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LIFE-HISTORY PATTERNS IN MARINE BIRDS[1]

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ABSTRACT

The parameters of the von Bertalanffy growth equation for seabirds were estimated from previously published growth curves to allow within and between group comparisons of their life-history patterns. Overall, growth data were available for 447 seabird populations breeding around the globe, corresponding to 137 species, 13 families and four orders. A negative relationship between the logarithmic values of W_∞ and K was identified for the orders of Charadriiformes, Pelecaniformes, Procellariiformes, and Sphenisciformes, as well as all seabird species combined. The values of the slope b ranged from -0.32 for the Sphenisciformes, to -0.12 for the Pelecaniformes, with a mean slope of -0.21, when all seabirds were considered.

INTRODUCTION

Seabirds can be broadly characterized as long-lived species, with delayed sexual maturation and breeding, as well as low annual reproductive rates. Many species have a life span well over 30 years (e.g., most species of albatrosses; Schreiber & Burger, 2002). In addition, most species start breeding when they are three years or older (e.g., over ten years in some albatross species; Schreiber and Burger, 2002). Most species lay not more than three eggs, and in some instances chick rearing lasts for a long time (e.g., 380 days in the Wandering albatross; Schreiber & Burger, 2002).

These life-history characteristics have been shaped as an evolutionary response to conditions of living in the marine environment, i.e, reflecting the patchy and unpredictable distribution of marine resources (Ricklefs, 1990; Hamer *et al.*, 2002; Weimerskirch, 2002), which poses challenges to seabirds in finding food and provisioning chicks. Nonetheless, Weimerskirch (2007) has recently suggested that prey dispersal may not be as unpredictable as we once thought. As a result, specialization of seabirds for use of a particular marine habitat may be the driving force for the evolution of a particular life history strategy (Weimerskirch, 2007).

Life-history strategies have been studied for a number of marine organisms (fish: e.g., Adams, 1980; Froese & Pauly, 1998; Pauly, 1998; Stergiou, 2000; marine mammals: e.g., Herzing, 1997; Trites & Pauly, 1998; sea turtles: e.g., Fraser & Ehrhart, 1985; van Buskirk & Crowder, 1994; marine birds: e.g., Ricklefs, 1990; Visser, 2002; Weimerskirch, 2007). In addition, examining relationships between life history traits and developing empirical equations has been proven useful for comparisons among different taxonomic groups (e.g., Peters, 1983; Froese & Pauly, 1998; Visser, 2002). Growth, in particular, has been described in seabirds with the use of several mathematical equations. Three of the most popular ones are listed in Table 1 (see also Table 8.1 in Peters, 1983). For all three equations, parameters are estimated by fitting the selected model to size-at-age data for each individual or population under study. These equations allow

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the estimation of the key parameters of chick growth, such as the growth constant, K, and the asymptotic weight, W_∞ and a measure of how rapidly this approached (K_1, K_G, K).

In the present study, we compiled information on growth parameters of seabird chicks, in an attempt to explore their life-history patterns. In addition, we established empirical relationships between life-history traits, in order to investigate potential differences in growth rates for a few seabird orders.

Table 1: Three equations most frequently used to describe chick growth in marine birds.

Growth curve	Equation	Description
1) Logistic	$W_t = W_\infty / (1 + e^{-K_L \cdot (t-t_L)})$	W_∞: asymptotic weight; K_L: logistic growth rate constant; t_L: the time of inflection point, which corresponds to the age of 50% of asymptotic weight of chicks.
2) Gompertz	$W_t = W_\infty \cdot e^{-e^{-K_G \cdot (t-t_G)}}$	W_∞: asymptotic weight; K_G: Gompertz growth rate constant; t_G: the time of inflection point.
3) Von Bertalanffy (VB)	$W_t = W_\infty \cdot (1 - e^{-K \cdot (t-t_0)})^b$	W_∞: asymptotic weight; K: VB growth rate constant; t_o: the theoretical 'age' the chick would have at weight zero; b: exponent indicating isometric growth pattern, when its value is 3.

METHODOLOGY

In the present study, we gathered all available information pertinent to growth patterns in seabird chicks, from studies conducted since 1937. Overall, growth data were available for 447 seabird populations, corresponding to 137 species, 13 families and four orders (Tables 2 to 4). For the purpose of this paper, we defined as seabird population a number of seabirds belonging to the same species and breeding at a certain location at a certain year (Tables 2 to 4). We gathered information using the following databases: (a) Aquatic Sciences and Fisheries Abstracts; (b) Web of Science - Thomson Scientific; (c) BioSciences Information Service of Biological Abstracts; and (d) the Searchable Ornithological Research Archive, which cover peer-reviewed journals and other literature sources. We also used some unpublished theses and technical reports that were available to us, and extracted information from the online database of Birds of North America, Cornell University (http://bna.birds.cornell.edu/BNA/).

The form of the VBGF used here is:

$$W_t = W_\infty \cdot (1-e^{-K \cdot (t-t0)})^3 \quad \ldots 1)$$

where W_t is the weight at age t, W_∞ the asymptotic size (here the size of a chick if it were to continue growing forever in the manner described by the equation), K is a parameter of dimension time^{-1} (here: year^{-1}), and t_o adjusts the function such that W_t=0 at t=t_o.

In case where the original graph of chick body weight-at-age was not available, we obtained data for the following life-history parameters, to fit the VBGF: (a) the asymptotic weight, W_∞ (g), the growth constant, K_L (in days^{-1}), and the inflection point, t_L (in days), of the logistic growth curve (Table 2); and (b) the asymptotic weight, W_∞ (in g), the growth constant, K_G (in days-1), and the inflection point, t_G (in days), of the Gompertz growth curve (Table 3). When information on K_L and t_L was not available, we used the following equations respectively to estimate the missing values:

$$K_L = 0.962 \cdot W_\infty^{-0.31} \quad \ldots 2$$

(Visser, 2002); and

$$t_L = ln\ (W_\infty/W0 - 1) / K_L \quad \ldots 3)$$

where W_o is the initial weight of the chicks at hatching (Navarro and Bucher, 1990).

For each seabird population, we calculated seven data points of time when chick body weight is equal to 1%, 5%, 10%, 25%, 50%, 75%, 90%, 95%, and 99% of W_∞, using the growth curve published by the corresponding study, and then used these data points to re-express growth parameters in terms of the VBGF (see Figure 1 for examples). As the VBGF and the other growth functions share one parameter (W_∞), we kept this constant, and used the least square optimization technique to estimate the other VBGF parameters (K, t_o), given the data points. An example is given in Figure 1, for the growth of the Crested auklet (*Aethia cristatella*) chicks of the Okhotsk Sea (Figure 1a), and of the Least auklet (*Aethia pussila*) chicks of the Pribilof Islands, Alaska (Figure 1b).

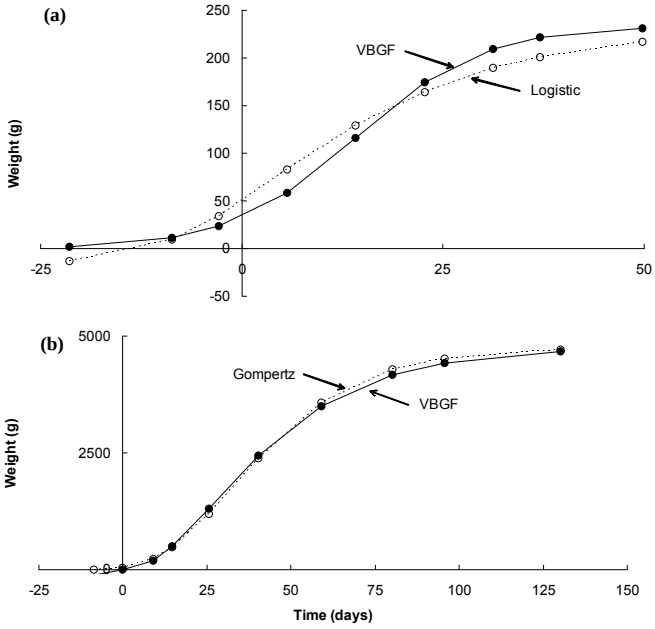

Figure 1. Comparison of the von Bertalanffy growth function (VBGF; black dot, solid line) with the growth curve originally used (open dot, dotted line) to describe weight-at-age data (not shown). (a) Crested auklet (*Aethia cristatella*) from the Okhotsk Sea, described with the logistic growth function (Kitaysky, 1999). (b) Light-mantled albatross (*Phoebetria palpebrata*) from Macquarie Island, Southern Ocean, described with the Gompertz growth function (Terauds and Gales, 2006).

When the chick body weight-at-age graph was provided in the original studies, data was traced and re-analyzed using the least square optimization technique to get growth parameter estimates in terms of the VBGF. An example is given in Figure 2, for the growth of Little shearwater (*Puffinus assimilis*) chicks of New Zealand.

The standard deviation (*SD*) was also estimated as a measure of effectiveness of the least-squares optimization. For all seabird populations, *SD* was then re-expressed as a % deviation (%D), i.e., relative to W_t=0.5* W_∞.

Pauly *et al.* (1996) proposed the auximetric plot as another tool for the comparison of within- and between- species growth patterns. The auximetric plot is a double logarithmic plot of the parameters K and the asymptotic size (W_∞ or L_∞) (Pauly *et al.*, 1996; Froese and Pauly, 2000). In such a plot, each set of growth parameters represents a point, with the different points for a species or higher taxon forming an ellipsoid cluster of points, whose surface area is related to the 'growth space' occupied by a given species or higher taxon (Pauly *et al.*, 1996; Froese and Pauly, 2000).

Table 2. Growth parameters of seabird chicks from the logistic growth curve (in normal font), and also estimated for this paper (in bold), using the von Bertalanffy (VB) growth model. W_∞ (in g): asymptotic weight of chicks for both the logistic and VB growth models; t_I (in days): inflection point of logistic curve; t_o (in years): hypothetical 'age' chicks would have had at zero weight; K_I (in days^{-1}) and K (in years^{-1}): growth coefficients for the logistic and VB models respectively. AK: Alaska; CA: California; WA: Washington State; and NY: New York State.

Species	Area (Year)	t_I	K_I	W_∞	K	t_o	Source
Alcidae							
Aethia cristatella	Okhotsk Sea (1994)	14.17	0.129	233	**20.96**	**-0.043**	Kitaysky (1999)
Cepphus columba	Farallon Is, AK (1989)	*14.01	¤0.150	401	**24.37**	**-0.032**	Shultz and Sydeman (1997)
Cepphus columba	Farallon Is, AK (1990)	*12.75	¤0.155	359	**25.19**	**-0.033**	Shultz and Sydeman (1997)
Cepphus columba	Farallon Is, AK (1991)	*15.86	¤0.143	466	**23.24**	**-0.031**	Shultz and Sydeman (1997)
Cepphus columba	Farallon Is, AK (1992)	*15.90	¤0.143	468	**23.24**	**-0.031**	Shultz and Sydeman (1997)
Cepphus columba	Farallon Is, AK (1993)	*15.91	¤0.143	469	**23.24**	**-0.031**	Shultz and Sydeman (1997)
Cepphus columba	Farallon Is, AK (1994)	*13.95	¤0.150	398	**24.37**	**-0.032**	Shultz and Sydeman (1997)
Cepphus columba	Farallon Is, AK (1995)	*15.26	¤0.145	443	**23.56**	**-0.031**	Shultz and Sydeman (1997)
Cerorhinca monocerata	Destruction Is, WA (1974)	*23.20	0.074	335	**12.02**	**-0.080**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Destruction Is, WA (1975)	*27.74	0.068	395	**11.05**	**-0.080**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Destruction Is, WA (1979)	*32.78	0.058	400	**9.43**	**-0.093**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Destruction Is, WA (1980)	*38.44	0.049	394	**7.96**	**-0.111**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Destruction Is, WA (1981)	*39.49	0.049	412	**7.96**	**-0.108**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Protection Is, WA (1975)	*24.61	0.076	412	**12.35**	**-0.072**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Protection Is, WA (1976)	*27.71	0.071	432	**11.54**	**-0.073**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Protection Is, WA (1979)	*25.88	0.076	432	**12.35**	**-0.069**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Protection Is, WA (1980)	*25.15	0.078	430	**12.67**	**-0.067**	Wilson and Manuwal (1986)
Cerorhinca monocerata	Protection Is, WA (1981)	*32.59	0.061	440	**9.91**	**-0.085**	Wilson and Manuwal (1986)
Fratercula cirrhata	Okhotsk Sea (1994)	20.41	0.118	621	**19.17**	**-0.034**	Kitaysky (1999)
Fratercula cirrhata	Buldir Is, AK (1975)	*19.35	0.074	360	**12.02**	**-0.090**	Wehle (1983)
Fratercula cirrhata	Ugaiushak Is, AK (1976)	*16.27	0.125	600	**20.31**	**-0.040**	Wehle (1983)
Fratercula cirrhata	Barren Is, AK (1976)	*18.53	0.111	600	**18.04**	**-0.045**	Wehle (1983)
Fratercula cirrhata	Chowiet Is, AK (1976)	*14.54	0.091	330	**14.79**	**-0.077**	Wehle (1983)
Fratercula cirrhata	Shumagin Is, AK (1976)	*12.90	0.145	520	**23.56**	**-0.038**	Wehle (1983)
Fratercula cirrhata	Wooded Is, AK (1976)	*16.13	0.120	550	**19.50**	**-0.044**	Wehle (1983)
Fratercula cirrhata	Ugaiushak Is, AK (1977)	*12.72	0.153	555	**24.86**	**-0.034**	Wehle (1983)
Fratercula cirrhata	Barren Is, AK (1977)	*18.62	0.110	595	**17.87**	**-0.045**	Wehle (1983)
Fratercula cirrhata	Sitkalidak, AK (1977)	*15.88	0.126	590	**20.47**	**-0.041**	Wehle (1983)
Fratercula cirrhata	Cathedral Is, AK (1977)	*15.71	0.127	580	**20.64**	**-0.040**	Wehle (1983)
Fratercula corniculata	Buldir Is, AK (1975)	*20.13	0.075	300	**12.18**	**-0.086**	Wehle (1983)
Fratercula corniculata	Barren Is, AK (1976)	*16.07	0.122	440	**19.82**	**-0.043**	Wehle (1983)
Fratercula corniculata	Chowiet Is, AK (1976)	*12.61	0.113	280	**18.36**	**-0.059**	Wehle (1983)
Fratercula corniculata	Shumagin Is, AK (1976)	*12.95	0.144	405	**23.40**	**-0.038**	Wehle (1983)
Fratercula corniculata	Ugaiushak Is, AK (1977)	*12.89	0.139	380	**22.59**	**-0.041**	Wehle (1983)
Fratercula corniculata	Barren Is, AK (1977)	*17.31	0.114	445	**18.52**	**-0.046**	Wehle (1983)
Hydrobatidae							
Oceanodroma homochroa	Farallon Is, CA (1985)	*13.56	0.108	49	**17.55**	**-0.061**	Ainley *et al.* (1990)
Laridae							
Larus atricilla	Florida (1972)	*13.45	¤0.162	310	**26.32**	**-0.029**	Dinsmore and Schreiber (1974)
Larus ridibundus	The Netherlands (2000)	9.90	0.200	237	**32.50**	**-0.026**	Eising and Groothuis (2003)
Sterna hirundo	Great Gull Is, NY (1968)	8.22	0.246	113	**39.97**	**-0.021**	LeCroy and Collins (1972)
Sterna paradisaea	Shetland Is (1975)	7.50	0.288	111	**46.80**	**-0.016**	Furness (1978)
Pelecanoididae							
Pelecanoides georgicus	S Georgia (1982)	14.90	0.145	148	**23.56**	**-0.032**	Roby (1991)
Pelecanoides urinatrix	S Georgia (1982)	15.60	0.146	139	**23.72**	**-0.030**	Roby (1991)
Phaethontidae							
Phaethon lepturus	Seychelles (2002)	35.00	¤0.155	362	**25.19**	**0.027**	Ramos and Pacheco (2003)

Table 2 continued.

Species	Area (Year)	t_l	K_l	W_∞	K	t_o	Source
Spheniscidae							
Eudyptula minor	Victoria, Australia (1980)	20.00	0.104	951	**16.90**	**-0.047**	Montague (1982)
	Victoria, Australia (1981)	21.40	0.168	793	**27.30**	**-0.004**	Montague (1982)
	Tasmania (1970)	17.10	0.152	836	**24.70**	**-0.023**	Hodgson (1975)
	New Zealand (1975)	16.10	0.158	642	**25.67**	**-0.023**	Jones (1978)
	New Zealand (1958)	21.40	0.123	1110	**19.99**	**-0.028**	Kinsky (1960)
	New Zealand (1938)	18.10	0.122	1148	**19.82**	**-0.037**	Richdale (1940)
	New Zealand (1983)	19.60	0.125	1154	**20.31**	**-0.031**	Gales (1987)
Stercorariidae							
Catharacta skua	Shetland Is. (1975)	16.96	0.176	1167	**28.60**	**-0.014**	Furness (1978)

* Estimated using equation 2 described in the methodology.
¤ Estimated using equation 3 described in the methodology.

RESULTS

Table 2 summarizes the logistic growth parameters as extracted from the corresponding studies, as well as the growth parameters we re-expressed using the VBGF. Similarly, Table 3 summarizes growth parameters derived from the Gompertz growth model, which we then re-expressed using the VBGF. Lastly, Table 4 summarizes VBGF parameters re-estimated after tracing and re-analyzing originally published weight-at-age data. W_∞ values ranged from 36 g for the Wilson's storm petrel (*Oceanites oceanicus*) chicks (Table 4), to 15,243 g for the Wandering albatross (*Diomedea exulans*) chicks both from the Crozet Islands, Southern Ocean (Table 4).

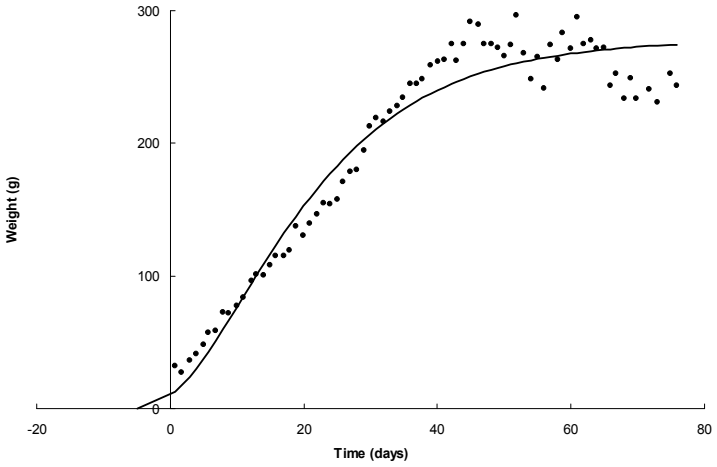

Figure 2. Von Bertalanffy growth function (solid line) for Little shearwater (*Puffinus assimilis*) chicks from Lady Alice Island, New Zealand, re-estimated using original weight-at-age data (black dot) published by Booth *et al.* (2000).

The most intensively studied species were the Pigeon guillemot (*Cepphus columba*), the Rhinoceros auklet (*Cerorhinca monocerata*), the Atlantic puffin (*Fratercula arctica*), the Tufted puffin (*Fratercula cirrhata*), the Horned puffin (*Fratercula corniculata*), the Common tern (*Sterna hirundo*), the Black-legged kittiwake (*Rissa tridactyla*), the Thick-billed murre (*Uria lomvia*), and the Blue penguin (*Eudyptula minor*). They were represented by more than 10 seabird populations each (Tables 2 to 4), and comprised 31% of all seabird populations compiled (138 out of 447; Tables 2 to 4). All the above-mentioned seabird species, with the exception of the Blue penguin, belong to the order Charadriiformes (Tables 2 to 4).

K_L values ranged from 0.049 days^{-1} for the Rhinoceros auklet chicks of Destruction Island, off the coast of Washington State (Table 2), to 0.288 days^{-1} for the Arctic tern (*Sterna paradisaea*) chicks of Shetland Islands, UK (Table 2). K_L values were not available for nine seabird populations (Table 2). These were estimated using equation 2 described above. The values of t_L ranged from 7.5 days for the Arctic tern chicks of Shetland Islands, UK (Table 2), to 39.5 days for the Rhinoceros auklet chicks of Destruction Island, off the coast of Washington State (Table 2). Values of t_L were lacking for 35 seabird populations (Table 2). These were estimated using equation 3 described in the methodology section.

Table 3. Growth parameters of seabird chicks from the Gompertz growth curve (in normal font), and also estimated for this paper (in bold), using the von Bertalanffy growth function (VBGF). W_∞ (in g): the asymptotic weight of chicks for both the Gompertz curve and VBGF; t_G (in days) and K_G (in days^{-1}): the inflection point and the growth constant for the Gompertz curve respectively; t_o (in years) and K (in years^{-1}): the hypothetical 'age' chicks would have at zero weight and the growth constant for VBGF respectively. AK: Alaska.

Species	Area (Year)	t_G	K_G	W_∞	K	t_o	Source
Diomedeidae							
Phoebastria immutabilis	Hawaii (1987)	19.00	0.050	2836	**14.84**	**-0.037**	Sievert and Sileo (1993)
Phoebastria nigripes	Hawaii (1987)	17.90	0.056	2714	**16.62**	**-0.010**	Sievert and Sileo (1993)
Phoebetria palpebrata	Macquarie Is (2000)	32.40	0.047	4760	**13.95**	**-0.006**	Terauds and Gales (2006)

K_G values ranged from 0.047 days^{-1} for the Light-mantled albatross (*Phoebetria palpebrata*) chicks of Macquarie Island, Southern Ocean (Table 3), to 0.056 days^{-1} for the Black-footed albatross (*Phoebastria nigripes*) chicks of Hawaii (Table 3). In addition, t_G ranged from 17.9 days for the Black-footed albatross chicks of Hawaii (Table 3), to 32.4 days for the Light-mantled albatross chicks of Macquarie Island, Southern Ocean (Table 3).

When re-expressed through VBGF, the logistic growth curve deviated from VBGF by 13%, while the Gompertz curve deviated by only 3%. This suggests that the VBGF and the Gompertz curves are equivalent.

Computed K values ranged from 3.22 years^{-1} for the Wandering albatross chicks of the Crozet Islands, Southern Ocean (Table A1), to 61.46 years^{-1} for the Cory's shearwater (*Calonectris diomedea*) chicks of Selvagem Grande, of the Madeira archipelago (Table A1). Moreover, t_o values ranged from -0.111 years for the Rhinoceros auklet chicks of Destruction Island, off the coast of Washington State (Table 2), to -0.001 years for the Whiskered auklet (*Aethia pygmaea*) chicks of Buldir Island, Alaska (Table A1), the Rhinoceros auklet chicks of Teuri Island, Japan (Table A1), and the Masked booby (*Sula dactylatra*) chicks, of Kure Atoll, Hawaii (Table A1).

A negative relationship between the logarithmic values of W_∞ and K was identified for the orders of Charadriiformes, Pelecaniformes, Procellariiformes, and Sphenisciformes as well as for all seabird species combined (Table 4, Figure 3). Each order was represented by 239, 50, 111 and 47 seabird populations respectively (Table 4, Figure 3). The values of the slope ranged

Table 4. Regression equations between the von Bertalanffy growth parameters K and W_∞, for four orders and all seabird species combined. SE(b): Standard error of the slope. r: The correlation coefficient. N: The number of seabird populations representing each order. All regressions were statistically significant (P<0.05).

Order	Regression	SE(b)	r	N	P
Charadriiformes	$LogK=2.18-0.31LogW_\infty$	0.03	-0.53	239	P<0.05
Pelecaniformes	$LogK=1.63-0.12LogW_\infty$	0.05	-0.35	50	P<0.05
Procellariiformes	$LogK=1.79-0.18LogW_\infty$	0.02	-0.61	111	P<0.05
Sphenisciformes	$LogK=2.35-0.32LogW_\infty$	0.05	-0.70	47	P<0.05
All seabirds	$LogK=1.93-0.21LogW_\infty$	0.01	-0.62	445	P<0.05

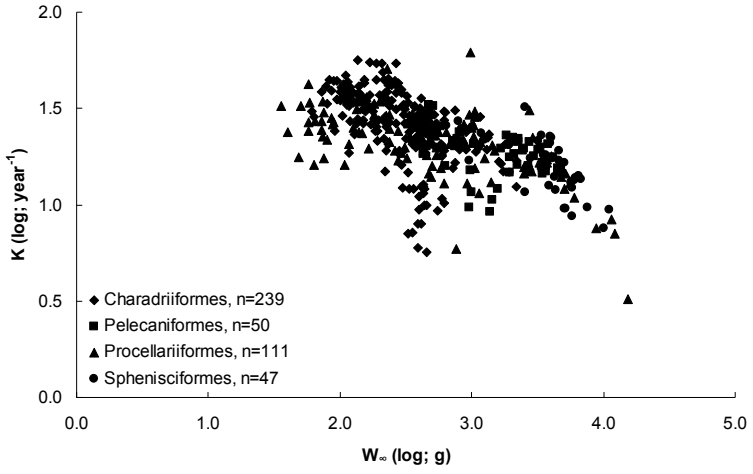

Figure 3. Auximetric plot for the four orders of Charadriiformes, Sphenisciformes, Procellariiformes and Pelecaniformes (see text).

from -0.32 for Sphenisciformes, to -0.12 for Pelecaniformes (Table 4). All regressions were statistically significant ($P<0.05$; Table 4). This justifies the use of auximetric plots in seabirds.

DISCUSSION

In the present study, relationships were established between the life-history parameters K and W_∞, for a number of seabird populations around the globe. However, these relationships were based on information available for about 39% of the world's seabirds (137 out of 351 in Karpouzi *et al.*, 2007). Thus, these relationships are provisional and subject to change when additional information becomes available. Nonetheless, they can be particularly useful in estimating approximate values of K from W_∞, and hence to obtain a preliminary growth curve for species without growth data. In addition, they allow us to compare growth patterns of seabirds to those from other groups of organisms, whose growth has also been described using the VBGF.

Similar studies that investigate the relationship between the growth parameters K and asymptotic size have also been conducted mainly for fish species of marine and freshwater ecosystems. In particular, Winemiller and Rose (1992) analyzed life-history patterns of 216 North American marine and freshwater fish species, belonging to 57 families. Pauly (1998) analyzed growth parameters for 4826 fish populations listed in FishBase (www.fishbase.org; Froese and Pauly, 2000). Stergiou (2000) explored life-history patterns for 40 fish species from Greek waters, belonging to 20 families, and compared them with those from Pauly (1998).

Starck and Ricklefs (1998) compiled information on the growth parameters K_L, K_G and W_∞ for 1117 populations, belonging to 557 bird species, from both terrestrial and aquatic ecosystems. Out of these, 366 belonged to marine birds and represented 114 seabird species, and 13 families (Starck and Ricklefs, 1998). Ricklefs *et al.* (1998) and later Visser (2002) used these data to examine the relationship between K_L and W_∞. Their analyses revealed that growth rates are particularly low for many pelagic seabird species, and tend to be higher in species that feed close to shore, such as the larid species. In addition, highest growth rates are observed among penguin species (Ricklefs *et al.*, 1998; Visser, 2002).

The VBGF parameters can be linked by the relation $W_\infty=a*K^{-b}$ (e.g., Beverton and Holt, 1959; Adams, 1980; Pauly, 1980; Charnov, 1993; Pauly, 1998; Froese and Pauly, 2000). For fish, the exponent b takes values that generally range from -0.27 to -0.80 (Charnov, 1993; Stergiou, 2000). The value of b for all Greek fish stocks is equal to -0.32 (Stergiou, 2000). In contrast, the value of b equals -0.57 for the 4826 populations analyzed by Pauly (1998). When all seabird populations were taken into account, the slope on the auximetric plot was equal to -0.21 (Table 5). This value was heavily influenced by 53% of the K and W_∞ values of Charadriiformes (239 out of 447 seabird populations; Table 5). Hence, it may be subject to change when growth parameter estimates from other seabird species belonging to the other three orders becomes available.

The auximetric plot revealed differences in the growth potential of the seabird species included in this study (Figure 3). Indeed, the growth spaces occupied by the four orders of seabirds seem to reflect differences in the seabirds' breeding biology (e.g., adult foraging behaviour during chick-rearing; e.g., Fernández *et al.*, 2001; parental feeding strategies; e.g., Ydenberg, 1989). In particular, tern and gull species with generally smaller body size exhibited faster growth rates (Figure 3). These are species that produce large clutches, which tend to transport food from areas close to shore to feed their young (e.g., Hulsman and Smith, 1988). On the other hand, alcid species, also characterized by small body size, grow more slowly (Figure 3). Alcid species produce single-egg clutches, and exhibit a more pelagic, nocturnal foraging behaviour (e.g., Sealy, 1973; Ricklefs, 1982, 1990). As a result, provisioning rates, and consequently growth rates of chicks, are reduced (e.g., Sealy, 1973; Ricklefs, 1982, 1990).

Some procellariiform species (e.g., storm petrels of the family Hydrobatidae) also displayed a growth pattern similar to that of the alcid species (Table 4; Figure 3). Storm petrels are small in size. However, the growth rates of their chicks are relatively low (Table 4; Figure 3). Storm petrels feed far from nesting colonies on prey that is sparse and unpredictably distributed. The single-clutch size may suggest that their ability to deliver energy to the brood is severely limited (e.g., Place *et al.*, 1989). Slow growth may be an adaptation to reduce the rate at which chicks require energy for development, thus making it easier for parents to utilize more distant and sparse food resources for breeding (e.g., Ricklefs *et al.*, 1980; Place *et al.*, 1989).

The large-bodied Sphenisciformes (i.e., penguins) exhibited high growth rates (Tables 2 and 4; Figure 3). A similar growth pattern was also observed by Visser (2002). This has been interpreted as an adaptation to the severe Antarctic conditions that shorten the breeding season. Indeed, faster growth rates enable chicks to leave the colony before the beginning of the winter (Volkman and Trivelpiece, 1980; Visser, 2002). Lastly, albatross species with large body size exhibited slow growth rates (Tables 3 and 4; Figure 3). This growth pattern is typical of the albatross family, which is dominated by long-distance foragers (e.g., Fernández *et al.*, 2001). Albatross chicks require nine to ten months to develop to adult body size at fledging (e.g., Berrow *et al.*, 1999; Mabille *et al.*, 2004). Thus, developmental period spans the winter season, and chicks must endure severe winter conditions and variability in parental provisioning efforts (e.g., Berrow *et al.*, 1999; Mabille *et al.*, 2004).

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Table A1. Growth parameters of seabird chicks re-estimated for this paper using the von Bertalanffy growth function (VBGF), from body weight-at-age data published in the original studies. W_∞ (g): the asymptotic weight of chicks; K (years^{-1}) and t_o (in years): the growth constant and the hypothetical 'age' chicks would have at zero weight respectively.

Species	Area (Year)	W_∞	K	t_o	Source
Alcidae					
Aethia cristatella	Buldir Is, Alaska (1996)	376	20.47	-0.011	Fraser *et al*. (1999)
	Buldir Is, Alaska (1997)	358	20.62	-0.011	Fraser *et al*. (1999)
	St Lawrence Is, Alaska (1987)	299	32.75	-0.018	Piatt *et al*. (1990)
Aethia pusilla	Kiska Is, Alaska (2003)	80	33.60	-0.018	Major *et al*. (2006)
	Pribilof Is, Alaska (1982)	114	34.41	-0.018	Roby and Brink (1986)
	St Lawrence Is, Alaska (1987)	95	35.40	-0.019	Piatt *et al*. (1990)
Aethia pygmaea	Buldir Is Alaska (1998)	113	32.92	-0.018	Hunter *et al*. (2002)
Alca torda	Machias Seal Is (1995)	189	44.81	-0.022	Bond *et al*. (2006)
	Machias Seal Is (2003)	208	54.25	-0.022	Bond *et al*. (2006)
Alle alle	Franz Josef Land (1993)	152	44.37	-0.021	Stempniewicz *et al*. (1996)
	Svalbard (1978)	138	41.05	-0.015	Clark and Ydenberg (1990)
	Svalbard (1984)	136	37.53	-0.019	Clark and Ydenberg (1990)
	Svalbard (1987)	178	30.53	-0.019	Konarzewski and Taylor (1989)
	Svalbard (1992)	138	37.80	-0.019	Stempniewicz *et al*. (1996)
Brachyramphus marmoratus	Barren Is, Alaska (1978)	152	42.84	-0.021	Simons (1980)
	Barren Is, Alaska (1979)	167	37.16	-0.020	Hirsch *et al*. (1981)
Cepphus carbo	Teuri Is, Japan (1989)	806	19.45	-0.017	Minami *et al*. (1995)
Cepphus columba	Farallon Is, California (1985)	447	28.59	-0.016	Ainley and Boekelheide (1990)
	Mandarte Is, British Columbia (1960)	476	27.19	-0.017	Drent (1965)
	Mitlenatch Is, British Columbia (1985)	421	29.61	-0.015	Emms and Verbeek (1991)
	Prince William Sound, Alaska (1978)	607	26.04	-0.015	Oakley (1981)
	Queen Charlotte Is, British Columbia (1991)	412	29.82	-0.016	Vermeer *et al*. (1993)
Cepphus grylle	Piqiuliit, Nunavut (1983)	404	28.10	-0.016	Cairns (1987)
	Pitsiulak, Nunavut (1981)	386	28.53	-0.017	Cairns (1987)
	Pitsiulak, Nunavut (1982)	408	26.76	-0.018	Cairns (1987)
	Pitsiulak, Nunavut (1983)	447	26.09	-0.017	Cairns (1987)
	Québec (1977)	448	25.60	-0.018	Cairns (1981)
Cerorhinca monocerata	Cleland Is, British Columbia (1969)	455	10.00	-0.054	Summers and Drent (1979)
	Protection Is, Washington (1989)	355	7.15	-0.076	Wilson (1993)
	Protection Is, Washington (1990)	392	6.01	-0.091	Wilson (1993)
	Protection Is, Washington (1991)	455	5.69	-0.104	Wilson (1993)
	Teuri Is, Japan (1994)	593	10.78	-0.005	Takahashi *et al*. (2001)
	Teuri Is, Japan (1995)	615	10.20	-0.001	Takahashi *et al*. (2001)
	Teuri Is, Japan (1996)	550	9.35	-0.006	Takahashi *et al*. (2001)
	Teuri Is, Japan (1997)	329	7.10	-0.072	Takahashi *et al*. (2001)
	Teuri Is, Japan (1998)	439	12.07	-0.004	Takahashi *et al*. (2001)
	Triangle Is, British Columbia (1978)	406	22.04	-0.026	Vermeer and Cullen (1982)
Cyclorrhynchus psittacula	Buldir Is, Alaska (1991)	266	26.47	-0.017	Hipfner and Byrd (1993)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Fratercula arctica	Bleiksøy, Norway (1982)	280	19.00	-0.039	Barrett *et al.* (1987)
	Bleiksøy, Norway (1986)	118	36.54	-0.030	Barrett and Rikardsen (1992)
	Bleiksøy, Norway (1987)	221	14.86	-0.053	Barrett and Rikardsen (1992)
	Farne Is, UK (1963)	195	27.51	-0.028	Pearson (1968)
	Gannet Is, Newfoundland (1996)	317	22.11	-0.028	Baillie and Jones (2003)
	Gannet Is, Newfoundland (1997)	442	18.01	-0.032	Baillie and Jones (2003)
	Gannet Is, Newfoundland (1998)	438	20.00	-0.029	Baillie and Jones (2003)
	Gull Is, Newfoundland (1998)	236	26.61	-0.028	Baillie and Jones (2003)
	Hornøy, Norway (1980)	387	29.49	-0.018	Barrett *et al.* (1987)
	Hornøy, Norway (1981)	372	32.72	-0.020	Barrett and Rikardsen (1992)
	Is May, UK (1975)	334	28.87	-0.018	Harris (1978)
	Is May, UK (1992)	265	31.23	-0.024	Wernham and Bryant (1998)
	Is May, UK (1995)	310	31.28	-0.019	Cook and Hamer (1997)
	Machias Seal Is (1997)	367	26.58	-0.019	Bond *et al.* (2006)
	Machias Seal Is (1999)	221	28.49	-0.029	Bond *et al.* (2006)
	Machias Seal Is (2003)	379	19.74	-0.029	Bond *et al.* (2006)
	Røst, Norway (1983)	377	27.15	-0.017	Barrett *et al.* (1987)
	Røst, Norway (1984)	222	35.49	-0.020	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1985)	292	16.10	-0.040	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1988)	182	26.37	-0.030	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1989)	326	33.76	-0.019	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1990)	304	31.81	-0.018	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1991)	306	29.50	-0.018	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1992)	368	32.27	-0.018	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1993)	228	43.54	-0.019	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1996)	219	37.92	-0.021	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (1999)	260	43.68	-0.020	Anker-Nilssen and Aarvak (2002)
	Røst, Norway (2000)	188	53.82	-0.022	Anker-Nilssen and Aarvak (2002)
	W Scotland, UK (1975)	339	21.81	-0.025	Harris (1978)
	Wales, UK (1977)	353	27.07	-0.016	Ashcroft (1979)
	Wales, UK (1978)	337	23.81	-0.017	Hudson (1979)
Fratercula cirrhata	Destruction Is, Washington (1975)	528	25.50	-0.017	Burrell (1980)
	Prince William Sound, Alaska (1995)	604	25.82	-0.017	Piatt *et al.* (1997)
	Triangle Is, British Columbia (2000)	517	29.38	-0.027	Gjerdrum (2004)
Fratercula corniculata	Duck Is, Alaska (1995)	511	20.31	-0.033	Harding *et al.* (2003)
	Duck Is, Alaska (1996)	371	26.23	-0.025	Harding *et al.* (2003)
	Duck Is, Alaska (1997)	472	20.43	-0.039	Harding *et al.* (2003)
	Duck Is, Alaska (1998)	303	33.01	-0.026	Harding *et al.* (2003)
	Duck Is, Alaska (1999)	402	31.80	-0.021	Harding *et al.* (2003)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Ptychoramphus aleuticus	California Channel Is (2001)	150	26.45	-0.027	Ackerman *et al*. (2004)
	California (1959)	155	30.42	-0.016	Thoresen (1964)
	Farallon Is, California (1971)	192	21.59	-0.014	Manuwal (1974)
	Triangle Is, British Columbia (1996)	118	32.70	-0.018	Hedd *et al*. (2002a)
	Triangle Is, British Columbia (1997)	149	31.15	-0.018	Hedd *et al*. (2002a)
	Triangle Is, British Columbia (1998)	136	27.99	-0.021	Hedd *et al*. (2002a)
	Triangle Is, British Columbia (1999)	187	25.48	-0.019	Hedd *et al*. (2002a)
Uria aalge	Farne Is, UK (1963)	169	55.21	-0.023	Pearson (1968)
	Is May, UK (1992)	267	54.34	-0.022	Harris and Wanless (1995)
	St Lawrence Is, Alaska (1972)	229	38.73	-0.026	Johnson and West (1975)
	Sweden (1974)	320	36.74	-0.021	Hedgren and Linnman (1979)
	Sweden (1975)	278	43.02	-0.021	Hedgren and Linnman (1979)
	Sweden (1976)	291	37.97	-0.022	Hedgren and Linnman (1979)
	Sweden (1977)	292	39.64	-0.021	Hedgren and Linnman (1979)
	Wales, UK (1987)	234	45.19	-0.022	Hatchwell (1991)
Uria lomvia	Cape Hay, Northwest Territories (1979)	215	44.67	-0.021	Birkhead and Nettleship (1981)
	Coats Is, Nunavut (1991)	268	41.66	-0.021	de Forest and Gaston (1996)
	Coats Is, Nunavut (1994)	268	37.92	-0.024	Hipfner *et al*. (2006)
	Coats Is, Nunavut (1995)	231	41.69	-0.023	Hipfner *et al*. (2006)
	Coburg Is, Northwest Territories (1979)	247	41.48	-0.021	Birkhead and Nettleship (1981)
	Digges Is, Nunavut (1999)	137	56.41	-0.023	Hipfner *et al*. (2006)
	Prince Leopold Is, Nunavut (2000)	305	33.09	-0.019	Gaston *et al*. (2005)
	Prince Leopold Is, Nunavut (2001)	200	36.92	-0.021	Gaston *et al*. (2005)
	Prince Leopold Is, Nunavut (2002)	117	41.05	-0.024	Gaston *et al*. (2005)
	St Lawrence Is, Alaska (1972)	211	48.51	-0.023	Johnson and West (1975)
Diomedeidae					
Diomedea amsterdamensis	Amsterdam Is (1984)	8818	7.58	-0.028	Jouventin *et al*. (1989)
Diomedea exulans	Crozet Is (1986)	12249	7.06	-0.033	Lequette and Weimerskirch (1990)
	Crozet Is (1994)	11557	8.35	-0.038	Weimerskirch and Lys (2000)
	Crozet Is (2000)	15243	3.22	-0.006	Mabille *et al*. (2004)
Phoebastria immutabilis	Midway Atoll, Hawaii (1965)	2478	15.72	-0.037	Fisher (1967)
Phoebetria palpebrata	Macquarie Is (2001)	3741	16.58	-0.011	Terauds and Gales (2006)
	S Georgia (1977)	3247	16.46	-0.017	Thomas *et al*. (1983)
Thalassarche cauta	Albatross Is, Australia (1998)	5986	10.84	-0.060	Hedd *et al*. (2002b)
Thalassarche chlororhynchos	Amsterdam Is (1996)	2921	22.29	-0.041	Weimerskirch *et al*. (2001)
	Amsterdam Is (1997)	2492	14.42	-0.086	Weimerskirch *et al*. (2001)
	Amsterdam Is (2001)	2732	31.01	-0.029	Pinaud *et al*. (2005)
Thalassarche chrysostoma	S Georgia (1976)	5090	12.02	-0.025	Ricketts and Prince (1981)
	S Georgia (1996)	3755	17.18	-0.003	Huin and Prince (2000)
Thalassarche melanophris	S Georgia (1976)	5540	12.92	-0.023	Ricketts and Prince (1981)
	S Georgia (1996)	4002	17.93	-0.006	Huin and Prince (2000)
Fregatidae					
Fregata magnificens	Baja California, Mexico (1988)	1424	10.58	-0.021	Carmona *et al*. (1995)
	Barbuda (1971)	1369	9.15	-0.042	Diamond (1973)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Hydrobatidae					
Fregetta tropica	Crozet Is (1982)	50	32.70	-0.023	Jouventin *et al*. (1985)
	S Shetland Is (1996)	118	20.74	-0.022	Hahn (1998)
Garrodia nereis	Chatham Is, New Zealand (1987)	74	22.53	-0.019	Plant (1989)
Hydrobates pelagicus	Shetland Is, UK (1992)	40	23.69	-0.024	Bolton (1995)
Oceanites oceanicus	Crozet Is (1982)	36	32.36	-0.023	Jouventin *et al*. (1985)
	S Shetland Is (1996)	59	33.99	-0.017	Quillfeldt and Peter (2000)
	W Antarctic Peninsula (1986)	58	26.92	-0.025	Obst and Nagy (1993)
Oceanodroma furcata	Barren Is, Alaska (1976)	87	26.24	-0.021	Boersma *et al*. (1980)
	Barren Is, Alaska (1977)	80	21.67	-0.028	Boersma *et al*. (1980)
	Barren Is, Alaska (1978)	86	28.28	-0.018	Simons (1981)
	Queen Charlotte Is, British Columbia (1983)	76	30.29	-0.020	Vermeer *et al*. (1988)
Oceanodroma leucorhoa	Kent Is, New Brunswick (1962)	73	27.30	-0.018	Ricklefs *et al*. (1985)
	Kent Is, New Brunswick (1972)	58	24.26	-0.023	Ricklefs *et al*. (1980)
	Kent Is, New Brunswick (1983)	72	24.29	-0.022	Ricklefs *et al*. (1985)
	Kent Is, New Brunswick (1988)	76	17.50	-0.041	Ricklefs and Schew (1994)
	Queen Charlotte Is, British Columbia (1983)	65	27.30	-0.020	Vermeer *et al*. (1988)
Oceanodroma tristrami	Laysan Is, Hawaii (1991)	90	26.89	-0.009	Marks and Leasure (1992)
Pelagodroma marina	Selvagem Grande (1996)	58	42.52	-0.019	Campos and Granadeiro (1999)
	Victoria, Australia (2003)	74	34.22	-0.017	Underwood and Bunce (2004)
	Victoria, Australia (2003)	63	16.12	-0.042	Underwood and Bunce (2004)
Laridae					
Anous minutus	Hawaii (1981)	117	33.44	-0.019	Pettit *et al*. (1984a)
Anous stolidus	Manana Is, Hawaii (1972)	171	31.73	-0.018	Brown (1976a)
	Puerto Rico (1989)	180	33.19	-0.018	Morris and Chardine (1992)
	Seychelles (1995)	214	21.94	-0.027	Ramos *et al*. (2006)
	Seychelles (1996)	187	27.39	-0.017	Ramos *et al*. (2006)
	Seychelles (2001)	226	19.06	-0.020	Ramos *et al*. (2006)
	Tern Is, Hawaii (1989)	222	25.36	-0.024	Megyesi and Griffin (1996)
Anous tenuirostris	Houtman Abrolhos, Australia (1991)	110	34.26	-0.020	Surman and Wooller (1995)
	Seychelles (1995)	100	34.61	-0.019	Ramos *et al*. (2006)
	Seychelles (1996)	106	37.33	-0.019	Ramos *et al*. (2006)
	Seychelles (1997)	104	28.84	-0.026	Ramos *et al*. (2006)
	Seychelles (2001)	100	38.66	-0.019	Ramos *et al*. (2006)
	Seychelles (2002)	83	44.31	-0.019	Ramos *et al*. (2006)
Chlidonias niger	The Netherlands (1995)	78	41.13	-0.019	Beintema (1997)
Creagrus furcatus	Galápagos (1966)	701	20.37	-0.015	Harris (1970a)
	Galápagos (1967)	752	16.55	-0.027	Harris (1970a)
Gygis alba	Hawaii (1981)	117	18.58	-0.021	Pettit *et al*. (1984a)
Larus argentatus	Appledore Is, New Hampshire (1973)	1084	18.87	-0.017	Dunn and Brisbin (1980)
	Germany (1996)	746	30.91	-0.012	Wilkens and Exo (1998)
Larus atricilla	Florida (1976)	353	25.89	-0.017	Schreiber and Schreiber (1980)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Larus audouini	Columbretes Is, Spain (2000)	620	30.40	-0.007	Villuendas and Sarzo (2003)
	Turkey (1974)	743	21.24	-0.018	Witt (1977)
Larus californicus	California (1986)	897	19.40	-0.010	Jehl *et al.* (1990)
Larus fuscus	Farne Is, UK (1963)	717	15.56	-0.030	Pearson (1968)
Larus glaucescens	Mandarte Is, British Columbia (1978)	1308	19.38	-0.013	Verbeek and Morgan (1980)
	Squab Is, Alaska (1979)	1326	22.25	-0.017	Murphy *et al.* (1984)
	Squab Is, Alaska (1980)	2189	12.43	-0.026	Murphy *et al.* (1984)
Larus modestus	Chile (1986)	302	19.11	-0.005	Guerra *et al.* (1988)
Larus occidentalis	Farallon Is, California (1970)	902	23.70	-0.016	Coulter (1979)
	San Nicolas Is, California (1968)	904	24.65	-0.016	Schreiber (1970)
Larus ridibundus	Germany (1986)	325	26.58	-0.018	Nelsen and Brandl (1987)
	The Netherlands (2002)	395	20.28	-0.023	Müller *et al.* (2005)
Larus schistisagus	Teuri Is, Japan (1984)	1612	16.67	-0.015	Watanuki (1992)
	Teuri Is, Japan (1985)	1668	16.38	-0.013	Watanuki (1992)
Procelsterna cerulea	Nihoa Is, Hawaii (1981)	63	28.54	-0.008	Rauzon *et al.* (1984)
Rissa brevirostris	St George Is, Alaska (1993)	422	29.68	-0.018	Lance and Roby (2000)
Rissa tridactyla	Bleiksøy, Norway (1986)	503	24.97	-0.017	Barrett (1989)
	Farne Is, UK (1963)	218	35.00	-0.020	Pearson (1968)
	Middleton Is, Alaska (1996)	402	31.26	-0.018	Gill *et al.* (2002)
	Middleton Is, Alaska (1997)	430	25.53	-0.023	Gill *et al.* (2002)
	Newfoundland (1970)	415	35.85	-0.018	Maunder and Threlfall (1972)
	Norway (1973)	518	25.50	-0.018	Barrett and Runde (1980)
	Norway (1974)	474	30.58	-0.017	Barrett and Runde (1980)
	Norway (1976)	476	30.90	-0.018	Barrett and Runde (1980)
	Prince William Sound, Alaska (1996)	497	29.46	-0.017	Suryan *et al.* (2002)
	Prince William Sound, Alaska (1997)	534	25.96	-0.016	Suryan *et al.* (2002)
	Prince William Sound, Alaska (1998)	451	28.70	-0.018	Suryan *et al.* (2002)
	Prince William Sound, Alaska (1999)	459	30.08	-0.017	Suryan *et al.* (2002)
	St George Is, Alaska (1993)	544	26.44	-0.017	Lance and Roby (2000)
Sterna albifrons	Portugal (2003)	61	30.60	-0.018	Paiva *et al.* (2006)
Sterna anaethetus	Great Barrier Reef (1980)	128	23.08	-0.031	Hulsman and Langham (1985)
	Penguin Is, Australia (1990)	119	27.28	-0.024	Garavanta and Wooller (2000)
Sterna caspia	California (1978)	624	30.25	-0.015	Schew *et al.* (1994)
	New Zealand (1993)	622	27.58	-0.018	Barlow and Dowding (2002)
Sterna dougallii	Great Barrier Reef (1986)	92	24.12	-0.029	Milton *et al.* (1996)
	Rhode Is (1967)	124	34.79	-0.018	LeCroy and Collins (1972)
	Rhode Is Sound (1990)	107	42.46	-0.018	Nisbet *et al.* (1995)
Sterna elegans	California (1999)	221	26.67	-0.020	Dahdul and Horn (2003)
Sterna fuscata	Hawaii (1972)	193	24.01	-0.025	Brown (1976b)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Sterna hirundo	Bird Is, Massachusetts (1999)	136	37.74	-0.019	Apanius and Nisbet (2006)
	Couquet Is, UK (1966)	181	27.70	-0.017	Langham (1972)
	Farne Is, UK (1963)	86	38.96	-0.021	Pearson (1968)
	Germany (1999)	150	33.83	-0.019	Becker and Wink (2003)
	Machias Seal Is (1995)	149	31.18	-0.018	Bond *et al*. (2006)
	Machias Seal Is (1996)	185	23.99	-0.017	Bond *et al*. (2006)
	Machias Seal Is (1997)	127	33.96	-0.019	Bond *et al*. (2006)
	Machias Seal Is (1999)	142	36.34	-0.018	Bond *et al*. (2006)
	Machias Seal Is (2000)	125	34.90	-0.019	Bond *et al*. (2006)
	Machias Seal Is (2001)	109	41.60	-0.019	Bond *et al*. (2006)
	Machias Seal Is (2002)	134	33.91	-0.017	Bond *et al*. (2006)
	Machias Seal Is (2003)	170	26.11	-0.016	Bond *et al*. (2006)
	Québec (1983)	145	37.28	-0.018	Chapdelaine *et al*. (1985)
	Rhode Is (1967)	102	35.24	-0.020	LeCroy and Collins (1972)
	The Netherlands (1989)	108	39.27	-0.018	Klaassen *et al*. (1994)
	The Netherlands (1990)	124	37.44	-0.017	Klaassen (1994)
Sterna paradisaea	Farne Is, UK (1963)	73	38.42	-0.021	Pearson (1968)
	Machias Seal Is (1996)	90	44.12	-0.019	Bond *et al*. (2006)
	Machias Seal Is (1997)	119	40.63	-0.019	Bond *et al*. (2006)
	Machias Seal Is (1998)	151	27.39	-0.017	Bond *et al*. (2006)
	Machias Seal Is (2002)	104	40.25	-0.018	Bond *et al*. (2006)
	Québec (1983)	125	38.74	-0.018	Chapdelaine *et al*. (1985)
	Svalbard (1986)	143	34.68	-0.018	Klaassen *et al*. (1989)
	The Netherlands (1989)	103	40.63	-0.018	Klaassen *et al*. (1994)
	The Netherlands (1990)	140	37.90	-0.017	Klaassen (1994)
Sterna sandvicensis	Farne Is, UK (1963)	114	43.36	-0.022	Pearson (1968)
	The Netherlands (1998)	245	34.80	-0.018	Stienen and Brenninkmeijer (2002)
Sterna sumatrana	Great Barrier Reef (1986)	133	26.55	-0.018	Hulsman and Smith (1988)
Sterna virgata	Crozet Is (1982)	94	44.17	-0.017	Weimerskirch and Stahl (1988)
	S Shetland Is (1979)	166	32.50	-0.017	Jabłoński (1995)
	S Shetland Is (1981)	216	34.48	-0.016	Jabłoński (1995)
	S Shetland Is (1991)	159	32.91	-0.018	Klaassen (1994)
Pelecanidae					
Pelecanus occidentalis	Florida (1972)	3812	20.72	-0.006	Schreiber (1976)
Pelecanoididae					
Pelecanoides georgicus	Crozet Is (1982)	126	25.09	-0.028	Jouventin *et al*. (1985)
Pelecanoides urinatrix	Crozet Is (1982)	134	31.40	-0.015	Jouventin *et al*. (1985)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Phaethontidae					
Phaethon lepturus	Aldabra Atoll (1968)	433	18.40	-0.029	Diamond (1975)
	Aldabra Atoll (1969)	387	20.84	-0.027	Diamond (1975)
	Puerto Rico (1986)	442	25.12	-0.012	Schaffner (1990)
	Seychelles (2002)	360	21.53	-0.015	Ramos and Pacheco (2003)
Phaethon rubricauda	Aldabra Atoll (1968)	985	15.11	-0.031	Diamond (1975)
	Aldabra Atoll (1969)	988	11.64	-0.038	Diamond (1975)
	Christmas Is (1967)	813	23.85	-0.016	Schreiber (1994)
	Christmas Is (1991)	624	15.80	-0.030	Schreiber (1994)
	Green Is, Hawaii (1965)	781	22.05	-0.015	Fleet (1974)
	Johnston Atoll (1986)	726	21.57	-0.011	Schreiber (1994)
	Johnston Atoll (1991)	801	20.88	-0.014	Schreiber (1994)
	Johnston Atoll (1992)	746	19.99	-0.017	Schreiber (1994)
Phalacrocoracidae					
Hypoleucos auritus	E Bic Reef, Québec (1978)	1997	21.88	-0.013	DesGranges (1982)
	E Bicquette Is, Québec (1978)	2446	19.09	-0.009	DesGranges (1982)
	Grand Metis Is, Québec (1978)	2131	21.33	-0.011	DesGranges (1982)
	Shoals Is, New Hampshire (1972)	3188	19.32	-0.009	Dunn (1975)
	SW Razade Reef, Québec (1978)	2288	22.07	-0.011	DesGranges (1982)
	W Bicquette Reef, Québec (1978)	3462	14.45	-0.007	DesGranges (1982)
Hypoleucos brasiliensis	Chile (1997)	1565	12.13	-0.007	Kalmbach and Becker (2005)
Microcarbo africanus	S Africa (1993)	477	33.14	-0.015	Kopij (1996)
Microcarbo pygmaeus	Israel (2001)	514	32.43	-0.012	Shmueli *et al*. (2003)
Notocarbo atriceps	Argentina (1993)	2475	19.58	-0.012	Punta *et al*. (2003)
	Heard and McDonald Is (1993)	3312	19.93	-0.012	Green (1997)
	S Georgia (1989)	2944	17.92	-0.027	Wanless and Harris (1993)
Phalacrocorax carbo	Greece (1994)	2735	21.18	-0.012	Goutner *et al*. (1997)
	Israel (2001)	2282	21.26	-0.004	Shmueli *et al*. (2003)
Strictocarbo aristotelis	Bleiksøy, Norway (1986)	2712	15.85	-0.011	Barrett (1989)
	Farne Is, UK (1963)	1027	20.60	-0.013	Pearson (1968)
	Is May, UK (1998)	1854	22.77	-0.011	Daunt *et al*. (2001)
	Norway (1995)	2046	22.19	-0.007	Østnes *et al*. (2001)
Procellariidae					
Bulweria bulwerii	Madeira (1995)	142	34.45	-0.017	Nunes and Vicente (1998)
Calonectris diomedea	Azores (1995)	1040	22.59	-0.016	Ramos *et al*. (2003)
	Portugal (1987)	1042	25.59	-0.015	Granadeiro (1991)
	Selvagem Grande (1969)	895	20.83	-0.026	Zino (1971)
	Selvagem Grande (1991)	977	61.46	-0.023	Hamer and Hill (1993)
Daption capense	S Shetland Is (1992)	582	20.61	-0.026	Weidinger (1998)
Fulmarus glacialis	Shetland Is, UK (1997)	959	29.38	-0.008	Phillips and Hamer (2000)
	Shetland Is, UK (1997)	879	26.20	-0.017	Gray *et al*. (2003)
	Shetland Is, UK (1998)	993	25.12	-0.017	Gray *et al*. (2003)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Fulmarus glacialoides	Prydz Bay, Antarctica (1989)	1059	28.59	-0.018	Norman and Ward (1992)
Halobaena caerulea	Crozet Is (1982)	222	28.72	-0.019	Jouventin *et al*. (1985)
	Prince Edward Is (1983)	198	34.51	-0.020	Fugler *et al*. (1987)
Lugensa brevirostris	Crozet Is (1982)	308	19.76	-0.052	Jouventin *et al*. (1985)
	Prince Edward Is (1980)	356	29.66	-0.022	Schramm (1983)
Macronectes giganteus	Prince Edward Is (1977)	4505	15.30	-0.008	Cooper *et al*. (2001)
Macronectes halli	Prince Edward Is (1977)	5194	14.43	-0.011	Cooper *et al*. (2001)
Pachyptila belcheri	Falkland Is (1978)	239	29.44	-0.016	Strange (1980)
	Falkland Is (2003)	263	19.12	-0.028	Quillfeldt *et al*. (2007)
	Falkland Is (2004)	181	29.15	-0.018	Quillfeldt *et al*. (2007)
	Falkland Is (2005)	155	31.60	-0.016	Quillfeldt *et al*. (2007)
Pachyptila desolata	S Georgia (1992)	225	35.35	-0.013	Reid *et al*. (1999)
Pachyptila salvini	Crozet Is (1982)	164	19.51	-0.035	Jouventin *et al*. (1985)
	Prince Edward Is (1981)	158	36.08	-0.020	Berruti and Hunter (1986)
Pachyptila turtur	S Georgia (1983)	182	33.60	-0.016	Prince and Copestake (1990)
Pagodroma nivea	Dronning Maud Land, Antarctica (1985)	322	17.51	-0.036	Røv (1990)
Procellaria aequinoctialis	Prince Edward Is (1981)	1429	20.36	-0.016	Berruti *et al*. (1985)
	S Georgia (1986)	1496	18.99	-0.013	Hall (1987)
Procellaria cinerea	Kerguelen Is (1988)	1394	13.14	-0.038	Zotier (1990a)
	Prince Edward Is (1982)	1247	17.31	-0.015	Newton and Fugler (1989)
Pseudobulweria rostrata	New Caledonia (2004)	583	15.52	-0.047	Villard *et al*. (2006)
Pterodroma arminjoniana	Mauritius (1978)	513	22.83	-0.024	Gardner *et al*. (1985)
Pterodroma atrata	Pitcairn Is (1990)	379	25.86	-0.015	de L. Brooke (1995)
Pterodroma axillaris	Chatham Is, New Zealand (1997)	328	26.44	-0.013	Gardner (1999)
Pterodroma hypoleuca	Midway Atoll, Hawaii (1981)	239	24.75	-0.022	Pettit *et al*. (1982)
Pterodroma incerta	Gough Is (2001)	762	5.89	-0.118	Cuthbert (2004)
Pterodroma lessoni	Kerguelen Is (1987)	108	16.13	-0.023	Zotier (1990b)
Pterodroma leucoptera	New South Wales, Australia (2001)	279	17.07	-0.038	O'Dwyer *et al*. (2006)
Pterodroma macroptera	Prince Edward Is (1980)	444	20.41	-0.022	Schramm (1983)
	Prince Edward Is (1982)	621	12.84	-0.037	Newton and Fugler (1989)
Pterodroma mollis	Crozet Is (1982)	295	18.60	-0.038	Jouventin *et al*. (1985)
	Prince Edward Is (1980)	341	22.44	-0.024	Schramm (1983)
Pterodroma nigripennis	Lord Howe Is, Australia (1990)	237	21.31	-0.024	Hutton and Priddel (2002)
Pterodroma phaeopygia	Galápagos (1986)	536	18.03	-0.032	Cruz and Cruz (1990)
	Galápagos (1966)	423	22.04	-0.034	Harris (1970b)
	Hawaii (1981)	540	19.84	-0.018	Simons (1985)
Pterodroma pycrofti	New Zealand (2001)	227	50.45	-0.025	Gangloff and Wilson (2004)
Puffinus assimilis	Lord Howe Is, Australia (1989)	222	28.83	-0.014	Priddel et al. (2003)
	New Zealand (1994)	278	24.13	-0.016	Booth et al. (2000)
Puffinus gravis	Gough Is (2001)	1157	21.12	-0.020	Cuthbert (2005)
Puffinus griseus	New Zealand (1944)	1147	11.50	-0.035	Richdale (1945)
Puffinus huttoni	New Zealand (1999)	507	23.17	-0.023	Cuthbert and Davis (2002)
Puffinus opisthomelas	Natividad Is, Mexico (1998)	395	25.96	-0.019	Keitt et al. (2003)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Puffinus pacificus	Kilauea Point, Hawaii (1978)	489	14.00	-0.039	Pettit et al. (1984b)
	Kilauea Point, Hawaii (1979)	479	21.89	-0.025	Pettit et al. (1984b)
	Kilauea Point, Hawaii (1980)	456	18.10	-0.031	Pettit et al. (1984b)
	Manana Is, Hawaii (1978)	427	19.19	-0.029	Pettit et al. (1984b)
	Manana Is, Hawaii (1979)	441	18.88	-0.030	Pettit et al. (1984b)
	Manana Is, Hawaii (1984)	476	14.50	-0.044	Fry et al. (1986)
	Tern Is, Hawaii (1979)	503	15.86	-0.033	Pettit et al. (1984b)
Puffinus puffinus	Faeroe Is (1981)	427	28.02	-0.015	Bech et al. (1982)
	Wales, UK (1995)	559	23.71	-0.016	Hamer and Hill (1997)
	Wales, UK (1996)	525	22.96	-0.018	Hamer et al. (1998)
	Wales, UK (1999)	680	20.55	-0.010	Gray et al. (2005)
Puffinus tenuirostris	Great Dog Is, Australia (1995)	930	12.85	-0.032	Hamer et al. (1997)
Thalassoica antarctica	Dronning Maud Land, Antarctica (1984)	640	23.89	-0.022	Røv (1990)
	Dronning Maud Land, Antarctica (1985)	1058	15.57	-0.027	Haftorn et al. (1991)
	Dronning Maud Land, Antarctica (1992)	852	22.14	-0.023	Lorentsen (1996)
	Prydz Bay, Antarctica (1989)	1057	30.53	-0.017	Norman and Ward (1992)
Spheniscidae					
Aptenodytes patagonicus	Crozet Is (2000)	5797	12.22	-0.024	de Margerie et al. (2004)
	Heard and McDonald Is (1992)	11010	9.38	-0.007	Moore *et al*. (1998)
	Prince Edward Is (1989)	10033	7.56	-0.037	van Heezik *et al*. (1993)
Eudyptes chrysocome	Macquarie Is (1956)	2786	17.35	-0.010	Warham (1963)
	Macquarie Is (1994)	2763	14.87	-0.004	Hull *et al*. (2004)
	Macquarie Is (1995)	2551	11.67	-0.013	Hull *et al*. (2004)
	Macquarie Is (1996)	2808	14.96	-0.010	Hull *et al*. (2004)
	Prince Edward Is (1985)	1902	20.26	-0.015	Brown (1987)
Eudyptes chrysolophus	Prince Edward Is (1985)	2609	15.57	-0.035	Brown (1987)
	S Georgia (1986)	4739	14.56	-0.017	Williams (1990)
	S Georgia (1998)	4369	11.89	-0.030	Barlow and Croxall (2002)
	S Georgia (1999)	3502	18.00	-0.015	Barlow and Croxall (2002)
	S Georgia (2000)	4302	14.00	-0.026	Barlow and Croxall (2002)
Eudyptula minor	Penguin Is, Australia (1989)	1018	25.46	-0.016	Wienecke *et al*. (2000)
	Penguin Is, Australia (1990)	1190	23.54	-0.017	Wienecke *et al*. (2000)
	Penguin Is, Australia (1991)	1242	21.77	-0.016	Wienecke *et al*. (2000)
Megadyptes antipodes	New Zealand (1937)	6026	13.37	-0.004	van Heezik (1991)
	New Zealand (1938)	7563	9.74	-0.020	van Heezik (1991)
	New Zealand (1940)	5640	13.10	-0.012	van Heezik (1991)
	New Zealand (1984)	6543	14.11	-0.003	van Heezik (1990)
	New Zealand (1985)	6078	13.76	-0.013	van Heezik (1990)
	New Zealand (1986)	4184	17.69	-0.010	van Heezik (1990)

Appendix 1. Continued

Species	Area (Year)	W_∞	K	t_o	Source
Pygoscelis adeliae	Humble Is, Antarctica (1989)	4134	17.47	-0.016	Salihoglu *et al*. (2001)
	Humble Is, Antarctica (1990)	5749	8.67	-0.072	Salihoglu *et al*. (2001)
	Lützow-Holm Bay, Antarctica (1989)	5107	16.52	-0.032	Watanuki *et al*. (1992)
	Lützow-Holm Bay, Antarctica (1990)	3983	20.84	-0.021	Watanuki *et al*. (1992)
	Lützow-Holm Bay, Antarctica (1991)	2567	32.00	-0.020	Watanuki *et al*. (1992)
	Ross Is, Antarctica (1970)	3420	22.97	-0.015	Ainley and Schlatter (1972)
	Torgersen Is, Antarctica (1989)	3651	16.77	-0.042	Salihoglu *et al*. (2001)
	Torgersen Is, Antarctica (1990)	5190	9.57	-0.064	Salihoglu *et al*. (2001)
Pygoscelis antarctica	S Shetland Is (1980)	3914	22.55	-0.012	Taylor (1985)
	S Shetland Is (1990)	4058	22.33	-0.020	Croll *et al*. (2006)
	S Shetland Is (1991)	4643	17.05	-0.014	Croll *et al*. (2006)
	S Shetland Is (1992)	4621	19.06	-0.015	Croll *et al*. (2006)
	S Shetland Is (1993)	3170	21.54	-0.013	Moreno *et al*. (1994)
Pygoscelis papua	S Shetland Is (1980)	6739	13.55	-0.012	Taylor (1985)
Spheniscus demersus	S Africa (1974)	1930	14.62	-0.026	Cooper (1977)
Spheniscus magellanicus	Argentina (1991)	3840	12.63	-0.018	Frere *et al*. (1998)
	Argentina (1992)	5030	9.53	-0.028	Frere *et al*. (1998)
	S Chile (1997)	3667	18.18	-0.008	Radl and Culik (1999)
Stercorariidae					
Catharacta antarctica	S Georgia (2001)	2199	16.89	-0.013	Phillips *et al*. (2004)
	S Georgia (2002)	1808	20.53	-0.012	Phillips *et al*. (2004)
	S Georgia (2003)	1938	20.55	-0.011	Phillips *et al*. (2004)
Catharacta maccormicki	Prydz Bay, Antarctica (1990)	1726	14.86	-0.030	Wang and Norman (1993)
	S Shetland Is (2001)	1347	23.05	-0.012	Ritz *et al*. (2005)
Stercorarius longicaudus	E Greenland (1975)	306	31.88	-0.015	de Korte (1986)
Sulidae					
Morus bassanus	Baccalieu Is, Newfoundland (1979)	4123	17.54	-0.006	Montevecchi *et al*. (1984)
	Magdalen Is, Québec (1979)	4477	15.48	-0.011	Kirkham and Montevecchi (1982)
	Québec (1965)	4708	15.15	-0.011	Poulin (1968)
	Scotland, UK (1962)	4746	15.39	-0.008	Nelson (1964)
	Scotland, UK (1976)	4732	15.33	-0.008	Wanless (1984)
Morus capensis	S Africa (1967)	3390	15.81	-0.009	Jarvis (1974)
	S Africa (1974)	3671	14.81	-0.007	Cooper (1978)
	S Africa (1988)	3461	15.41	-0.009	Navarro (1991)
Morus serrator	Victoria, Australia (1995)	3668	15.82	-0.006	Gibbs *et al*. (2000)
	Victoria, Australia (1999)	3457	16.58	-0.007	Bunce (2001)
Sula dactylatra	Ascension Is (1960)	1952	17.60	-0.009	Dorward (1962)
	Kure Atoll, Hawaii (1965)	2107	18.25	-0.001	Kepler (1969)
	Lord Howe Is, Australia (2002)	2260	17.74	-0.011	Priddel *et al*. (2005)
Sula nebouxii	Galápagos (1964)	1939	14.74	-0.005	Duffy and Ricklefs (1981)
	Lobos de Tierra Is, Peru (1979)	1669	19.54	-0.020	Duffy and Ricklefs (1981)
Sula sula	Galápagos (1963)	956	9.63	-0.014	Nelson (1969)