The diving behaviour of Pigeon Guillemots (*Cepphus columba*) off southern Vancouver Island

JAMES S. CLOWATER

2080 Chaucer Street, Victoria, B.C. V8R 1H7, Canada
and
Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

AND

ALAN E. BURGER

Biology Department, University of Victoria, Victoria, BC V8W 2Y2, Canada

CLOWATER, J.S., and BURGER, A.E. 1994. The diving behaviour of Pigeon Guillemots (*Cepphus columba*) off southern Vancouver Island. Can. J. Zool. **72**: 863–872.

The foraging behaviour of Pigeon Guillemots (*Cepphus columba*) was observed off southern Vancouver Island, British Columbia. Diving bouts comprised 1–24 dives. Birds returned to the surface with prey in 22 of 248 (9%) dives, and mean handling time for prey was 34.7 s. Dives averaged 87 s (ranging from 37 s in water 14 m deep to 144 s at 34 m) and the mean postdive pause lasted 98 s (range 24–232 s). Birds foraged in water depths from 6 to 45 m. The duration of both dives and pauses increased with water depth. Our model of Pigeon Guillemot diving behaviour predicts foraging time at the bottom to be maximized during dives to depths of 22–24 m, while foraging efficiency, (foraging time)/(dive + recovery time), is maximized at 10 m. Calculated work to resist buoyancy and drag during descent and foraging phases of the dive cycle suggest that energetic savings from reduced buoyancy at depth may not explain how birds increase dive duration with increasing depth. Pigeon Guillemots appear to maximize time spent in the foraging patch. In 82% of transects, the most frequently chosen foraging depth was 15–20 m (mode). Model predictions were supported by observations that 43.6% of Pigeon Guillemots preferred water depths of 15–20 m, while 19% preferred water depths of 10–15 m.

CLOWATER, J.S., et BURGER, A.E. 1994. The diving behaviour of Pigeon Guillemots (*Cepphus columba*) off southern Vancouver Island. Can. J. Zool. **72** : 863–872.

Le comportement de quête de nourriture du Guillemot colombin (*Cepphus columba*) a fait l'objet d'une étude au large de la côte sud de l'Île de Vancouver, Colombie-Britannique. Les cycles de plongée comptaient de 1 à 24 plongées. Les oiseaux sont revenus en surface avec des proies après 22 (9%) des 248 plongées observées et la durée de manipulation des proies était de 34,7 s en moyenne. Les plongées duraient en moyenne 87 s (étendue de 37 s à 14 m de profondeur à 144 s à 34 m de profondeur) et l'intervalle moyen entre les plongées était de 98 s (étendue de 24 à 232 s). Les oiseaux cherchaient leur nourriture entre 6 et 45 m de profondeur. La durée des plongées et des intervalles augmentait en fonction de la profondeur des plongées. Notre modèle du comportement de plongée du Guillemot colombin permet de prévoir que la durée des plongées au fond est maximisée au cours des plongées à 22–24 m de profondeur, alors que l'efficacité de la quête de nourriture, (durée de la quête)/(durée de la plongée + durée de l'intervalle avant la plongée suivante), est maximisée à une profondeur de 10 m. Le calcul du travail nécessaire pour résister à la flottaison et à la traînée durant les phases de descente en profondeur et de quête de nourriture au cours d'une plongée indique que les économies énergétiques reliées à une flottaison réduite en profondeur n'expliquent pas nécessairement comment les oiseaux augmentent la durée de leurs plongées aux profondeurs plus grandes. Les Guillemots colombins semblent maximiser le temps qu'ils passent dans une zone d'alimentation. Dans 82% des transects examinés, la profondeur choisie le plus fréquemment par les oiseaux était de 15–20 m (mode). Les prédictions du modèle ont pu être appuyées par des observations : 43,6% des guillemots préféraient les profondeurs situées entre 15 et 20 m et 19% préféraient les profondeurs situées entre 10 et 15 m.

[Traduit par la Rédaction]

Introduction

Foraging models that incorporate the physiological constraints of breath-hold diving have created new insights into ecological aspects of underwater foraging by diving animals (Kramer 1988; Ydenberg 1988; Ydenberg and Clark 1989; Burger 1991; Houston and Carbone 1992; Ydenberg et al. 1994). Although birds can utilize anaerobic metabolism to prolong underwater time (Kooyman et al. 1992; Croll et al. 1992), most foraging dives are conducted within aerobic limits (Butler and Woakes 1982; Butler and Stephenson 1987). For diving birds, both the time at the surface between dives and the time in the foraging patch offer rates of resource gain that diminish with time (Kramer 1988; Houston and Carbone 1992). Models developed to predict optimal diving behaviour under these constraints have used both efficiency maximization and rate maximization currencies (Ydenberg et al.

1994; Houston and Carbone 1992). If we assume net energetic gain as the optimal strategy for foraging birds, then energetic efficiency (EE) can be defined as

$$EE = \frac{\text{energy gained}}{\text{energy expended}}$$

If we assume that birds will maximize the net rate of energetic gain (R), then optimal behaviour will maximize the currency

$$R = \frac{\text{energy gained} - \text{energy expended}}{\text{time}}$$

A special case of rate-maximizing currency used by Kramer (1988) is the proportion of time spent in the foraging area that is equivalent to maximizing the gross rate of energetic gain (Houston and Carbone 1992). In this discussion of diving birds we will refer to this currency as foraging efficiency (FE), since it measures gain acquired at the foraging site (foraging
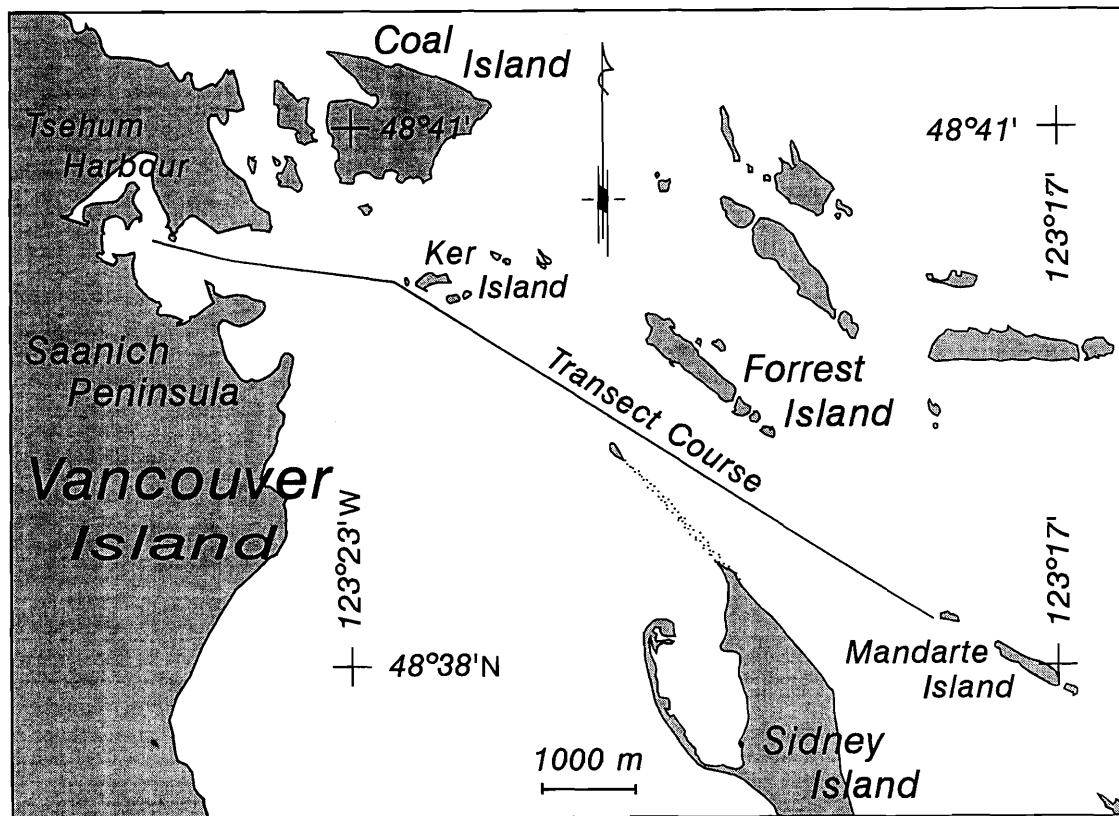
FIG. 1. Location of the transect course off southern Vancouver Island, British Columbia.

time) with respect to the costs of underwater travel time and surface recovery time:

$$FE = \frac{\text{foraging time}}{\text{travel time} + \text{foraging time} + \text{recovery time}}$$

The duration of dives in bottom-feeding birds is often a function of water depth (Dewar 1924; Wilson and Wilson 1988). The duration of postdive recovery periods (pauses) is in turn largely a function of dive duration (Wilson and Wilson 1988; Ydenberg 1988). There is thus a dynamic interaction between water depth, dive times, pause times, and the bird's physiological limitations, which ultimately determines optimal foraging behaviour.

We investigated these interactions in a study of diving of Pigeon Guillemots (*Cepphus columba*) off southern Vancouver Island, British Columbia. This bird has a widespread distribution in inshore waters of the North Pacific and is largely a bottom feeder. Although its diet varies somewhat with geographical location, epibenthic fish species are the primary prey items (Drent 1965; Scott 1973; Follett and Ainley 1976; Kuletz 1983; Ainley et al. 1990). In studies conducted on Mandarte Island, within our study area, it was found that blennies (Stichaeidae) and sculpins (Cottidae) made up 75% of prey items returned to guillemot chicks (Drent 1965; Koelink 1972). A few studies have reported diving behaviour, but sample sizes were generally small (Cody 1973; Thoreson 1989). Diving behaviour in the closely related Black Guillemot (*Cepphus cepphus*) was reported by Cairns (1987, 1992).

We measured the durations of dives and postdive pauses made at a variety of water depths at sea and used these data in a model of foraging behaviour to predict the optimal depth

at which Pigeon Guillemots should forage. We compared the model predictions with the distribution of Pigeon Guillemots determined during a series of boat transects on inshore waters of various depths.

Methods

Observations of diving were made between 7 September 1991 and 17 May 1992 in the sea adjacent to Victoria and Sidney, British Columbia, from a 5.5-m kayak or a 6.5-m sailboat. Binoculars were used to view the birds and the timing and duration of dive events were recorded on a cassette recorder. Water depths were measured to the nearest 1 m with a Scubapro Personal Dive Sonar or a Humminbird LCR 4004D Depth Sonar.

Dives resulting in prey capture were removed from the data set prior to the analysis of pause values because the pauses were prolonged as the bird manipulated prey. Mean values for dive duration, pause duration, and water depth were calculated from a series of dives by each bird. Birds that performed less than three dives were excluded from the data set.

The distribution of foraging Pigeon Guillemots with respect to available water depths was recorded during transects conducted between 15 May 1992 and 17 May 1993. The transects began at a navigational marker in Tsehum Harbour, near Sidney, Vancouver Island, and continued 9.5 km to Mandarte Island (Fig. 1). Observations were made from a 6.5-m boat travelling at constant speed (10 km·h^{-1}) along the transect. Water depths were recorded at 2-min intervals and whenever Pigeon Guillemots were sighted. Birds within 150 m on each side of the transect were included; water depths recorded under the boat were assumed to approximate the depth at the birds' positions. Transects containing fewer than 20 observations of Pigeon Guillemots were excluded from the analysis. The Kolmogorov–Smirnov goodness-of-fit test for grouped data (Zar 1984) was applied to determine if the distribution of birds with respect to water depth was significantly different from a random distribution over available water depths.

TABLE 1. Summary of Pigeon Guillemot diving behaviour measured in 21 bouts of diving

	Mean	SE	N	n	Range
Dive duration (s)	87	6.13	21	168	37–133
Pause duration (s)	98	10.82	21	168	24–233
Dive:pause ratio	1.04	0.10	21	168	0.49–2.01
Depth (m)	20	2.45	19	153	6–45

NOTE: Only birds performing more than two dives in a bout have been included. N is the number of bouts; n is the number of dives.
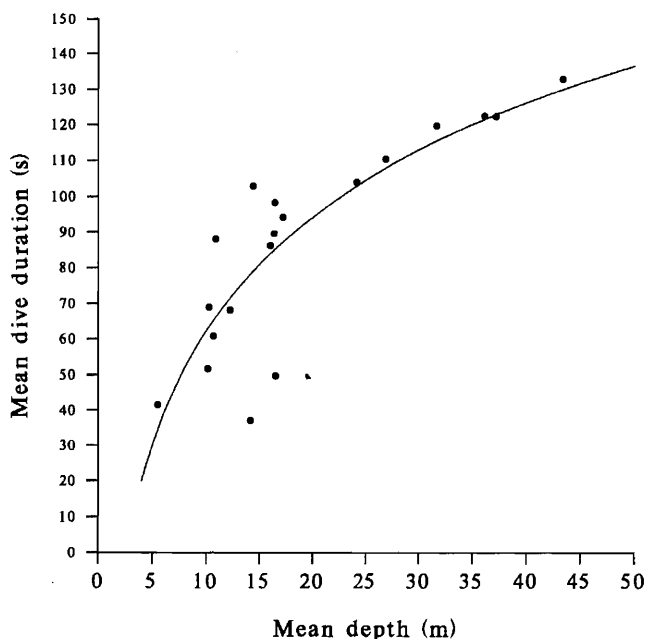

FIG. 2. Dive duration of Pigeon Guillemots off southern Vancouver Island increased logarithmically with water depth ($r^2 = 0.71, p < 0.001$).

Results

In 21 bouts of diving, the mean number of dives per bout was 8 (range 3–36 dives), mean dive and pause durations were 87 and 98 s, respectively, and mean dive:pause ratio was 1.04 (Table 1). Twelve dive bouts that were observed from start to finish averaged 23.1 min in duration (range 0.6–58.1 min). A significant positive relationship was found between dive duration, T_d (in seconds), and water depth, d (in metres), which was best described by a logarithmic equation:

[1] $T_d = 46.11 \ln d - 43.833$

$$(r^2 = 0.712, p < 0.001; \text{Fig. 2})$$

Similarly, we found a positive relationship between pause duration, T_r (in seconds), and the duration of the preceding dive, T_d, which best fitted a power function:

[2] $T_r = 0.422 T_d^{1.217}$ $(r^2 = 0.520, p < 0.001; \text{Fig. 3})$

Pause duration also varied significantly with water depth as follows:

[3] $T_r = 18.625 d^{0.579}$ $(r^2 = 0.440, p < 0.001; \text{Fig. 4})$

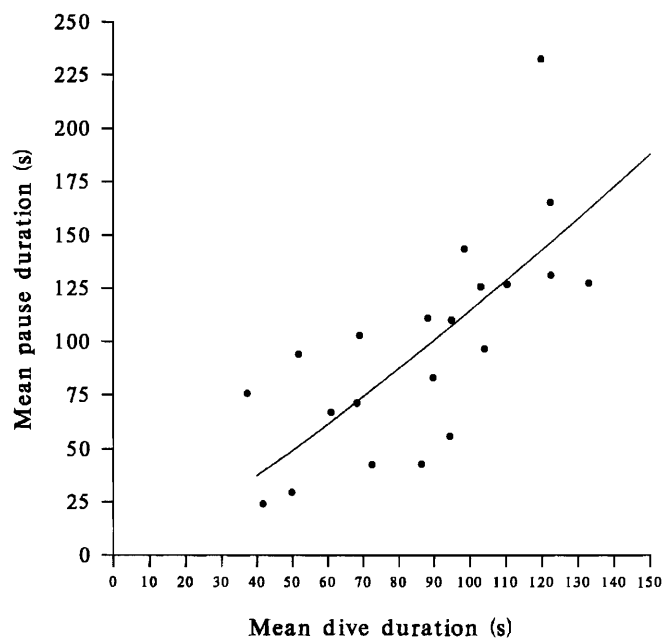
FIG. 3. Pause duration of Pigeon Guillemots off southern Vancouver Island increased as a power function of dive duration ($r^2 = 0.52$, $p < 0.001$).
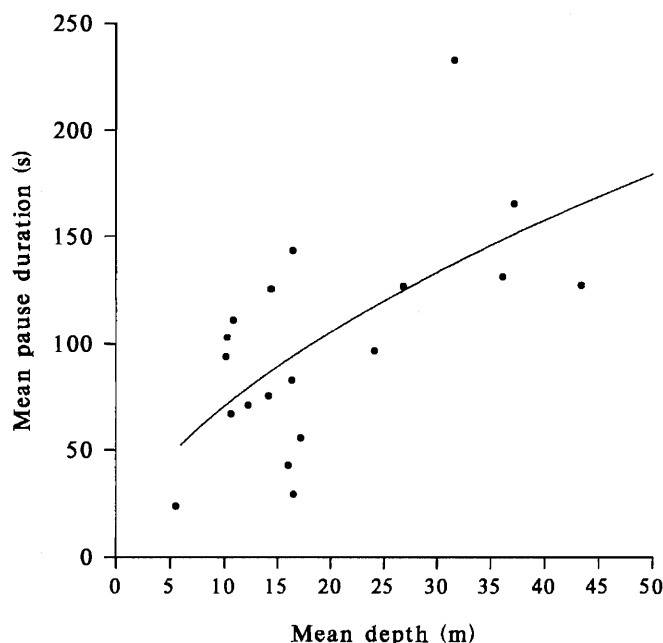

FIG. 4. Pause duration of Pigeon Guillemots off southern Vancouver Island increased as a power function of water depth ($r^2 = 0.44$, $p < 0.001$).

Birds returned to the surface with prey in 22 (9%) of the 248 dives observed, and shrimp, blennies (pricklebacks), and sculpins were the most common prey identified (Table 2). Prey were captured in water 10–45 m deep, and mean handling time of prey was 33 s (Table 2). An estimate of vertical velocity was obtained from successful dives. By assuming that the guillemot caught prey immediately on reaching the bottom and then ascended directly to the surface, the vertical velocity could be approximated by $2d/T_d$. In most

TABLE 2. Summary of successful dives by Pigeon Guillemots observed in the waters off southern Vancouver Island

Bird No.	Dive duration (s)	Pause duration (s)	Depth (m)	Handling time (s)	Prey	Comments
39	64	57		28		
39	81	120		51 (37)	Shrimp	Drop and recapture
39	61	230		19		
39	69	92				
39	51	143		44	Shrimp	
39	62	258		40 (11)		Drop and recapture
39	87	68				
57	69	393	12	470 (47)	Flounder	Drop and recapture twice
79	119		45		Blenny	
81	62		23	72	Sculpin	
82	141		34	21	Blenny	
84	129		37			
85		123	35			
87	103	567	36	19		
87	88	518	36	41	Blenny	
87	127		36	23		
88	124	132	36	40	Blenny	
88	88	644	36			
93	90	392	29	37		
99	93		43			
103	111		24		Blenny	
113	61	101	10	41 (23)	Blenny	Drop and recapture

NOTE: Values in parentheses show handling time from surfacing after recapture to swallowing prey.

cases, the guillemot would spend more time at the bottom searching for prey, and our estimate of travel time would be low, leading to an underestimate of vertical velocity. In the 14 successful dives where the depth and dive times were known, the highest estimate of vertical velocity was 0.95 m · s^{-1}. Since it is unlikely that a guillemot would capture prey without time spent for search, capture, and handling, this approximation of vertical velocity is likely underestimated.

Modelling foraging behaviour

We employed a simple model of foraging behaviour (Ydenberg and Clark 1989; Burger 1991) to examine the effects of diving to various depths. We assumed that Pigeon Guillemots will attempt to maximize total daily energetic gain (Houston 1987; Ydenberg et al. 1994).

We set the rate of vertical descent and ascent at 1 m · s^{-1}, based on our estimates from successful dives and estimates made of alcids of similar size: Cairns (1992) used a vertical velocity of 1 m · s^{-1} for Black Guillemots based on estimates in Burger (1991); Croll et al. (1992) used a depth gauge and found mean rates of ascent and descent in Thick-billed Murres (Uria lomvia) to be 0.86 and 0.94 m · s^{-1}, respectively; Burger et al. (1993) estimated vertical velocity in Rhinoceros Auklets (Cerorhinca monocerata) to be 0.9 m · s^{-1}.

The dive cycle consists of dive time (T_d) and recovery time at the surface (T_r), with T_d further divided into vertical travel time (T_t) (down and up) and foraging time (T_f). We modelled dive duration (T_d) and pause duration (T_r) as a function of water depth from eqs. 1 and 3. To obtain estimates of foraging time (T_f) and foraging efficiency, T_t was first approximated assuming a vertical velocity of 1 m · s^{-1}:

$$[4] \quad T_t = \frac{2(\text{depth})}{1 \text{ m} \cdot \text{s}^{-1}}$$

Foraging time was then calculated as

$$[5] \quad T_f = T_d - T_t$$

Foraging efficiency (FE) is the proportion of each dive cycle that could be spent foraging at the bottom. Therefore

$$[6] \quad \text{FE} = \frac{T_f}{(T_f + T_t + T_r)}$$

This model suggests that if vertical velocity is 1 m · s^{-1}, foraging time is maximized at 22–24 m (Table 3, Fig. 5). Foraging efficiency is maximized at 10 m (Fig. 6). To evaluate the sensitivity of our model to variations in velocity estimates, we ran the model over a range of feasible velocities (Fig. 6).

Observed distribution of Pigeon Guillemots

Eleven of 15 transects (73%) that returned significant results showed that Pigeon Guillemots were not distributed randomly with respect to water depths (Table 4, Fig. 7). The most frequently used depth intervals (mode) were 15–20 m in 9 (82%) transects and 10–15 m in 2 (18%) transects. Figure 7 summarizes water depths preferred by Pigeon Guillemots over the period May 1992 to May 1993. The mean percentage of birds observed in the depth ranges 10–15 m and 15–20 m for all transects was 19.0 and 43.6%, respectively. Only 4% of birds were observed in water 0–10 m deep and 33.4% of birds in all depth categories greater than 20 m.

Estimate of work required to resist buoyancy and drag

To estimate the work performed by diving Pigeon Guillemots we calculated the work done against buoyancy

TABLE 3. Dive parameters estimated by a model based on dive-depth and pause-depth regressions

Depth (m)	Dive duration,[a] T_d (s)	Pause duration,[b] T_r (s)	Foraging time,[c] T_f (s)	Foraging efficiency[d] (%)
4	20.1	41.6	12.1	19.6
6	38.8	52.6	26.8	29.3
8	52.1	62.1	36.1	31.6
10	62.3	70.6	42.3	31.8
12	70.7	78.5	46.7	31.3
14	77.9	85.8	49.9	30.5
16	84.0	92.7	52.0	29.4
18	89.4	99.3	53.4	28.3
20	94.3	105.5	54.3	27.2
22	98.7	111.5	54.7	26.0
24	102.7	117.3	54.7	24.9
26	106.4	122.8	54.4	23.7
28	109.8	128.2	53.8	22.6
30	113.0	133.5	53.0	21.5
32	116.0	138.5	52.0	20.4
34	118.8	143.5	50.8	19.4
36	121.4	148.3	49.4	18.3
38	123.9	153.0	47.9	17.3
40	126.3	157.6	46.3	16.3
42	128.5	162.2	44.5	15.3
44	130.7	166.6	42.7	14.4
46	132.7	170.9	40.7	13.4
48	134.7	175.2	38.7	12.5
50	136.6	179.4	36.6	11.6

[a]Predicted as a function of depth from eq. 1 (Fig. 2).
[b]Predicted as a function of depth from eq. 3 (Fig. 4).
[c]Calculated as $T_d - 2$(depth/velocity).
[d]Calculated as $(T_f/(T_d + T_r)) \times 100$.

and drag during the descent phase and against buoyancy during the foraging phase of the dive cycle. The ascent phase of the dive was considered passive and so was not included in the calculations. Total work performed was calculated for dives ranging in depth from 2 to 50 m. We assumed a body mass of 500 g and a vertical swimming velocity of 1 m · s⁻¹. Foraging times were calculated using eq. 5 (Table 3). The body density of Pigeon Guillemots was approximated using the value given for Common Murres (*Uria aalge*) by Wilson et al. (1992). Upward buoyant force (F_{up}) was calculated using the equation and estimates provided by Wilson et al. (1992):

$$[7] \quad F_{up} = pg\left(\frac{P_s(V_{Ls} + V_{Fs})}{P_s + pgd} + V_T\right) - gm$$

where p = density of fluid, taken to be 1.0×10^3 kg · m⁻³
  g = gravitational acceleration (9.807 m · s⁻²)
  P_s = atmospheric pressure, taken to be 1.0×10^5 Pa
  V_{Ls} = lung and air sac volume (m³ · kg⁻¹);
    $V_{Ls} = 1.61 \times 10^{-4}$ m⁰·⁹¹
  V_{Fs} = volume of air in feathers (m³ · kg⁻¹);
    $V_{Fs} = 0.44 (8.11 \times 10^{-2}$ m⁰·⁶⁶⁷ BFT) $- 1.38 \times 10^{-4}$,
    where BFT = 0.018 (for *Uria aalge*)
  m = mass (0.500 kg)
  d = depth (m)
  V_T = volume of body tissues (m³ · kg⁻¹);

$$V_T = \frac{m}{\text{density}} = \frac{0.500 \text{ kg}}{1.00 \times 10^3 \text{ kg} \cdot \text{m}^{-3}}$$
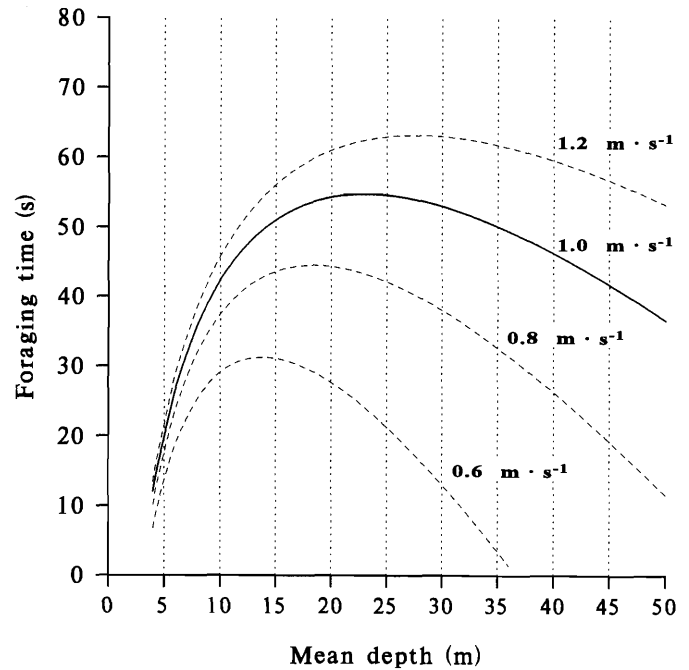
FIG. 5. Model predictions of foraging time ($T_f = T_d - T_t$) vary with depth. An increase in the estimate of swimming speed (0.6, 0.8, 1.0, 1.2 m · s⁻¹) causes an increase in the depth at which foraging time is maximized.
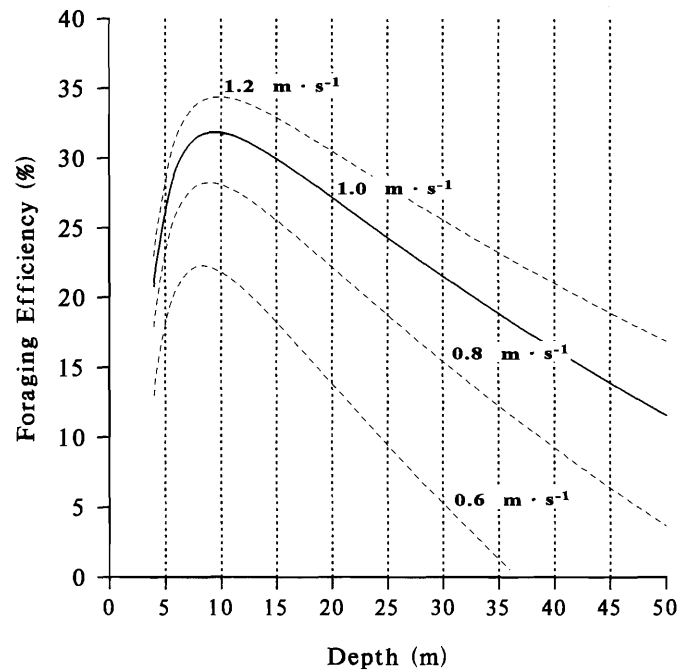
FIG. 6. Our model predicts that foraging efficiency (FE = $T_f/(T_f + T_t + T_r)$) varies with water depth. Although variations in swimming speed (0.6, 0.8, 1.0, 1.2 m · s⁻¹) change the magnitude of the foraging efficiency estimate, they cause little change in the depth at which efficiency is maximized.

Work is performed during the dive to overcome buoyancy during descent and foraging, and against drag during descent. Because the buoyant force on a diving bird is a nonlinear function of depth (Wilson et al. 1992), we approximate work

TABLE 4. Summary of transects conducted to determine the distribution of Pigeon Guillemots with respect to water depth, showing significant differences between the depths used by birds and those available in the transects, tested with the Kolmogorov–Smirnov (KS) test (Zar 1984)

Transect	No. of birds	Results from KS tests			Mean depth (m)	Most frequent depth category (mode)
		K	D_{max}	p		
15 May 1992	34	11	3.8	ns	24.2	15–20
3 June 1992	62	11	25.0	<0.001	16.3	15–20
15 June 1992	32	10	13.8	<0.001	19.5	15–20
1 July 1992	50	10	15.0	<0.001	21.9	15–20
7 July 1992	25	11	5.5	ns	22.2	15–20
15 July 1992	27	11	8.6	<0.050	29.4	15–20
28 July 1992	29	10	12.6	<0.001	22.3	15–20
9 Aug. 1992	31	11	12.5	<0.001	19.6	15–20
13 Aug. 1992	40	10	14.0	<0.001	20.1	10–15
11 Oct. 1992	50	11	7.2	ns	23.2	15–20
11 Nov. 1992	111	11	37.5	<0.001	18.2	15–20
12 Dec. 1992	88	11	26.4	<0.001	22.0	15–20
08 Feb. 1993	57	10	7.6	ns	28.0	30–35
13 March 1993	102	10	22.8	<0.001	21.5	10–15
18 April 1993	28	12	9.6	<0.010	22.2	15–20

NOTE: ns, not significant.

FIG. 7. Mean number of Pigeon Guillemots (percentage of total) observed for each water depth category in transects conducted from May 1992 to May 1993. Solid bars show the mean percentage of birds sighted in each depth category and open bars the mean percentage of depths available during the transect. Values are monthly means from 15 transects ($N = 724$ bird sightings).

required to overcome buoyancy during descent (W_d) as the summation of the mean work calculated for each 2-m interval.

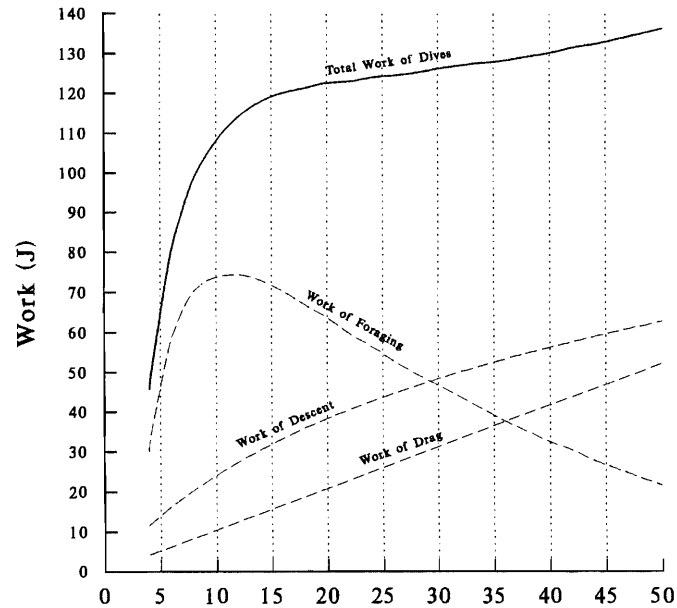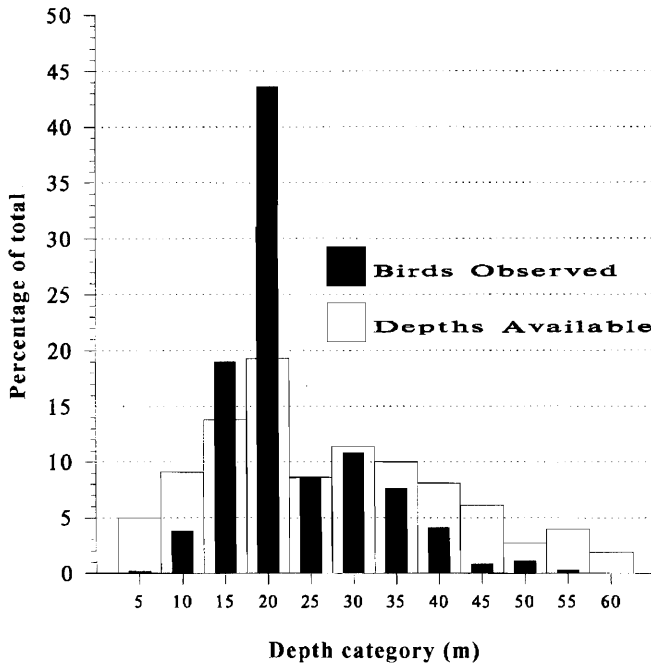$$[8] \qquad W_d = \sum_{x=2}^{50} 2F_{x-1}$$

FIG. 8. Approximations of work required to resist buoyancy during descent, to resist drag during descent, and to resist buoyancy during foraging. Total work = work of foraging + work of descent + work of drag.

where work = force × displacement
F_{x-1} = buoyant force at depth $x - 1$
x = 2, 4, . . . 50.

Subsurface drag was estimated using the equation provided by Stephenson et al. (1989) for Lesser Scaup (*Aythya affinis*):

$$[9] \qquad drag = -0.144 + 0.562V + 0.622V^2$$

where V is velocity.

Work to counter drag during the descent was approximated using the equation

$$[10] \qquad \text{work} = \text{drag} \times \text{depth}$$

Work to resist buoyancy while foraging at the bottom was approximated by multiplying the calculated work output during the descent by the ratio of the bottom time and the descent time (Stephenson et al. 1989, Lovvorn et al. 1991).

$$[11] \qquad \text{total work} = \text{work of descent} \times \frac{\text{bottom time}}{\text{descent time}}$$

$$= (\text{depth} \times F_{up}) \times \frac{\text{foraging time}}{\text{depth} \div \text{velocity}}$$

Our approximations of work required to overcome buoyancy are based on observed dive durations by Pigeon Guillemots in waters of 6–45 m depth. Because of this, Fig. 8 represents an approximation of the typical work output of foraging Pigeon Guillemots at increasing depths. Although the work of foraging reaches a maximum at 12 m depth, the total work of diving continues to increase with depth (Table 5).

Discussion

Compared with other alcids, Pigeon Guillemots are capable of relatively long dive durations. Mean durations of dives for Pigeon Guillemots range from 36 to 87 s, while mean durations of dives are 41–81 s for Common Murres, 55 s for Thick-billed Murres, 37–58 s for Tufted Puffins, 34–45 s for Rhinoceros Auklets, and 28–44 s for Marble Murrelets (Tables 6, 7). Although Thick-billed Murres and Common Murres are the largest alcids ($\approx$1000 g) and perform the longest and deepest dives (Croll et al. 1992; Burger 1991; Wanless et al. 1988; Piatt and Nettleship 1985), Pigeon Guillemots ($\approx$500 g) often have longer mean dives than both these murres. Longer dives performed by Pigeon Guillemots are likely the result of a foraging strategy adapted to the pursuit of solitary epibenthic prey. Birds that feed primarily on nonschooling epibenthic prey may perform relatively long dives and spend more time recovering between dives (Ainley et al. 1990; Ydenberg and Guillemette 1991). Common and Thick-billed murres, on the other hand, when feeding on pelagic schooling fish, may refrain from excessively long dives so that they can keep surface recovery periods relatively short. Although Croll et al. (1992) found that Thick-billed Murres were capable of making very long and deep dives (224 s, 210 m), mean dive duration and depth were only 55 s and 18 m. Croll et al. (1992) pointed out that Thick-billed Murres appeared to balance the benefit of a longer time at the foraging site with the cost of increased surface recovery time, which could lead to a reduced prey encounter rate in the subsequent dive.

Our study, as well as others, showed that dive durations increased with depth (Dewar 1924; Stonehouse 1967; Batulis and Bongiorno 1972; Wilson and Wilson 1988; Cairns 1992; Croxall et al. 1991; Croll et al. 1992). Assuming that swimming speed remains constant, our model indicates that in shallow waters, Pigeon Guillemots increased their foraging time rapidly with depth (Fig. 5, Table 3). As central place foragers (Lessells and Stephens 1983; Houston and McNamara 1985), guillemots would likely increase bottom time (T_f) to

TABLE 5. Calculation of work required to resist buoyancy and drag during the descent and foraging phases of a dive cycle

Depth (m)	$F_{up}{}^a$ (N)	Work during descent[b] (J)	Work during drag[c] (J)	Work during foraging[d] (J)	Total work[e] (J)
4	2.48	11.63	4.16	30.01	45.80
6	2.18	16.26	6.24	58.42	80.92
8	1.94	20.36	8.32	70.03	98.71
10	1.74	24.03	10.40	73.60	108.03
12	1.59	27.35	12.48	74.25	114.08
14	1.46	30.39	14.56	72.85	117.80
16	1.35	33.18	16.64	70.20	120.02
18	1.25	35.77	18.72	66.75	121.24
20	1.17	38.19	20.80	63.53	122.52
22	1.09	40.44	22.88	59.62	122.94
24	1.03	42.56	24.96	56.34	123.86
26	0.97	44.57	27.04	52.77	124.38
28	0.92	46.46	29.12	49.50	125.08
30	0.88	48.26	31.20	46.64	126.10
32	0.84	49.97	33.28	43.68	126.93
34	0.80	51.60	35.36	40.64	127.60
36	0.76	53.16	37.44	37.54	128.14
38	0.73	54.65	39.52	34.97	129.14
40	0.70	56.08	41.60	32.41	130.09
42	0.68	57.46	43.68	30.26	131.40
44	0.65	58.78	45.76	27.76	132.30
46	0.63	60.06	47.84	25.64	133.54
48	0.61	61.29	49.92	23.61	134.82
50	0.59	62.48	52.00	21.59	136.07

[a]Force up resulting from buoyancy calculated from eq. 7.
[b]Calculated from eq. 8.
[c]Calculated from eqs. 9 and 10.
[d]Calculated from eq. 11.
[e]Work of descent + work of drag + work of foraging.

compensate for increases in foraging costs ($T_t + T_r$). Kramer (1988) presented the idea that increasing oxygen stores allow dive durations to increase with depth. A dynamic balance of optimal surface time and underwater foraging time (Kramer 1988) allows birds to dive in shallow water with an optimal but not maximum oxygen load. As depth increases, optimal surface time will increase, providing greater oxygen stores and allowing longer dive durations within aerobic limits.

In 82% of transects, the most frequently chosen foraging depth was 15–20 m (mode) (Table 4). Mean monthly data show that 43.6% of Pigeon Guillemots preferred water depths of 15–20 m, while 19.0% preferred water depths of 10–15 m (Fig. 7). If we accept depths that fall within 1 s of predicted maximum foraging time (20–28 m), these observations match our model predictions (Table 3, Fig. 5). Only 4% of Pigeon Guillemots in all transects were observed in waters 0–10 m deep. One might expect shallow water to provide maximum time at the foraging site, since vertical travel time would be very short. Birds may avoid shallow water primarily because of the increased cost of resisting buoyancy (Wilson et al. 1992). Variations in prey density and abundance must also be considered as possible factors in guillemots' avoidance of shallow water.

Although 51% of the transect length was over water greater than 20 m deep, only 33.4% of guillemots preferred these depths. Birds diving deeper than 20 m experience an increase in the cost of resisting buoyancy and drag during a longer descent (Fig. 8). Our model predicts that foraging efficiency

TABLE 6. Summary of dive parameters for Pigeon Guillemots from this study and published literature

Study site	Dive duration (s)		Mean pause duration (s)	Depth (m)	No. of dives	Source
	Mean	Max.				
Southern Vancouver Island, B.C.	87	144	98	10–45	246	This study
Prince William Sound, Alaska						
Benthic foraging	86		40		140	Kuletz 1983
Pelagic foraging	47		18		125	Kuletz 1983
Rosario Head, Washington	67	105	24		50	Thoresen 1989
Farallon Islands, California	75	110	34	20	156	Ainley et al. 1990
Yaquina Head, Oregon	36	69			259	Scott 1973
Olympic Peninsula, Washington	41				10	Cody 1973

TABLE 7. Summary of dive parameters for other alcid species

Study site	Dive (s)		Mean pause duration (s)	Depth (m)	No. of dives	Source
	Mean	Max.				
Black Guillemot						
Northeastern Hudson Bay	70.8		31.2	4–48		Cairns 1992
Common Murre						
Farallon Is., California	55	70		20	39	Ainley et al. 1990
Olympic Peninsula, Washington	41	71			82	Cody 1973
Yaquina Head, Washington	71	140			228	Scott 1973
Isle of May, Scotland	67	202			245	Wanless et al. 1988
Barkley Sound, B.C.	81	150			63	J.S. Clowater, unpublished data
Victoria, B.C.	46	64			123	J.S. Clowater, unpublished data
Thick-billed Murre						
Coats Is., N.W.T.	55	224		5–210	1052	Croll et al. 1992
Marbled Murrelet						
Barkley Sound, B.C.	28	87		10–30	119	Carter and Sealy 1990
Rosario Head, Washington	44	115			14	Thoresen 1989
Barkley Sound, B.C.	28	33			89	J.S. Clowater, unpublished data
Rhinoceros Auklet						
Farallon Is., California	37				46	Ainley et al. 1990
Vancouver Is.	45	53	10.8		75	Burger et al. 1993
Barkley Sound, B.C.	30	38			94	J.S. Clowater, unpublished data
Victoria, B.C.	34	48		34	130	J.S. Clowater, unpublished data
Tufted Puffin						
Farallon Is., California	58	80			16	Ainley et al. 1990
Olympic Peninsula, Washington	37	60			16	Cody 1973

will decrease in depths greater than 10 m and foraging time in depths greater than 25 m. We have also noted that while foraging efficiency varies little with assumed swimming velocity, foraging time is affected by changes in velocity (Figs. 5, 6). To some extent birds may mitigate the negative effect of increasing depth on foraging time by increasing foraging velocity in deeper waters (Wilson and Wilson 1988).

While the distribution and density of prey remain of prime importance in determining preferred foraging depths for Pigeon Guillemots, it has been pointed out in some studies that energetic costs of resisting buoyancy may also be an important factor (Stephenson et al. 1989; Burger 1991; Lovvorn et al. 1991; Lovvorn and Jones 1991; Wilson et al. 1992). We calculated the work performed by Pigeon

Guillemots in dives at depths from 4 to 50 m (Fig. 8). Since guillemots spend little foraging time at depths of less than 10 m (Fig. 5), the work output at these depths is also relatively low. The work output at depths over 15 m is greater than in shallow water and increases more slowly with depth. Birds appear to prefer to work in deep water (>15); this may be in response to greater benefits available at these depths. From Fig. 8 we can see that although work required to resist buoyancy during foraging is reduced at depths greater than 12 m, the increased work required to resist buoyancy and drag during the longer travel times results in a total work function that continues to increase with depth. Wilson et al. (1992) suggest that an increase in dive duration with depth may be attributed to energetic savings resulting from reduced buoyancy at depth.

Our model of diving behaviour suggests that energetic savings resulting from reduced buoyancy may not explain why dive durations increase with depth.

Model predictions of the foraging efficiency of Pigeon Guillemots indicate that efficiency is low in shallow water and increases rapidly to a maximum at 10 m depth (Fig. 6). Pigeon Guillemots seem to respond to increased foraging costs as predicted by optimal foraging theory by increasing dive duration with depth. As well as an increase in costs of travel time and recovery time with depth, our calculations suggest that the cost of resisting buoyancy may be considered an important factor in understanding choice of foraging depth by diving birds.

During the winter, the diving behaviour of Pigeon Guillemots is primarily directed at locating and capturing prey for their own consumption. Under the constraints imposed by physiological and environmental factors we would expect guillemots to develop foraging strategies that maximize long-term energy gain (Ydenberg et al. 1994). Our model provides two predictions of optimal foraging depth for diving Pigeon Guillemots. If bird behaviour followed predictions of foraging efficiency (eq. 6), then the chosen foraging depth would be approximately 10 m. If foraging behaviour maximized foraging time at the bottom, then the chosen depth would be approximately 22.5 m. Our transects show that water depths of 15–20 m were chosen most often by Pigeon Guillemots. These results suggest that guillemots are maximizing the time spent at the site of resource gain (foraging time). This currency can be considered to be like maximizing the gross foraging rate and unlike foraging efficiency, does not account for energetic losses incurred during travel and surface recovery.

If we assume that the Pigeon Guillemot is not restricted in daily foraging time and that feeding bouts are terminated when no more prey can be consumed without digestive processing, we can examine some possible reasons for the behaviour observed. As a bird that feeds mostly on epibenthic solitary prey, the Pigeon Guillemot may not experience the same cost due of prolonged dives as a bird that feeds on schooling pelagic prey, which may escape during surface recovery times. The calculations of foraging efficiency in this study take into account the cost of recovery. If the Pigeon Guillemot does not experience a significant net cost of prolonging surface recovery, it may spend more time per dive at the foraging patch than is predicted by a foraging efficiency currency. Loss of prey contact is not a consideration with solitary prey species, and if the Pigeon Guillemot is not restricted in daily foraging time it can take a longer time to recover.

Pigeon Guillemot diving behaviour is considered to represent an optimal hunting solution resulting from a number of environmental and physiological constraints. Without consideration of environmental factors such as buoyancy and prey distribution we might suspect that guillemots which maximize foraging time should forage at the minimum depths available. The Pigeon Guillemots in this study appeared to maximize gross foraging time; however, they do not forage at minimum depths. Although our model lacked direct empirical data on the distribution of prey, our calculations suggest that the cost of resisting buoyancy is likely an important factor in the choice of optimal foraging depth for Pigeon Guillemots.

Ainley, D.C., Strong, C.S., Penniman, T.M., and Boekelheide, R.J. 1990. The feeding ecology of farallon seabirds. *In* Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. *Edited by* D.C. Ainley and R.J. Broekelheide. Stanford University Press, Stanford, Calif. pp. 51–127.

Batulis, J.C., and Bongiorno, S.F. 1972. Effect of water depth on diving times in the American Coot (*Fulica americana*). Auk, **89**: 665–667.

Burger, A. E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. Can. Wildl. Serv. Occas. Pap. No. 68.

Burger, A.E., Wilson, R.P., Garnier, D., and Wilson, M.-P.T. 1993. Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia. Can. J. Zool. **71**: 2528–2540.

Butler, P.J., and Stephenson, R. 1987. Physiology of breath-hold diving: a bird's eye view. Sci. Prog. (Oxford), **71**: 439–458.

Butler, P.J., and Woakes, A.J. 1982. Telemetry of physiological variables from diving and flying birds. Symp. Zool. Soc. Lond. No. 49. pp. 107–128.

Cairns, D.K. 1987. Diet and foraging ecology of Black Guillemots in northeastern Hudson Bay. Can. J. Zool. **65**: 1257–1263.

Cairns, D.K. 1992. Diving behaviour of Black Guillemots in Northeastern Hudson Bay. Colon. Waterbirds, **15**: 245–248.

Cody M.L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology, **54**: 31–44.

Croll, D.A., Gaston, A.J., Burger, A.E., and Konnoff, D. 1992. Foraging behaviour and physiological adaptation for diving in Thick-billed Murres. Ecology, **73**: 344–356.

Croxall, J.P., Naito, Y., Kato, A., Rothery, P., and Briggs, D.R. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Palacrocorax atriceps*. J. Zool. (Lond.), **225**: 177–199.

Dewar, J.M. 1924. The bird as a diver. H.F. & G. Witherby Ltd., London.

Drent, R.H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba*. Ardea, **53**: 99–160.

Follett, W.I., and Ainley, D.G. 1976. Fishes collected by Pigeon Guillemots, *Cepphus columba* (Pallas), nesting on southeast Farallon Island, California. Calif. Fish Game, **62**: 28–31.

Houston, A.I. 1987. Optimal foraging by parent birds feeding dependant young. J. Theor. Biol. **124**: 251–274.

Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the dive cycle. Behav. Ecol. **3**: 255–265.

Houston, A.I., and McNamara, J.M. 1985. A general theory of central place foraging for single-prey loaders. Theor. Popul. Biol. **28**: 233–262.

Koelink, A.E. 1972. Bioenergetics of growth in the Pigeon Guillemot, *Cepphus columba*. M.Sc. thesis, University of British Columbia, Vancouver.

Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V., and Kooyman, C.A. 1992. Diving behavior and energetics during foraging cycles in King Penguins. Ecol. Monogr. **62**: 143–163.

Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. Can. J. Zool. **66**: 89–94.

Kuletz, K.J., 1983. Mechanisms and consequences of foraging behavior in a population of breeding Pigeon Guillemots. M.Sc. thesis, University of California, Irvine.

Lessells, C.M., and Stephens, D.W. 1983. Central place foraging: single prey loaders again. Anim. Behav. **31**: 238–243.

Lovvorn, J.R., and Jones, D.R. 1991. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can. J. Zool. **69**: 2879–2887.

Lovvorn, J.R., Jones, D.R., and Blake, R.W. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. J. Exp. Biol. **159**: 89–108.

Piatt, J.F., and Nettleship, D.N. 1985. Diving depths of four alcids. Auk, **102**: 293–297.

Scott, J.M. 1973. Resource allocation in four syntopic species of marine diving birds. Ph.D. thesis, Oregon State University, Corvallis.

Stephenson, R., Lovvorn, J.R., Heieis, M.R.A., Jones, D.R., and Blake, R.W. 1989. A hydromechanical estimate of the power requirements of diving and surface swimming in the Lesser Scaup (*Aythya affinis*). J. Exp. Biol. **147**: 507–519.

Stonehouse, B. 1967. Feeding behaviour and diving rhythms of some New Zealand shags, Phalacrocoracidae. Ibis, **109**: 600–605.

Thoresen, C. 1989. Diving times and behavior of Pigeon Guillemots and Marbled Murrelets off Rosario Head, Washington. West. Birds, **20**: 33–37.

Wanless, S., Morris, J.A., and Harris, M.P. 1988. Diving behavior of guillemot *Uria aalge*, puffin *Fratercula arctica* and razorbill *Alca torda* as shown by radio-telemetry. J. Zool. (Lond.), **216**: 73–81.

Wilson, R.P., and Wilson, M.T. 1988. Foraging behaviour in four sympatric cormorants. J. Anim. Ecol. **57**: 943–955.

Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E., and Nöldeke, E.C. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? Am. Nat., **140**: 179–200.

Ydenberg, R.C. 1988. Foraging by diving birds. Proc. Int. Ornithol. Congr. **19**: 1831–1842.

Ydenberg, R.C., and Clark, C.W. 1989. Aerobiosis and anaerobiosis during diving by Western Grebes: an optimal foraging approach. J. Theor. Biol. **139**: 437–449.

Ydenberg, R.C., and Guillemette, M. 1991. Diving and foraging in the Common Eider. Ornis Scand. **22**: 349–352.

Ydenberg, R.C., Welham, C.V.J., Schmid-Hempel, R., Schmid-Hempel, P., and Beauchamp, G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. Behav. Ecol. In press.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J. pp. 53–58.