large numbers of ommastrephid squid (mainly *Ommastrephes bartrami*) from the nets (Gould *et al.* 1997a, 1997b). Because of a ban on high-seas gillnetting in the North Pacific, that source of squid is no longer available. It would be interesting to know if Hawaiian albatrosses are still feeding on ommastrephid squid.

Another possibility is that albatrosses from Hawaii forage in different areas than those used by the Guadalupe Island birds and therefore have access to different prey. In either case, we agree with Harrison *et al.* (1983: 53) that, to properly describe the diet of Hawaiian albatrosses, it will be necessary to identify a much larger proportion of the cephalopods taken, both from the preserved samples from their study and from more recent samples.

A prevalence of ommastrephid squid in the diet also has implications for both how and when albatrosses catch their prey. Many ommastrephids are diurnal migrants. They are often the most abundant and conspicuous cephalopods found alive at the sea surface at night (e.g. Roper & Young 1975, Nesis 1987). They are also negatively buoyant and rarely float when dead (Clarke *et al.* 1979, Lipinsky & Jackson 1989). Therefore, once it was concluded that Laysans feed mainly on ommastrephid squids, it followed that the birds must be capturing the squid alive and at night (Harrison *et al.* 1983, Harrison & Seki 1987, Harrison 1990).

We suggest, however, that Laysan Albatrosses feed mainly on dead rather than live squid. Nesis *et al.* (1998) reported that among mesopelagic and bathypelagic squid that spend their entire lives in deep water, many species have females that die and float to the surface after mating. (Males apparently remain either neutrally buoyant or sink.) It was further suggested that these spent females could account for the regular occurrence of deep-water squid in the diets of seabirds (Nesis *et al.* 1998). The squid families that were cited as important in this regard were “Onychoteuthidae, Gonatidae, Histioteuthidae, Cranchiidae, etc.” (Nesis *et al.* 1998). Those four families alone accounted for 81% of the identified squid in our sample. In addition, frequency distributions of DML for individual species were in most cases strongly unimodal and clustered around the maximum size classes reported for the individual species (Fig. 3), providing further evidence that

albatrosses are targeting spawned-out adults (Rodhouse *et al.* 1987). Finally, the two fish identified in our sample were hagfish; these are epibenthic deepwater species that were probably also scavenged at the surface.

Scavenging albatrosses are likely better suited for daytime foraging when, in addition to any potential olfactory capabilities, they can use their vision effectively to locate either prey or other feeding birds (Verheyden & Jouventin 1994). Using satellite telemetry and immersion detectors, Fernández & Anderson (2000) found that, during the breeding season, foraging Laysan Albatrosses landed on the water more often during the daytime than at night. From that finding, they inferred that daytime foraging was more important for Laysan Albatrosses than had been previously suspected, although it was not known if the prey they were taking was alive or dead. Our results, in conjunction with theirs, suggest that Laysans may feed primarily as diurnal scavengers, as has also been suggested for Wandering Albatrosses *Diomedea exulans* (Weimerskirch & Wilson 1992, Croxall & Prince 1996) and White-chinned Petrels *Procellaria aequinoctialis* (Lipinsky & Jackson 1989). More work, especially in Hawaii, on the diet and foraging activities of Laysan Albatrosses will be necessary to resolve these issues.

#### ACKNOWLEDGEMENTS

Funding for the Guadalupe 2000 Bi-national Biocomplexity Survey Expedition was provided, in part, by the US National Science Foundation’s Special Grant for Exploratory Research 0074462 to W.T. Everett and E. Escurra of the San Diego Natural History Museum. W. Perryman and the Photogrammetry Program at Southwest Fisheries Science Center and M. Cain provided outstanding helicopter support for our surveys. L. Ballance, D. Hyrenbach and L. Spear improved an earlier draft with their comments; M. Clarke provided consultation on squid beak identification; R. Rowlett, E. Mellink and C. Navarro assisted with the field work.

#### REFERENCES

- CHEREL, Y. & KLAGES, N. 1997. A review of the food of albatrosses. In: Robertson, G. & Gales, R. (Eds). Albatross biology and conservation. Chipping Norton: Surrey Beatty & Sons. pp. 113–136.
- CLARKE, M.R. 1980. Cephalopods in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Reports* 37: 1–324.
- CLARKE, M.R. 1986. A handbook for the identification of cephalopod beaks. Oxford: Clarendon Press.
- CLARKE, M.R., DENTON, E.J. & GILPIN-BROWN, J.B. 1979. On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the United Kingdom* 59: 259–276.
- CROXALL, J.P. & PRINCE, P.A. 1994. Dead or alive, night or day: how do albatrosses catch squid? *Antarctic Science* 6: 155–162.
- EVERETT, W.T. 1988. Notes from Clarion Island. *Condor* 90: 512–513.
- FERNÁNDEZ, P. & ANDERSON, D.J. 2000. Nocturnal and diurnal foraging activity of Hawaiian albatrosses detected with a new immersion monitor. *Condor* 102: 577–584.
- FURNESS, B.L., LAUGKSCH, R.C. & DUFFY, D.C. 1984. Cephalopod beaks and studies of seabird diets. *Auk* 101: 619.

- GALES, R. 1998. Albatross populations: status and threats. In: Robertson, G. & Gales, R. (Eds). Albatross biology and conservation. Chipping Norton: Surrey Beatty & Sons. pp. 20-45.
- GALLO-REYNOSO, J.P. & FIGUEROA-CARRANZA, A.L. 1996. The breeding colony of Laysan Albatrosses on Isla de Guadalupe, Mexico. *Western Birds* 27: 70-76.
- GOULD, P., OSTROM, P. & WALKER, W. 1997a. Trophic relationships of albatrosses associated with squid and large-mesh drift-net fisheries in the North Pacific Ocean. *Canadian Journal of Zoology* 75: 549-562.
- GOULD, P.J., OSTROM, P., WALKER, W. & PILICHOWSKI, K. 1997b. Laysan and Black-footed Albatrosses: trophic relationships and driftnet fisheries associations of non-breeding birds. In: Robertson, G. & Gales, R. (Eds). Albatross biology and conservation. Chipping Norton: Surrey Beatty & Sons. pp. 199-207.
- HARRISON, C.S. 1990. Seabirds of Hawaii: natural history and conservation. Ithaca: Cornell University Press.
- HARRISON, C.S., HIDA, T.S. & SEKI, M.P. 1983. Hawaiian seabird feeding ecology. *Wildlife Monographs* 85: 1-71.
- HARRISON, C.S. & SEKI, M.P. 1987. Trophic relationships among tropical seabirds in the Hawaiian Islands. In: Croxall, J.P. (Ed). Seabirds: feeding ecology and role in marine systems. Cambridge: Cambridge University Press. pp. 305-326.
- HODUM, P.J. & HOBSON, K.A. 2000. Trophic relationships among fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ( $d^{15}N$  and  $d^{13}C$ ) analyses. *Marine Ecology Progress Series* 198: 273-281.
- HOWELL, S.N.G. & WEBB, S. 1989. Additional notes from Isla Clarion, Mexico. *Condor* 91: 1007-1008.
- HOWELL, S.N.G. & WEBB, S. 1992. Changing status of the Laysan Albatross in Mexico. *American Birds* 46: 220-223.
- LIPINSKI, M.R. & JACKSON, S. 1989. Surface-feeding on cephalopods by procellariiform seabirds in the southern Benguela region, South Africa. *Journal of Zoology, London* 218: 549-563.
- NESIS, K.N. 1987. Cephalopods of the world. Neptune City: TFH Publications, Inc.
- NESIS, K.N., NIGMATULLIN, C.H.M. & NIKITINA, I.V. 1998. Spent females of deepwater squid *Galiteuthis glacialis* under the ice at the surface of the Weddell Sea (Antarctic). *Journal of Zoology, London* 244: 185-200.
- PITMAN, R.L. 1985. The marine birds of Alijos Rocks, Mexico. *Western Birds* 16: 81-92.
- PITMAN, R.L. & BALLANCE, L.T. 2002. The changing status of the marine birds breeding at San Benedicto Island, Mexico. *Wilson Bulletin* 114: 11-19.
- RODHOUSE, P.G., CLARKE, M.R. & MURRAY, A.W.A. 1987. Cephalopod prey of the wandering albatross (*Diomedea exulans*). *Marine Biology* 96: 1-10.
- ROPER, C.F.E. & YOUNG, R.E. 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* 209:1-51.
- SANTAELLA, L. & SADA, A.M. 1991. The avifauna of the Revillagigedo Islands, Mexico: additional data and observations. *Wilson Bulletin* 103:668-675.
- SWEET, P.R., BARROWCLOUGH, G.F., KLIČKA, J.T., MONAÑEZ-GODOY, L. & ESCALANTE-PLIEGO, P. 2001. Recolonization of the flicker and other notes from Isla Guadalupe, Mexico. *Western Birds* 32:71-80.
- TICKELL, W.L.N. 2000. Albatrosses. New Haven, CT: Yale University Press.
- VERHEYDEN, C. & JOUVENTIN, P. 1994. Olfactory behavior of foraging procellariiforms. *Auk* 111:285-291.
- WEIMERSKIRCH, H. & WILSON, R.P. 1992. When do wandering albatrosses *Diomedea exulans* forage? *Marine Ecology Progress Series* 86:297-300.
- WHITTOW, G.C. 1993. The Laysan Albatross (*Diomedea immutabilis*). In: Pooley, A. & Gill, F. (Eds). The birds of North America. Vol. 66. Philadelphia: The Academy of Natural Sciences. pp. 1-20.
- WOLFF, G.A. 1982. A beak key for eight eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size. *Fishery Bulletin, US* 80:355-368.



Nesting Laysan Albatross *Phoebastria immutabilis* on Guadalupe Island, Mexico. Robert L. Pitman