PLUMAGE-BASED AGEING CRITERIA FOR THE BLACK-FOOTED ALBATROSS
PHOEBASTRIA NIGRIPES

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SUMMARY

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I describe plumage-based ageing criteria for the Black-footed Albatross *Phoebastria nigripes* and assess the utility of this technique using known-age museum specimens and at-sea observations. First, I quantify the repeatability of the plumage assessments and document that 95%, 95%, and 100% of the inspected specimens were reliably scored into one of three standardised plumage classes. Next, I assess the correspondence between the three plumage classes described here and three age groups: juvenile (0.5 years), immature (0.5–4.5 years), and mature (>4.5 years) birds. Overall, 82%, 68%, and 100% of age class 1, 2, and 3 specimens inspected were juvenile, immature, and mature birds, respectively. Finally, to illustrate the applicability of the ageing criteria, I characterise the monthly age-class composition of the Black-footed Albatross population off southern California (29–35°N, 117–124°W) from February through to December. I surveyed albatross population structure during 19 cruises between August 1996 and April 2000. Overall, 97% of the 294 birds sighted during surveys were aged using the plumage-based criteria. I used hierarchical clustering to identify time periods with similar age-class population composition. This analysis revealed four distinct stages: (1) the incubation period (November–December), characterised by the absence of white-rumped (breeding age) individuals; (2) the chick-brooding period (February–March), characterized by the numerical dominance of juvenile birds; (3) the chick-rearing (April–June) and post-breeding (August–October) period, characterised by the presence of all three age classes with mature birds being numerically dominant; and (4) the period of dispersal from breeding colonies (July), characterised by the absence of juvenile birds and the numerical dominance of mature individuals. These observations are in agreement with previous studies of Black-footed Albatross distributions off the west coast of North America. Despite substantial individual variability in moulting and bursa involution patterns, this study suggests that plumage characteristics can be effectively used to discriminate between different albatross age classes at sea.

Keywords: Black-footed Albatross, *Phoebastria nigripes*, age determination, Bursa of Fabricius, plumage, population age structure, population composition

INTRODUCTION

Studies of marine bird distributions provide valuable information about important habitats including foraging and moulting grounds (Hunt *et al*. 1996, Huettmann & Diamond 2000). Additionally, at-sea surveys can enhance our ability to monitor seabird population trends, especially for species that are difficult to count at breeding colonies (Spear *et al*. 1995, Woehler 1996). In particular, it is inherently difficult to monitor petrel and albatross populations due to their life-history characteristics and their habit of nesting underground and/or in difficult-to-access locations (Warham 1990). In albatrosses, for instance, delayed maturity, skipping of breeding seasons by mature birds and complex interactions between breeding and moulting schedules introduce substantial variability into colony-based population counts (Tickell 2000).

The accurate determination of albatross population numbers has become a conservation priority in the light of pervasive mortality in longline fisheries (Croxall 1998, Tasker *et al*. 2000, Tickell 2000). In the North Pacific Ocean, the Black-footed Albatross *Phoebastria nigripes* is considered to be Vulnerable according to World Conservation Union (IUCN) criteria, due to a projected 20% decrease in the next 45 years (three generations) (Croxall & Gales 1998). Assessing Black-footed Albatross population trends is inhibited by substantial inter-annual fluctuations in the proportion of adult birds that breed each year (mean: 0.80, range: 0.43–1.00) and by the delayed and variable age of first breeding (mean: 8.6, range: 5–16 years) (Cousins & Cooper 2000, Cousins 2001). In addition to counts of breeding birds and chicks at colonies, at-sea surveys can improve our ability to monitor albatross populations and fishery impacts in a variety of ways. For

instance, an improved understanding of the marine distribution of different age classes can help assess potential population-level impacts of fisheries bycatch (Weimerskirch & Jouventin 1987, Brothers *et al.* 1997, Croxall *et al.* 1999). Moreover, information on population composition can be used to test the predictions of modeling studies, which often involve shifts in population age structure (Wooller *et al.* 1992, Moloney *et al.* 1994, Cousins & Cooper 2000). However, this valuable information can only be gained once reliable field ageing techniques have been developed.

A widely-used technique for age determination in seabirds is based on the size and condition of the Bursa of Fabricius, a dorsal diverticulum of the cloaca that serves an immunosuppressive function in immature individuals (Glick 1983). In particular, the width and length of the bursa are commonly measured and used to calculate the organ's surface area, expressed in mm^2. Because the width and length measurements tend to compensate each other, this metric provides a very convenient index of the organ's size; because some bursas are short and wide, whereas others are long and narrow. Broughton (1994) characterized the pattern of bursa involution in Black-footed and Laysan Albatrosses *P. immutabilis*

using known-age banded specimens taken by high-seas driftnet fisheries operating within the North Pacific Ocean during 1990–1991. Because of their close taxonomic relationship, this analysis combined the data from both species. Bursa size, calculated as the product of the organ's maximum length and width, decreased with increasing age.

Particularly, there was a significant difference in the surface area of the bursa of newly-fledged birds (0.5-year class) and older individuals in the 1.5- and 2.5-year classes, suggesting that the size of this organ decreases drastically during the first year of life. Accordingly, Broughton (1994) classified Black-footed and Laysan Albatross specimens into three age classes:

(1) juveniles (bursa >600 mm^2);
(2) immature non-breeders (bursa 500–75 mm^2); and
(3) adult breeders with vestigial (<50 mm^2) or lacking bursas.

Unfortunately, the value of the bursa for age determination is limited because its size and condition can only be assessed in dead specimens.
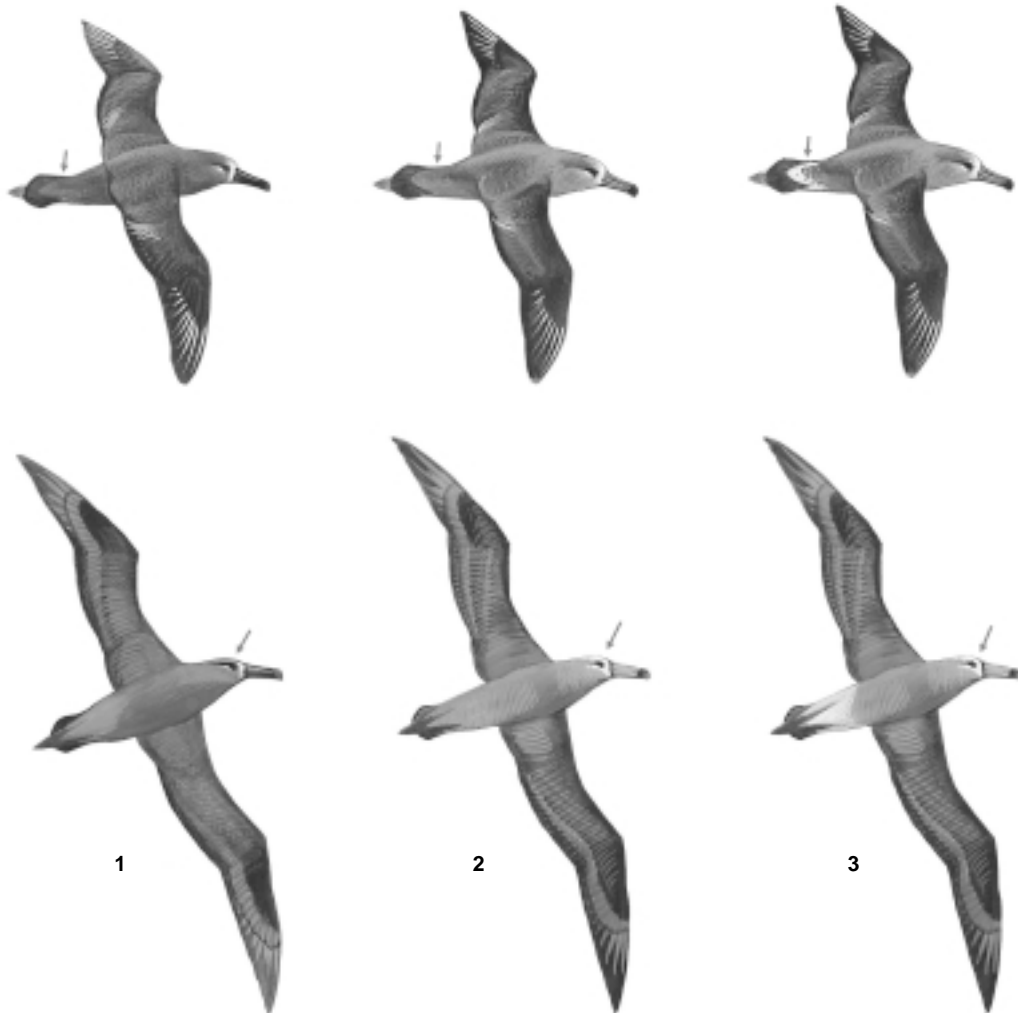
Fig. 1. Illustration of the plumage-based ageing criteria used to discriminate between three plumage classes in Black-footed Albatrosses: (1) juvenile (first year), (2) immature (pre-breeding), and (3) mature (breeding age) birds. The arrows highlight the extent of white on the rump and face. Illustrations have been modified from Sibley (2000).

TABLE 1

Reliability of plumage assessments for 67 Black-footed Albatross specimens. Raw counts and proportions (in parentheses) are shown for two independent inspections. Bold font highlights specimens that were consistently assigned to the same plumage classes, illustrated in Fig. 1

		First inspection					
		Plumage Class 1		Plumage Class 2		Plumage Class 3	
Second inspection	**Plumage Class 1**	**11**	**(16.42)**	1	(1.49)	0	(0)
	Plumage Class 2	2	(2.99)	**44**	**(64.67)**	0	(0)
	Plumage Class 3	0	(0)	0	(0)	**9**	**(13.43)**

Traditionally, sightings and returns of banded and colour-marked individuals have provided information about gender and age-specific distributions (Brothers *et al*. 1997, Croxall *et al.* 1999, Cousins & Cooper 2000). Additionally, differences in plumage and bill colouration have been used to discriminate between juvenile (first year), immature (pre-breeding), and mature (breeding-age) individuals in many species, including Short-tailed *P. albatrus*, Wandering *Diomedea exulans*, Black-browed *Thalassarche melanophrys*, Indian Yellow-nosed *T. carteri* and Shy *T. cauta* Albatrosses (Weimerskirch and Jouventin 1987, Sherburne 1993, Tickell 2000). However, the lack of conspicuous plumage differences across age classes has inhibited the development of similar ageing methods for Black-footed Albatrosses.

The extent of the white plumage on the rump (upper tail coverts) and head increases in Black-footed Albatrosses up to the age of first breeding, five and six years for females and males, respectively (Bourne 1982, Cousins & Cooper 2000, Tickell 2000). First-year (juvenile) birds appear generally darker than adults, except for a whitish area around the base of the bill, and are characterised by the absence of a white band along the base of the tail (age class 1 birds in Fig. 1). Juveniles turn progressively sooty-brown as they age (age class 2 birds in Fig. 1). This change in colouration occurs between 16 and 21 months (1.25–1.75 years), with the whitening of the head, belly, upper tail and under tail coverts increasing in size with successive moults, until the birds are five to six years old (age class 3 birds in Fig. 1) (van Ryzin & Fisher 1976, Bourne 1982, Cousins & Cooper 2000, Tickell 2000).

In this paper, I develop plumage-based ageing criteria for identification of Black-footed Albatross age classes in the field. I also examine the utility of these criteria by assessing how reliably observers score birds into distinct age groups, and by quantifying the correspondence between age classes determined on the basis of these plumage-based criteria and bursa characteristics previously described in the literature (Broughton 1994). Finally, to illustrate the applicability of the ageing criteria developed here, I characterise the monthly age class composition of the Black-footed Albatross population off southern California.

METHODS AND RESULTS

Development of plumage-based ageing criteria

Developing reliable plumage-based ageing criteria involves three steps: (1) defining a plumage-scoring system based on a set of conspicuous and easily identifiable characteristics; (2) assessing the reproducibility of these criteria; and (3) quantifying the statistical relationship between these plumage characteristics and other established ageing criteria described in the literature.

I compiled 67 Black-footed Albatross skins catalogued at the University of Washington's Burke Museum, that had been sexed using gonads and had complete data on bursa size (length and width) and condition. Without consulting the bursa and gender information, I scored each of these specimens into one of three possible age classes on the basis of their plumage colouration patterns: age class 1 birds were homogeneously dark, with a white outline around the periphery of the bill, but lacked a white band along the rump; age class 2 birds were sooty-brown in appearance, with a larger extent of white around the face and head, but still lacking a white band along the rump; and class 3 birds were sooty-brown with a white band along the rump (Fig. 1). I scored all the specimens in the

TABLE 2

Results of two-way analysis of variance of bursa size. Bold font denotes statistically significant results. Dependent variables: bursa surface area (mm^2). Independent variables: plumage score (class 1, class 2, class 3) and gender (female, male)

Source	% Variance	*P* value
Plumage	49.32	**<0.001**
Gender	2.29	0.099
Plumage × Gender	1.24	0.470
Error	47.14	–

TABLE 3

Bursa size (mm²) of 64 unknown-age Black-footed Albatross and a sample of known-age banded birds, including eight Black-footed and 10 Laysan Albatrosses (Table 1 from Broughton 1994)

	Plumage scores			Age groups (years)		
	Class 1	Class 2	Class 3	0.5	1.5–4.5	>4.5
Sample size	11	44	9	7	7	4
Mean	761	275	16	830	161	20
S.D.	230	240	23	161	139	23
Median	800	222.5	0	770	150	20
Maximum	1012	819	65	1100	434	40
Minimum	264	0	0	630	0	0

collection twice, with a one-hour interval between successive inspections. I quantified whether I had scored an individual bird into the same plumage class both times, and used this information to gauge the repeatability of the plumage-based ageing criteria (Table 1). The plumage assessments were consistent, with 100% (9/9) of class 3 and 95% (55/58) of class 1 and 2 specimens inspected receiving the same plumage score both times they were inspected. Three specimens were not consistently classified into the same plumage class. The bursa dimensions (560 mm²) of one misclassified specimen fell between the ranges used by Broughton (1994) to separate recently-fledged (large bursa >600 mm²) and pre-breeding (bursa between 500 and 75 mm²) birds. The other two misidentified individuals fell along the lower tail of the immature bird distribution, with bursa sizes of 630 and 646 mm², respectively. Moreover, all three birds had 'fleshy' bursas, suggesting they were in their first year of life (Broughton 1994). The three misidentified specimens were removed from the data set. Thus, the sample size for subsequent analyses is 64 birds.

The next step involved determining if there were significant differences in the size and condition of the bursa of specimens belonging to the three plumage classes described above (Fig. 1). The surface area and the condition of the bursa were related: fleshy, regressing, and vestigial bursas were the largest, intermediate, and smallest in size, respectively (Spearman Rank Test, n: 64, R_S: –0.839, $P < 0.001$). Thus, I focused on size, the more quantitative metric describing the condition of the bursa. I used a two-way analyses of variance (ANOVA) to test for differences in bursa size (mm²) across genders and plumage classes (Zar 1984). The ANOVA revealed significant differences in bursa surface area across plumage classes (Table 2), but no gender-based differences, and no significant interaction effect between gender and age class. Because there were no significant gender differences, I combined observations from males and females for subsequent analyses. The ANOVA residuals were normally distributed (Kolmogorov–Smirnoff Test, n: 64, $0.50 < P < 0.75$).

Finally, to assess the validity of the plumage-based ageing criteria, I compared the bursa size of the specimens belonging to different plumage classes and age groups (Table 3) using Mann-Whitney tests (Zar 1984). The three pair-wise comparisons involving birds of different plumage classes revealed significant differences,

TABLE 4

Comparison of bursa sizes for albatrosses belonging to the different plumage classes and age groups described in Table 3. Plumage scores refer to 64 Black-footed Albatrosses of unknown age from the Burke Museum collections, and age groups refer to the 18 birds (10 Laysan and 8 Black-footed Albatrosses) analysed by Broughton (1994). Mann Whitney *U* test statistics and *P* values are listed for each pair-wise comparison. Bold font denotes statistically significant results

		Plumage scores			Age groups (years)		
		Class 1	Class 2	Class 3	0.5	1.5–4.5	>4.5
Plumage scores	**Class 1**	–	**<0.001**	**<0.001**	0.820	**0.001**	**0.004**
	Class 2	465	–	**<0.001**	**<0.001**	0.304	**0.009**
	Class 3	108	362	–	**0.001**	**0.009**	0.614
Age groups	**0.5**	36	12.5	0	–	**0.002**	**0.008**
	1.5–4.5	76	191.5	7.5	49	–	**0.035**
	>4.5	44	158	15	28	25	–

suggesting that the plumage scores are indicative of age (Table 4). Moreover, the nine pair-wise comparisons involving the three plumage classes (1, 2, 3) and banded birds belonging to the three age groups (juvenile, immature, mature) confirmed the value of the surface area of the bursa as a useful albatross ageing metric. Six of the nine comparisons revealed significant differences (Table 4). However, bursa sizes for birds in plumage classes 1, 2 and 3 were indistinguishable from those of the juvenile, immature, and mature age classes. These results highlight the concordance between the plumage classes defined here and the three distinct age groups described by Broughton (1994): class 1 birds are juveniles (0–6 months), class 2 birds are immatures (1.5–4.5 years), and class 3 birds are mature individuals (>4.5 years). Immature specimens with regressing bursas were occasionally misclassified as mature birds. Conversely, mature individuals were not misclassified as immatures according to their plumage characteristics (Table 5). In summary, age 1 and age 3 birds were exclusively non-breeders (largely juveniles) and mature birds, respectively. Age 2 birds were more difficult to characterise because they included 14%, 68%, and 18% juvenile, immature, and mature individuals, respectively.

Application of the plumage ageing criteria during at-sea surveys

I characterised the Black-footed Albatross population age structure during 19 California Cooperative of Oceanographic Fisheries Investigations (CalCOFI) cruises between August 1996 and April 2000. These cruises survey a standardised grid of hydrographic stations extending between 29–35°N, and from the southern California coast to 124°W. The data presented here comprise 235 days at sea and over 24 000 km of survey effort.

Because albatrosses approach and follow survey vessels, I used a modified 300-m strip transect methodology, designed to account for these vessel-attraction and ship-following behaviours (Tasker *et al.* 1984, Hyrenbach 2001). Over 95% of the sighted birds occurred within the 300-m survey strip, which greatly facilitated the use of this field ageing technique (Hyrenbach 2001). Overall, 287 (96.6%) of the 294 albatrosses sighted during surveys were aged using the plumage-based criteria described here. The remaining seven 'unknown' age birds were not used in any subsequent analyses (Table 6).

Temporal variability in the albatross population age structure

I used the 287 birds aged using plumage-based criteria to characterise the monthly age composition of the Black-footed Albatross population off southern California between February and December (Fig. 2). Instead of stratifying the observations on the basis of the different stages of the breeding cycle (e.g. incubation, brooding, chick-rearing, post-breeding dispersal), I allowed the data themselves to describe the temporal variability of the population age structure (Fig. 2, Table 6). I combined all birds sighted during a given month and used hierarchical clustering, with the single-linkage Euclidean distance metric, to identify months with similar age-class population composition (Manly 1994). This analysis revealed four distinct stages (Fig. 3): (1) incubation period (November–December), characterised by the absence of white-rumped (breeding age) individuals; (2) chick-brooding period (February–March), characterised by the numerical dominance of juvenile birds; (3) chick-rearing (April–June) and post-breeding (August–October) periods, characterised by the presence of all three age classes with mature birds being numerically dominant; and (4) the period of dispersal from breeding colonies (July), characterised by the absence of juvenile birds and the numerical dominance of mature birds.

DISCUSSION

A better understanding of albatross dispersion patterns and population structure is urgently needed because many of their populations are decreasing precipitously (e.g. Woehler 1996, Croxall & Gales 1998, Tickell 2000). In particular, information about the abundance and distribution of different genders and age classes is especially important to assess the potential population-level impacts of fisheries bycatch. The susceptibility of albatross populations to bycatch is frequently exacerbated by differential age-specific and gender-based mortality rates (Prince *et al.* 1992, Moloney *et al.* 1994), as a result of gender-based and age-specific segregation at sea (Weimerskirch & Jouventin 1987, Brothers *et al.* 1997). In addition to assessing the susceptibility to bycatch, information on age composition of albatross populations is useful to test the predictions of modelling studies (Moloney *et al.* 1994, Cousins 2001).
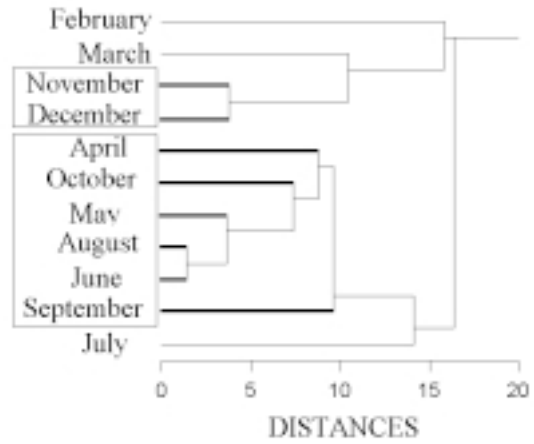
TABLE 5

Correspondence between the plumage assessments and the age of 64 Black-footed Albatrosses determined on the basis of their bursa characteristics (Broughton 1994). Raw counts and proportions (in brackets) are shown for each pair-wise comparison. Bold font highlights specimens that were classified into corresponding plumage classes and age groups

		Age group (years)							
		0.5		**1.5–4.5**		**>4.5**		**Total**	
Plumage score	Class 1	**9**	**(81.82)**	2	(18.18)	0	(0)	11	(100)
	Class 2	6	(13.64)	**30**	**(68.18)**	8	(18.18)	44	(100)
	Class 3	0	(0)	0	(0)	**9**	**(100)**	9	(100)
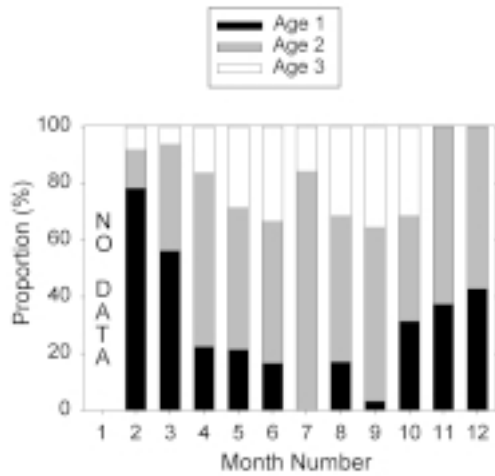
Fig. 2. Summary of Black-footed Albatross monthly population age composition data, obtained by combining surveys between August 1996 and April 2000.

Fig. 3. Results of hierarchical clustering of Black-footed Albatross monthly population age composition data (August 1996–April 2000), highlighting two clusters of months with a similar population age structure composition.

TABLE 6

Summary of albatross at-sea observations off southern California. For each survey, the total number (proportion) of individuals aged using the plumage criteria is shown, in addition to the relative contribution of juvenile (age 1), immature (age 2), and mature (age 3) birds

Survey period	Birds aged		Plumage score (%)		
	No.	(%)	Class 1	Class 2	Class 3
August 1996	15	(100)	35.8	7.1	57.1
October 1996	10	(100)	70.0	10.0	20.0
February 1997	11	(100)	54.5	27.3	18.2
July 1997	8	(100)	0.0	75.0	25.0
September 1997	15	(100)	6.7	60.0	33.3
December 1997	7	(100)	42.9	57.1	0.0
February 1998	26	(100)	88.5	7.7	3.8
March 1998	16	(100)	56.3	37.4	6.3
April 1998	33	(100)	33.3	54.6	12.1
May 1998	14	(100)	21.4	50.0	28.6
June 1998	6	(85.7)	16.7	50.0	33.3
July 1998	11	(100)	0.0	90.9	9.1
September 1998	16	(100)	0.0	62.5	37.5
October 1998	10	(100)	0.0	60.0	40.0
November 1998	8	(100)	37.5	62.5	0.0
April 1999	36	(100)	8.3	77.8	13.9
August 1999	21	(100)	4.7	81.0	14.3
October 1999	15	(78.9)	26.7	40.0	33.3
April 2000	11	(100)	36.4	27.2	36.4

Sightings of banded birds and recoveries of individuals caught as fisheries bycatch provide valuable information about the age and gender composition of albatross populations at sea (Brothers *et al.* 1997, Croxall *et al.* 1999, Cousins & Cooper 2000). However, these observations are constrained by the paucity of banding data, and by the generally low coverage (<10% of total effort) of most fishery observer programmes. The ability to age albatrosses visually from platforms of opportunity, including fishing and oceanographic vessels, on the basis of plumage characteristics would augment existing observations of banded and bycatch individuals (Weimerskirch & Jouventin 1987, Sherburne 1993, Croxall *et al.* 1999). The ability to discriminate between juvenile (first year), immature (pre-breeding), and mature (breeding-age) individuals would be particularly suited to match at-sea and colony-based surveys with population modelling efforts (Weimerskirch & Jouventin 1987, Moloney *et al.* 1994, Cousins & Cooper 2000, Cousins 2001).

The high reliability of the plumage assessments using museum specimens (95% for class 1, 95% for class 2, 100% for class 3) indicates that the criteria used here are conspicuous and easily discernible upon visual inspection (Table 1). Furthermore, the correspondence between the plumage classes and distinct age groups defined on the basis of bursa characteristics (Broughton 1994) suggests that these ageing criteria can be readily used to identify different age classes (Tables 4 & 5). The relative proportion of white-rumped birds may be an especially appropriate metric to characterise the age population composition of Black-footed Albatrosses, because these conspicuous individuals are easily identifiable and comprise only mature (age >4.5 year) birds (Tables 1 & 5).

Previous vessel-based surveys failed to identify temporal patterns in the relative proportion of white-rumped Black-footed Albatrosses off southern California (Miller 1940, Yocom 1947). Miller's (1940) monthly observations between San Diego and Point Conception (117–123°W, 31–35°N) in 1937–1938 documented that white-rumped individuals accounted for up to 10% of all birds sighted during summer months (June–September). Yocom's (1947) larger-scale surveys off the west coast of North America (130–136°W, 31–43°N) during February–September 1945 revealed that the proportion of white-rumped (mature) birds changed little across seasons or areas, accounting for between 10–12.5% of the population. These results suggested that the broad range of Black-footed Albatross plumage colouration did not depend on the gender, season, or age of the birds (Miller 1940, Yocom 1947). Conversely, this study did reveal a yearly cycle in the proportion of white-rumped birds sighted off southern California (Fig. 2). Overall, dark-rumped individuals accounted for 81.2±13.8% (S.D.) of all birds sighted per month, (average monthly proportions ranging from 64.5% in September to 100% in November–December). Conversely, white-rumped individuals accounted for 18.8±13.8% of the birds seen monthly, with a minimum (0%) during the November–December incubation period and a maximum in September (35.5%).

The analysis of the Black-footed Albatross population age composition off southern California revealed four distinct time periods associated with specific stages of the reproductive cycle: (1) incubation (November–December), (2) chick-brooding (February–March), (3) a prolonged period including the chick-rearing (April–June) and post-breeding (August–October) stages, and (4)

the period of dispersal from breeding colonies (July) (Figs 2 & 3). These results are in agreement with previous studies of Black-footed Albatross distributions off the west coast of North America. Namely, banding and telemetry studies have revealed that breeding age birds occur off California predominantly between late spring and early fall (March–September), and that juvenile birds are most numerous during winter months (November–February) (Robbins & Rice 1974, Cousins & Cooper 2000, Fernández *et al.* 2001, Hyrenbach & Dotson 2003).

Data from Black-footed Albatrosses banded at Midway between 1963–1969 and observed until August 1998 reinforce the vessel-based observations reported here (Fig. 2). Band returns are concentrated near breeding colonies (monthly mean position south of 35°N, and west of 140°W during the incubation and chick-brooding periods, from December to February). The distribution of banded birds shifts north and east during March, and reaches the west coast of North America in April. From May through to July, the population range shifts northward and is restricted to the east of the international dateline (180°W). During fall (August–October), the distribution shifts to the west and south. By November, the population is focused around the breeding colonies, west of 140°W and south of 40°N. Even though there are no significant differences in the temporal patterns of band returns and the spatial distributions (mean latitude and longitude) of immature (0–5 year old) and older birds, the banding data provide evidence of age-specific spatial segregation. Immature birds occur farther east, on average, than do older birds during January–July, suggesting an eastward shift in the distribution of mature birds once breeding is completed (Cousins & Cooper 2000).

Additionally, a recent (1998–1999) satellite telemetry study revealed that mature albatrosses breeding at Tern Island, Hawaii, forage close to their colony during the brooding period (first 18 days after chicks hatch, January–February), commute to the west coast of North America during the chick-rearing stage (19–140 days after chicks hatch, February–June), and remain off the west coast during the post-breeding dispersal, once they have completed breeding (Fernández *et al.* 2001).

Telemetry and banding results support the increased occurrence of mature (plumage class 3) birds off southern California between spring and fall (March–September). However, these studies cannot explain the observed lack of juvenile (plumage class 1) birds off southern California during July (Fig. 2). Two possible explanations for this disjunct occurrence pattern are: (1) a seasonal population shift across latitude, and (2) a change in the appearance of juvenile birds after their first year of life.

At-sea surveys suggest there are seasonal changes in Black-footed Albatross distributions along the west coast of North America, with populations shifting northwards during spring (March–May), and southwards during fall (September–November) (McHugh 1955, Briggs *et al.* 1987). Conceivably, if different age classes were segregated across latitude, cruises within a fixed survey grid could perceive a temporal change in the population age composition, solely due to the latitudinal shift in the entire population. For instance, the observed lack of juvenile and mature birds during summer (July) and winter (December) off southern California could be attributable to a scenario where juvenile and mature birds preferentially occupied the northern and southern edges of the population range, respectively.

Another explanation for the lack of juvenile birds off southern California during July entails a lag in the arrival of first-year birds on the west coast. Because juveniles change from plumage class 1 (0.5-year class) to 2 (1.5–4.5-year classes) during their first year at sea, by the 19th month of their life (July of their second year) they probably resemble immature individuals. Thus, the lack of juvenile birds off California at this time can be attributed to a lack of first-year birds, which likely do not arrive at the west coast until August (Fig. 2).

Additional research is needed to quantify bursa size and plumage characteristics in the Black-footed Albatross more accurately. The observed variability in the plumage of same age class specimens, probably arising from differences in the trade-offs between reproductive success and moulting (Langston & Rohwer 1996), blurs the plumage-based ageing assessments. In addition to individual differences in plumage patterns, there is substantial unexplained variability in the pattern of bursa involution for Black-footed Albatrosses (r^2: 0.48, Broughton 1994). Observations of known-age bycatch birds would improve the existing model of Black-footed Albatross bursa involution. In particular, a finer temporal resolution is needed during the transition between the immature and mature stages, between 3–16 years of age. Moreover, plumage assessments of known-age birds at breeding colonies could help develop and test improved ageing criteria for field identification (Frings & Frings 1961, Weimerskirch & Jouventin 1987).

The results of this study should be interpreted with caution because they are based on small sample sizes (Tables 1, 3 & 6). Additionally, the annual cycle in the population age structure described in this paper provides a composite of highly variable monthly data collected over five years (1996–2000) (Figs 2 & 3). Yet, these same observations suggest there is substantial year-to-year variability in the albatross population composition during any given month (Table 6).

Large-scale, multi-year surveys will be necessary to characterise the spatial and temporal patterns of Black-footed Albatross population age structure across the North Pacific Ocean. The plumage-based ageing technique described here offers a broadly applicable tool, useful to assess the age composition of both fisheries-caught and live albatrosses observed at sea from vessels of opportunity and dedicated surveys.

ACKNOWLEDGEMENTS

REFERENCES

BOURNE, W.R.P. 1982. The colour of the tail coverts of the Black-footed Albatross. *Sea Swallow* 31: 56–57.

BRIGGS, K.T., DETTMAN, K.F., LEWIS, D.B. & TYLER, W.B. 1987. Bird communities at sea off California. *Studies in Avian Biology* 11: 1–74.

BROTHERS, N.P., REID, T.A. & GALES, R.P. 1997. At-sea distribution of Shy Albatrosses *Diomedea cauta cauta* derived from records of band recoveries and colour-marked birds. *Emu* 97: 231–239.

BROUGHTON, J.M. 1994. Size of the Bursa of Fabricius in relation to gonad size and age in Laysan and Black-footed Albatrosses. *Condor* 96: 203–207.

COUSINS, K.L. 2001. The Black-footed Albatross population biology workshop: a step to understanding the impacts of longline fishing on seabird populations. In: Melvin, E. & Parrish, J. (Eds). Seabird bycatch: trends, roadblocks, and solutions. Anchorage: University of Alaska Sea Grant. pp. 95–114.

COUSINS, K.L. & COOPER, J. (Eds). 2000. The population biology of the Black-footed Albatross in relation to mortality caused by longline fishing. Honolulu: Western Management Regional Fishery Management Council.

CROXALL, J.P. 1998. Research and conservation: a future for albatrosses? In: Robertson, G. & Gales, R. (Eds). Albatross biology and conservation. Chipping Norton: Surrey Beatty and Sons. pp. 269–290.

CROXALL, J.P., BLACK, A.D. & WOOD, A.G. 1999. Age, sex and status of Wandering Albatrosses *Diomedea exulans* in Falkland Islands waters. *Antarctic Science* 11: 150–156.

CROXALL, J.P. & GALES, R. 1998. An assessment of the conservation status of albatrosses. In: Robertson, G. & Gales, R. (Eds). Albatross biology and conservation. Chipping Norton: Surrey Beatty and Sons. pp. 46–65.

FERNÁNDEZ, P., ANDERSON, D.J., SIEVERT, P.R. & HUYVAERT, K.P. 2001. Foraging destinations of three low-latitude albatross species. *Journal of Zoology* 254: 391–404.

FRINGS, H. & FRINGS, M. 1961. Some biotic measurements of the albatrosses of Midway Atoll. *Condor* 61: 305–314.

GLICK, B. 1983. Bursa of Fabricius. In: Farner, D.S., King, J.R. & Parkes, K.C. (Eds). Avian biology, Vol. 7. New York: Academic Press. pp. 443–500.

HUETTMANN, F. & DIAMOND, A.W. 2000. Seabird migration in the Canadian northwest Atlantic Ocean: moulting locations and movement patterns of immature birds. *Canadian Journal of Zoology* 78: 624–647.

HUNT, G.L., Jr., COYLE, K.O., HOFFMAN, S., DECKER, M.B. & FLINT, E.N. 1996. Forageing ecology of Short-tailed Shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series* 141: 1–11.

HYRENBACH, K.D. 2001. Albatross response to survey vessels: implications for studies of the distribution, abundance, and prey consumption of seabird populations. *Marine Ecology Progress Series* 212: 283–295.

HYRENBACH, K.D. & DOTSON, R.C. 2003. Assessing the sus-

ceptibility of female Black-footed Albatross (*Phoebastria nigripes*) to longline fisheries during their post-breeding dispersal: an integrated approach. *Biological Conservation*. In press.

LANGSTON, N.E. & ROHWER, S. 1996. Molt–breeding tradeoffs in albatrosses: life history implications in big birds. *Oikos* 76: 498–510.

MANLY, B.F.J. 1994. Multivariate statistical methods. A primer. 2nd Edition. New York: Chapman & Hall.

McHUGH, J.L. 1955. Distribution of Black-footed Albatross, *Diomedea nigripes*, off the west coast of North America, 1949 and 1950. *Pacific Science* 9: 375–381.

MILLER, L. 1940. Observations on the Black-footed Albatross. *Condor* 42: 229–239.

MOLONEY, C.L., COOPER, J., RYAN, P.G. & SIEGFRIED, W.R. 1994. Use of a population model to assess the impact of longline fishing on Wandering Albatross *Diomedea exulans* populations. *Biological Conservation* 70: 195–203.

PRINCE, P.A., WOOD, A.G., BARTON, T. & CROXALL, J.P. 1992. Satellite tracking of Wandering Albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science* 4: 31–36.

ROBBINS, C.S. & RICE, D.W. 1974. Recoveries of banded Laysan Albatrosses (*Diomedea immutabilis*) and Black-footed Albatrosses (*D. nigripes*). In: Pelagic studies of seabirds in the central and eastern Pacific Ocean. King, W.B. (Ed). *Smithsonian Contributions in Zoology* 158: 232–277.

SHERBURNE, J. 1993. Status report on the Short-tailed Albatross *Diomedea albatrus*. Anchorage: Alaska Natural Heritage Program.

SIBLEY, D.A. 2000. The Sibley guide to birds. New York: Alfred A. Knopft.

SPEAR, L.B., AINLEY, D.G., NUR, N. & HOWELL, S.N.G. 1995. Population size and factors affecting the at-sea distribu-

tions of four endangered procellariids in the tropical Pacific. *Condor* 97: 613–638.

TASKER, M.L., JONES, P.H., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of the methods employed and a suggestion for a standardized approach. *Auk* 101: 567–577.

TASKER, M.L., CAMPHUYSEN, C.J., COOPER, J., GARTHE, S., MONTEVECCHI, W.A. & BLABER, S.J.M. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science* 57: 531–547.

TICKELL, W.L.N. 2000. Albatrosses. London: Yale University Press.

VAN RYZIN, M.T. & FISHER, H.I. 1976. The age of Laysan Albatrosses, *Diomedea immutabilis*, at first breeding. *Condor* 78: 1–9.

WARHAM, J. 1990. The petrels: their ecology and breeding systems. New York: Academic Press.

WEIMERSKIRCH, H. & JOUVENTIN, P. 1987. Population dynamics of the Wandering Albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos* 49: 315–322.

WOEHLER, E.J. 1996. Concurrent declines in five species of Southern Ocean seabirds in Prydz Bay. *Polar Biology* 5: 379–382.

WOOLLER, R.D., BRADLEY, J.S. & CROXALL, J.P. 1992. Long-term population studies of seabirds. *Trends in Ecology and Evolution* 7: 111–114.

YOCOM, C. 1947. Notes on behavior and abundance of the Black-footed Albatrosses in the Pacific waters off the continental north American shores. *Auk* 64: 507–523.

ZAR, J.H. 1984. Biostatistical analysis. New Jersey: Prentice-Hall.