

AGE AND SEX OF COMMON MURRES *URIA AALGE* RECOVERED DURING THE 1997-98 POINT REYES TARBALL INCIDENTS IN CENTRAL CALIFORNIA

HANNAHROSE M. NEVINS¹ & HARRY R. CARTER^{2,3}

¹Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039 USA, e-mail: hrnevins@hotmail.com

²Department of Wildlife, Humboldt State University, Arcata, CA 95521 USA

³Present address: 5700 Arcadia Road, Apt #219, Richmond, B.C. V6X2G9 Canada

Received 9 April 2003, accepted 11 October 2003

SUMMARY

NEVINS, H. M. & CARTER, H. R. Age and sex of Common Murres *Uria aalge* recovered during the 1997-98 Point Reyes Tarball Incidents in central California. *Marine Ornithology* 31: 51-58.

We examined 1,138 Common Murre *Uria aalge* carcasses recovered along the central California coast from November 1997 through March 1998 during the Point Reyes Tarball Incidents, a prolonged oiling event traced to the sunken vessel *S. S. Jacob Luckenbach*. We used head plumage, supraorbital ridge, and bursa of Fabricius, to classify age among carcasses as hatch-year (HY), or after-hatch year (AHY). We then separated AHY birds into two maturity categories based on gonad development: subadult and adult. The observed age class composition (14.6% HY, 37.6% subadult, and 47.8% adult) was not different from expected values generated with a stage-based matrix model that assumed a year-round resident population. The sex ratio for HY birds was equal (1.2:1), indicating little difference in at-sea distribution among male and female HY birds during winter. We found male-biased sex ratios in subadult (1.6:1) and adult (1.5:1) age classes. Sex-based differences in winter dispersal or colony attendance may have caused different risks to oiling among AHY birds. Mortality of mostly AHY murres during the Point Reyes Tarball Incidents and other oil spills has contributed to slow recovery of the central California population following historic and recent declines.

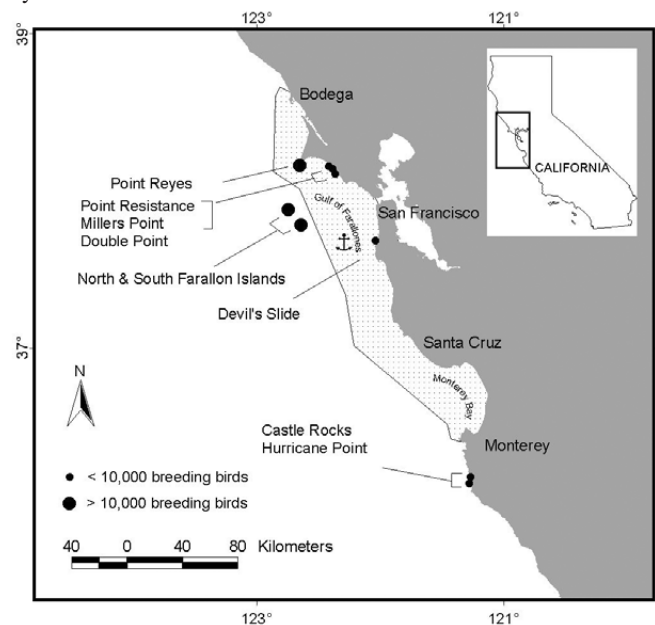
Keywords: age, California, Common Murre, dispersal, oil pollution, sex, *Uria aalge*

INTRODUCTION

Large numbers of Common Murres *Uria aalge* have been killed by oil spills off central California since the early 20th century (Carter *et al.* 2001). Common Murres are abundant near breeding colonies on the continental shelf in the Gulf of the Farallones region where oil spills occur from marine vessels visiting San Francisco Bay (Ainley & Lewis 1974, Briggs *et al.* 1987, Ainley *et al.* 1996, Manuwal & Carter 2001). Since the mid 1980s, considerable effort has been made to quantify numbers of seabirds killed by major oil spills and chronic oiling off central California (Ford *et al.* 1987, Stenzel *et al.* 1988, Page *et al.* 1990, Nur *et al.* 1997, Carter *et al.* 2003b). This study is one of the first to quantify age and sex of all Common Murres recovered during an oiling event in California.

During the Point Reyes Tarball Incidents (PRTI), state and federal agencies recovered oiled seabirds on beaches from Bodega to Monterey Bay, California (Fig. 1). During November 1997 through March 1998, searchers recovered a total of 1,858 Common Murres, 720 live and 1,138 dead. An estimated 9,094 murres were killed in this oil spill (Hampton *et al.* 2003, Himes Boor *et al.* 2003), the greatest reported number of murres killed during a single oiling event in central California (Carter *et al.* 2001). PRTI oil samples were eventually matched to oil leaking from the vessel *S.S. Jacob Luckenbach* which sank in 1953, after colliding with another ship in the Gulf of the Farallones.

Fig. 1. Coastal areas in central California where Common Murres were recovered during the Point Reyes Tarball Incident (shaded). Murre breeding colonies >10,000 breeding pairs indicated with large circles, colonies <10,000 breeding pairs indicated by smaller circles. The sunken vessel *S.S. Luckenbach* is indicated by anchor symbol.



Common Murres from southern regions are resident throughout the year and do not undertake large-scale migrations characteristic of populations in northern regions (Harris & Wanless 1990a, Gaston & Jones 1998). Winter dispersal patterns of murres in California, however, are not well known. Briggs *et al.* (1987) attributed greater densities of murres at-sea off California during winter to an influx of migrants from northern populations, as suggested by earlier reports (Smail *et al.* 1972, Storer 1952). Others have questioned these conclusions, arguing instead that Common Murres in central California are resident year-round (Manuwal & Carter 2001, Carter *et al.* 2003b). Because breeding adults and non-breeding subadults are thought to remain within 40-60 km of colonies during winter (Ainley *et al.* 2002), we assumed that murres killed by this oil spill were primarily from the central California population. Age and sex related differences in at-sea distribution may result in differential oil exposure and subsequent mortality. Differential mortality among age classes and sexes is expected to affect population growth unequally (Coulson *et al.* 2001). Murres are long-lived, with delayed maturity, low juvenile survival, and high adult survival; therefore, greater relative adult mortality will be more detrimental than juvenile mortality to population growth-rate (Russell 1999).

Examination of carcasses recovered during oil spills can provide important information regarding differential mortality of age classes and sexes (Anker-Nilssen *et al.* 1988, Anker-Nilssen & Lorentsen 1995). Our primary objective was to determine the age and sex of Common Murre carcasses recovered during the PRTI and to evaluate the potential impact of this mortality to the central California population. We compared the observed age and sex composition of our sample to expected values generated with a stage-based matrix model to determine if the PRTI affected the entire population or affected specific age or sex classes differently. Finally, we compared the age structure and sex ratio of the PRTI sample to data from three other winter oil spills in central California: the January 1971 San Francisco, February 1986 *Apex Houston*, and September 1998 *Command* spills (Smail *et al.* 1972, Page *et al.* 1990, Boyce & Hampton 2002, Carter *et al.* 2003b).

METHODS

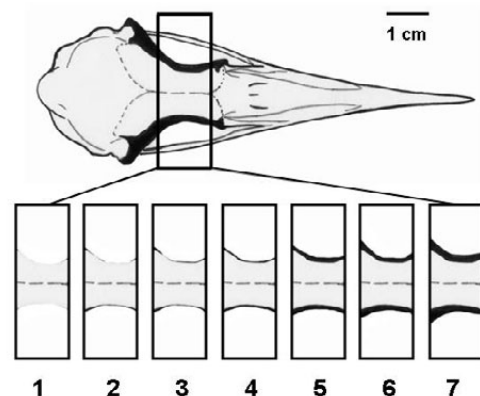
Carcasses were stored frozen after collection from beaches or after they died in rehabilitation facilities. We examined all 1,138 dead murres recovered during the PRTI, regardless of the extent of oiling. Approximately 90% were oiled, 8% were not visibly oiled, 2% were unknown oiling (heavily scavenged), and <0.1% died from other causes (Himes Boor *et al.* 2003). We did not examine 720 live oiled birds that were rehabilitated and released, but 110 of these birds that were photographed had similar head plumage proportions to our sample (44% black, 24% mottled, and 33% white; P. Capitolo *pers. comm.*). We classified age, using head plumage, supraorbital ridge, and the presence of the bursa of Fabricius (Davis 1947, Gaston 1984, Broughton 1994, Thompson *et al.* 1998). We determined sex and maturity by inspecting and measuring gonads.

We assigned head plumage to one of seven categories: (1) *White with a thin neck ring*, a lightly-flecked <1.0 cm wide ring of dark feathers at the base of the throat (juvenile plumage); (2) *White with a thick neck ring*, a heavily-flecked band of dark feathers >1.0 cm wide at the base of the throat (juvenile or basic plumage); (3) *White – Mottled*, with approximately 51-99% white feathers

(transitioning from basic to alternate plumage); (4) *White* (basic or winter plumage); (5) *Black – Mottled*, with approximately 51-99% black feathers (transitioning from basic to alternate plumage); (6) *Black* (alternate or breed plumage); and (7) *Unknown* (i.e., head missing or heavy oiling). Hatching year (HY) murres do not attain complete alternate head plumage until May or later, and most breeding adults and older subadults molt into alternate head plumage during October and February (Verwey 1922, Storer 1952, Harris & Wanless 1990a, Ainley *et al.* 2002). We considered all birds with black, black-mottled, or white-mottled head plumage during the November to February period to be more than 1 year old (after hatch year; AHY). Nestlings depart colonies in juvenile head plumage with a thin neck ring with varying amounts of white on the sides of the head (Hope Jones and Rees 1985). By late September and early October, the thin neck ring is no longer visible in the field in HY birds. Remnants of a thin neck ring are apparent on some birds during the fall and as late as February. We classified all birds with a thin neck ring as HY. Birds in basic head plumage or with thick neck rings were difficult to age, and may included some first year birds changing into alternate plumage (Gaston & Jones 1998). Therefore, we used development of supraorbital ridge and bursa to resolve ambiguities in these head plumage categories and among specimens with heavily oiled plumage.

We removed the skin from the top of the skull to examine development of the supraorbital ridge (SOR). The SOR is a skeletal structure bordering the salt gland, which ossifies during the first winter and continues to thicken with age (Gaston 1984). We classified SOR development into seven categories modified after Gaston (1984): (1) *Not present* (cartilage or no ossification); (2) *Thin* (~0.5 mm band of cartilage with ossified processes at distal ends); (3) *Thin-medium* (~0.5-1.0 mm wide bone ridge); (4) *Medium* (~1.0 mm wide bone ridge, slightly thinner middle section); (5) *Medium-thick* (~1.0 mm wide uniformly thickened ridge); (6) *Thick* (~1.5 – 2.0 mm uniformly thickened ridge); and (7) *Very thick* (> 2.0 mm heavily thickened ridge; Fig. 2). We opened the body cavity and inspected the cloaca region for the presence or absence of the bursa of Fabricius, a lymphatic gland, which is largest in first-year birds and atrophies with age and maturation (King 1956, Siegel-Causey 1990). We measured gonad length, and width (widest part of the ovary, center of the testis), and

Fig. 2. Supraorbital ridge structure of a Common Murre skull (box) and scoring system used in this study. See text for description of codes. The ridge is located at edge of the salt gland depression. It is cartilaginous or non-existent in the youngest birds, SOR = 1, and ossifies with age, forming a thickened ridge in the oldest individuals SOR = 7.



diameter of the largest ovarian follicle (DLF) with a ruler to the nearest 0.5 mm. We used a two-step process to determine age and maturity classes. First, we used head plumage, SOR, and bursa, to separate HY from AHY birds. Second, we divided AHY birds into two maturity classes, subadult and adult, using gonad size (testis width for males and DLF for females). We assumed birds with wider testes and larger ovarian follicles had a high likelihood of past breeding activity.

We used a birth pulse, pre-breeding, 3 x 3 stage-based matrix model to predict a stable stage distribution of HY, subadult, and adult stages. We used the model-derived stage structure to approximate expected age proportions for comparison with observed age class proportions of PRTI birds. The stage-based model has two main assumptions: stages are biologically representative, and matrix probabilities apply equally to all individuals within the stage (Crouse *et al.* 1987, Caswell 2001). We converted stage durations to a common time unit (years), and based fertility probabilities on the number of females giving birth to female offspring (Caswell 2001). In this model, it is necessary to incorporate fledging success into the fertility parameter (H. Moller, *pers. comm.*). We used vital statistics from the literature to calculate matrix parameters for each of three stages: (1) *First year*, from colony departure to second summer including the at-sea chick rearing period (mean annual survivorship [s] = 0.58, Ydenberg 1989), (2) *Subadult*, non-breeding two to four years old (s = 0.89, Ydenberg 1989), and (3) *Breeding adult*, five or more years old (s = 0.94, Sydeman 1993; fledging success = 0.80; Boekelheide *et al.* 1990). We used PopTools (Microsoft Excel) to calculate the expected stable stage distribution.

We examined the age structure of murres collected during other oil spills in California for comparison with the PRTI sample. During the San Francisco spill, Smail *et al.* (1972) provided age classes of 292, and sexes of 324, from a total of 542 carcasses recovered from four rehabilitation centers. During the *Apex Houston* spill, H. R. Carter (unpublished data) examined 167 murres recovered from the South Farallon Islands (n = 21), mainland beaches (n = 48), and the Agnew Rehabilitation Center (n = 98). During the *Command* spill, 129 Common Murres were recovered, 30 were found live, rehabilitated and released, and 99 were recovered dead. We examined 90 of those found dead during the *Command* spill using the same protocol as described for the PRTI sample.

We compared both the observed PRTI two-stage (HY and AHY), and three-stage (HY, subadult, and adult) distributions to model-

derived expected age class frequencies with 2 x 2 (two stage distribution) and 3 x 3 (three stage) chi-square contingency tables (alpha = 0.05). We also compared age distributions from other oil spills in central California with the PRTI and the model using chi-square tests. We tested sex ratio within age groups for equality (1:1, males to females) with a chi-square test with Yates' correction for continuity (Zar 1984).

RESULTS

We were able to classify all carcasses collected during the PRTI into age categories using a combination of SOR, bursa, and head plumage. Our ability to use all age-related characters for each specimen was determined by the condition of the carcass. We could not determine head plumage for heavily oiled or scavenged carcasses, and those missing heads (4%; Table 1). We could not score SOR on carcasses that were heavily scavenged or missing skulls (8%). Decomposition of the bursa prevented age determination in 25% of the carcasses examined. These biases resulted in differing percentages of the total sample classified with each character: head plumage 95.7%; SOR 91.7 %; and bursa 75.0 % (Table 1).

We classified HY birds as those with juvenal head plumage, SOR = 1-4, and bursa present. Most birds with incomplete SOR ossification were in juvenal plumage (SOR = 1-4; 86%; Fig. 3). We classified AHY birds as those with basic, transitional or alternate head plumage, SOR = 5 or greater, and bursa absent. Murres with SOR = 5 were a mix of plumages: alternate (44%); basic (21%); white-mottled (8%); and black-mottled (21%). Most birds with SOR = 6-7 were in alternate plumage (62% and 69%; Fig. 3). We found differences in mean testis width and DLF between SOR 5 and 6 to reflect differences in reproductive maturity states among these age classes (Fig. 4). For both sexes, we further characterized AHY birds with SOR = 5 as subadult and SOR = 6 as adult.

We determined sex for 80% of murre carcasses examined (915 of 1,138). Scavenging and decomposition, exacerbated by freezing and thawing, prevented us from sexing the remaining birds. Sex

Fig. 3. Proportion of plumage states, including black (alternate), black-mottled (transitional to alternate), white-mottled (transitional from basic), white (basic), and juvenal (white with thin neck ring), classified by supraorbital ridge (SOR) score.

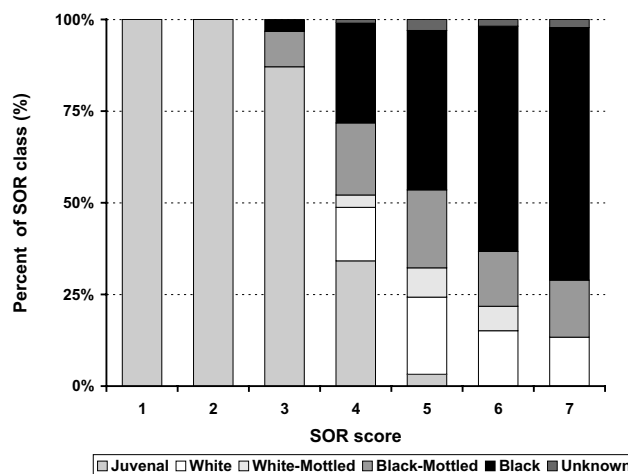
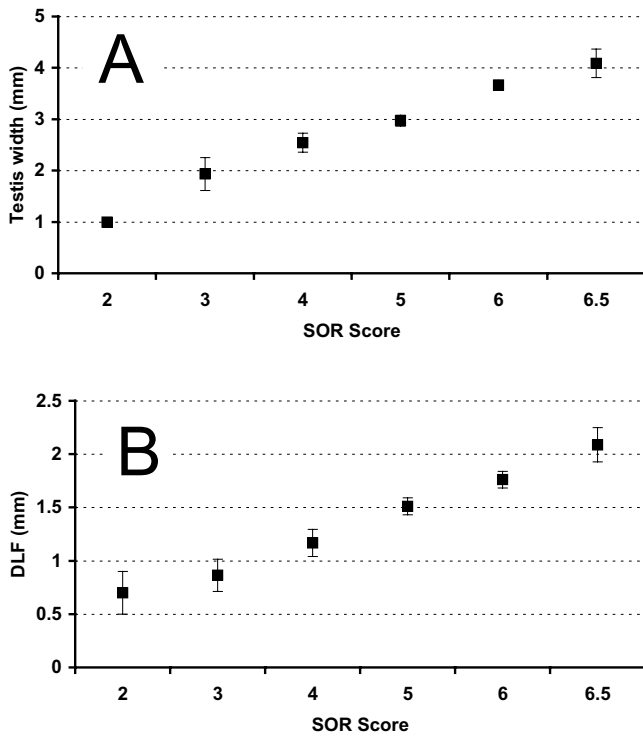


Table 1
Age classification of hatch-year (HY) and after hatch-year (AHY) Common Murres, based on each aging criterion or two or more criteria.

Aging Criterion	Age-Class				Total	
	n	%	n	%	n	%
Head Plumage	102	9.4	987	90.6	1089	95.7
Supra-orbital Ridge	162	15.5	881	84.5	1043	91.7
Bursa of Fabricius	151	17.7	703	82.3	854	75.0
Combined	160	14.1	978	85.9	1138	100.0

ratios differed among age classes. There was no significant difference in numbers of male and female HY birds (1.2:1; $\chi^2 = 1.01$, $df = 1$, $P > 0.05$), but greater numbers of male than female AHY birds (1.5:1; $\chi^2 = 31.12$, $df = 1$, $P < 0.001$; Table 2). Among AHY birds, males outnumbered females for both subadult (1.6:1; $\chi^2 = 18.84$, $df = 1$, $P < 0.001$) and adult age-classes (1.5:1; $\chi^2 = 14.66$, $df = 1$, $P < 0.001$; Table 2). Similar percentages of unsexed birds occurred in each age class (11% HY, 21% subadult, 19% adult), thus the skewed sex ratio in the subadult and adult age classes likely were not affected by our inability to sex birds in a given age class.

Fig. 4. Gonad development increases with age-related supraorbital ridge (SOR) score, a) testis width vs. SOR for males, and b) diameter of largest ovarian follicle (DLF) for females. Mean represented by middle of black square. Error bars represent +/- 1 SD.



Observed percentages of HY (14.6%) and AHY (85.4%) birds did not differ from expected values from the model (13.0% HY and 87% AHY; $\chi^2 = 0.23$, $df = 1$, $P = 0.66$; Table 3). Observed percentages for all three age classes (14.6% HY, 37.6% subadult, 47.8% adult) also did not differ from expected values (13.0% HY, 32.2% subadult, and 54.8% adult; $\chi^2 = 2.00$, $df = 2$, $P = 0.37$; Table 3).

During the San Francisco oil spill, Smail *et al.* (1972) separated carcasses into two age groups based on plumage; “immatures in winter plumage” (n = 198), and “adults in breeding plumage” (n = 94). We assumed Smail *et al.* (1972) combined HY and subadult birds (e.g. juvenal or basic plumage) as immature and re-calculated the PRTI distributions accordingly. The San Francisco oil spill sample had more immatures (67.8%) and fewer adults (32.2%) than the PRTI (52.2% immatures and 47.8% adults; $\chi^2 = 16.0$, $df = 2$, $P < 0.001$; Table 3). The sex ratio was reported as equal in both age groups. However, they sub-sampled 324 of a total of 562 birds at rehabilitation centers and no dead birds were collected from shorelines.

The sample of birds from the *Apex Houston* spill included 36.5% HY in juvenal plumage, 20.4% subadults in basic plumage, and 43.1% adults in alternate or transitional plumage (n = 167). Likewise, the *Apex Houston* spill affected more HY and fewer AHY than expected from the PRTI sample ($\chi^2 = 16.03$, $df = 2$, $P < 0.001$; Table 3). However, AHY birds predominated at the South Farallon Islands and mainland beaches whereas HY birds predominated at rehabilitation centers. Sex ratios of murres from the *Apex Houston* spill were male-biased only among subadults (1.4:1 HY, $\chi^2 = 1.05$, $df = 1$, $P > 0.25$, n = 61; 2.8:1 sub-adult, $\chi^2 = 6.62$, $df = 1$, $P = 0.01$, n = 34; and 0.8:1 adult, $\chi^2 = 0.68$, $df = 1$, $P = 0.37$, n = 72).

During the *Command* spill, only five murres were classified as HY (6%), and the rest of the carcasses were AHY (94%). The age distribution of the *Command* spill was not different from the PRTI sample (9.4% HY and 90.6% AHY; $\chi^2 = 1.36$, $df = 1$, $P = 0.25$; Table 3). Small sample size of HY birds precluded analysis of sex ratio in this age class. In the AHY age class, there were more males than females but the difference was not significant (1.6:1, $\chi^2 = 3.11$, $df = 1$, $P > 0.05$).

TABLE 2
Sex composition of Common Murres within each age class, and maturity category: subadult (SA) and adult (AD). Sex ratio tested against expected 1:1 ratio.

Age-Class	Sex			Total	Sex ratio (M:F)	$\chi^2_{0.05, 1}$	P
	M	F	U				
HY Total	78	65	17	160	1.2 : 1	1.01	"> 0.05, ns"
AHY SA	201	122	85	408	1.6 : 1	18.84	< 0.001
AHY AD	247	168	95	510	1.5 : 1	14.66	< 0.001
AHY U	16	18	26	60	0.8 : 1	0.03	"> 0.05, ns"
AHY Total	464	308	206	978	1.5 : 1	31.12	< 0.001
Grand Total	542	373	223	1138	1.5 : 1	30.85	< 0.001

DISCUSSION

Proportions of age classes killed during the PRTI were similar to the expected age class structure of the model. These results suggest a winter at-sea distribution consistent with a resident population without large age-related differences in dispersal. Experienced breeders often attend colonies during the winter in temperate regions (Harris & Wanless 1989, 1990a, b). Off central California, murres frequently attend colonies between November and the start of egg-laying in April (Boekelheide *et al.* 1990). HY birds are not known to attend colonies in winter and may be more widely dispersed during this time. In the North Atlantic, some HY Common Murres occasionally undergo long-distance southward winter dispersal (Birkhead 1974, Mead 1974). However, based on our sample, a substantial proportion of HY and subadult birds appeared to remain near breeding colonies in the Gulf of the Farallones region during the El Niño winter 1997-98. It is likely that all age classes of the central California murre population were distributed in shelf waters of the Gulf of the Farallones during this spill and thus had similar exposure to oiling during the PRTI.

We found no apparent difference in the sex ratio of HY birds killed during the PRTI. Given an equal sex ratio of chicks at colony departure (Parker *et al.* 1991), these results indicated no difference in winter dispersal and survivorship among male and female HY murres during the El Niño winter 1997-98. We found greater number of males than females among our AHY sample. Whereas breeding adult females may have slightly lower survivorship than males (i.e., 93% vs. 99%; Sydeman 1993), this difference is not likely to account for the large bias in the observed sex ratio. It seems more probable that AHY males were more abundant than

females in the spill-affected area, perhaps because AHY males have lower dispersal and greater colony attendance during winter. At the Isle of May, Scotland, fall colony attendance was mainly by experienced breeding birds of both sexes, but a greater proportion of male non-breeders attend the colony in fall (i.e., 33% male versus 18% female; Harris & Wanless 1989, 1990a, b). The close proximity of the PRTI oil source (*S.S. Jacob Luckenbach*) to breeding colonies in the Gulf of the Farallones may have caused increased oil exposure to subadult and adult males because they are attending colonies and foraging nearby. To elucidate sex-related differences in colony attendance and dispersal patterns, detailed studies of banded pairs and winter radio telemetry studies are needed in central California during winter.

Like the PRTI, other oil spills in California killed mostly adult murres, presumably from central California breeding colonies. The sex ratio was equal among HY birds in all spills, but skewed to males among subadults in *Apex Houston* and among subadults and adults in PRTI, suggesting greater colony attendance of AHY males in the Gulf of the Farallones during winter when these spills occurred. The *Command* and PRTI spills had similar age structure, whereas the San Francisco and *Apex Houston* spills apparently killed proportionately greater numbers of HY birds. We strongly suspect the latter samples were not random or representative of the age groups because of the reliance on carcasses recovered at rehabilitation centers.

Cumulative mortality from oil spills is probably the greatest source of human-related mortality affecting the central California murre population (Nur *et al.* 1997, Carter *et al.* 2001). This population has been recovering since the 1950s from historic declines due to egg

TABLE 3
Comparison of observed age-class distribution from the 1997-98 Point Reyes Tarball Incidents and other oil spills and expected distribution from a stage-based matrix model.

Distribution	Age-Class				n	χ^2	df	P
	% HY	% AHY	% SA	% AD				
1997-98 Point Reyes								
Obs-PRTI	14.6	85.4			1138	0.23	1	0.66, ns
Model (two-stage)	13.0	87.0						
Obs-PRTI	14.6		37.6	47.8	1078	2.00	2	0.37, ns
Model (three-stage)	13.0		32.2	54.8				
1998 <i>Command</i>								
Obs-Cmd	6.0	94			78	1.36	1	0.25, ns
Obs-PRTI ¹	9.4	90.6			1089			
1986 <i>Apex Houston</i>								
Obs-Apex	36.5		20.4	43.1	167	41.18	2	<0.001*
Obs-PRTI	14.6		37.6	47.8	1078			
1971 <i>San Francisco</i>								
Obs-SFO	32.2			67.8	292	16.03	1	<0.001*
Obs-PRTI ²	52.2			47.8	1138			

¹ Age classification based on head plumage only (see Table 1).

² HY and SA classes combined into "immature" category for comparison with Smail *et al.* (1972).

harvesting, oil pollution, and human disturbance (Ainley & Lewis 1974, Boekelheide *et al.* 1990). Recovery stopped with declines in the 1980s resulting from extensive gill net by-catch, oil pollution, and other factors (Ainley & Lewis 1974, Takekawa *et al.* 1990, Carter *et al.* 2001). Many past threats have been lessened, such as a curtailment of coastal gill-net fishing, but oil pollution continues to impact significant numbers of Common Murres (Carter *et al.* 2001).

Because the PRTI killed many thousands of breeding adults from colonies in central California, significant effects on population growth are expected. Since 1998, numbers of murres attending large breeding colonies (i.e. >10,000 pairs) have remained stable or increased despite mortality from past oil spills and continued mortality from the leaking *Lukenbach* (1997-2002; Hampton *et al.* 2003, Himes Boor *et al.* 2003, Knectel *et al.* 2003). These observations suggest that larger colonies have a greater capacity to buffer impacts of oil spills. Density-dependent compensation presumably occurs through increased subadult recruitment. For instance, assuming the population is below historic carrying capacity, vacant breeding sites may allow murres to attempt to breed at a younger age. In contrast, number of murres attending smaller colonies (<10,000 pairs) within the Drake's Bay colony complex (Point Resistance, Miller's Point Rocks, and Double Point; see Fig. 1) were 13% lower during 1999-2000 than in 1997 and growth at these colonies had stalled by 2000 (Carter *et al.* 2003a). PRTI mortality apparently had greater impacts at these smaller colonies. Male-biased mortality of adults may have contributed to reduce attendance at these colonies as males maintain nest sites and attract recruiting subadults to the colony. Future research into age-specific and sex-related demographics of Common Murres is needed to gain a better understanding of how oil spill mortality affects the central California population.

We reduced possible sampling biases associated with non-random sub-sampling by examining all PRTI carcasses available. We assumed that including a small proportion of birds that were not visibly oiled (<10%) did not significantly affect our results. If ages or sexes were distributed differently with respect to distance from shore, some bias may have occurred, because we examined only birds that reached shore. These potential sampling errors aside, we believe the sample we examined was representative of the age structure and sex ratio of the population killed during the PRTI.

By using a combination of age-related traits to classify age classes, we overcame biases associated with any one single criterion. The bursa was useful for aging oiled birds in juvenal or basic plumage when combined with SOR. However, small bursae sometimes were present in birds with high SOR scores and well-developed gonads. This finding is consistent with observations showing the bursa may be retained in some adult breeding birds (Broughton 1994) or become enlarged with immune stress caused by oil exposure (Lowenstein & Fry 1985). In future studies, difficulties in aging murres with the bursa may be resolved by using a gradation of bursa categories (e.g. small, fleshy, thin; Thompson *et al.* 1998) or quantified bursa area (Siegel-Causey 1990).

Overall, the SOR was excellent for separating HY and AHY murres because it was easily located and scored, even among heavily oiled specimens. The main disadvantage to relying solely on the SOR is that heavily scavenged carcasses often are missing skulls. Our results support Gaston's (1984) observation that the SOR does not

develop completely by the end of the first winter. Thus, complete ossification of the SOR apparently occurs during the second year, with additional thickening of the ridge during subsequent years. In several cases, birds with alternate head plumage had lower SOR than expected, suggesting observer error in scoring or variation in ossification among some birds. To reduce observer variability in scoring SOR, we recommend measuring SOR width in future studies. Determination of ages at which stages of ossification occur will require validation with studies of using banded, known-aged birds in the wild or captivity.

ACKNOWLEDGEMENTS

Permission to examine carcasses from the Point Reyes Tarball Incidents and the *Command* oil spill was provided by the California Department of Fish & Game (S. Hampton), National Park Service (S. Allen), U. S. Fish & Wildlife Service (J. Haas), and National Oceanic & Atmospheric Administration (J. Roletto). Administrative support for this work was provided by Moss Landing Marine Laboratories (J. Harvey), Humboldt State University (R. Golightly), and U.S. Geological Survey (D. Orthmeyer). We are particularly thankful to D. Jessup, M. Miller, E. Dodd, and staff at California Department of Fish & Game Marine Wildlife Veterinary Care and Research Center, Santa Cruz who provided facilities and other support. We are extremely grateful to the numerous "murre-a-thoners" who assisted with carcass examinations: L. Algee, J. Adams, D. Adams, S. Allen, K. Andrews, P. Capitolo, M. Chapla, G. Cunningham, A. Den Besten, C. Hamilton, H. Harris, J. Harvey, J. Hawkes, L. Henkel, M. McMurphy, K. Neuman, S. Oates, H. Steed, & G.-J. "JR" Veldink. G. Page, N. Warnock, and L. Spear assisted Carter with carcass collection and examinations during the *Apex Houston* oil spill. P. Capitolo and P. Herbert provided valuable unpublished information. H. Moller provided valuable help with calculating model parameters. Comments from J. Harvey, J. Adams, A. J. Gaston, P. Herbert, and an anonymous reviewer improved the manuscript.

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