Patterns of energy expenditure influence various aspects of animal life histories, geographic distributions, resource requirements, and energy flow in ecosystems (Weathers 1979; Wiens 1984; Trevelyan et al. 1990). Basal metabolic rates (BMR) and field metabolic rates (FMR) are among the most important indices of energy expenditure. BMR represents the minimum amount of energy required to maintain essential life processes (Schmidt-Nielsen 1997), while FMR represents the daily expenditure of energy by an animal living under natural conditions in its normal habitat (Nagy 1987). Although previous studies have measured these indices (Ricklefs et al. 1996; Nagy et al. 1999), the number of studies of seabirds in which both BMR and FMR have been measured remains small; therefore, more information on these metabolic rates is required to verify their relationships with behavioural and ecological factors.

Shearwaters, petrels, and albatrosses are ecologically adapted for long-distance and wide-ranging flight; they have proportionately larger wings with...
high aspect ratios than other birds (Prince & Morgan 1987). BMR and FMR have been measured in several shearwater and petrel species during chick-rearing periods (Adams & Brown 1984; Ellis 1984; Pettit et al. 1985; Weathers et al. 2000; Hodum & Weathers 2003; Weimerskirch et al. 2003). Their FMR/BMR ratios (3.2–4.6 times BMR), which represent metabolic intensity (Nagy 1987), are clearly higher than those of albatrosses (1.8–3.3 times BMR: Brown & Adams 1984; Adams et al. 1986; Costa & Prince 1987; Shaffer et al. 2001). In different species, BMR may be influenced by body mass, the latitude of the breeding colony, breeding stage, and/or activity mode (Ellis 1984; Niizuma & Watanuki 1997; Ellis & Gabrielsen 2002). In addition, FMR can also vary depending on body mass, ocean regime, and/or activity mode (Birt-Friesen et al. 1989; Furness & Bryant 1996; Nagy et al. 1999). To understand the factors that affect BMR and FMR among species in the Procellariiformes, it is necessary to conduct further research and to compare species.

Streaked Shearwaters *Calonectris leucomelas* breed on offshore islands of East and Southeast Asia (Oka 2004). Recent studies have investigated their breeding ecology (e.g., growth rate and meal mass) and foraging behaviour (e.g., diet and foraging areas) (Oka et al. 2002; Lee & Yoo 2004; Matsumoto 2008; Inoue et al. 2009; Ochi et al. 2010). Streaked Shearwaters fly several hundreds to more than a thousand kilometres from their breeding sites to their foraging grounds (Matsumoto 2008), as do other shearwaters, petrels, and albatrosses (Klomp & Schultz 2000; Shaffer et al. 2003; Awkerman et al. 2005; Freeman et al. 2010). There have been no previous investigations into this species’ BMR and FMR; thus this paper provides the first descriptions of them. BMR and FMR for breeding Streaked Shearwaters was determined by means of respirometry and doubly labelled water (DLW) methods.

**MATERIALS AND METHODS**

1) **Study site and species**

Our experiments were conducted on Awa Island (38°27′N, 139°13′E, Niigata, Japan), which is located within the Tsushima Warm current region of the Sea of Japan. Approximately 84,000 Streaked Shearwaters breed on the island (Maki Yamamoto, unpublished data). Streaked Shearwaters rear a single chick between mid-August and early-November (Yoshida 1981; Oka et al. 2002). They only return to the colony to provision their chick at night (Yoshida 1981). The duration of foraging trips during the chick-rearing period varies widely from 1 to 15 days on Mikura Island (33°52′N, 139°14′E, Izu Islands, Japan; Ochi et al. 2010). In this study, shearwater gender was determined based on their vocalizations: males give high-pitched calls, whereas females give low-pitched calls (Arima & Sugawa 2004).

2) **Respirometry measurements**

We measured the oxygen consumption rates (V\textsubscript{O2}) of four adult Streaked Shearwaters (two males and two females, body mass 512±71 g, means±1 standard deviation) between 13 and 19 October 2009 to estimate their BMR. The birds were captured in their nest burrows and transported to a field laboratory on the island and placed in individual cages for at least nine hours to ensure they were in a post-absorptive state. All birds were released in their nests within 49 h of capture. Since the mean provisioning rate of Streaked Shearwaters is 0.46 meals day\textsuperscript{-1} (Inoue et al. 2009), it was assumed that our experimental procedure would have little impact on the breeding performance of the experimental individuals.

Oxygen consumption rates were measured using an open circuit respirometry system composed of a 20 L acrylic metabolic chamber and an oxygen analyser (Xentra 4100, Servomex Ltd). The metabolic chamber was submerged in a thermostatic water bath that was set to 25°C, which was assumed to be within the thermoneutral zone of Streaked Shearwaters. Based on an equation given by Ellis and Gabrielsen (2002), we assumed their lower critical temperature was 15°C. A temperature logger (Thermocron Type-SL, KN Laboratories, Inc.) was used to record the ambient temperature (T\textsubscript{a}) in the metabolic chamber every minute. The flow rate (V\textsubscript{f}) of the respirometer was fixed at 2.0 L min\textsuperscript{-1} using a mass flow controller (+2%, Type HM1171A, Tokyo Keiso Co., Ltd). Effluent air was dried over silica gel and a fraction of the dry effluent air was directed into the oxygen analyser. The oxygen analyser was calibrated using dry outside air (set to 20.946% oxygen) and pure stock nitrogen (set to 0.000% oxygen). A computer was used to read oxygen concentrations in effluent air (F\textsubscript{EO2}) every minute.

When the birds were in a post-absorptive condition, they were put into the metabolic chamber and measuring was begun. We collected F\textsubscript{EO2} data for 26 h; however, we did not use the first two hours of F\textsubscript{EO2} data because this period might have included habitu-
ation to the metabolic chamber. $V_{O2}$ was calculated using formula 3A in Withers (1977) as follows:

$$V_{O2} = V_E \times (F_{I02} - F_{E02}) / [1 - (1 - RQ) \times F_{I02}],$$

where RQ represents the respiratory quotient. We assumed that RQ was 0.8 and the oxygen concentration in influent air ($F_{I02}$) was 20.946%. To calculate metabolic rate from $V_{O2}$, we used the conversion coefficient of 20.1 kJ L$^{-1}$ (Schmidt-Nielsen 1997).

BMR was calculated from the lowest 60-min running average of instantaneous metabolic rate. The body mass of each bird was measured before and after each experiment using a Pesola spring balance (accurate to the nearest 10 g). A linear decrease in body mass was assumed when assessing the body mass value used for calculating the mass-specific metabolic rate. All results are given at standard temperature (0°C) and pressure (1 atm) under dry (STPD) conditions.

During the experiments on Awa Island, sunrise occurred between 0522 and 0527 and sunset between 1747 and 1755. Therefore, in the data analysis, we divided each day into daytime and nighttime periods based on these time frames.

3) Field procedure for the DLW method

The DLW method has been used as one of the least-invasive field research methods as it allows an estimate to be made of the energy expended by subjects as they go about their normal activities (Lifson & McClintock 1966; Speakman 1997; Butler et al. 2004). Theoretically, when water labelled with stable isotopes of oxygen and hydrogen (i.e. deuterium) ($^{18}$O and $^2$H) is injected into a subject, the isotopes are mainly eliminated as CO$_2$ and H$_2$O gradually from the subject. Because $^2$H leaves as H$_2$O while $^{18}$O leaves as CO$_2$ and H$_2$O, it is possible to estimate the CO$_2$ production rate, which is an indicator of metabolic rate, from the differences in the elimination rates of each isotope.

Fourteen Streaked Shearwaters were captured at night in their nest burrows on Awa Island between 17 September and 1 October 2008. We used the two-sample technique for the DLW method following Speakman (1997). After collecting a 1 mL blood sample as a background sample, the shearwaters were injected with 2 mL DLW. The DLW dose contained 10.3 atom percent $^{18}$O, 4.0 atom percent $^2$H, and 0.9 % NaCl. The DLW dose was injected intraperitoneally by carefully elevating the skin to avoid damage to the air sacs. To quantify the administered dose, the syringe was weighed before and after the injection using a portable electronic balance that was accurate to the nearest 0.01 g (SJ-420JS, Shinko Denshi Co.) in the field laboratory.

After injection, these experimental subjects were kept individually in plastic boxes for 90 min. Then, we took a 1 mL blood sample from the brachial or tarsal vein as an initial sample and measured their initial body mass ($W_i$) with a Pesola spring balance (accurate to the nearest 10 g). The birds were ringed with individually numbered metal rings and released back into their nests. After a period of two to eight days, the experimental subjects were recaptured in their burrows at night. Immediately after recapture, we took a 1 mL blood sample from the brachial or tarsal vein as a final sample for each individual and measured final body mass ($W_f$).

Each blood sample was placed in a heparinized tube (Nipro Neo-Tube, NT-HE 1000 Nipro, Japan) and immediately centrifuged (5 min, 6200 rpm). After centrifugation, the serum was transferred to a 0.5 mL plastic screw cap vial with an O-ring (Asahi Techno Glass Co.) and frozen at $-25\degree$ C until the isotope analysis.

4) Isotope analysis

All of the serum samples and the DLW doses were analysed for $^2$H and $^{18}$O isotope concentrations using an isotope ratio mass spectrometer (IRMS; ANCA-GSL, Sercon Ltd; Yamada et al. 2009). To estimate the enrichment of the DLW doses, a 0.050 g injected sample was diluted with 49.867 g distilled water prior to the analysis (Speakman 1997). Similarly, all serum samples were diluted six times with distilled water. The IRMS was used to measure the enrichment of the distilled water used for the analyses and the diluted serum and injected samples.

The distilled water and diluted samples were put into cylindrical tubes, and were analyzed in duplicate using the water equilibration method (Horita et al. 1989). First, for the $^{18}$O analysis, the cylindrical tubes were filled with CO$_2$ gas and kept at 25°C for a minimum of eight hours to allow the substitution of $^{18}$O between the sample and the CO$_2$ gas. Then the substituted CO$_2$ gas was transferred to the IRMS for analysis. The cylindrical tubes were then put in minivials with a platinum (Pt) catalyst for $^2$H analysis (Herd et al. 2000). The cylindrical tubes were filled with hydrogen gas and kept at 25°C for at least 36 h to allow substitution to occur between the $^2$H sample and the hydrogen gas. Then the substituted hydrogen
gas was transferred to the IRMS for analysis. We discarded data for birds for which the final isotopic enrichment was too close to the background abundance (difference <20 ppm; Thums et al. 2003) to maintain analytical precision.

5) Calculations for the DLW method

Turnover rates for $^2$H ($k_d$, day$^{-1}$) and $^{18}$O ($k_o$, day$^{-1}$) were determined using the two-sample technique and calculated as follows:

\[
k_d = \left[ \ln(H_i - H_b) - \ln(H_f - H_b) \right] / t
\]

\[
k_o = \left[ \ln(O_i - O_b) - \ln(O_f - O_b) \right] / t
\]

where $H_b$, $H_i$, $H_f$, $O_b$, $O_i$, and $O_f$ represent the isotope concentrations ($^2$H or $^{18}$O, ppm) of the background, initial, and final samples, respectively, and $t$ represents the time interval (days) between the initial and final samples (Lifson & McClintock 1966; Speakman 1997).

The plateau method was used to determine the isotope dilution spaces for $^2$H ($N_d$) and $^{18}$O ($N_o$), and to estimate total body water (Speakman 1997). Calculations were performed for $N_d$ and $N_o$ using the general equations:

\[
N_d (\text{mol}) = H_{inj} \times (H_d - H_i) / (H_b - H_d)
\]

\[
N_o (\text{mol}) = O_{inj} \times (O_d - O_i) / (O_b - O_d)
\]

where $H_{inj}$ and $O_{inj}$ represent the quantities of the isotopic doses ($^2$H or $^{18}$O, mol), and $H_d$ and $O_d$ represent the isotope concentrations ($^2$H or $^{18}$O, ppm) in the doses, respectively.

To calculate the $CO_2$ production rate, two main models (one-pool and two-pool models) were used. The one-pool model regards the oxygen isotope dilution space as the body water, while the two-pool method is based on both the hydrogen and oxygen isotope dilution spaces in the animal (Speakman 1997). Speakman (1997) and Butler et al. (2004) suggested that the one-pool model is more appropriate for small birds (<4 kg), therefore the $CO_2$ production rate ($rCO_2$, mL day$^{-1}$) of Streaked Shearwaters was computed using Speakman’s one-pool model (Speakman 1997; equation 7.17). The equation was as follows:

\[
rCO_2 = (N / 2.078) \times (k_o - k_d) - (0.0062 \times k_d \times N),
\]

where $N = N_o$.

To convert units of mL $CO_2$ day$^{-1}$ to energy equivalents, we assumed that 1 mL $CO_2 = 25.11$ J (Gessaman & Nagy 1988).

6) Activity loggers

We deployed activity loggers (GLS-Mk4, 25×18×7 mm, 4.5 g, British Antarctic Survey) on experimental subjects using plastic leg rings (Takahashi et al. 2008). The total mass of the logger, including the plastic leg ring, was 7 g (1.5% of the mean initial body mass of the experimental birds). The loggers (sampling every three seconds) recorded time, and immersion (1) or non-immersion (0) in seawater. These data were pooled during each 10-min recording period, thereby providing a value from 0 to 200 to represent the proportion of time the logger was immersed during the 10-min period. We used the immersion data to calculate the number of landings birds made, and the proportion of time spent on the sea surface, during the period between the collection of the initial and the final blood samples (see above) following Yamamoto et al.’s (2008) method.

RESULTS

We measured oxygen consumption in four resting Streaked Shearwaters that were kept in a constant dark environment for 24 h (see Fig. 1). The mean BMR of the birds was 0.0124±0.0153 kJ g$^{-1}$ h$^{-1}$ (N=4) during daytime.

We recaptured 12 out of 14 experimental subjects and obtained activity data from their loggers. However, in nine of the birds, the final isotopic enrichment was lower than the background abundance. Therefore, data were only available for three individuals (body mass 500±43 g; FMR 759.2±362.8 kJ day$^{-1}$). Using the plateau method, the mean $^2$H and

![Fig. 1. Metabolic rate (kJ g$^{-1}$ h$^{-1}$) of a resting Streaked Shearwater maintained in continuous dark at 25°C. Dotted lines represent the time of dawn or dusk on Awa Island. Arrows represent the time when the lowest metabolic rate (i.e. BMR) of the bird was recorded.](image-url)
18O dilution spaces ($N_d$ and $N_o$) of the birds (calculated from FMR) were $331.8\pm17.3$ mL (total body water [TBW] content: $65.4\pm2.3\%$, $N=3$) and $322.0\pm21.2$ mL (TBW: $63.4\pm1.4\%$, $N=3$), respectively. The dilution space ratio ($N_d:N_o$) of the birds ranged from 1.02 to 1.04. The $k_d/k_o$ ratio, an indicator of the turnover rates of the two isotopic labels, was $0.78\pm0.08$ ($N=3$). Experimental subjects spent, on average, $44.8\pm8.0\%$ ($N=12$) of their time on water and landed on the water surface $50.3\pm9.8$ times day$^{-1}$ ($N=12$) during the period studied.

**DISCUSSION**

1) **Basal metabolic rate**

The lowest metabolic rate (i.e. BMR) of each of the four resting Streaked Shearwaters was recorded during the daytime. This is similar to the daily rhythm in metabolic rates in resting Kerguelen Petrels *Pterodroma brevirostris* (Adams & Brown 1984) and Leach’s Storm-petrels *Oceanodroma leucorhoa* (Niizuma & Watanuki 1997), whereas Sooty Albatrosses *Phoebetria fusca* show an inverse rhythm (Adams & Brown 1984). Aschoff and Pohl (1970) have shown that avian resting metabolic rates are lower during the inactive phase of the circadian rhythm than during the active phase. Our data indicate that the inactive phase in the metabolic rhythm of Streaked Shearwaters occurs during the daytime.

The BMR of the Streaked Shearwaters was equal to 54% of the predicted BMR that was calculated (using body mass=512 g) from an allometric equation for seabirds (Ellis & Gabrielsen 2002). In general, it is likely that BMR of Procellariiformes are lower than those of other seabirds (Warham 1996), due to their lower body temperatures (Warham 1990). The measured BMR of the Streaked Shearwaters also corresponded to 59% of the predicted BMR that was calculated from the allometric equation for Procellariiformes (Ellis & Gabrielsen 2002). This means that the measured BMR of Streaked Shearwaters is not only low among seabirds, but also more specifically in the Procellariiformes. Ellis (1984) and Pettit et al. (1985) suggested that seabirds that breed at lower latitudes also have BMR that are lower than predicted: 65% of the predicted value for Christmas Shearwaters *Procellaria nativitatis* breeding at 24°N, and 58% for Wedge-tailed Shearwaters *Puffinus pacificus* at 24°N (summarised by Ellis & Gabrielsen 2002). Although previous studies show that breeding stage influences BMR in seabirds (e.g. Niizuma & Watanuki 1997; Bech et al. 1999), the effect of breeding stage in this study was not known because it was conducted during a single stage. Activity modes, such as flight patterns and feeding methods, also affect the BMR of seabirds. Seabirds that fly by means of gliding, soaring or flapping/gliding and feed by dipping or seizing prey are likely to have low BMR (Ellis 1984). Since many Procellariiformes glide during flight and seize prey when feeding (Warham 1996), our result may indicate a relationship between BMR and activity mode.

2) **Field metabolic rates and activity at sea**

Unfortunately, we were only able to calculate FMR from three Streaked Shearwaters because the final isotopic enrichment in nine birds was lower than the acceptable level (above 20 ppm of the background enrichment). Presumably the relatively long experimental periods and/or the high activity levels (the number of landings on water) caused the low final isotope enrichment (Table 1). However, we found that the range of dilution space ($N_d:N_o$) ratio was 1.02–1.04 using data from the three shearwaters for which FMR was calculated. Variation in the $N_d:N_o$ ratio is influenced by analytical noise, and the acceptable range is between 0.97 and 1.10 (Speakman et al. 1993). Therefore, the analytical error in our results is negligible. The $k_d:k_o$ ratio represents the similarity between the 18O and 2H turnover rates and is used as an indicator of the precision of the DLW method (Speakman 1997). High $k_d:k_o$ ratios (>0.9) indicate that an estimate of CO2 production is not reliable (Jones et al. 2009). However, in the shearwaters, the $k_d:k_o$ ratio was 0.78±0.08. This indicates that our FMR results for the three shearwaters were highly reliable.

The FMR of the three birds were 3.1, 4.1 and 8.1 times BMR, and, on average, FMR was 5.1 times BMR in Streaked Shearwaters (Table 1). Drent and Daan (1980) proposed that FMR values that are four times BMR may represent “the maximum sustained working level for parent birds,” and Weathers and Sullivan (1989) revised that value to 5.0–5.7 times BMR. Despite the limited sample size, the mean
FMR of Streaked Shearwaters was within the maximum sustained working level and was similar to values for other shearwaters and petrels (3.2–4.6 times BMR; summarised by Ellis & Gabrielsen 2002). The mean FMR of the Streaked Shearwaters was equal to 80% of the predicted FMR calculated from an allometric equation for seabirds using a body mass of 500 g (Ellis & Gabrielsen 2002). Previous studies found FMR to be low in seabirds living in warmer waters and using gliding flight (Birt-Friesen et al. 1989; Ellis & Gabrielsen 2002). Since Streaked Shearwaters have both of these characteristics (Warham 1990, 1996), our results support the previous analyses.

We found that, on average, Streaked Shearwaters landed on water 50.3 times day$^{-1}$ and spent 44.8% of the foraging period on water, where they might either forage or rest (Table 1). Previous studies have shown that several albatross species land on the water surface less frequently than do Streaked Shearwaters during foraging trips (15–26 times day$^{-1}$), but albatross species spend similar proportions of their time on the water (35–53%) (Weimerskirch et al. 2000; Shaffer et al. 2001; Weimerskirch & Guionnet 2002). Our results show that Streaked Shearwaters land on the water more frequently than albatrosses; therefore, shearwaters have higher energetic costs because they take off more frequently. Taking off from the water surface is energetically demanding, especially for seabirds that have large wings with high aspect ratios (Weimerskirch et al. 2000; Shaffer et al. 2001). Therefore, frequent landings may increase the energy expenditure of Streaked Shearwaters. Usually, shearwaters and petrels have higher FMR values than albatrosses (shearwaters and petrels: 3.2–4.6 times BMR; albatrosses: 1.8–3.3 times BMR, summarised by Ellis & Gabrielsen 2002). To the best of our knowledge, in medium-sized breeding Procellariiformes, data on the number of landings per day are only available for Sooty Puffinus griseus (26.3 times day$^{-1}$, Shaffer et al. 2009) and Cory’s Calonectris diomedea shearwaters (104–140 times day$^{-1}$, Ramos et al. 2009), and no data are available regarding their FMR. To understand differences in foraging strategies among the Procellariiformes, it is necessary to investigate their FMR in association with their foraging behaviours.

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BMR and FMR of shearwaters

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