AGE-RELATED TIMING OF PRIMARY MOULT IN SHY ALBATROSS *THALASSARCHE [C.] CAUTA/STEADI* LONGLINE CASUALTIES FROM SOUTH AFRICA

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SUMMARY

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A provisional schedule is given for the age-related timing of primary moult in White-capped Albatross *Thalassarche [c.] steadi* based on an analysis of primary moult in 575 Shy Albatross *T. [c.] cauta/steadi* caught as bycatch on longlines off South Africa (mostly White-capped Albatross). Our analysis draws upon basic principles for age-related moult timing established in studies of other mollymawks. The principles involve combined assessment of an alternate-year primary moult schedule, maturation of plumage aspect, and maturation of bill colour and pattern. There is good evidence that adult/definitive prebasic moult of White-capped Albatross occurs mainly in August–October, which is between breeding seasons, and continues into the austral summer. After a successful breeding attempt, most White-capped Albatrosses skip the following breeding season and may be less constrained in the timing of moult relative to breeding. The third and fourth prebasic moults occur December–June, considerably earlier than the definitive prebasic moult; the fifth prebasic moult appears to occur April–September, closer in timing to the definitive prebasic moult. Observations from 10 Shy Albatross *T. [c.] cauta* provide some evidence that they moult slightly earlier than White-capped Albatross, which is consistent with their earlier breeding period.

Key words: Shy Albatross, White-capped Albatross, primary moult in albatross

INTRODUCTION

Patterns in the timing of primary moult in mollymawks—small albatrosses of the genus *Thalassarche*—in relation to age have been reported for Atlantic Yellow-nosed *T. chlororhynchos*, Black-browed *T. melanophris*, and Grey-headed *T. chrysostoma* albatross (e.g. Brooke 1981, Prince *et al.* 1993, Prince & Rodwell 1994, Bugoni & Furness 2009, Howell 2012, Flood 2015, Flood *et al.* 2015, Flood & Fisher 2016, Pyle 2016). The patterns, which are based on combined assessments of moult cycles, maturation of plumage aspect, and maturation of bill colour, reveal general principles for the assessment of age-related timing of primary moult in mollymawks and likely also apply broadly to *Phoebastria*, a genus of small albatross from the North Pacific Ocean (Pyle 2008, Rohwer *et al.* 2011, Howell 2012).

Age-related timing of primary moult in Shy Albatross *T. [c.] cauta/steadi* is relatively poorly known. They are one of the most abundant mollymawks off South Africa, where approximately 95% are from the New Zealand population of *T. [c.] steadi*—hereafter White-capped Albatross—and the rest are from the Tasmanian population *T. [c.] cauta*—hereafter Shy Albatross (Hockey *et al.* 2005). They are the second most frequent bycatch victim of the pelagic longline fishery operating off South Africa after White-chinned Petrel *Procellaria aequinoctialis* (Petersen *et al.* 2009, Rollinson *et al.* 2017). Here, we applied the general principles for age-related timing of primary moult to 575 longline casualties and established a provisional primary moult schedule for White-capped Albatross, presented in terms of moult cycles from juvenile to adult. Observations from 10 Shy Albatross provided some evidence that they moult slightly earlier, which is consistent with their earlier breeding period.

Ageing Mollymawks

Mollymawks typically moult in cycles (first cycle (1c), second cycle (2c), third cycle (3c), and so on), replacing subsets of primaries each year from the 3c onwards (Tickell 2000). The 1c starts with a complete prebasic moult in the nest; this moult produces the juvenile plumage. Fledging occurs upon completion of this first prebasic moult, and virtually all feathers are of the same generation and appear uniform for the six to nine months after. The 2c and all subsequent cycles involve head, body, and tail moult. The second prebasic moult is the first moult post-fledging and the start of the 2c, and it may be preceded by a preformative moult (Howell 2012). After this, fresh head, body, and tail feathers contrast with worn and bleached juvenile upperwing feathers. The 3c and all subsequent cycles involve wing moult. The pattern of primary moult in P5–P10 is key to ageing. Together, the third prebasic moult (start of the 3c) and the fifth prebasic moult (start of the 5c) compose the phase 1 primary moult, which typically includes the renewal of P8–P10 but not P5–P7. These latter primaries are usually replaced in the phase 2 primary moult, which comprises the fourth prebasic moult (start of the 4c) and the sixth prebasic moult (start of the 6c). This alternate-year primary moult strategy continues throughout adulthood. Hence, from the third prebasic moult onwards, moult contrast is evident between P5–P7 and P8–P10. The maturation of plumage aspect, bill colour, and bill pattern distinguish birds in the

3c, 5c, and 7c (all with relatively fresh outer primaries) from those in the 4c and 6c (with worn outer primaries contrasting with fresh inner ones).

There is considerable variation in the detail of primary moult between individuals, although the general principles hold true in most cases (likewise *Phoebastria*; Rohwer *et al.* 2011). Further, a small minority may not follow a precise alternate-year strategy, as occurs in some *Phoebastria*, and could be incorrectly aged (Pyle 2008, Rohwer *et al.* 2011, Howell 2012). Research is required into the variation in alternate-year primary replacement in mollymawks, especially for prebreeding moult cycles.

The pattern of secondary moult also provides a clue to the age of immature birds. Juvenile secondaries are replaced mainly during prebasic moults at the start of the 3c, 4c, and 5c. By the 3c many of the retained juvenile secondaries are bleached, abraded, and give a jagged trailing edge to the inner wing in flight. Some are retained until the 4c, when they are strongly bleached and heavily abraded. Most, if not all, juvenile secondaries are replaced by the 5c. The sequence of secondary replacement is probably similar to that of *Phoebastria*, with moult centres at the tertials (distal replacement), S1 (proximal replacement), and S5 (proximal replacement). In *Phoebastria*, the last juvenile secondaries to be replaced are among S3–S4 and those midway between S5 and the tertials, usually among S12–S19 (Edwards & Rohwer 2005, Pyle 2008). A similar pattern appears to occur in yellow-nosed albatrosses (Pyle 2016).

Adult mollymawks follow an annual moult cycle related to the breeding cycle. Young immatures (i.e., 1c to 4c birds) moult earlier than adults, whereas the timing of moult cycles for old immatures (i.e., 5c to 7c birds) typically synchronizes with adults by the 5c. Prior to the 5c, moult only approximately follows an annual cycle. Smaller species such as yellow-nosed albatrosses attain adult plumage aspect and bill colour and pattern by about the 5c, whereas the larger mollymawks, including Shy Albatross and White-capped Albatross, take up to the 7c to do so (Flood & Fisher 2016).

Current Knowledge About Moult Timing in Shy and White-capped Albatross

The breeding period (i.e., from mean egg-laying date to mean fledging date) for White-capped Albatross occurs mainly in the Auckland Islands from November to July/August, whereas the Shy Albatross breeds in Tasmania between August and April (Marchant & Higgins 1990; ACAP 2009, 2011). Melville (1991) found no evidence of flight-feather moult at breeding colonies for either taxon, despite it having been observed in other albatross species (e.g., Black-browed Albatross; Catry *et al.* 2013). All 45 presumably White-capped Albatross wrecked on North Island, New Zealand, after a tropical cyclone in April 1968 were in primary moult (Kinsky 1968); only one bird showed signs of immaturity in the colouring of its bill. However, those in adult plumage may have been either pre-breeders, failed breeders, or birds skipping breeding that year. (Most White-capped Albatross skip breeding in the year following a successful breeding attempt (ACAP 2011).) New Zealand beach-wrecked seabird surveys from 1960 to 1983 found monthly peaks in the mortality of presumed White-capped Albatross in May–June and October–December (Powlesland 1985); the peak in the austral winter could reflect vulnerability of birds in primary moult to harsh weather. Howell (2012) suggests that the first primary moult (in the third prebasic moult) of Shy Albatross and White-capped Albatross occurs between January and April (17–20 months after fledging, depending on taxon), which allows White-capped Albatross to complete primary moult prior to the austral winter. Hockey *et al.* (2005) noted that active moult in Shy/White-capped albatross off South Africa is observed in all months, but they did not link months, age groups, and regions of feather moult. In a preliminary study of Shy Albatross and White-capped Albatross bycatch victims off South Africa, we found that adults were in active primary moult mainly in the non-breeding season from August to October/November (but ranging from April until December), while immatures were in active primary moult mainly in December–June (Flood & Ryan 2016).

METHODS

Almost all bycatch victims in this study came from the pelagic longline fishery targeting tunas *Thunnus* spp. and Broad-billed Swordfish *Xiphias gladius*. This is the longline fishery that kills the most seabirds in the region (Petersen *et al.* 2009), although bycatch rates have dropped steadily in the last decade (Rollinson *et al.* 2017).

Primary moult was recorded for 632 Shy/White-capped albatross longline victims returned to port between 2004 and 2017. The month of capture was not recorded for 57 birds, which were thus omitted from the analysis entirely, leaving 575 birds to study moult phenology. Secondary, tail, head, and body moult were recorded on a subset of these birds. The primaries were given a moult score using the standard method of 0 = old, 1–4 = progress in growth, and 5 = new (e.g., Ginn & Melville 1983), although it was not always easy to differentiate old from new feathers. This difficulty arose from feathers being thoroughly soaked, having been submerged for a day or so. Primaries are not replaced from fledging until the 3c and become very old. Thus, we introduced an additional category that helped to distinguish 1c birds from 2c birds: individuals were categorised by active moult or moult contrast in the primaries (none, phase 1, phase 2) and aged using criteria for maturation of plumage aspect and maturation of bill pattern and colour (Flood & Fisher 2016).

Immature birds lacking primary moult contrast and showing a dark-grey hindneck shawl, complete neck collar, and blackish ungues (pale tip at most) were aged 1c/2c. Of this group, birds showing fresh or moderately worn primaries and no head, body, or tail moult were aged 1c (juvenile); those showing worn or moderately worn primaries and head, body, and tail moult were aged 2c. Immature birds showing phase 1 primary moult and immaturity in plumage aspect and bill colour and pattern were aged 3c/5c. Of this group, birds with much immaturity in plumage aspect and bill colour and pattern were aged 3c, while those showing an adult-like head pattern (though not pristine and silky) and an adult-like bill colour and pattern with a small dark mark on the mandibular unguis (some with smudgy mark on the maxillary unguis) were aged 5c. Immature birds showing phase 2 primary moult and clear signs of immaturity in plumage aspect and bill colour and pattern were aged 4c. Our studies found that plumage aspect and bill colour and pattern of presumed 6c, presumed 7c, and adult birds are similar, and their moult timing largely in synch, so these age groups were combined.

Shy Albatross and White-capped Albatross are cryptic (sub-) species that breed and thus might moult two to three months apart. The only way the two (sub-)species can reliably be told apart is

by using genetic markers (Abbott *et al.* 2006). Small samples of pectoral muscle were collected from 258 bycatch victims from 1992 and from 2004–2006, of which all but three could be assigned to (sub-)species: approximately 95% were White-capped Albatross (n = 242), and approximately 5% Shy Albatross (n = 13). We assumed this ratio in our study.

TABLE 1
Shy Albatross *T. [c.] steadi* (typed) killed off the coast of South Africa and returned to port 2004–2017. Presented by moult cycle and month, starting in July (the month of fledging; ACAP 2011).[a]

	1c	2c	3c		4c		5c		6c–adult		Σ	
	n	*n*	*n*	a	*n*	a	*n*	a	*n*	a	*n*	b
Jul	1	16	10	1/10, 10%	9	0/9, 0%	4	0/4, 0%	8	0/8, 0%	48	1/31, 3%
Aug	2	5	2	0/2, 0%	3	0/3, 0%	1	0/1, 0%	4	1/4, 25%	17	1/10, 10%
Sep	2	13	8	0/8, 0%	8	0/8, 0%	2	0/2, 0%	16	6/16, 38%	49	6/34, 18%
Oct	2	31	4	1/4, 25%	3	0/3, 0%	4	0/4, 0%	6	5/6, 83%	50	6/17, 35%
Nov	1	1	-	-	-	-	-	-	1	1/1, 100%	3	1/1, 100%
Dec	-	1	-	-	-	-	-	-	-	-	1	-
Jan	1	-	-	-	-	-	-	-	-	-	1	-
Feb	1	-	2	2/2, 100%	-	-	-	-	-	-	3	2/2, 100%
Mar	1	-	-	-	-	-	-	-	-	-	1	-
Apr	-	-	3	3/3, 100%	1	0/1, 0%	2	2/2, 100%	1	1/1, 100%	7	6/7, 86%
May	-	-	-	-	1	0/1, 0%	1	0/1, 0%	2	0/2, 0%	4	0/4, 0%
Jun	-	2	2	0/2, 0%	4	1/4, 25%	-	-	2	1/2, 50%	10	2/8, 25%
Σ	11	69	31	7/31, 23%	29	1/29, 3%	14	2/14, 14%	40	15/40, 38%	194	25/114, 22%

[a] n = number of birds inspected; a = ratio of birds in active primary moult, expressed as a fraction and as a percentage; b = ratio of 3c and older birds in active primary moult (the cycles in which primary moult occurs), expressed as a fraction and as a percentage. Percentages are to the nearest whole number.

TABLE 2
Shy Albatross, taxon unknown (not typed), killed off the coast of South Africa and returned to port 2004–2017. Presented by moult cycle and month starting in July, the month of fledging for *T. [c.] steadi* (ACAP 2011), which makes up approximately 95% of the birds in this table.[a]

	1c	2c	3c		4c		5c		6c–adult		Σ	
	n	*n*	*n*	a	*n*	a	*n*	a	*n*	a	*n*	b
Jul	1	17	20	0/20, 0%	10	0/10, 0%	7	4/7, 57%	9	0/9, 0%	64	4/46, 9%
Aug	8	17	25	0/25, 0%	12	1/12, 8%	6	0/6, 0%	25	5/25, 20%	93	6/68, 9%
Sep	2	3	9	0/9, 0%	5	0/5, 0%	6	1/6, 17%	7	1/7, 14%	32	2/27, 7%
Oct	-	5	8	0/8, 0%	1	0/1, 0%	1	0/1, 0%	11	2/11, 18%	26	2/21, 10%
Nov	-	1	-	-	2	0/2, 0%	-	-	-	-	3	0/2, 0%
Dec	2	2	3	2/3, 67%	3	3/3, 100%	1	1/1, 100%	1	0/1, 0%	12	6/8, 75%
Jan	-	-	-	-	-	-	-	-	-	-	-	-
Feb	-	-	1	1/1, 100%	-	-	-	-	-	-	1	1/1, 100%
Mar	2	-	8	8/8, 100%	2	0/2, 0%	-	-	-	-	12	8/10, 80%
Apr	-	-	4	2/4, 50%	3	0/3, 0%	-	-	6	1/6, 17%	13	3/13, 23%
May	-	13	17	2/17, 12%	6	1/6, 17%	-	-	6	0/6, 0%	42	3/29, 10%
Jun	1	11	12	2/12, 17%	4	0/4, 0%	1	1/1, 100%	5	1/5, 20%	34	4/22, 18%
Σ	16	69	107	17/107, 16%	48	5/48, 10%	22	7/22, 32%	70	10/70, 14%	332	39/247, 16%

[a] n = number of birds; a = ratio of birds in active primary moult, expressed as a fraction and as a percentage; b = ratio of 3c and older birds in active primary moult (the cycles in which primary moult occurs), expressed as a fraction and as a percentage. Percentages are to the nearest whole number.

RESULTS AND DISCUSSION

Just over 95% of birds were killed between March and October, thus few data were available to draw conclusions about moult timing in the austral summer (November–February). Primary moult contrast in 39 birds 3c and older could not be ascribed with confidence to either phase 1 or phase 2; this is an example of variation in moult and a reminder that age-related moult timing schedules are guides only. Thus, of the 575 Shy/White-capped Albatross available to study moult phenology, only 536 were included: 10 Shy, 194 White-capped, and 332 Shy/White-capped albatross (all except Shy Albatross analysed in Tables 1–3).

Of the 165 birds aged 1c/2c, 27 were aged 1c, with fresh primaries and no evidence of head, body, or tail moult. Only one 1c bird was killed between April and June, which is consistent with commencement of the 2c (i.e., by about 9 months after fledging). Of the 138 birds aged 2c (with old juvenile primaries), a good number showed evidence of head, body, and/or tail moult.

Of the 138 birds aged 3c, 24 (17%) were in active primary moult. Of these 24 moulting birds, 20 (83%) were in active primary moult February–June (41% of the 49 bycatch victims for those months); two (8%) were in active primary moult July–October (2% of the 86 bycatch victims for those months); and two (8%) were in active primary moult in December (67% of the three bycatch victims for that month). There were no bycatch victims in November or January for this age group. This suggests that the primary moult in the third prebasic moult ranges from December to June (i.e., from about 17 months after fledging), with most occurring between February and April.

Of the 77 birds aged 4c, only six (8%) were in active primary moult, including all three birds killed in December. The rest of the 74 bycatch victims were killed March–November, and only three of them (4%) were in active primary moult. Such a low percentage indicates that the fourth prebasic moult occurred mainly December–February (i.e., from about 29 months after fledging) in the austral summer, when few killed birds were returned to port. This is rather early compared to Black-browed Albatross, which commences the 4c about 35 months after fledging (Flood & Fisher 2016), and compared to the minimal data that we have for Shy Albatross.

Of the 36 birds aged 5c, nine (25%) were in active primary moult. The sample size is small and interpretation thus somewhat speculative, especially given that just one bird was killed November–March. Eight birds were in active primary moult April–October (from about 45 months after fledging). Of these eight, four were found in July (36% of the 11 birds killed that month), indicating that July is one of the main months in the fifth prebasic primary moult. July is consistent with the synching of primary moult timing with adults (see below), as observed in other mollymawks.

Of the 110 birds aged either 6c, 7c, or adult, 25 (23%) were in active primary moult. Twenty of the 25 (80%) were in active primary moult August–October, making up 29% of the 69 bycatch victims for those months. Adult primary moult in other large mollymawks mainly occurs within a six-month period (Flood & Fisher 2016). Thus, it is likely that primary moult in this group occurs largely July–January and peaks August–October (in the 6c, from about 61 months after fledging); this is between breeding seasons, and accounts for primary moult in the single November bycatch victim of this age group. Among other possibilities, two birds in active

TABLE 3
Shy Albatross, combined *T. [c.] steadi* with taxon unknown (combined Tables 1, 2), killed off the coast of South Africa and returned to port 2004–2017. Presented by moult cycle and month starting in July, the month of fledging for *T. [c.] steadi* (ACAP 2011), which makes up approximately 98% of the birds in this table.[a]

	1c	2c	3c		4c		5c		6c–adult		Σ	
	n	*n*	*n*	a	*n*	a	*n*	a	*n*	a	*n*	b
Jul	2	33	30	1/30, 3%	19	0/19, 0%	11	4/11, 36%	17	0/17, 0%	112	5/77, 7%
Aug	10	22	27	0/27, 0%	15	1/15, 7%	7	0/7, 0%	29	6/29, 21%	110	7/78, 9%
Sep	4	16	17	0/17, 0%	13	0/13, 0%	8	1/8, 13%	23	7/23, 30%	81	8/61, 13%
Oct	2	36	12	1/12, 8%	4	0/4, 0%	5	0/5, 0%	17	7/17, 41%	76	8/38, 21%
Nov	1	2	-	-	2	0/2, 0%	-	-	1	1/1, 100%	6	1/3, 33%
Dec	2	3	3	2/3, 67%	3	3/3, 100%	1	1/1, 100%	1	0/1, 0%	13	6/8, 75%
Jan	1	-	-	-	-	-	-	-	-	-	1	_
Feb	1	-	3	3/3, 100%	-	-	-	-	-	-	4	3/3, 100%
Mar	3	-	8	8/8, 100%	2	0/2, 0%	-	-	-	-	13	8/10, 80%
Apr	-	-	7	5/7, 71%	4	0/4, 0%	2	2/2, 100%	7	2/7, 29%	20	9 /20, 45%
May	-	13	17	2/17, 12%	7	1/7, 14%	1	0/1, 0%	8	0/8, 0%	46	3/33, 9%
Jun	1	13	14	2/14, 14%	8	1/8, 13%	1	1/1, 100%	7	2/7, 29%	44	6/30, 20%
Σ	27	138	138	24/138, 17%	77	6/77, 8%	36	9/36, 25%	110	25/110, 23%	526	64/361, 18%

[a] *n* = number of birds in the given month; a = ratio of birds in the given month in active primary moult, expressed as a fraction and as a percentage; b = ratio of birds in active primary moult for 3c and older birds (the cycles in which primary moult occurs), expressed as a fraction and as a percentage. Percentages are to the nearest whole number.

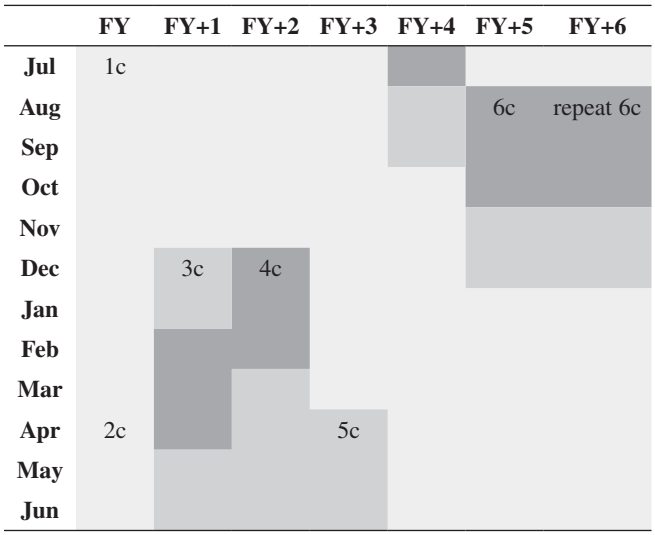
primary moult in both April and June may have commenced primary moult earlier than expected because they were skipping a breeding season (following a successful breeding attempt), were sick, or were Shy Albatross, which breeds two to three months earlier than White-capped Albatross.

We were unable to find a pattern in the progress of active primary moult that correlated to the period of primary moult. An example of such a pattern might be growing P8 toward the start of the 5c period (say August) and P10 at the end (say October).

The percentage of 3c and older birds in primary moult is rather low (18%). This may be because birds in primary moult are less active (Gutowsky *et al.* 2014) or less aerodynamic (Hedenström & Sunada 1999), and they are consequently ineffective competitors behind longliners compared to birds with a full set of primaries.

The sample size of 10 typed Shy Albatross (i.e., those positively identified by genetic means) is too small to make any generalised conclusions about primary moult timing. A few tentative observations follow: No 1c birds were captured. Three 2c birds were captured in August–September, which is consistent with both the 3c primary moult commencing at least 17 months after fledging and the provisional schedule for White-capped Albatross. Of the two 3c birds captured in March, one had completed primary moult and the other had completed primary moult except for P1 with a score of 4, which is consistent with the 4c primary moult commencing from about 30 months after fledging (Black-browed Albatross commences from about 31 months after fledging; Flood & Fisher 2016). None of the three birds aged 4c—one caught in each of July, August, and September—were in primary moult, which is consistent with the 5c primary moult commencing later than 42 months after fledging. (Our provisional schedule for White-capped Albatross indicates the 5c commencing from about 44 months after fledging.) The one 5c-aged bird captured in October was not in primary moult about 53 months after fledging; this fits the timing in our provisional primary moult schedule for White-capped Albatross. The one bird aged 6c or older (an adult captured in August) was not in primary moult, which is consistent with an adult schedule where primary moult is expected to follow fledging, mainly May–July.

TABLE 4
Provisional age-related primary moult timing schedule by age and month for White-capped Albatross *T. [c.] steadi* off the coast of South Africa; based on Table 3 (about 98% *T. [c.] steadi*).[a]



[a] FY = fledging year. In the table, '1c', '2c', '3c' and so on indicate the start of the given moult cycle; the start of the 3c onward is at the start of primary moult. Dark-grey shading highlights the most likely months for primary moult; light-grey shading proposes additional months in which primary moult is to be expected, based on our limited data and established knowledge about moult duration in other large mollymawks (Flood & Fisher 2016).

A contingency table showed that the bycatch population exhibited a strong likelihood for secondaries to be moulted at the same time as primaries ($X^2 = 32.80$, $df = 1$, $P < 0.001$). Of the 225 birds checked for active moult in the primaries and secondaries, more were moulting secondaries (19%) than primaries (12%). Of the birds in primary moult, 61% were replacing secondaries, but only 40% of birds in secondary moult were replacing primaries.

CONCLUSIONS

The schedule indicated in Table 4 is our best interpretation of the data in Tables 1–3. It is the first attempt at working out a schedule for either Shy Albatross or White-capped Albatross, and further research is needed. That said, the data behind our schedule are broadly consistent with data for better-studied mollymawks (e.g., Black-browed Albatross).

In our schedule, head, body, and tail moult occur by nine months after fledging (preformative moult or a prolonged second prebasic moult). From the 3c onward, the start of each cycle is marked by commencement of primary moult, with the advantage that primary moult can be seen on birds in flight. There is reasonable evidence that the third prebasic moult occurs in December–June, with most concentrated in February–April; this is considerably earlier than the adult/definitive prebasic moult. Such timing aligns with the idea that the first primary moult of White-capped Albatross occurs before the harsh austral winter (Howell 2012). Timing estimates for the fourth and fifth prebasic moults are the most tentative due to limited data. The fourth prebasic moult may occur mainly in summer. The fifth prebasic moult probably occurs later, closer to the adult/definitive prebasic moult. There is good evidence that adult/definitive prebasic moult of White-capped Albatross occurs mainly between breeding seasons, i.e., August–October, with some continuing into the austral summer. Timing may vary in non-breeding adults. After a successful breeding attempt, most White-capped Albatross skip the following breeding season and so might be less constrained in terms of timing of moult relative to breeding; however, there is no solid evidence that they shift timing of the primary moult. Primary moult timing in the small number of Shy Albatross bycatch victims is consistent with primary moult timing in other mollymawks.

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