CHARACTERISTICS OF DIVING IN RADIO-MARKED XANTUS'S MURRELETS

CHRISTINE D. HAMILTON[1,2], RICHARD T. GOLIGHTLY[1] & JOHN Y. TAKEKAWA[3]

[1]Department of Wildlife, Humboldt State University, Arcata, California, 95521, USA
(chamilton13@hotmail.com)
[2]Current address: US Fish and Wildlife Service, 2493 Portola Road, Suite B, Ventura, California, 93003, USA
[3]US Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station,
505 Azuar Drive, Vallejo, California, 94592, USA

Received 7 April 2005, accepted 15 January 2006

SUMMARY

HAMILTON, C.D., GOLIGHTLY, R.T. & TAKEKAWA, J.Y. 2005. Characteristics of diving in radio-marked Xantus's Murrelets. *Marine Ornithology* 33: 155–159.

We monitored diving activity of radio-marked Xantus's Murrelets *Synthliboramphus hypoleucus* near Anacapa Island, California, during the breeding season. Thirteen radio-marked murrelets were remotely monitored from Anacapa Island with a handheld antenna and radio receiver for 29 hours in three sample periods in April and May 2003. Mean dive durations in the sample periods were 18 s ± 2 s, 28 s ± 2 s, and 24 s ± 4 s, suggesting that dives were less than 21 m from the surface. Dive duration and subsequent time on the surface differed between the sample periods. Dive duration and subsequent time on the surface were not correlated in observations stratified by individual bird or by sample period. Further, dive duration and subsequent time on the surface were not correlated within foraging bouts. Dive characteristics measured near Anacapa Island suggested that Xantus's Murrelets have the ability to capture prey found at varying depths, but will feed on prey that is most available near the surface of the water.

Key words: Xantus's Murrelet, *Synthliboramphus hypoleucus,* Anacapa Island, radio telemetry, dive duration, dive depth, surface times

INTRODUCTION

Xantus's Murrelets *Synthliboramphus hypoleucus* are found near islands off the west coast of Baja California and within the Southern California Bight during the breeding season from March through June (Jehl & Bond 1975, Hunt *et al.* 1979, Briggs *et al.* 1987, Drost & Lewis 1995). Like other alcids, they are wing-propelled pursuit-divers and forage almost exclusively by diving (Ashmole 1971, Gaston & Jones 1998). They feed in small, dispersed groups, usually in singles and pairs, but occasionally in groups of up to eight individuals (Howell 1910, Hunt *et al.* 1979, Drost & Lewis 1995). They feed on small fish and zooplankton and may use prey concentrated near the surface in ocean fronts and along convergence lines (Hunt *et al.* 1979, Hamilton *et al.* 2004, Hamilton 2005). At-sea distribution of murrelets relative to nesting colonies is variable within and between years (Whitworth *et al.* 2000, Hamilton 2005). Presumably this variation occurs because abundance, distribution, depth and availability of prey are patchy and variable in the Southern California Bight (Mais 1974, Roesler & Chelton 1987, Cross & Allen 1993). Rather than feeding at fixed depths, murrelets may exercise flexibility in the depth and length of time they spend underwater to obtain prey. Prey depth, availability and flexibility in foraging behaviors can be inferred from an examination of dive duration, time on the surface following a dive, variation in dive duration between time periods and within foraging bouts (series of consecutive dives), and variation in dive duration among individuals (Wanless *et al.* 1997, Jodice & Collopy 1999). These diving characteristics have not yet been examined for Xantus's Murrelets. In 2003, we examined the diving characteristics of radio-marked Xantus's Murrelets near Anacapa Island, California, during the breeding season.

METHODS

Anacapa Island (34°01′N, 119°24′W) is the easternmost of the northern four Channel Islands in the Southern California Bight. In 2001/02, Black Rats *Rattus rattus* were eradicated from Anacapa Island to protect Xantus's Murrelet (hereafter murrelet) nests from depredation (American Trader Trustee Council 2001). An estimated 200–600 murrelet pairs nest on Anacapa Island (Whitworth *et al.* 2003). During 14–16 April and 28–29 April 2003, we captured 44 murrelets from within nocturnal congregations near Anacapa Island using a night-lighting capture technique (Whitworth *et al.* 1997). Radio transmitters (model PD-2, Holohil Systems, Woodlawn, Ontario, Canada) were attached to murrelets using a subcutaneous anchor technique (Mauser & Jarvis 1991, Newman *et al.* 1999). In conjunction with this project, we also examined at-sea distribution, nocturnal colony attendance and foraging habitat of the 44 radio-marked murrelets (Hamilton 2005).

We used a three-element Yagi antenna and receiver (model R-4000: Advanced Telemetry Systems, Isanti, MN, USA) to remotely monitor diving activity from Anacapa Island during three sample periods of one to three days each. To select a radio-marked bird to monitor, we scanned all 44 frequencies with the receiver to determine which transmitters could be detected with a strong signal. We then randomly selected and monitored one of the detected frequencies for at least 30 minutes. During each monitoring session, we estimated sea state using the Beaufort scale. Transmitter signals were detected when the bird was on the surface and were interrupted when the bird dove (Wanless *et al.* 1993). Thus, we considered a dive to start when the radio signal became inaudible and to end when the signal was once again audible.

Start time and end time of each dive were voice recorded on a tape recorder. A dive was defined as a signal loss of more than four seconds, because in Marbled Murrelets *Brachyramphus marmoratus,* shorter signal losses were reported only when waves over-topped the birds, when preening activities resulted in the antenna dipping underwater or when birds executed very short dives (Jodice & Collopy 1999). Jodice & Collopy (1999) found that shorter signal losses represented only 3.3% of all signal losses, and so we believe that few potential dives were discarded by using the four-second criterion. A surface interval was defined as less than three minutes between successive dives, and a foraging bout was defined as three or more consecutive dives that ended with an interval of more than three minutes (Jodice & Collopy 1999). Diving efficiency was calculated as the ratio of dive duration to subsequent surface interval (Wanless *et al.* 1988). When we could record a complete foraging bout, the number of dives per bout was calculated. Percentage of time underwater during a foraging bout was estimated as the quotient of dive duration over foraging bout duration. We determined these diving characteristics for the monitored murrelets: dive duration, surface interval, diving efficiency, duration of foraging bout, number of dives per foraging bout and percentage of time spent underwater during each foraging bout.

We used two-way analysis of variance (ANOVA: SPSS, version 11.5, 2002, Chicago, IL, USA) to test for differences in dive duration between the sample periods. Because repeated dives were recorded for each bird, we controlled for pseudoreplication by using the bird as a factor in the two-way ANOVA. We used two-way ANOVA to also test for differences in surface intervals between the sample periods. We used single-factor ANOVA, where the mean for the individual bird was the experimental unit, to compare mean diving efficiency, duration of foraging bout, number of dives per foraging bout and percentage of time spent underwater during each foraging bout between sample periods.

We used analysis of covariance (ANCOVA) to determine whether there was a relationship between dive duration and subsequent surface interval for individual birds and by sample period (SAS Institute, 2001, Cary, NC, USA). A strong relationship between dive duration and subsequent surface interval was expected if the bird was diving to maximum effort or depth as limited by physiology (Jodice & Collopy 1999). To determine whether there was a relationship between dive duration and subsequent surface interval for individual birds within foraging bouts, we averaged dive durations and surface intervals by foraging bout, and tested for differences between foraging bouts and between birds. We treated dives by the three birds recorded in two sample periods as separate samples because we found significant differences between sample periods in dive duration and surface intervals.

We estimated the direction of each bird from Anacapa Island by estimating the direction of the strongest signal. To estimate the location of the radio-marked murrelets during diving trials, we determined the maximum distance that a radio transmitter on the surface of the water could be detected from the island. On 28 April 2003, two transmitters were attached to 470 mL plastic bottles half-filled with water. The bottles were floated on the surface at various locations and were recorded using a global positioning system [GPS (model 12XL, Garmin, Olathe, KS, USA]. Each time the transmitters were placed on the surface, an observer with a receiver and handheld antenna on Anacapa Island determined whether they could be detected. Distance from each test location to the observer was calculated using a Geographic Information System (GIS) program (ArcView 3.3, ESRI, Redlands, CA, USA).

RESULTS

During 19–20 April, 9–11 May, and 24–26 May 2003 (periods 1, 2, and 3 respectively), diving activity of radio-marked murrelets was monitored for a total of 29 hours. Diving occurred across all daylight hours (06h00–20h00 PDT; Table 1). Sea state was mild during all monitoring sessions [Beaufort 1 (1–3 knots) or 2 (4–6 knots)], with the exception of 9 May (within Period 2), which scored a Beaufort 6 (22–27 knots). In total, we recorded 447 individual dives and 23 complete foraging bouts for 13 murrelets during the three sample periods. All of the murrelets were south of Anacapa Island where water depth ranged from 50 m to 700 m. Based on our assessment of transmitter range, we estimated that the murrelets were detected only when they were within 5 km of the island.

Dive duration varied between the three periods ($F = 75.0$, $P < 0.001$, df = 2) and between individuals ($F = 2.8$, $P = 0.001$, df = 12), but we observed a significant interaction between period and individual ($F = 5.9$, $P = 0.016$, df = 1). The shortest dives were in period 1: 18 ± 2 s [mean ± standard error (SE)]; the longest dives were in period 2: 28 ± 2 s. Dive duration in period 3 was 24 ± 4 s. Surface interval varied between periods ($F = 7.3$, $P = 0.001$, df = 2) and between individuals ($F = 3.7$, $P < 0.001$, df = 12), and we observed no interaction between period and individual ($F = 1.5$, $P = 0.220$, df = 1). The surface intervals in period 1 were shorter (14 ± 5 s) than those in period 2 (22 ± 8 s) and period 3 (24 ± 12 s).

There were no significant differences between the three periods in diving efficiency, duration of foraging bouts, number of dives per foraging bout and percentage of time spent underwater (Table 2). There was no relationship between dive duration and surface interval for individuals (ANCOVA: $F = 1.34$, n = 16, $P = 0.18$), or for the three periods (ANCOVA: $F = 0.91$, n = 3, $P = 0.41$), and there was no relationship between average dive duration and surface interval within a foraging bout for individuals (ANCOVA: $F = 0.10$, n = 5, $P = 0.98$).

TABLE 1
Number of dives per minute and monitoring effort for radio-marked Xantus's Murrelets from Anacapa Island, California, during three sample periods in 2003

Time of day (PDT)	Number of dives per minute (total minutes monitored)		
	19, 20 April	9, 10, 11 May	24, 25, 26 May
06h00–08h00	—	0.37 (90)	0.10 (175)
08h00–10h00	0.65 (120)	0.23 (220)	0.42 (55)
10h00–12h00	—	0 (50)	0.17 (180)
12h00–14h00	1.67 (15)	0.20 (40)	0.23 (110)
14h00–16h00	—	0.27 (15)	0.24 (225)
16h00–18h00	—	0.35 (190)	0.18 (60)
18h00–20h00	—	—	0.12 (200)
Time spent monitoring (hours)	2.25	9.75	17
Murrelets monitored (n)	4	8	4

DISCUSSION

Based on the allometric relationship between maximum diving depth and body mass developed by Schreer & Kovacs (1997) for alcids, the predicted maximum diving depth of murrelets would be approximately 25 m. This value is similar to the estimated diving depths for the murrelets in the present study. Based on average dive duration, and assuming that the average swimming speed was 1.5 m/s or less as measured for Thick-billed Murres *Uria lomvia* (Lovvorn *et al.* 1999), murrelets likely dove to depths of less than 21 m to capture prey. Smaller divers are not expected to swim as fast as larger ones, and thus swimming speeds of murrelets are not expected to be greater than those of the larger Thick-billed Murres (Lovvorn & Jones 1991, Schreer & Kovacs 1997).

Because water depth where the murrelets were foraging was greater than 50 m, birds must have been foraging within the water column and not on the bottom. Murrelets likely exhibited V-shaped dives, representing capture of single prey items; U-shaped dives, with a horizontal phase at shallow depths; or underwater undulations (rapid depth changes) during dives, indicating pursuit of prey and possibly ingestion of multiple prey items within a single shallower dive (or some combination of these). Thick-billed Murres foraging on epibenthic and epipelagic prey were shown to use U-shaped dives with a clear horizontal phase (Watanuki *et al.* 2001). Rhinoceros Auklets *Cerorhinca monocerata,* which feed on prey types similar to those observed for murrelets (euphausiids and epipelagic schooling fishes; Hamilton *et al.* 2004), were shown to exhibit both underwater undulations and V-shaped dives to capture prey within the water column (Kuroki *et al.* 2003). Although Rhinoceros Auklets exhibited longer dives (mean ± standard deviation: 53 ± 8 s) than the murrelets in this study, the median diving depth of the auklets was only 14.0 ± 1.8 m. Thus, seabirds that feed on epipelagic prey may spend time pursuing prey in the water column rather than spending time diving to maximum depths. Duration and depth of dives in pursuit-diving seabirds are generally less than the maximum attainable (Burger 1991).

Dive duration and surface intervals for murrelets were similar to those for Ancient Murrelets *S. antiquus* observed foraging within two kilometres of a nesting colony in water less than 100 m deep (Gaston 1992), and Marbled Murrelets foraging within one kilometre from shore where water depths ranged from three metres to 50 m (Carter & Sealy 1990, Strachan *et al.* 1995, Jodice & Collopy 1999, Henkel *et al.* 2004). Despite differences in foraging habitats, these three similar-sized murrelet species would be expected to exhibit similar diving durations because dive duration and maximum depth of dives are correlated with body mass (Piatt & Nettleship 1985). Further, all three species feed on small schooling fishes and euphausiids and are considered to be generalist feeders (Sealy 1975, Gaston 1992, Gaston *et al.* 1993, Gaston & Jones 1998, Hamilton *et al.* 2004). They probably feed on the prey types that are most available near the surface of the water.

Diving efficiency was slightly less than the value of 2.3 reported for Marbled Murrelets in central California (Henkel *et al.* 2004), 2.0–3.0 for Marbled Murrelets in Oregon (Jodice & Collopy 1999), and 3.9 for Marbled Murrelets in British Columbia (Carter & Sealy 1990). Diving efficiency should decrease with increasing dive duration and depth of dives (Wanless *et al.* 1988, Wanless *et al.* 1997, Jodice & Collopy 1999), and such a decrease could occur as a result of reduced prey availability near the surface of the water. Thus, prey may have been less available to the murrelets in this study.

Assuming aerobic diving, subsequent surface intervals are expected to increase as dive duration increases so that the bird can recover and replenish oxygen stores (Lea *et al.* 1996). The lack of correlation between dive duration and subsequent surface interval within foraging bouts for individual birds and between the three periods indicates that the murrelets did not dive to their maximum depth as limited by physiology or maximize the amount of time they could have spent underwater to obtain prey (Lea *et al.* 1996). This suggests that prey were available and able to be located and captured at less than maximum effort during the time of this study. Stronger relationships between dive duration and surface intervals may occur in years when prey availability is reduced and capture effort must be increased. This has been shown to occur in Adélie Penguins *Pygoscelis adelie,* Common Murres *U. aalge* and European Shags *Phalacrocorax aristotelis* (Chappell *et al.* 1993, Wanless *et al.* 1993, Monoghan *et al.* 1994).

The shortest average dive durations and surface intervals occurred in period 1, suggesting that prey may have been more available earlier in the breeding season. The ability of murrelets to capture

TABLE 2

Summary of diving characteristics measured for radio-marked Xantus's Murrelets from Anacapa Island, California, during three sample periods in 2003 (mean ± standard error)[a]

	19, 20 April	9, 10, 11 May	24, 25, 26 May	*F* Value	*P* Value
Diving efficiency	1.8±0.2	1.8±0.2	1.8±0.3	0.02	0.98
	(n=4)[b]	(n=8)[b]	(n=4)[b]		
Duration of foraging bout (min)	4.7	8.7±1.5	7.5±0.8	0.79	0.49
	(n=1)[c]	(n=6)[c]	(n=4)		
Number of dives per foraging bout	10	13±3	9±2	0.60	0.57
	(n=1)	(n=6)	(n=4)		
Percent of foraging bout spent underwater	61	59±4	57±8	0.08	0.93
	(n=1)	(n=6)	(n=4)		

[a] Each bird represents a sample unit within a period.

[b] The total number of individual birds monitored was 13. Three birds were monitored in two separate sample periods.

[c] Sample size includes only birds for which complete foraging bouts were recorded.

prey may be reduced when turbidity of the water increases as a result of windy conditions (Jodice & Collopy 1999). Thus, the longest average dive durations in period 2 may have been a result of the windy conditions that occurred on 9 May.

The lack of correlation between dive duration and surface intervals also suggests that murrelets used flexible foraging techniques and captured prey found at varying depths. Strong relationships between dive duration and surface intervals have been shown to occur in seabirds that feed on the bottom such as Red-legged Cormorants *P. gaimardi* (Frere *et al.* 2002). Variability in dive durations and surface intervals has been shown to occur in Neotropic Cormorants *P. brasilianus* that exhibit more flexible foraging techniques in that they forage both on the bottom and on pelagic schooling fishes (Quintana *et al.* 2004). Our data do not suggest that murrelets were feeding at the bottom; however, they do indicate that the murrelets foraged at varying depths and pursued prey underwater for varied amounts of time. Several studies have shown that diving depth of seabirds is positively correlated with dive duration (e.g. Wanless *et al.* 1997, Luna-Jorquera & Culik 1999, Mills 2000, Kuroki *et al.* 2003). However, this correlation did not occur in Marbled Murrelets and may not occur in murrelets or other seabirds that forage throughout the water column (Jodice & Collopy 1999).

There were several indications that prey resources were abundant and available near Anacapa Island in 2003. Nesting murrelets exhibited high hatching success (88%), and densities of murrelets attending nocturnal congregations adjacent to the island were high in comparison with other years (Whitworth *et al.* 2005). Among all 44 radio-marked murrelets from Anacapa Island (13 sampled for this study), 88% of at-sea locations were within 40 km south of the island (Hamilton 2005). In other years, murrelets have been documented foraging farther from nesting colonies (Whitworth *et al.* 2000, Hamilton 2005). Some of the 44 radio-marked murrelets in 2003 were associated with ocean fronts that were 10–30 km south of Anacapa Island and persisted for at least three weeks until mid-May (Hamilton 2005). Ocean fronts concentrate zooplankton and schooling fish near the surface of the water (Owen 1981, Olson & Backus 1985, Mann & Lazier 1996). Although the murrelets that we monitored were feeding less than 5 km south of Anacapa Island, they may have been responding to the same upwelling, because seabird associations may extend up to 9.3 km beyond fronts (Hoefer 2000). It was unknown whether the murrelets foraging farther than 5 km from the island exhibited similar dive characteristics or if they needed to dive deeper to obtain prey. Our results suggest that murrelets have the ability to capture prey at varying depths. However, when prey are available near the surface of the water, the murrelets will probably feed on that prey.

ACKNOWLEDGMENTS

We thank J. Ackerman, H. Carter, M. Colwell, W. McIver, S. Sealy and one anonymous reviewer who made helpful comments on this manuscript. Funding and in-kind support were provided by the US Geological Survey (Dixon Field Station and San Francisco Bay Field Station), Humboldt State University, California Department of Fish and Game (E. Burkett, Habitat Conservation Planning Branch; and P. Kelly, Office of Spill Prevention and Response), and US Navy (T. Keeney and S. Schwartz, Legacy Resources Management Program and Naval Air Weapons Station, Point Mugu). Coordination and assistance with the study were provided by Channel Islands National Park (T. Hofstra, P. Martin, and K. Faulkner). Murrelet captures were supported by Channel Islands National Park vessel *Pacific Ranger* (Captain B. Wilson). Biologists that assisted with field research included J. Ackerman, J. Adams, H. Carter, E. Craig, E. Creel, G. Howald, P. Martin, J. Mason, W. McIver, D. Whitworth and R. Young. Research was conducted with permits from Humboldt State University (HSU IACUC protocol 01/02.W.106.A), US Geological Survey (banding permit 22911, Animal Care and Use Committee Review), Channel Islands National Park (research permit CHIS-2003-SCI-0005), and California Department of Fish and Game (scientific collecting permit 000392).

REFERENCES

AMERICAN TRADER TRUSTEE COUNCIL (ATTC). 2001. Final restoration plan and environmental assessment for seabirds injured by the American Trader oil spill [Unpublished report]. Sacramento, CA: American Trader Resource Trustee Council, US Fish and Wildlife Service, California Department of Fish and Game, and National Oceanic and Atmospheric Administration. 43 pp.

ASHMOLE, N.P. 1971. Seabird ecology and the marine environment. In: Farner, D.S., King, J.R. & Parkes, K.C. (Eds). Avian biology. New York: Academic Press. pp. 223–286.

BRIGGS, K.T., TYLER, W.B., LEWIS, D.B. & CARLSON, D.R. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology* 11: 1–74.

BURGER, A.E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. Ottawa, ON: Canadian Wildlife Service. pp. 9–15. [Occasional paper No. 68]

CARTER, H.R. & S.G. SEALY. 1990. Daily foraging behavior of Marbled Murrelets. *Studies in Avian Biology* 14: 93–102.

CHAPPELL, M.A., SHOEMAKER, V.H., JANES, D.N. & BUCHER, T.L. 1993. Diving behavior of Adélie Penguins. *Ecology* 74: 1204–1215.

CROSS, J.N. & ALLEN, L.G. 1993. Fishes. In: Dailey, M.D., Reish, D.J. & Anderson, J.W. (Eds). Ecology of the Southern California Bight: a synthesis and interpretation. Los Angeles: University of California Press. pp. 459–540.

DROST, C.A. & LEWIS, D.B. 1995. Xantus' Murrelet (*Synthliboramphus hypoleucus*). In: Poole, A. & Gill, F. (Eds). The birds of North America, No. 164. Philadelphia & Washington, DC: The Academy of Natural Sciences & American Ornithologists' Union.

FRERE, E., QUINTANA, F. & GANDINI, P. 2002. Diving behavior of the Red-legged Cormorant in southeastern Patagonia, Argentina. *Condor* 104: 440–444.

GASTON, A.J. 1992. The Ancient Murrelet: a natural history in the Queen Charlotte Islands. London: T&AD Poyser.

GASTON, A.J., CARTER, H.R. & SEALY, S.G. 1993. Winter ecology and diet of Ancient Murrelets off Victoria, British Columbia. *Canadian Journal of Zoology* 71: 64–70.

GASTON, A.J. & JONES, I.L. 1998. The auks. New York: Oxford University Press.

HAMILTON, C.D. 2005. At-sea distribution, habitat, and foraging behavior of Xantus's Murrelets (*Synthliboramphus hypoleucus*) during the breeding season in the Southern California Bight [MSc thesis]. Arcata, CA: Humboldt State University. 82 pp.

HAMILTON, C.D., CARTER, H.R. & GOLIGHTLY, R.T. 2004. Diet of Xantus's Murrelets in the Southern California Bight. *Wilson Bulletin* 116: 152–157.

HENKEL, L.A., BURKETT, E.E. & TAKEKAWA, J.Y. 2004. At-sea activity and diving behavior of a radio-tagged Marbled Murrelet in central California. *Wilson Bulletin* 27: 9–12.

HOEFER, C.J. 2000. Marine bird attraction to thermal fronts in the California Current system. *Condor* 102: 423–427.

HOWELL, A.B. 1910. Notes from the Los Coronados Islands. *Condor* 12: 184–187.

HUNT, G.L. Jr, PITMAN, R.K., NAUGHTON, M., WINNETT, K.A., NEWMAN, A., KELLY, P.R. & BRIGGS, K.T. 1979. Distribution, status, reproductive ecology and foraging habits of breeding seabirds. In: Summary of marine mammal and seabird surveys of the Southern California Bight area, 1975–1978. Los Angeles, CA: US Department of the Interior, Bureau of Land Management. [PB-81–248–205]

JEHL, J. Jr & BOND, S.I. 1975. Morphological variation and species limits in murrelets of the genus *Endomychura. Transactions of the San Diego Society for Natural History* 20: 9–24.

JODICE, P.G.R. & COLLOPY, M.W. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. *Canadian Journal of Zoology* 77: 1409–1417.

KUROKI, M., KATO, A., WATANUKI, Y., NIIZUMA, Y., TAKAHASHI, A. & NAITO, Y. 2003. Diving behavior of an epipelagically feeding alcid, the Rhinoceros Auklet (*Cerorhinca monocerata*). *Canadian Journal of Zoology* 81: 1249–1256.

LEA, S.E.G., DALEY, C., BODDINGTON, P.J.C. & MORISON, V. 1996. Diving patterns in shags and cormorants (*Phalacrocorax*): tests of an optimal breathing model. *Ibis* 138: 391–398.

LOVVORN, J.R. & 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.). *Canadian Journal of Zoology* 69: 2879–2887.

LOVVORN, J.R., CROLL, D.A. & LIGGINS, G.A. 1999. Mechanical versus physiological determinants of swimming speeds in diving Brunnich's guillemots. *Journal of Experimental Biology* 202: 1741–1752.

LUNA-JORQUERA, G. & CULIK, B.M. 1999. Diving behavior of Humboldt Penguins (*Spheniscus humboldti*) in northern Chile. *Marine Ornithology* 27: 67–76.

MAIS, K.F. 1974. Pelagic fish surveys in the California Current. Sacremento, CA: California Department of Fish and Game. 79 pp. [Fish Bulletin 162]

MANN, K.H. & LAZIER, J.R.N. 1996. Dynamics of marine ecosystems: biophysical interactions in the oceans. 2nd ed. Cambridge: Blackwell Science.

MAUSER, D.M. & JARVIS, R.J. 1991. Attaching radio transmitters to 1-day-old mallard ducklings. *Journal of Wildlife Management* 55: 488–491.

MILLS, K.L. 2000. Diving behavior of two Galapagos Penguins (*Spheniscus mendiculus*). *Marine Ornithology* 28: 75–79.

MONOGHAN, P., WALTON, P., WANLESS, S., UTTLEY, J.D. & BURNS, M.D. 1994. Effects of prey abundance on foraging behavior, diving efficiency and time allocation of breeding guillemots (*Uria aalge*). *Ibis* 136: 214–222.

NEWMAN, S.H., TAKEKAWA, J.Y., WHITWORTH, D.L. & BURKETT, E.E. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on seabirds: Xantus' and Marbled Murrelets. *Journal of Field Ornithology* 70: 520–534.

OLSON, D.B. & BACKUS, R.H. 1985. The concentration of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. *Journal of Marine Research* 43: 113–137.

OWEN, R.W. 1981. Fronts and eddies in the sea. In: Longhurst, A.R. (Ed). Analysis of marine ecosystems. New York: Academic Press. pp. 197–233.

PIATT, J.F. & NETTLESHIP, D.N. 1985. Diving depths of four alcids. *Auk* 102: 293–297.

QUINTANA, F., YORIO, P., LISNIZER, N., GATTO, A. & SORIA, G. 2004. Diving behavior and foraging areas of the Neotropic Cormorant at a marine colony in Patagonia, Argentina. *Wilson Bulletin* 116: 83–88.

ROESLER, C.S. & CHELTON, D.B. 1987. Zooplankton variability in the California Current, 1951–1982. *California Cooperative Oceanic Fisheries Report* 28: 59–96.

SCHREER, J.F. & KOVACS, K.M. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* 75: 339–358.

SEALY, S.G. 1975. Feeding ecology of Ancient and Marbled Murrelets near Langara Island, British Columbia. *Canadian Journal of Zoology* 53: 418–433.

STRACHAN, G., MCALLISTER, M. & RALPH, C.J. 1995. Marbled Murrelet at-sea and foraging behavior. In: Ralph, C.J., Hunt, G.L. Jr, Raphael, M.G. & Piatt, J.F. (Eds). Ecology and conservation of the Marbled Murrelet. [General Technical Report PSW-GTR-152] Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station. pp. 247–254.

WANLESS, S., CORFIELD, T., HARRIS, M.P., BUCKLAND, S.T. & MORRIS, J.A. 1993. Diving behavior of the Shag *Phalacrocorax aristotelis* (Aves: Pelecaniformes) in relation to water depth and prey size. *Journal of Zoology, London* 231: 11–25.

WANLESS, S., HARRIS, M.P., BURGER, A.E. & BUCKLAND, S.T. 1997. Use of time-at-depth recorders for estimating depth and diving performance of European Shags. *Journal of Field Ornithology* 68: 547–561.

WANLESS, S., MORRIS, J.A. & HARRIS, M.P. 1988. Diving behavior of Guillemot *Uria aalge,* Puffin *Fratercula arctica,* and Razorbill *Alca torda* as shown by radio-telemetry. *Journal of Zoology, London* 216: 73–81.

WATANUKI, Y., MEHLUM, F. & TAKAHASHI, A. 2001. Water temperature sampling by foraging Brünnich's Guillemots with bird-borne data loggers. *Journal of Avian Biology* 32: 189–193.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R. 1997. Night-lighting as a capture technique for Xantus' Murrelets in the Southern California Bight. *Colonial Waterbirds* 20: 525–531.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R., NEWMAN, S.H., KEENEY, T.W. & KELLY, P.R. 2000. Distribution of Xantus' Murrelet (*Synthliboramphus hypoleucus*) at sea in the Southern California Bight, 1995–97. *Ibis* 142: 268–279.

WHITWORTH, D.L., CARTER, H.R., YOUNG, R.J., CREEL, E., GRESS, F. & FANGMAN, S. 2003. Spotlight survey monitoring plan for Xantus's Murrelets (*Synthliboramphus hypoleucus*) at Anacapa Island, California, after eradication of Black Rats (*Rattus rattus*) [Unpublished report]. Davis, CA & Arcata, CA: California Institute of Environmental Studies & Humboldt State University, Department of Wildlife. 25 pp.

WHITWORTH, D.L., CARTER, H.R., KOEPKE, J.S., YOUNG, R.J., GRESS, F. & FANGMAN, S. 2005. Initial recovery of Xantus's Murrelets following rat eradication on Anacapa Island, California. *Marine Ornithology* 33: 131–137.