NUTRIENT RESERVE DIFFERENCE BETWEEN YOUNG AND ADULT SHORT-TAILED SHEARWATERS, *PUFFINUS TENUIROSTRIS*, BEFORE AND AFTER TRANS-EQUATORIAL MIGRATION

by Nariko Oka

(with five text-figures and one table)

The Short-tailed Shearwater, *Puffinus tenuirostris*, is a trans-equatorial migrant, breeding in Tasmania and other parts of southeastern Australia during the Austral summer and migrating to the northern North Pacific for the Boreal summer. Juveniles, in particular, suffer considerable mortality during the migration. Body composition of juveniles and adults in terms of body mass, lipid content, pectoral muscle mass and bone marrow content, before and after migration was investigated. Juveniles varied greatly in body composition pre- and post-migration and took longer to recover their nutritional status than adults. Adults sustained a better body composition, showing a moderate decrease in body fat upon arrival in the north and recovering their body mass and lipid supply during their stay. The lipid content of beachcast bird carcasses (mean, 4 g) was the minimum necessary for cell membranes and was not metabolisable for energy. Pectoral muscle protein remained high among birds under hyper-nutritional conditions, and decreased gradually at first as lipids decreased, and then rapidly at late malnutritional stages when most lipids had been utilised for energy. Although adults sustained their nutritional status, the amount of lipids in adults leaving the Tasmanian colony was insufficient to accomplish the long-distance migration, so post-breeding adults probably first visited Antarctic waters to accumulate fat reserves before commencing their northward migration.
Key Words: age group, body composition, fat deposit, marrow, nutritive difference, pectoral muscle, protein, *Puffinus tenuirostris*, Short-tailed Shearwater, trans-equatorial migrant.

INTRODUCTION

Long-distance migrations through areas with poor nutrient productivity are critical events for some animals. Recent evidence has shown that the Sooty Shearwater, *Puffinus griseus* (J.F. Gmelin, 1789), a New Zealand trans-equatorial migratory seabird, traversed low-latitude waters with low productivity at mean speeds as high as 910 km per day while rarely foraging (Shaffer *et al.* 2006). To accomplish these long journeys without refueling, they must have sufficient energy reserves, though the storage abilities of most birds are limited by the constraints of flight and wing loading.

The Short-tailed Shearwater, *Puffinus tenuirostris* (Temminck, 1835), which breeds in Tasmania and other parts of southeastern Australia during the Austral summer (October to April), migrates one of the longest distances of any migratory bird, annually completing a trans-equatorial migration to spend the Boreal summer (May to September) in the highly productive waters of the northern North Pacific, Okhotsk Sea and Bering Sea (Serventy *et al.* 1971, Shuntov 1974, Warham 1996). This species has evolved a feeding apparatus that allows it to take small marine animals effectively (Morgan & Ritz 1982), which are sparsely distributed in tropical and sub-tropical oceans along its migratory pathway (Reid 1962). Thus, the survival of the migrants may depend greatly on energy deposits acquired before departure from the cool waters of the higher latitudes of both hemispheres.

The Nemuro Strait (about 44°N latitude), which separates eastern Hokkaido from the Kuril Islands, is the southernmost limit of the waters where the Short-tailed Shearwater spends the Austral winter. Along the Japanese coast, bathed by the warm Kuroshio Current 1300 km south of the strait, comprising the final stretch of the shearwaters' northward trans-equatorial migration, mortalities occur regularly during the two weeks from late May to early June (Oka *et al.* 1986).

Mass mortalities occurred at about 10-year intervals in the second half of the twentieth century: 1964, 1973–75, 1983–85 and 1996 (Kawaguchi & Marumo 1964, Sugimori *et al.* 1976, Oka & Maruyama 1986, Taguchi & Kato 1997). Age estimates based on skull ossification of the 2250 beachcast bird carcasses collected along the central Japanese coast from the mass mortality events of the mid-1980s revealed that almost all of them (99.5%) were four-month-old juveniles that had died from starvation (Oka & Maruyama 1986).

In the current century mass mortalities continued occurring along the central Japanese coast in the same period of late May–early June in 2003, 2005 and 2006, suggesting that those casualties were also migrating juveniles.

During the Boreal summer, mass mortalities of Short-tailed Shearwaters occurred in the Bering Sea in 1997 (Baduini *et al.* 2001a, b) and in the Okhotsk Sea in 2007 (Hokkaido Government, unpublished data). These mortalities suggest that some birds postponed recovering from energy shortage. Unfortunately the age of the birds in both these mass mortality events was not determined, but evidence from previous events suggests that it is more likely that they were inexperienced fledglings rather than experienced sub-adult or adult birds. As shearwater fledglings migrate independently to the Northern Hemisphere and remain apart from older birds while there, they have little foraging experience or knowledge of local waters suitable for feeding; thus, their survival is most likely lower than that of older birds, with differing energy storage among age groups.

Knowledge of energy storage differences among the shearwater age classes before and after the northern migration and the time to recover from energy shortage is important not only to clarify the reasons for the recent mortality

events observed in the Northern Hemisphere but also to understand the higher survivorship of adults (Bradley *et al.* 1989) from the viewpoint of nutritional ecology. I here report body composition differences in juvenile and adult Short-tailed Shearwaters and composition changes pre- and post-migration, focusing in particular on the disparity in nutritional recovery in the far northern waters of the Northern Hemisphere.

MATERIALS AND METHODS

Study animals

The Short-tailed Shearwater, *Puffinus tenuirostris*, is a long-distance migrant, which breeds in Tasmania and in other parts of southeastern Australia and overwinters in the North Pacific and Bering Sea and Okhotsk Sea (Marchant & Higgins 1990). The breeding season of Short-tailed Shearwaters comprises the 195 days from October to April (53% of each year; Warham 1990). The female lays a single egg in a burrow in late November (Marchant & Higgins 1990, Warham 1990). After the chick hatches in mid-January, the adults rear the nestling for about 85 days, until early April (Oka 1989). During this time, the chick increases its body mass until it weighs on average 1.4 times at maximum the weight of adults (Marchant & Higgins 1990). Beginning in early April, after provisioning the nestlings with a final meal, the adults leave their breeding grounds for the trans-Pacific migration, probably via Antarctic waters as a satellite tracking experiment suggests (Nicholls *et al.* 1998). During the subsequent two or three weeks, the body mass of the nestlings decreases, and they fledge in late April (Oka 1989), after their feathers have developed to adult condition (Lill & Baldwin 1983, Oka 1989). Most juveniles depart their hatching sites shortly after fledging (Naarding 1980). Since the juveniles depart later than the adults, they also arrive later at their overwintering sites in the North Pacific than the adults (Marchant & Higgins 1990). Large flocks of birds (presumably adults, judging from the departure schedule from the breeding grounds) first appear along northern Japanese coasts in the westernmost North Pacific in late April to early May (Niizuma & Shibano 1983, Watabe *et al.* 1987), and they first appear in the Bering Sea around the end of April (Shuntov 1974). Large flocks of fledglings appeared in Japanese waters from around 20 May to early June (Oka 1986). Adults leave the northern North Pacific and Bering Sea for their Australian breeding sites in September. They are followed by sub-adults and young one or two months later. Short-tailed Shearwaters are long-living seabirds, with 87–95% annual survivorship (Bradley *et al.* 1989). They begin to breed at about 6–7 years of age (Bradley *et al.* 1989).

Materials

A total of 263 Short-tailed Shearwaters were used in this study: 31 birds (17 nestlings, 14 adults) were captured in burrows at the Clifton Bluff breeding colony in Tasmania, Australia (42°55'S, 147°19'E)(fig.1, location 1), in April 1983, weighed using a spring balance with 10 g calibration, and immediately released after these measurements were taken. A further 232 birds were collected from 4 April 1983–30 May 1984, euthanased (if not already dead) and frozen for later laboratory analysis. Of these birds 59 (50 adults, nine nestlings) were caught from burrows at their breeding grounds
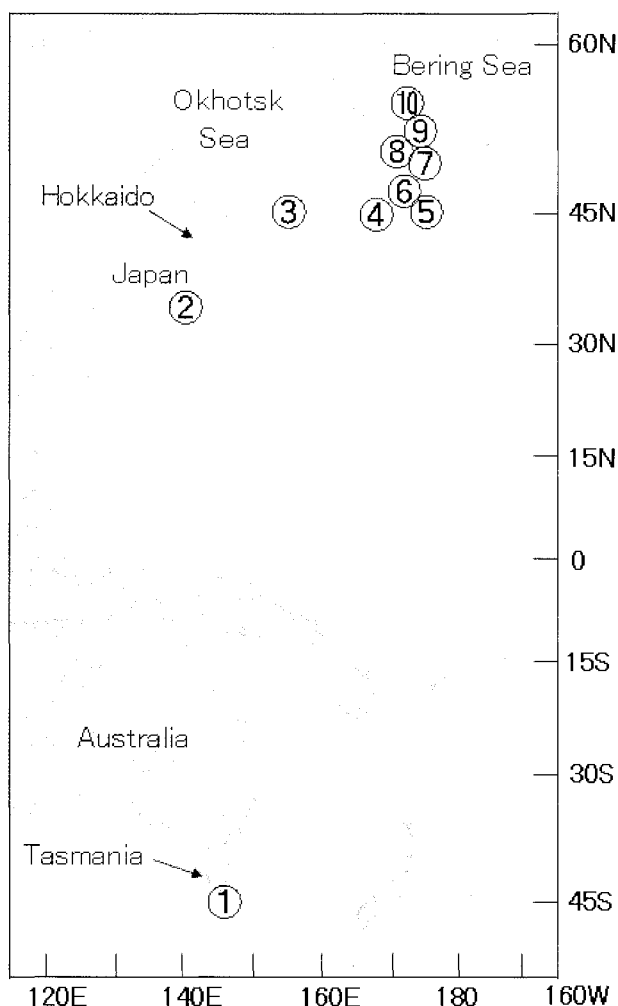

FIG. 1 — Short-tailed Shearwater sampling locations.

at the Clifton Bluff colony in Tasmania from 23 November 1983 to 20 April 1984; 60 fresh beachcast bird carcasses and 23 accidental bycatch birds from fishing nets were collected from Japan (collection points about 36°N in the North Pacific along the Japanese coast) (fig.1, location 2), from 24 May to 7 June 1983 and on 30 May 1984, when the shearwaters are at the final stretch of their migration; and 90 bycatch birds were collected from drift nets in the northern North Pacific and Bering Sea (between 44.50–55°25'N) from 5 May to 23 July 1983, where they spend the boreal summer (fig. 1, locations 3–10). Except for beachcast birds, all birds collected from the North Pacific waters and Bering Sea were bycatch, so they were alive at the time of capture.

Age and phase groups

Birds were classified into two age groups: young (n = 147 with 26 nestlings and 121 juveniles) and adults (n = 116). Young birds were further classified into four phase groups: old nestlings (n =26) (captured in burrows in Tasmania in fledging period); dead juveniles (n = 60) from Japanese coasts (beachcast birds from around 36°N); juveniles (n = 23) collected in late May or early June upon their arrival (AR) at 45–48°N in the North Pacific, in the convergence zone of the warm Kuroshio Current with the sub-Arctic Oyashio Current; and juveniles (n = 15) collected from the

sub-Arctic Current waters north of 48°N to 55°N in the North Pacific and Bering Sea in July, during their stay (ST) in the Northern Hemisphere.

Adults collected from the North Pacific and Bering Sea during the Boreal summer were divided into two phase groups: those collected upon arrival (AR) in early to mid-May from the waters at 45–48°N in the North Pacific (n = 37), and those collected from sub-Arctic current waters north of 48°N to 55°N in the North Pacific and Bering Sea in late June to July during their Northern Hemisphere stay (ST) (n = 15). The timing of the AR and ST periods differed between the age groups, because, conservatively estimated, adults in Australia start their northward migration two weeks before the juveniles.

The ages of the birds collected outside the burrows at the colony were determined via skull ossification (Sugimori *et al.* 1986), which distinguishes juvenile Short-tailed Shearwaters from older birds. This method cannot be used to divide older birds into adults and sub-adults, so the adults collected from waters of the North Pacific may have included sub-adults.

Laboratory procedure

The 232 birds used for the laboratory analysis were deep-frozen in zippered plastic bags soon after collection to prevent desiccation and were preserved in good condition until examination in 1984. Wet body and pectoral muscle masses and liver and stomach contents were weighed using a top-loading precision electronic balance (±0.01 g). Wet pectoral muscle weights were doubled for the analysis (i.e., full breast).

The carcasses were plucked by hand before dissection to prepare them for body lipid extraction. The following parts were removed from the naked body: the head (for aging); the bones of the legs and wings (for marrow analyses); the stomach and its contents; the intestines; the liver; and one side of the pectoral muscle. The liver and the one side of the pectoral muscles were first weighed and then individually minced by scissors and homogenised well; about 7 g of each sample was then collected for determination of the dry weight/wet weight ratio and the lipid and protein contents. The body carcass was minced, by passing it through a meat grinder three times using two kinds of grid sizes of

blade, with hand mixing between passes to homogenise the sample. After thorough homogenisation, 7 g of each wet minced sample was individually weighed in the extraction thimbles using a top-loading precision electronic balance (±0.001 g) and dried in a convection oven at 50 °C for 8 hours until a constant weight was reached. The femora were cracked, and the marrow was removed as completely as possible from the bone with forceps and weighed. The marrow was dried to constant weight in a convection oven at about 50 °C for 3 hours, and the dry weight % (ratio of the dry weight to the wet weight) was recorded. Because not all measures were available for all birds sampled, sample sizes in the laboratory analyses differed from the numbers of birds collected.

Lipids were extracted from each dried sample by a Soxhlet extractor for 12 hours using an alcohol-benzene (1:1) solution. The lipid content and the lipid-free contents dried to a constant weight were weighed. The body lipid content given in this study is the total of the lipids extracted from the minced body and those in the liver and pectoral muscle side previously removed.

Statistical analysis

Because no significant differences were found in any variable of the body composition of the 60 beachcast juvenile Short-tailed Shearwaters between 1983 and 1984 (table 1), I pooled the data for those two years. To test for significant differences in the beachcast juveniles between the two years, I used the Student *t*-test, as all variables were homoscedastic (body mass, $F_{10,48} = 0.530$, $p = 0.2102$; body lipids, $F_{4,16} = 4.433$, $p = 0.0932$; dry body weight %, $F_{4,16} = 5.76$, $p = 0.5072$; wet pectoral muscle mass, $F_{10,48} = 0.4353$, $p = 0.5915$; protein content in pectoral muscles, $F_{5,23} = 0.838$, $p = 0.8070$; liver mass, $F_{10,33} = 2.024$, $p = 0.1810$; dry femur marrow weight %, $F_{10,47} = 1.018$, $p = 0.9714$; dry tibia marrow weight %, $F_{10,44} = 0.633$, $p = 0.3670$).

There were no significant differences in body mass in old nestlings (n = 26) in late April or in adults (n = 27) at the final landing period in late March and/or early April between 1983 and 1984 (between nestlings for two years: unpaired *t*-test, $t_{24} = 0.365$, $p = 0.7185$; between adults for two years: unpaired *t*-test, $t_{25} = 0.658$, $p = 0.5164$), using the Student *t*-test for significant differences, as variances

Table 1
Comparison of body composition of beachcast birds in Japan between 1983 and 1984

	1983			1984			
	n	Mean	SD	*n*	Mean	SD	*p*
Body mass (g)	11	297.3	17.54	49	285	24.09	ns
Body lipids (g)	5	4.79	2.881	17	4.29	1.368	ns
Body lipids (%)	5	1.63	0.905	17	1.45	0.367	ns
Dry body weight (%)	5	12.1	1.65	17	12	2.18	ns
Pectoral muscle mass (g)	11	26.6	4.13	49	27.5	5.03	ns
Dry pectoral muscle content (%)	11	22.7	1.99	47	22.5	1.73	ns
Dry tibia marrow content (%)	11	11.1	4.41	48	8.9	4.37	ns
Dry femur marrow content %	11	19.8	4.77	45	12.6	5.99	ns
Liver weight (g)	11	4.8	1.37	34	4.2	0.96	ns
Pectoral muscle protein (g)	6	4.4	1.08	24	5	1.18	ns
Pectoral muscles/body mass (%)	11	8.9	1.09	49	9.6	1.55	ns

were homoscedastic, respectively. I, therefore, used the data set of those birds collected in 1984 to compare the body composition variables among the different phase groups collected in 1983.

Because the body mass and body composition variables of both adults and young among three phase groups, before migration (i.e., shortly before leaving the colony in Tasmania), after migration (AR), and during their stay in the northern North Pacific and Bering Sea (ST), were heteroscedastic (i.e., with statistically unequal variances), I used the non-parametric Kruskal-Wallis rank test to determine significant differences in body mass and in body composition among these phase groups for both age groups. This was followed by non-parametric Mann-Whitney U-tests to compare the heteroscedastic variables between the two age groups. Statistical analyses were performed with Statview 5.0. All measurements in the text are given as means ± 1 standard deviation.

RESULTS

Body mass before and after migration

The mean body mass of young and adult Short-tailed Shearwater groups differed among the three phase groups, before migration (i.e., shortly before leaving the colony in Tasmania), after migration (AR) (i.e., shortly after arriving at the boreal summering waters), and during their stay in the northern North Pacific and Bering Sea (ST) (Kruskal-Wallis rank test, adults: $H = 22.37, p < 0.0001, n = 66$; juveniles: $H = 36.15, p < 0.0001, n = 55$) (fig. 2). The lowest mean body masses were found in both age groups upon arrival in the North Pacific (AR group). The body mass of adults was low (517 ± 31.4 g, $n = 37$) and that of juveniles was the lightest (397 ± 41.0 g, $n = 26$) among all age and phase groups. During their stay in the northern North Pacific and Bering Sea in July (ST group), adults recovered their mean body mass to 583 ± 68.3 g ($n = 15$), a value significantly similar to that of adults at the final landfall in early April (AR group; Mann-Whitney U-test, $U = 91, z = -0.611, p = 0.5407$), whereas juveniles in the ST group showed only a moderate increase in body

mass to 449 ± 61.5 g ($n = 12$) (Mann-Whitney U-test, $U = 75, z = -2.544, p = 0.011$), compared with the AR group, a value about 130 g lighter than the mass of adults spending the boreal summer in the northern North Pacific or Bering Sea and 160 g lighter than the mean value for old nestlings in fledgling period in Tasmania in late April.

Relationship between body mass and body lipid content by weight

Body mass and the amount body lipids (g) were highly correlated ($r^2 = 0.79, p < 0.001, n = 153$) in the pooled data set of Short-tailed Shearwater age and phase groups ranging from 220–701 g in body mass, and from 2.6–149.3 g in body lipids, excluding nestlings. That was because the nestlings were in hyper-nutritive condition, characterised by a large amount of body lipids (262.3 ± 38.5 g, $n = 9$) accounting for 42.0% of their average body mass (622 ± 68.4 g, $n = 9$). The equation of the exponential correlation function is:

$$y = 10.932 - 0.151x + (4.564)^{-4}x^2$$

where y is body lipids and x is body mass. Body lipids reached a minimum of a few grams when the body mass had decreased to around 300 g or less (fig. 3).

Relationship between body lipids and muscle protein

Body lipids and protein in the pectoral muscles were also highly correlated in the Short-tailed Shearwaters ($y = 4.65 + 0.285x - 0.002x^2$; $r^2 = 0.76, p < 0.001, n = 76$) where y is protein in pectoral muscles (g) and x is body lipids (g) (fig. 4).

Protein content was approximately constant at a high level in birds storing large amounts of fat, but decreased gradually as body lipids decreased below about 60 g. In birds that had lost most of their body lipids, the protein content had decreased to just a few grams (fig. 4).
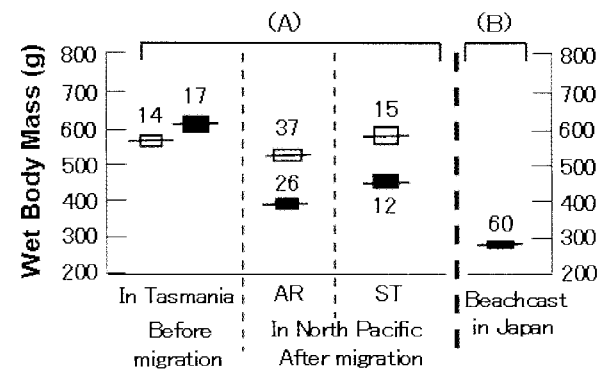

FIG. 2 — Comparison of the body masses of young (black symbols) and adult (open symbols) Short-tailed Shearwaters before and after migration (A) and of beachcast birds that died during migration (B). AR indicates data collected at the time of the birds' arrival at the North Pacific for the Boreal summer, and ST indicates data collected later during their stay in the North Pacific. The mean (horizontal line) and standard error are shown.
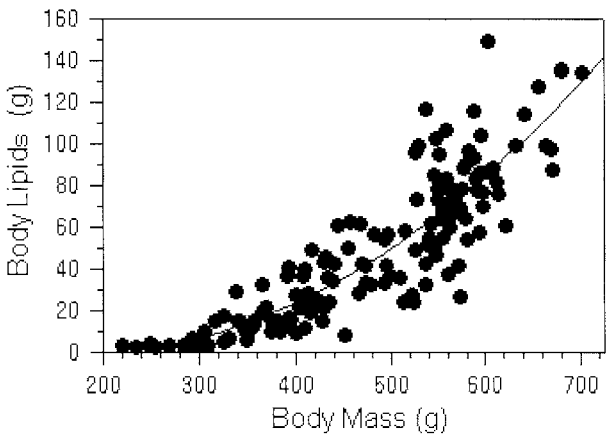

FIG. 3 — Relationship between body mass and body lipid content in Short-tailed Shearwaters.

Beachcast birds

The mean body mass of beachcast young Short-tailed Shearwaters dying during migration was significantly lower than that of AR group (Mann-Whitney U test, U = 8.5, z = 7.255, p < 0.0001) (fig. 2B). The beachcast birds retained only a mean lipid content of 4.4 ± 1.74 g (range, 2.62–9.84 g, n = 22) (fig. 5), accounting for a mean 1.5 ± 0.51% (range, 1.1–3.2%, n = 22) of the very lean average body mass of 287 g. They also had a small pectoral mass (fig. 5B); the pectoral muscle weighed 27.3 ± 4.86 g (range, 17.2–41.1 g, n = 60), with only 4.9 ± 1.17 g of protein (range, 3.4–8.2 g, n = 30). Liver mass was 4.6 ± 1.25 g (range, 3.0–8.3 g, n = 45) (fig. 5B). The marrow content of the dried femur and tibia was only 14.0 ± 6.43% (range, 5.0–32.7%, n = 56) (fig. 5B) and

9.8 ± 4.85% (range, 1.9–26.4%, n = 59), respectively. These low marrow values indicated that the birds were alive until the suspension of their hematopoietic stem cell activities.

All of the lines of evidence showed that the beachcast young Short-tailed Shearwaters had exhausted their nutrients to critical levels by the time they had reached the Japanese coast, which is the final and westernmost stretch of their migration pathway to the northern North Pacific.

BODY COMPOSITION

Post-migratory birds

Post-migratory AR young stored 26.2 g (± 15.22 g, n = 23) of body lipids (fig. 5), which accounted for 6.6% of the lean average body mass of 397 g, whereas post-migratory AR adults stored 41.0 g (± 13.03g, n = 13) of body lipids, accounting for 7.9% of the average 517 g of body mass. The amount of fat stored by the post-migratory young was therefore only 10% of that of the obese nestlings sampled during the fledging period at the colony in Tasmania (mean body lipids, 262.3 g, 42% of the 622 g body mass; 20 April 1984) (fig. 5). Moreover, upon their arrival in the northern North Pacific (AR group), juveniles had similar fat levels to juveniles that were collected later, i.e., during their stay in the North Pacific and Bering Sea (unpaired t-test, t_{30} = 0.066, p = 0.948). On the other hand, post-migratory adults stored 71.4 g (±30.94g, n = 15) lipid, that was similar to the body lipids stored by pre-migratory adults leaving the colony in Tasmania in 1984 (84.4 ± 16.15 g, n = 13)(Mann-Whitney U test, U = 71, z = -1.221, p=0.222). Though the pectoral muscle mass decreased significantly even in the adults from before to after migration (unpaired t-test, t_{48} = 2.703, p = 0.01), the decrease was moderate (<10%) (fig. 5).
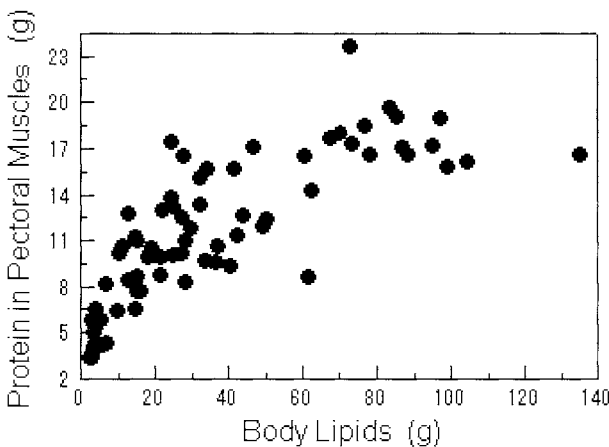

FIG. 4 — Relationship between the protein content in pectoral muscles and the body lipid content in Short-tailed Shearwaters.
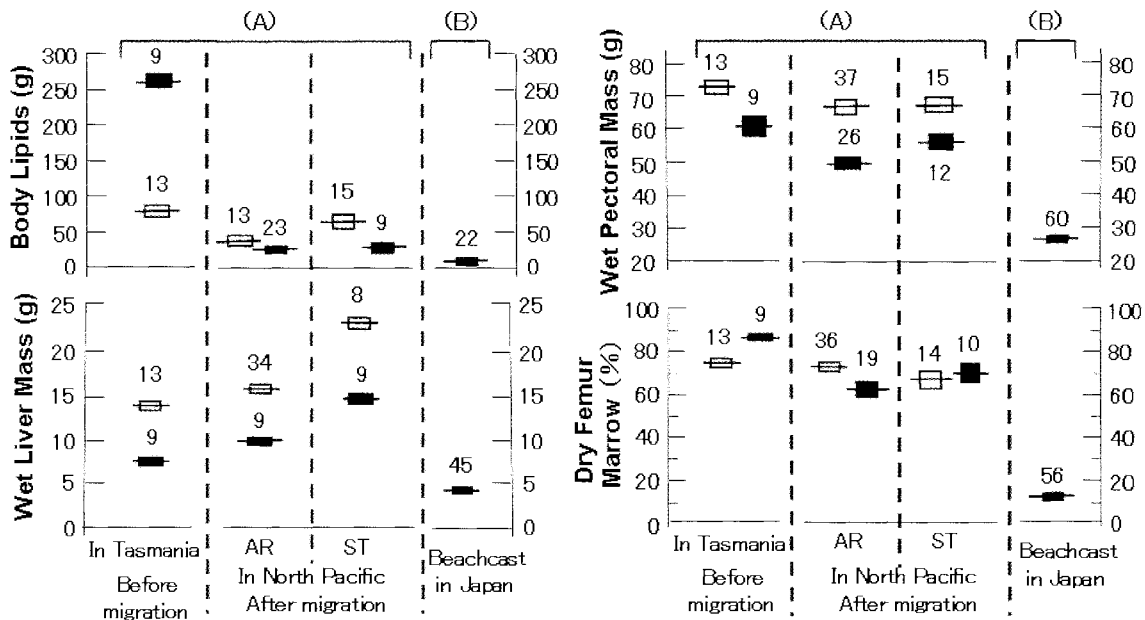

FIG. 5 — Comparison of the body masses of young (black symbols) and adult (open symbols) Short-tailed Shearwaters before and after migration (A) and of beachcast birds that died during migration (B). AR indicates data collected at the time of the birds' arrival at the North Pacific for the boreal summer, and ST indicates data collected during their stay in the North Pacific. The mean (horizontal line) and standard error are shown.

The fat levels after migration (AR groups) were larger in both young (26.2 ± 15.21 g, *n*=23) and adults (41.0 ± 13.03 g, n=13) than the mean minimum value found in the dead birds (beachcast birds: 4.4 g, n=22). Their residual lipid capacities therefore were sufficient for use not only for energy for basal metabolism but also for foraging in local waters. Although the AR young had lost their nutritive reserves to some degree during migration, they sustained high contents of dry femur marrow (AR group, 62 ± 21.5%, *n* = 19; ST group, 70 ± 17.5%, *n* = 10) (fig. 5) that did not differ significantly from the adult AR (mean, 72.9 ± 6.23%, *n* = 13) and ST (mean, 68.0 ± 19.16%, *n* = 14) groups (Kruskal-Wallis rank test, K_5 = 3.684, *p* = 0.595).

Adults in the northern North Pacific in late June to July (ST group) had the largest wet liver mass (23.0 ± 2.55 g, *n* = 8) among all phase and age groups (fig. 5), indicating a high intake efficiency while foraging.

DISCUSSION

Body lipids in Short-tailed Shearwaters are both a structural component necessary for cell membranes, and thus not available as a metabolic energy source, and a stored body fat component, including a distinctive oil stored in the upper layer of the stomach, which can be mobilised as a metabolic energy source.

The data presented here on lipid content from beachcast juvenile birds and from adults at the breeding colony led to a number of important observations.

The juvenile Short-tailed Shearwaters beachcast along Japanese shores during the northern migration had a remaining mean body lipid content of 4 g, which is comparable to the mean value of 3 g in starved birds of unknown age in the Bering Sea, reported by Baduini *et al.* (2001b). Oka & Okuyama (2000) reported that beachcast Rhinoceros Auklets, *Cerorhinca monocerata* (Pallas, 1811), found after an oil spill, had a mean body lipid content of 7 g and dry femur marrow content of 24%. These auklets, which are short-distance migrants and a slightly heavier species than the shearwaters, had also lost most of their nutritional energy reserves and had suspended hematopoietic stem cell activity.

The body lipids remaining in the beachcast Short-tailed Shearwaters, therefore, should not be regarded as available for metabolic energy needs but as structural components of cell membranes (Klasing 1998). Thus, this species of bird requires extra lipids for energy, in addition to the 4 g needed for structural components. The beachcast juveniles also had only a small amount of protein in their muscles, as has been found in starved penguins (Cherel *et al.* 1994). The present study also shows that protein had a tendency to be consumed at the malnutritional stage after body lipid was mostly consumed.

The two mean body mass values (564 g with empty stomachs, and 569 g, possibly including stomach contents) for the adult birds collected in this study at the colony in southern Tasmania during the departure period compares well with adult values measured by other studies at colonies during the late chick-rearing season (e.g., 574 g mean body mass with empty stomachs; northernmost Montague Is. population, New South Wales, Schultz & Klomp 2000; and 583 g mean body mass, possibly including stomach content; Cape Woolamai population on Phillip Island, Victoria, Lill & Baldwin 1983). The data can thus be interpreted as

indicating the standard nutritive condition of adults.

As body mass and body fat have been previously shown to be positively correlated in Rhinoceros Auklets (Oka & Okuyama 2000) and Short-tailed Shearwaters (Baduini *et al.* 2001b), consistent with the results of the present study, the moderate body mass of 564 g with a mean body fat content of 83 g can be considered optimal from the viewpoint of keeping wing loading at a minimum to increase flight efficiency. This stable nutritive condition among adults is maintained by commuting from the breeding sites far south to abundantly productive Antarctic waters, where Antarctic Krill, *Euphausia superba* (Dana, 1852), is captured to replenish their energy reserves during the chick-rearing season (Weimerskirch & Cherel 1998, Klomp & Schultz 2000, Cherel *et al.* 2005). Even if the birds minimise energy expenditure during flight by dynamic soaring, their fat deposits are too small to accomplish the 9000-km long-distance migration from 42°S to 45°N through the low-productivity low-latitude waters. During the final long-distance foraging trip to Antarctic waters south of Tasmania prior to the equatorial migration, adults may replenish their fat deposit and distinctive stomach oil to some extent. During the trans-equatorial migration over low-productivity tropical waters, the birds would metabolise not only their stored fat but also some of the stomach oil for their energy requirements. Birds probably complete their trans-equatorial migration in minimal time to avoid wasting their limited amount of energy on opportunistic foraging efforts in areas of low productivity.

Body lipids reached a minimum of a few grams when the body mass had decreased to around 300 g or less. This suggests that the decrease in body mass during the final stages of malnutrition may reflect decreases in components other than body fat. Unlike lipid, protein generally is not viewed as an energy storage, but is considered to be used only after lipid reserves are exhausted (Blem 1990). Protein content in the pectoral muscles in the shearwaters was accelerated to decrease during the final critical stage of malnutrition. Though the pectoral muscle mass decreased significantly even in adults from before to after migration, the decrease was moderate, compared with the decrease in body lipid, that showed Short-tailed Shearwaters depend largely on body lipids to accomplish their long-distance migration.

Post-migratory juveniles sustained a low body mass with a small amount of body lipids. The results of this study indicate that juveniles take longer to recover from energy shortages than adults, possibly because they lack skill and experience in feeding on prey organisms.

During anomalous weather and oceanic conditions in the Bering Sea in 1997 and 1998, the shearwaters failed to accumulate sufficient energy, storing only a mean of 31 g and 45 g body fat by each North Pacific autumn, respectively. They also had lighter pectoral masses (Baduini *et al.* 2001a) at the time when the shearwaters usually commence their southward migration to Australia. In the North Pacific autumn of 1997, up to 200 000 individuals were estimated to have starved to death (Baduini *et al.* 2001b). Interestingly, these fatalities had body and pectoral masses 25% larger than those of the beachcast juveniles along the Japanese coast in this study (380 g *vs.* 287 g for body mass, and 36 g *vs.* 27 g for pectoral mass, respectively). The ages of the dead birds in the 1997 mass mortality were not determined.

Comparison of the body and pectoral masses of these fatalities with those of the adult birds in this study suggests that many older age classes were involved in these events, as

the structural weights of bone and organs such as muscles increase and develop with age. These mass mortalities in the Bering Sea differ ecologically from the mass mortalities in temperate waters in which migratory juveniles are repeatedly involved. The ages of the dead birds should be determined to understand the effects of these mass mortalities on the population ecology of Short-tailed Shearwaters, and long-term monitoring is essential to understand the nature of these events.

ACKNOWLEDGEMENTS

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