AGE-SPECIFIC SURVIVAL, BREEDING SUCCESS, AND RECRUITMENT IN COMMON MURRES (*URIA AALGE*) OF THE CALIFORNIA CURRENT SYSTEM

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Abstract.—Estimating age-specific vital rates and determining which of them have the greatest influence on population trajectory is very useful for conservation and management of at-risk species. We created multistate capture–recapture models to provide estimates of age-specific variation in survival, recruitment, breeding propensity, and breeding success of Common Murres (*Uria aalge*) breeding at Southeast Farallon Island, California. Model-averaged age functions indicated that a "plateauing" (inverse age) function best characterized recruitment probability (transition from nonbreeder to breeder state) and breeding success (fledglings per pair). Adult and juvenile survival and breeding propensity were best modeled as constant with age. We modeled the population using an extended Leslie matrix and determined elasticity values for each of our estimated parameters to determine which have the greatest influence on population growth. Elasticities indicated that variation in adult survival had the greatest influence on population growth rate, but juvenile survival was also important. Increased juvenile survival since 1999, a period of cooler and more productive oceanic conditions, is probably largely responsible for the population growth observed during this period. *Received 5 January 2007, accepted 31 May 2007.*

Key words: age at first breeding, Alcidae, Common Murre, demography, elasticity, mark–recapture, multistate, *Uria aalge*.

Estimados de Supervivencia, Éxito Reproductivo y Reclutamiento Específicos para Distintas Edades en *Uria aalge* en el Sistema de Corrientes de California

Resumen.—Estimar las tasas vitales específicas de distintas edades y determinar cuáles de ellas tienen la mayor influencia en la trayectoria de las poblaciones es muy útil para la conservación y el manejo de las especies en riesgo. Creamos modelos de captura-recaptura de estados múltiples para brindar estimados de la variación relacionada con la edad de la supervivencia, el reclutamiento, la propensión a reproducirse y el éxito reproductivo de individuos de la especie *Uria aalge* que nidifican en la Isla Southeast Farallon, California. Las funciones de la edad promediadas entre los modelos indicaron que una función con una "meseta" (edad invertida) caracterizó mejor la probabilidad de reclutamiento (transición del estado no reproductivo al estado reproductivo) y el éxito reproductivo (volantones por pareja). La supervivencia de los adultos y de los juveniles y la propensión a reproducirse fueron modeladas mejor como constantes con la edad. Modelamos la población usando una matriz de Leslie extendida y determinamos los valores de elasticidad para cada uno de nuestros parámetros estimados para determinar cuáles tienen la mayor influencia en el crecimiento poblacional. Las elasticidades indicaron que la variación en la supervivencia de los adultos tuvo la mayor influencia en la tasa de crecimiento de la población, pero la supervivencia de los juveniles también fue importante. El incremento en la supervivencia de los juveniles desde 1999, un período de condiciones oceánicas más frías y productivas, es probablemente el principal responsable del crecimiento poblacional observado durante este período.

Development of effective conservation and management measures for at-risk species is facilitated by understanding age-specific demography and the relative influence of various parameters on population growth rates. Seabird species are of particular conservation concern, because of their vulnerability to a variety of human activities, including direct (bycatch) and indirect (prey depletion) effects of fisheries, disturbance at nesting colonies, global climate change, oil spills, and other factors (Boersma et al. 2002).

Seabirds typically have life histories characterized by low productivity, delayed maturity, and relatively high adult survival probabilities, though there is a wide spectrum of strategies along

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the *r*-selected to *k*-selected gradient (Weimerskirch 2002). Of these components, adult survival has high elasticity values and, as such, strongly influences population dynamics (Russell 1999, Crone 2001). However, both juvenile survival and the age at which an organism starts to reproduce (called "primiparity," "age of first breeding," or "recruitment age"), parameters that are much more difficult to estimate, are important traits that also influence population dynamics (Croxall and Rothery 1991, Hatchwell and Birkhead 1991, Charnov 1997, Morris and Doak 2002). Recruitment age is considered an important life-history trait with a profound influence on fitness (Cole 1954, Stearns 1992). Variation in recruitment age can also strongly influence population growth (Caswell 2001). However, reproductive success and survival commonly increase with age (Sæther 1990, Forslund and Pärt 1995, Reid et al. 2003), and the strength of this increase will greatly influence whether or not early maturity is favored by selection.

Here, we estimate age-specific demographic traits of Common Murres (*Uria aalge*; hereafter "murres") in the eastern north Pacific Ocean. We studied murres on Southeast Farallon Island (SEFI), California, in the central portion of the California Current System (CCS). Murres on SEFI feed primarily on euphausiid crustaceans, California Market Squid (*Loligo opalescens*), and a wide range of pelagic schooling fish including California Anchovy (*Engraulis mordax*) and juvenile rockfish (*Sebastes* spp.) (Ainley et al. 1996, Sydeman et al. 2001, Miller and Sydeman 2004). The murre population on SEFI has suffered historical declines attributed to egg collecting, gill-net bycatch, oil spills, and human disturbance (Boekelheide et al. 1990, Manuwal et al. 2001), and they continue to be severely affected by interactions with humans. The murre is often the species affected in the greatest numbers by oil spills (e.g., Page et al. 1990, Piatt et al. 1990). Also, murres consume a significant proportion of the forage biomass in the CCS (Wiens and Scott 1975, Briggs and Chu 1987), which places them in direct competition with human commercial fisheries (Dayton et al. 2002). These interactions, coupled with historical population declines, make this a species of conservation concern (U.S. Fish and Wildlife Service [USFWS] 2005) and one that warrants detailed estimates of demographic traits for population-dynamics modeling.

The objectives of the present study were to (1) estimate age-specific variation in survival, recruitment probability, breeding propensity, and breeding success; (2) select a model of age functions using five competing age-specific curves and model averaging; and (3) develop a matrix population model to identify the demographic parameters that have the greatest potential effect on the finite rate of population growth (λ). In this context, we were not interested in temporal variation in parameter estimates; thus, to focus on age-specific patterns, we constrained estimates to be equal across years, using separate estimates for El Niño years only.

Methods

Data collection.—Data for this study were collected from 1986 to 2004 on SEFI, Farallon Island National Wildlife Refuge, California (37°42′N, 123°00′W), site of one of the largest murre populations in the continental United States. Biologists from PRBO Conservation Science (formerly Point Reyes Bird Observatory; hereafter "PRBO") have been monitoring the population size, reproductive success, and diet of murres on SEFI since 1972.

We surveyed the murre breeding population every year during peak incubation (late May to early June) over a period of two to three days, using a combination of land- and boat-based surveys, weather permitting. For these surveys, the island is divided into sectors and all individual birds are counted by experienced observers from standardized locations using binoculars or a spotting scope. A correction factor was applied to the raw count of individuals to account for adults that were not attending the colony at the time of the census. The correction factor is derived by multiplying the number of breeding sites in monitored productivity plots by 2, to obtain the number of breeding adults, and then dividing the product by the mean number of adults present on the study plots during the survey (N. Nur and W. J. Sydeman unpubl. data). In years when the boat-based portion of the survey could not be completed (because of prolonged rough sea conditions), we applied a second correction factor to account for the proportion of the population that would normally be surveyed from the boat. This correction factor was computed from years in which the entire survey was completed.

Chicks aged 10–20 days were captured from 1986 to 2001 at a small colony (Colony UU; called "Colony II" in Sydeman 1993) at the peak of the breeding season and banded with a federal band and three color bands, producing a unique band combination for each individual. Each year from April through mid-July, we searched for banded birds daily; typically, 3–4 h per day were spent on resighting efforts, especially early in the nesting period. Birds were confirmed as resighted if their color-band combination was recorded at least three times during the season. Each time an individual was resighted, its breeding status ("breeder" or "nonbreeder") was determined on the basis of whether an egg was laid at its site. Annual records of resightings and breeding status were compiled as individual encounter histories through time. Breeding success of birds that attempted to breed was coded as 0 or 1, depending on whether their chick survived to 16 days posthatching, which is considered the minimum fledging age for a chick (Boekelheide et al. 1990).

Statistical analyses.—We followed the example of Cam et al. (2005) and used multistate modeling to model and obtain estimates of the demographic traits of interest. Annual observations for each individual were classified according to breeding "state" (nonbreeder = N, breeder = B). When data from both prebreeders and breeders are available, multistate models (e.g., Brownie et al. 1993, Nichols et al. 1994, Nichols and Kendall 1995) should be used to address recruitment and survival while accounting for age- and state-specific recapture probability (e.g., Cam et al. 2002, 2003). For multistate models, codes are used in the longitudinal individual encounter histories to distinguish the state of an individual at each sampling occasion (year). Multistate models allow estimation of age- and state-specific survival probabilities (e.g., S^N_i, the probability that a nonbreeding individual survives between age *i* and age *i* + 1) and age-specific transition probabilities (Ψ) between nonbreeder and breeder states (e.g., Ψ^{NB}_i, the probability that an individual that is in state N at age *i* and that survives to age *i* + 1 is in state B at the latter age [Nichols et al. 1994]); Ψ^{NB}_i for young birds corresponds to the recruitment probability.

Recruitment is a probabilistic event that is conditional on three different, potentially independent probabilities (Clobert

et al. 1993): (1) that an individual survives from birth to age $i - 1$, (2) that it exhibits fidelity to the natal area, and (3) that, alive and in the "prebreeder" state at age $i - 1$, it survives and is in the "breeder" state at age i. Hereafter, when we refer to "recruitment probability," we mean this transition probability from nonbreeder to first-time breeder (Pradel and Lebreton 1999). As Clobert et al. (1993) emphasized, unless relevant data from colonies within the plausible range of natal dispersal are available, the first two components cannot be separated and their product is "apparent survival" (S). Because there are no banding and resighting data from nearby colonies, we will deal only with apparent survival here.

These models also estimate the parameter Ψ^{BN}_i, which is the probability of transitioning from breeder to nonbreeder, also called "skipping probability." The complement of this parameter, Ψ^{BB}_i, is "breeding propensity," the conditional probability that an individual that bred in year $i - 1$ will breed in year i, given that it has survived to that year. Breeding propensity is difficult to measure and is often ignored (Nur and Sydeman 1999).

The parameter p is "recapture probability." The recapture probability of species with high natal-site fidelity, such as seabirds, is interesting with regard to young, nonbreeding birds because it incorporates the probability that birds of a given age will return to their natal area to prospect for mates and nest sites. Recapture probability of breeders in this model is essentially a "nuisance parameter," but a necessary one if the analysis is to provide less biased estimates of survival and transition probabilities.

Previous studies on marine birds have documented the age-specific survival curve as a constant (Potts et al. 1980, Nur and Sydeman 1999, Lee et al. 2007), as a negative linear function (Dunnett and Ollason 1978, Spear et al. 1987, Crespin et al. 2006b), as a constant that exhibits senescent decline in the oldest individuals (Buckland et al. 1983, Bradley et al. 1989, Aebischer and Coulson 1990, Croxall et al. 1990), or as a quadratic curve whereby survival increases with age to a midlife optimum, then declines as the oldest individuals senesce (Rattiste and Lilleleht 1987, Frederiksen and Bregnballe 2000). Age-specific breeding success in seabirds has been estimated as a positive linear relationship (Mills 1989, Sæther 1990), as a positive quadratic curve (Wooller et al. 1989, Forslund and Pärt 1995, Crespin et al. 2006b), or as steadily increasing to an asymptote and then remaining constant (Wooller et al. 1992, Mauck et al. 2004, Lee et al. 2007). Age-specific breeding propensity has been described infrequently for seabirds, but varying patterns have been observed: a linear increase with age (Ollason and Dunnett 1988, Thomas and Coulson 1988); a steady increase to an asymptote, then constancy (Wooller et al. 1989); or a linear decrease with age (Mills 1989).

With these previous studies in mind, our *a priori* model set for age functions included S, p, and Ψ parameters modeled separately for each state (N and B), and the *rs* (breeding success) parameter as (1) "constant," (2) linear (increase or decrease) with age ("linear age"), (3) quadratic with age (age + age^2; "age^2"), (4) increasing, deceleratingly, with age ("ln(age)"), and (5) plateauing with age ("1/age").

To obtain age-specific survival, recapture, and transition probability estimates, we used multistate mark–recapture models in MARK (White and Burnham 1999). We used a fully age-specific model with 15 age classes to obtain age-specific

estimates and assess goodness of fit. Age classes >14 years were pooled because of small sample sizes in the oldest age classes. The program U-CARE (Choquet et al. 2005) indicated some lack of fit between our data and the JollyMove model S(state*time)p(state*time)Ψ(state*time) because of age-dependant or age-like overdispersion (tests 3G.SR and M.ITEC), but the age structures we went on to investigate accounted for this lack of fit in the state- and time-dependent JollyMove model. We used the bootstrap approach available in MSSURVIV (Hines 1994) to estimate an overdispersion parameter ($\hat{c}$) based on 100 simulations of our state- and age-dependent general model S(state*age15)p(state*age15)Ψ(state*age15). The value of $\hat{c}$ was 1.464, which indicates minimal overdispersion of our state- and age-dependent general model (Cooch and White 2007) and confirms our decision to model temporal variation as a constant. Model selection was subsequently based on QAIC$_c$ (Akaike's Information Criterion corrected for small sample sizes, based on quasi-likelihood; Burnham and Anderson 2002) in MARK (White and Burnham 1999). All age-specific estimates were generated using a time-constant model.

We also examined breeding success (fledglings pair^{-1}) of known-age birds from 1989 to 2004. Breeding success (*rs*) in relation to age was assessed using a generalized linear model (GLM). Because the reproductive output included failed breeding attempts, we used a binomial error structure and logit link function (Nielsen and Drachmann 2003).

We used QAIC$_c$ weights as a measure of the strength of evidence for a given model. Because of uncertainty in model selection, information from all models in the set with QAIC$_c$ weight > 0 should be considered when making inferences (Burnham and Anderson 2002). The ratio of QAIC$_c$ weights between two models computes how many times better the evidence is that the numerator model is better than the denominator model (Burnham and Anderson 2002). We computed model-average parameters using QAIC$_c$ weights as the weighting factor.

We performed model selection on each parameter sequentially, obtaining model ranks and weights and computing model average curves in this order: p^N, p^B, Ψ^{NB}, Ψ^{BN}, S^B, and S^N. In each sequential step, we kept previously modeled parameters in their most parsimonious form (Lebreton et al. 1992). We confirmed earlier sequential model rankings by repeating model selection on each parameter with all other parameters in their most parsimonious form. We selected models for each parameter individually, but we also examined the evidence for equality of survival in breeders and nonbreeders using all possible age functions. We used the logit link function throughout, and second-part variance-estimation procedure. Model selection for *rs* was performed in STATA, version 8.2 (Stata, College Station, Texas), using the *a priori* age models described above for p, Ψ, and S, as well as additional models that controlled for El Niño years in 1992 and 1998 because island-wide productivity was known to be >1 SD lower than average in those years (PRBO unpubl. data).

Using the program ULM (Legendre and Clobert 1995), we created an extended Leslie matrix population model with 15 age classes, where birds remain in the oldest age class as adults, with no mandatory mortality. Fecundity for each age class was calculated using recruitment and breeding success (halved, assuming an equal sex ratio at fledging). Survival for each age class from 0

to 12 years was parameterized with estimated model average values for breeders in the present study. Survival of the oldest age class was taken from mean annual survival estimated over 19 years for birds captured as adults in the same area (PRBO unpubl. data). Elasticity values for each parameter, and population-stable age-distribution, were calculated in ULM (Legendre and Clobert 1995).

RESULTS

The population of murres on SEFI was fairly stable from 1986 to 1993, then rose to a new level from 1995 to 2001, and has been growing dramatically since then (Fig. 1). By contrast, the population of the UU colony grew rapidly in the first years after colony initiation but has declined since its peak in 1989 (Fig. 1). The primary reason for the difference between this colony and the overall population is the small size of the UU colony and its consequent vulnerability to predation and disturbance by Peregrine Falcons (*Falco peregrinus*) and Western Gulls (*Larus occidentalis*) (Sydeman 1993, PRBO unpubl. data).

From 1986 to 2001, we marked and released 375 murre chicks (age 0) at the UU colony; only chicks that fledged were considered released. Model-selection results for recapture, transition, and survival probabilities are given in Table 1. The only strong age effects were found in recapture probability of nonbreeders (Fig. 2),

and recruitment (Fig. 3). The recapture probability of nonbreeders indicates return to the natal colony to prospect for a breeding site and mate. Both these parameters were most parsimoniously modeled by the inverse age function.

The recapture probability of nonbreeders climbed to an asymptote at age seven years, and recapture probability of breeders was nearly constant at 0.964 ± 0.034 (mean $\pm$ SE) but declined slightly with age (Fig. 2). Recruitment remained near zero until age four years, climbed to 0.51 by age nine years (Fig. 3), and remained constant through the older age classes. Most individuals of a cohort recruit at age six (22%) or seven (22%); by age nine, an average of 91% of a given cohort will have recruited (Fig. 3). The skipping probability (transition probability from breeder to nonbreeder) was nearly constant at 0.037 ± 0.037. Given the very high breeding-site fidelity in this species, it is logical that the recapture rate of breeders and skipping probability are complementary.

The model average age curve for apparent survival of breeders showed decelerating increase with age (Fig. 4; mean survival age $6–15 = 0.895 \pm 0.047$). Nonbreeder survival is essentially constant at 0.667 ± 0.058. There was little evidence supporting equal survival of breeders and nonbreeders (Table 2); the model of differential constant survival was $>12\times$ better than the highest-ranking model of equal survival. Multiple models of breeding success received high $QAIC_c$ weight (Table 3). The model average curve shows an increase in breeding success as birds reached ages 9–10,
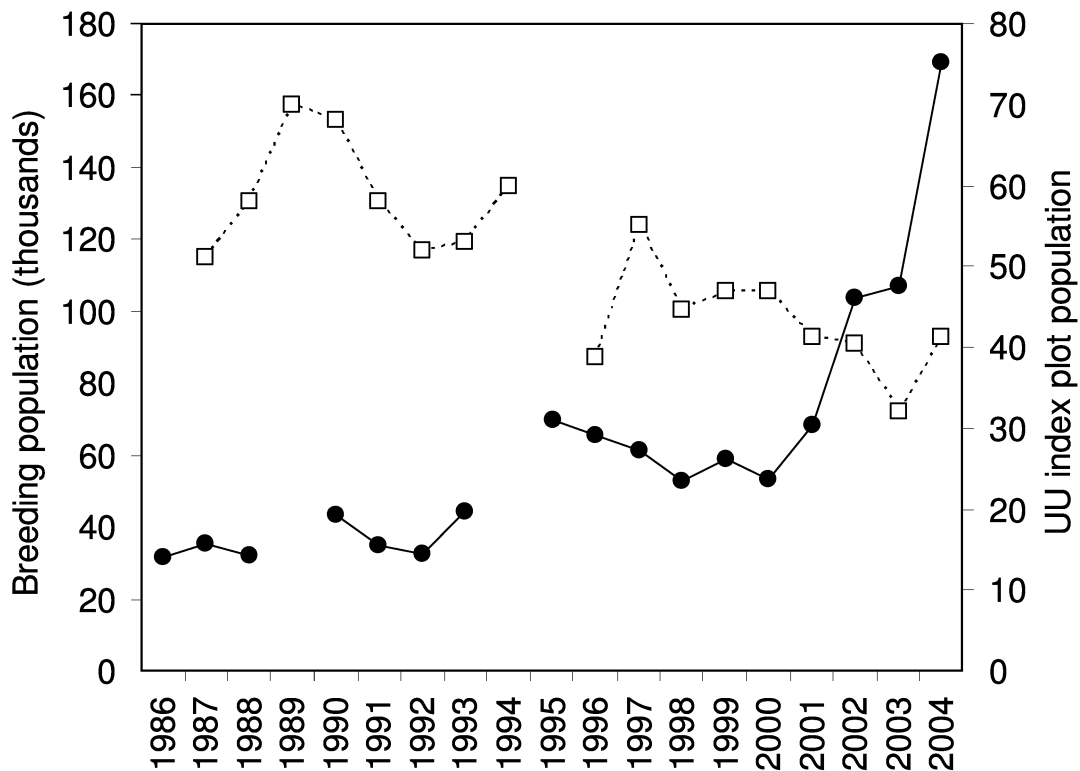

FIG. 1. Breeding population of Common Murres in the southern Farallon Islands (filled circles), California, and in the UU colony (unfilled squares) on Southeast Farallon Island, 1986–2004.

TABLE 1. Table of model-selection results for age effects on recapture (*p*), transition (Ψ), and survival (S) probabilities of nonbreeder (N) and breeder (B) Common Murres on Southeast Farallon Island, California, from 1986 to 2004; *ĉ* = 1.464. The most parsimonious model for each parameter is in bold; weights in bold indicate the strength of evidence that the most parsimonious model is the best of the set.

Parameter	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	*k*	QDeviance
p^N	**1/age**	875.99	0	**0.97**	77	327.97
	ln(age)	883.19	7.20	0.03	77	335.17
	age^2	893.93	17.94	0	78	343.26
	linear age	897.86	21.87	0	77	349.85
	age categorical	903.20	27.21	0	90	319.84
	constant	942.08	66.09	0	76	396.71
p^B	**constant**	845.35	0	**0.50**	63	333.44
	linear age	847.73	2.39	0.15	64	333.31
	ln(age)	847.77	2.42	0.15	64	333.35
	1/age	847.80	2.45	0.15	64	333.38
	age^2	850.20	4.85	0.04	65	333.25
	age categorical	875.99	30.65	0	77	327.97
Ψ^{NB}	**1/age**	824.21	0	**0.65**	50	344.16
	age^2	825.84	1.63	0.29	51	343.40
	ln(age)	828.93	4.72	0.06	50	348.88
	linear age	838.27	14.06	0	50	358.22
	age categorical	845.35	21.14	0	63	333.44
	constant	866.86	42.65	0	49	389.20
Ψ^{BN}	**constant**	795.47	0	**0.43**	36	348.05
	1/age	797.32	1.86	0.17	37	347.64
	ln(age)	797.35	1.88	0.17	37	347.66
	linear age	797.35	1.89	0.17	37	347.67
	age^2	799.62	4.16	0.05	38	347.65
	age categorical	824.21	28.74	0	50	344.16
S^B	**constant**	773.81	0	**0.35**	22	357.43
	linear age	774.94	1.13	0.20	23	356.39
	ln(age)	775.08	1.27	0.19	23	356.53
	1/age	775.19	1.38	0.18	23	356.64
	age^2	776.80	2.99	0.08	24	356.08
	age categorical	795.47	21.65	0	36	348.05
S^N	**constant**	753.00	0	**0.43**	8	366.15
	ln(age)	754.90	1.90	0.17	9	365.98
	1/age	754.93	1.93	0.16	9	366.01
	linear age	754.96	1.96	0.16	9	366.05
	age^2	756.47	3.47	0.08	10	365.49
	age categorical	773.81	20.81	0	22	357.43

a plateau, and a slight decrease in the oldest age classes that possibly indicates breeding senescence (Fig. 5).

We parameterized our extended Leslie matrix population model for UU murres using values in Table 4. The finite rate of population growth (lambda) from the model was 0.978, indicating a population declining at 2.2% per annum. The value of lambda calculated for this site from 1987–2004 using the population census data is 0.987 (Fig. 1). Elasticities indicated that changes in adult survival had the greatest proportional effect on lambda (Table 4); however, elasticities for adults are biased high, because individuals recycle within that matrix cell for many years. When the matrix is expanded to 40 age classes, juvenile survival probabilities are the matrix cells with the highest elasticity values.

DISCUSSION

Here, we provide estimates of age-specific variation in survival, recruitment, breeding propensity, and breeding success for Common Murres in the eastern north Pacific Ocean. Our model selection of age functions for these demographic parameters indicated that the inverse age function best characterized the relationship between age and the probability of recruiting, followed closely by the quadratic model. Our results show that most murres on SEFI recruit at age six or seven. Our estimates of recruitment age for murres in the Pacific closely resemble estimates made at colonies in Great Britain (Birkhead and Hudson 1977, Swann and Ramsay 1983, Harris et al. 1994). Crespin et al. (2006a) showed that recruitment of cohorts in this species varies in relation to ocean climatic
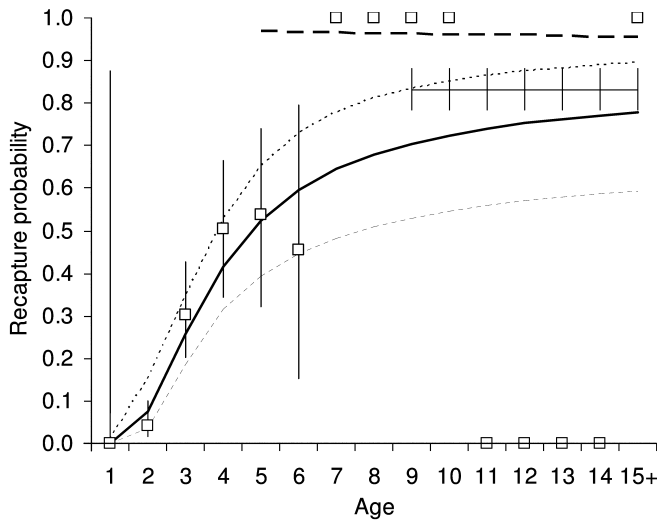
FIG. 2. Age-specific estimates (squares) of recapture probability for non-breeding Common Murres fledged at the UU colony of Southeast Farallon Island, California, 1986–2001. Recapture probability of nonbreeders indicates probability of returning to the colony to prospect for mates and nest sites, a prerequisite to primiparity. Error bars indicate 95% confidence intervals (CI) of estimates. The heavy black line indicates the model average age-curve for nonbreeders, and the dotted black lines are 95% CI of model average age-curve for nonbreeders. The dashed black line is recapture probability of breeders. The thin line is recapture probability of breeding birds banded as adults at the same site, and error bars indicate 95% CI.

FIG. 4. Age-specific estimates (squares) of local survival probability for breeding Common Murres fledged at the UU colony of Southeast Farallon Island, California, 1986–2001. Error bars indicate 95% confidence intervals (CI) of estimates. The heavy black line indicates model average age curve, and the dotted black lines are 95% CI of model average curve. The thin line is mean local survival probability of breeding birds banded as adults at the same site, and error bars indicate 95% CI.

conditions; murres begin breeding at an earlier age when environmental conditions are favorable, presumably because of enhanced prey availability. Colony size may also influence recruitment, because young birds may have to wait longer for a breeding site in dense colonies (Swann and Ramsay 1983).

Our results also show that murres rarely skip a year once they have initiated breeding. The probability of skipping is ~4%, which means that 96% of birds that bred the previous year remain in the breeder state the following year. This skipping probability is similar to, but slightly lower than, estimates from North Sea colonies (5–10%; Harris and Wanless 1995, Harris et al. 1996b). Generally, birds that skip a year of breeding have lost a mate, lost their breeding site, or suffered low breeding success in the previous year (Harris et al. 1996b, PRBO unpubl. data). Beyond age 10,
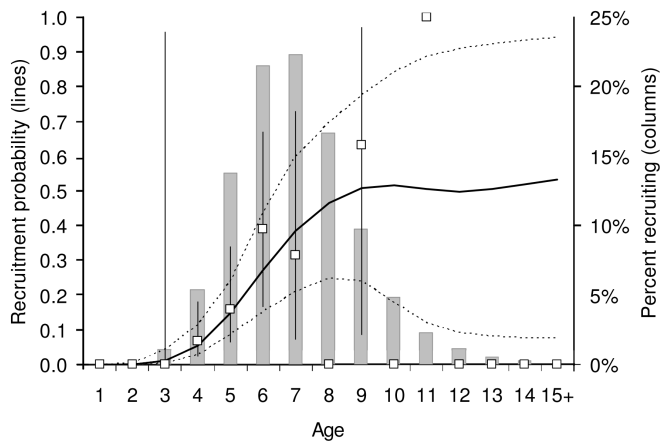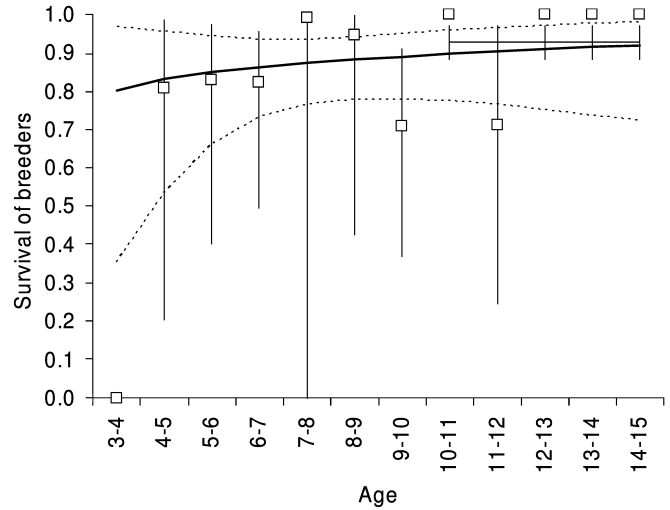

FIG. 3. Age-specific estimates (squares) of transition probability from nonbreeding to breeding state for Common Murres fledged at the UU colony of Southeast Farallon Island, California, 1986–2001 (left axis). Transition probability from nonbreeding to breeding state indicates recruitment, or probabilistic age of first breeding. Error bars indicate 95% confidence intervals (CI) of estimates. The solid black line indicates model average age curve, and the dotted black lines are 95% CI of model average age curve. Columns represent the mean proportion of each cohort that would recruit at each age, given the model average age-specific recruitment probabilities (right axis).

TABLE 2. Table of model-selection results for evaluating whether local survival (S) is identical for breeding and nonbreeding Common Murres on Southeast Farallon Island, California, from 1986 to 2004; $\hat{c} = 1.464$.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	k	QDeviance
S^{N+B} (constant)	753.00	0	**0.85**	8	366.15
$S^{N=B}$ (age^2)	758.11	5.11	0.07	9	369.20
$S^{N=B}$ (linear age)	758.36	5.36	0.06	8	371.51
$S^{N=B}$ ln(age)	761.02	8.02	0.02	8	374.17
$S^{N=B}$ (1/age)	763.09	10.09	0.01	8	376.24
$S^{N=B}$ (constant)	766.28	13.28	0	7	381.49
$S^{N=B}$ (age categorical)	769.27	16.28	0	21	355.05

TABLE 3. Model-selection results for breeding success (*rs*) of Common Murres on Southeast Farallon Island, California, from 1986 to 2004; EN controls for El Niño effects in 1992 and 1998 breeding seasons.

Model	AIC_c	ΔAIC_c	AIC_c weight	*k*	Deviance
EN + 1/age	156.22	0.00	**0.28**	2	76.06
EN + age^2	156.63	0.41	0.23	3	75.22
EN	156.65	0.43	0.22	1	77.31
EN + ln(age)	157.47	1.25	0.15	2	76.69
EN + linear age	158.31	2.09	0.10	2	77.11
1/age	162.97	6.75	0.01	1	80.47
age^2	164.06	7.84	0.01	2	79.98
ln(age)	164.17	7.95	0.01	1	81.07
linear age	165.20	8.98	0.00	1	81.58
EN + age categorical	169.37	13.15	0.00	13	70.06
age categorical	175.51	19.29	0.00	12	74.38

we observed nearly constant transition probability of nonbreeder to breeder, at ~50%. After age 10, this transition parameter largely represents adult birds that returned to breeding after a failure to breed for a year or more, because >95% of juvenile birds have begun breeding by age 10. So, of the ~4% of adult birds that skip breeding in any given year, ~50% return to breed in the next year. The slight positive trend in skipping probability with age may indicate some senescence in breeding effort or it may reflect the time it takes to acquire a new mate or site if one member of the breeding pair dies.

Breeding success was the only other parameter to show evidence of age effects, and the inverse of age was the most parsimonious function. However, the quadratic age function and the constant (no age effect) model also performed well. Because of uncertainty in model selection and the high rank of the constant model, age effects in breeding success are only weakly supported, and interpretations are speculative. The model average curve
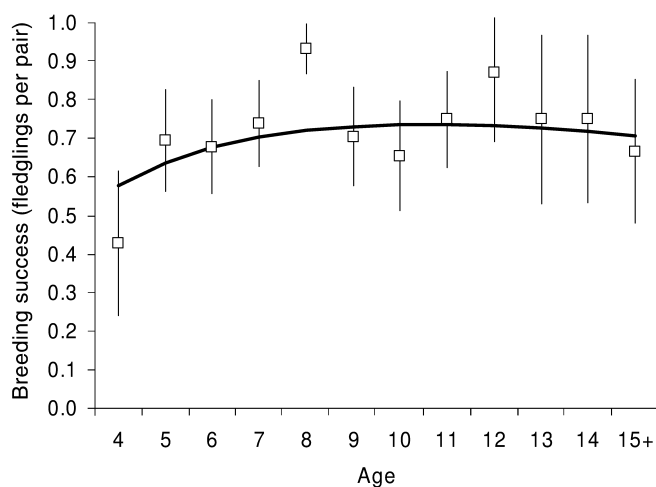

FIG. 5. Age-specific estimates (squares) of breeding success for Common Murres fledged at the UU colony of Southeast Farallon Island, California, 1986–2001. Error bars indicate 95% confidence intervals of estimates. The solid black line indicates model average age curve for breeding success.

TABLE 4. Model average parameter estimates used in Leslie matrix population model of Common Murres on Southeast Farallon Island, California, from 1986 to 2004; SAD = stable age distribution. The finite population-growth rate (λ) from the matrix thus parameterized was 0.978.

Fecundity	Matrix value	Elasticity	Survival	Matrix value	Elasticity	SAD
f1	0	0	s1	0.596	0.040	
f2	0	0	s2	0.671	0.040	0.174
f3	0	0	s3	0.754	0.040	0.107
f4	0.003	0.000	s4	0.803	0.040	0.074
f5	0.019	0.001	s5	0.831	0.039	0.057
f6	0.065	0.001	s6	0.849	0.039	0.047
f7	0.142	0.001	s7	0.862	0.038	0.040
f8	0.226	0.002	s8	0.873	0.036	0.035
f9	0.291	0.002	s9	0.882	0.034	0.030
f10	0.331	0.002	s10	0.890	0.033	0.030
f11	0.352	0.002	s11	0.897	0.031	0.030
f12	0.360	0.002	s12	0.904	0.029	0.020
f13	0.363	0.002	s13	0.910	0.027	0.020
f14	0.362	0.002	s14	0.915	0.026	0.020
adult	0.362	0.026	adult	0.927	0.470	0.298

indicates a peak in breeding success at age 10–11 and a decrease thereafter. The lower breeding success among young birds is predicted by life-history-strategy theory: young animals should invest less in reproduction than older birds (Pianka and Parker 1975; Pugesek 1981, 1983). Age-related differences in breeding success could also be the result of differences in foraging abilities among age classes, though this has been studied infrequently (Burger 1980). Another explanation is a decrease in the heterogeneity in individual quality with age, owing to selection pressure (Cam and Monnat 2000). The decrease in breeding success among older birds, coupled with increased skipping probability with age, may indicate reproductive senescence, but patterns of decline are not particularly convincing. Reproductive senescence has been suggested for murres in the North Sea, with an age curve for reproductive success similar to that reported here (Crespin et al. 2006b), but this may also be attributable to long-term environmental change.

Survival of known-age breeders compares well with survival estimates of murres banded as adults at the same site (Fig. 3; Sydeman 1993, D. E. Lee et al. unpubl. data). Local apparent survival is composed of true survival and permanent emigration, but the high site-fidelity of this species leads us to believe that variation in local survival is largely attributable to mortality. Observations of banded birds at the UU colony indicate a very low rate of movement or dispersal among closely situated subcolonies (PRBO unpubl. data). However, the presence of any permanent emigration would bias our survival estimates lower than the true survival probability. Prebreeding murres often prospect at their natal colony before dispersing to other sites (Halley et al. 1995, Harris et al. 1996a, Crespin et al. 2006a), and that emigration would be mistaken for mortality. Harris et al. (2007) found that most young murres at Isle of May, Scotland, that survive their first two years at sea return to the natal colony. Fidelity to age two years was estimated as 96%, though confidence limits were very wide. Fidelity decreased gradually after the age of three, falling to 69% from the sixth year onward. This reflects permanent emigration from the colony, loss of color bands, and breeding birds being less visible

than prebreeders (Harris et al. 2007). Prospecting birds thus favor their natal colony, and prebreeders decide to disperse to other colonies if conditions are bad at the natal colony or if they are unable to secure a site there (Dittmann et al. 2005, Harris et al. 2007). We found no evidence of actuarial senescence, in contrast to the findings of Crespin et al. (2006b), but the birds in that study were banded as adults and reached much higher ages than our sample.

Population modeling.—Our matrix population model identified adult survival as the demographic parameter with the greatest influence on the finite rate of population change (lambda). However, adult survival encompasses many age classes, leading to biased elasticity for that matrix cell value compared with the single age class in every other cell of the matrix. It is more informative to look at the elasticities of younger age classes and note the inverse relationship of elasticity and age. Survival elasticities were all an order of magnitude greater than elasticities for fecundity rates.

Recently, the murre population on SEFI has grown dramatically; this is presumably attributable to a few productive years in 1999–2002 (Peterson and Schwing 2003; Goericke et al. 2004, 2005). This pattern of ecosystem productivity reversed after 2003 (Peterson et al. 2006, Sydeman et al. 2006). We observed no increase in breeding success during the productive 1999–2002 period when the new recruits contributing to population growth were fledged, which indicates that juvenile survival was most likely the driving force behind population growth; however, immigration could also play a part. Another important consideration is that adverse environmental changes, such as severe El Niño events, that reduce adult survival in every age (Sydeman 1993, Ainley et al. 1994) will cause population declines and reduce future growth. Therefore, for murres of the central CCS, boom-and-bust cycles hinge on variation in both survival and recruitment probabilities. Boom years apparently result from higher-than-normal survival of young birds to recruitment age, not from hugely successful reproduction. It remains to be seen whether bust years are a function of reduced survival across all age classes, or whether certain groups or ages are harder-hit. Differential mortality could result in different population-level responses. The age-specific parameter estimates presented here provide the basis for future population-modeling efforts, including estimates of damage from oil spills.

It should be understood that the demographic parameters we estimated and used to parameterize our population model were from a small sample of birds from a single subcolony on the Farallons that may or may not reflect the demographic parameters at other locations. We know that parameters are lower at the UU colony than at other monitored areas of the SEFI population (PRBO unpubl. data), and our population model closely matched the observed population trajectory for the UU subcolony. Therefore, we believe that the model is valid but that the parameters may need to be adjusted upward to reflect the positive population trend at most other subcolonies. Future efforts with larger sample sizes would also permit more precise modeling of age-specific curves.

Acknowledgments

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