Age-specific birth rates of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico

CLAUDIA J. HERNÁNDEZ-CAMACHO

Laboratorio de Ecología de Pinnípedos "Burney J. Le Boeuf,"
Centro Interdisciplinario de Ciencias Marinas,
Instituto Politécnico Nacional,
Ave. IPN s/n Colonia Playa Palo de Santa Rita,
La Paz, Baja California Sur, Mexico 23096
and
School of Life Sciences,
Arizona State University,
P. O. Box 874601, Tempe, Arizona 85287-4601, U.S.A.
E-mail: Claudia.J.Hernandez@asu.edu

DAVID AURIOLES-GAMBOA

Laboratorio de Ecología de Pinnípedos "Burney J. Le Boeuf,"
Centro Interdisciplinario de Ciencias Marinas,
Instituto Politécnico Nacional,
Ave. IPN s/n Colonia Playa Palo de Santa Rita,
La Paz, Baja California Sur, Mexico 23096

LEAH R. GERBER

School of Life Sciences,
Arizona State University,
P. O. Box 874601, Tempe, Arizona 85287-4601, U.S.A.

ABSTRACT

Estimates of demographic parameters are essential for assessing the status of populations and assigning conservation priority. In light of the difficulties associated with obtaining such estimates, vital rates are rarely available even for well-studied species. We present the first estimates of age-specific birth rates for female California sea lions (*Zalophus californianus*) >10 yr of age. These rates were estimated from the reproductive histories of five cohorts of animals branded as pups between 1980 and 1984 at Los Islotes colony in the Gulf of California, Mexico. Age-specific birth rates varied among age classes and ranged between 0.06 and 0.80. The highest birth rates were observed for females between 10 and 15 yr of age, with decreased birth rates among older females. The effect of age, year, and resighting effort were explored using logistic regression analysis. Based on Akaike Information Criteria, birth rates were best explained by female age, while year and resighting effort did not have a significant effect. The odds ratio of producing a pup decreased with age but did not change significantly for middle-aged females. Our estimates of age-specific birth rates are consistent with general patterns observed for other large vertebrates.

Age-specific survival and fecundity estimates are essential for understanding the evolution of life history traits and the dynamics of animal populations (Fox 1993, Caswell 2001). Age-specific fecundity rates in long-lived species can be estimated in two ways: by following naturally or artificially marked individuals through time, and by examining the reproductive organs of sacrificed animals (Bester 1995, Coulson *et al.* 2000). The first approach requires years of data collection for multiple cohorts, which can be very labor intensive. The second approach may underestimate fecundity rates because an unknown proportion of pregnant females fail to give birth (McKenzie *et al.* 2005). As a result of these challenges, detailed fecundity estimates do not exist for many long-lived species such as California sea lions, limiting the predictive ability of quantitative population models that rely on age-specific survival and fecundity estimates (Morris and Doak 2002).

The California sea lion (*Zalophus californianus*) is one of the most widely distributed pinnipeds in the North Pacific (King 1983, Le Boeuf *et al.* 1983). Breeding colonies are distributed from the Channel Islands in California to the southern tip of the Baja California Peninsula in Mexico, including the Gulf of California (GoC; King 1983, Le Boeuf *et al.* 1983). Females reach sexual maturity at 4 or 5 yr of age (Lluch-Belda 1969, Mate 1978, Melin 2002) and generally produce one pup per year, although births of twins have been reported infrequently (King 1983). Birthing is concentrated in a relatively short period of time, from the end of May to the middle of July, with a peak between 15 and 21 June (Odell 1975, García-Aguilar and Aurioles-Gamboa 2003*a*). The lactation period generally lasts 1 yr although juveniles may suckle for two or more years (Peterson and Bartholomew 1967, Francis and Heath 1991, Bonner 1984, Newsome *et al.* 2006). Despite the widespread distribution of California sea lions, little is known about the basic population biology of the species. Detailed birth rates are not available and survival rates have only recently been estimated (Hernández-Camacho *et al.*, in press).

California sea lions occupy 13 island breeding sites in the GoC (Fig. 1). These colonies have been monitored regularly since the mid-1970s (Szteren *et al.* 2006). Previous studies suggest that colonies are fairly isolated units (Maldonado *et al.* 1995, Hernández-Camacho 2001, Schramm-Urrutia 2002, Bowen *et al.* 2006), although some limited movement of individuals occurs between them (Young *et al.* 2007). The study site, Los Islotes, is the southernmost breeding colony in the entire range for the species. Its current population is estimated at 400 individuals (Szteren *et al.* 2006). Los Islotes is one of the few colonies in the GoC that has exhibited a consistent increase in abundance over the past two decades (Szteren *et al.* 2006). This site is also a popular tourist destination due to its proximity to the city of La Paz (Labrada-Martagón *et al.* 2005).

California sea lions were intensively harvested throughout their range in the 19th century, causing a dramatic reduction in their population number (Cass 1985, Zavala and Mellink 2000). During the 20th century the population exhibited a remarkable recovery as the species was protected by both Mexican (*i.e.*, NOM-059-ECOL-1994) and United States laws (*i.e.*, Marine Mammal Protection Act) (Cass 1985, Zavala and Mellink 2000). However, despite this recovery, some populations in the GoC have declined in recent years (Szteren *et al.* 2006). A greater understanding of demographic
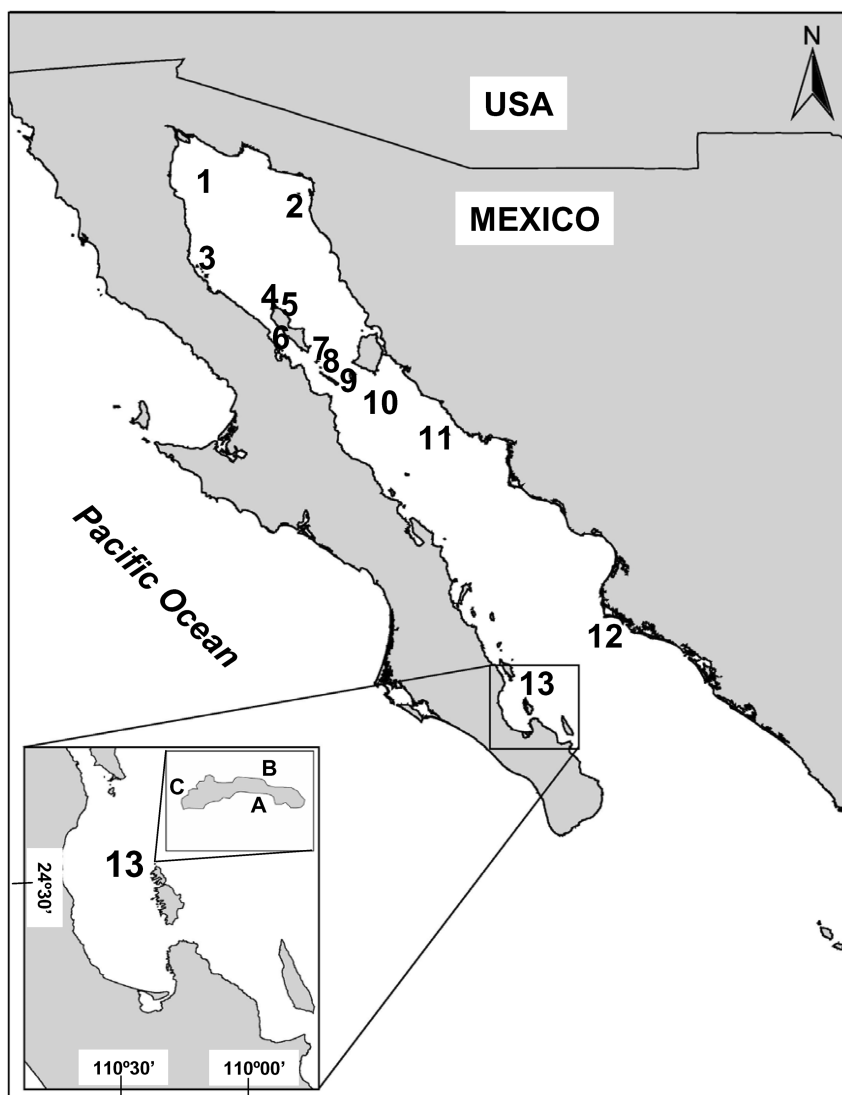
Figure 1. Map of the study area. Los Islotes rookery (13) is located in the southern part of the Gulf of California. Breeding colonies: 1. Rocas Consag, 2. San Jorge, 3. Isla Lobos, 4. Isla Granito, 5. Los Cantiles, 6. Los Machos, 7. El Partido, 8. Rasito, 9. San Esteban, 10. San Pedro Mártir, 11. San Pedro Nolasco, 12. Farallón de San Ignacio, 13. Los Islotes.

parameters is critical to ensuring an accurate assessment of population status for California sea lions.

We estimated age-specific birth rates for females greater than 10 yr of age from the reproductive histories of five California sea lion cohorts (1980–1984) at Los Islotes, GoC, Mexico. We also evaluated the effect of age and other covariates on birth rates using logistic regression analysis.

Methods

Field Methods

Branding—Ninety-four female pups born during the breeding season (June–July) between 1980 and 1984 were captured and hot-branded on the dorsal surface using a unique code of letters or numbers (Table 1). Individuals were branded during the second week of July of each year when they were approximately 1-mo old (Aurioles-Gamboa and Sinsel 1988). The mean birth date for this colony is 11–12 June (García-Aguilar and Aurioles-Gamboa 2003*a*). Pups were captured at random and held in a small stone corral in the shade. Individuals were measured and weighed before branding. The brands were legible throughout the study period (>25 yr). Branding did not compromise the survival of young sea lions. Early survival was >0.90 during the first 6 mo of age and was not different from that of unbranded pups (Aurioles-Gamboa and Sinsel 1988).

Resighting effort—Resighting trips were conducted during the years immediately following branding as part of a separate study on survival (Hernández-Camacho *et al.*, in press). However, we did not record whether branded females were with a pup until 1994. We conducted three resighting trips (June, July, and August) per year at Los Islotes between 1994 and 2006 (except 1995). Only two trips (June and July) were made in 1997 and 1998. Sampling occurred during and/or after the peak of birthing (García-Aguilar and Aurioles-Gamboa 2003*a*). Visits to the study site lasted between 6 and 8 d and consisted of 6–8 continuous h of observation per day. During each resighting trip, two or three observers searched for branded animals. This field strategy was designed to provide adequate time to locate and identify marked females. At Los Islotes, females alternate 2.05 (SD 0.87) d of foraging with 1.22 (SD 1.33) d of nursing on land (García-Aguilar and Aurioles-Gamboa 2003*b*); thus females are expected to visit land every two to four days. Surveys at the colony were conducted on land and from a small boat approximately 50 m from shore (three times per day) using 20 × 50 power binoculars. When we initiated our study in 1994, branded females were between 10 and 14 yr of age. Birth rates for animals between 5 (the age of sexual maturity, Melin 2002) and 9-yr old were therefore not estimated.

For each observation of marked individuals, we recorded the date, time, age, and reproductive status of females (with or without pup). A female was considered to be with a pup when it was observed on at least one occasion giving birth, engaged in mother-response calls, or nursing, nuzzling, or sniffing the pup. Females that were not

Table 1. Number of females branded and alive at the beginning of this study (breeding season 1994) at Los Islotes rookery, GoC (Modified from Hernández-Camacho 2001). The percentage of branded female pups in a cohort is also given. Females alive in 1994 include those seen that year or in any subsequent year.

Cohort	Branded females	Females alive 1994	Branded (%) (relative to total population)
1980	8	2	45
1981	17	3	76
1982	18	6	68
1983	26	11	100
1984	25	18	88
Total	94	40	80

observed nursing a pup or were absent during the breeding season, but known to be alive because they were seen in subsequent years, were considered to be without a pup.

Data Analysis

Our estimates represent apparent birth rates because an unknown number of females may have been missed, died, or emigrated to other colonies during the study period. Because our sample size was small, we pooled the number of branded females into five age-classes to estimate apparent birth rates and examine the effect of age and other covariates on birth rates: (1) 10–12-yr old, (2) 13–15- yr old, (3) 16–18-yr old, (4) 19–21-yr old, and (5) 22–25-yr old. Apparent birth rates were estimated as the number of branded females in a given age-class that were lactating divided by the number of branded females of that age-class known to be alive. The number of females known to be alive (observed during the study period; Hernández-Camacho 2001) and the number of females estimated to be alive (capture-recapture analysis) (Hernández-Camacho *et al.*, in press) were very similar (0.95 and 0.91, respectively), thus it was not necessary to adjust our estimate of total females.

Reproductive status is a binary response variable (with pup = 1, without pup = 0), so we used logistic regression analysis to determine the effect of age, resighting effort (two or three resighting trips during the breeding season) and year on birth rates (Kutner *et al.* 2005). We grouped years into two classes: normal years (1996, 1998–2001, 2003, 2005–2006) and El Niño years (1994, 1997, 2002, and 2004). Resighting effort was considered a covariate with reproductive status because of the potential influence on the probability of detecting a female with a pup during a specific breeding season. Similarly, year was considered as a covariate because variations in environmental conditions may influence the probability of giving birth (*e.g.*, food availability during El Niño years).

We first constructed a global model (all variables included) and tested its goodness-of-fit using the Hosmer and Lemeshow test (Kutner *et al.* 2005). This test, appropriate for data sets with few replicates, groups data into classes with similar fitted values to compute a chi-square value (Kutner *et al.* 2005). We then explored a set of candidate models to determine how well each variable explained the probability of giving birth.

The most parsimonious model was selected using Akaike Information Criterion (AIC). Models with ΔAIC < 2 and highest AIC weights were considered to have substantial support (Burnham and Anderson 2002). The relative importance of each predictor variable was estimated by summing the Akaike weights across all the models in the set where each variable occurs. Variables with larger values are considered to be more important relative to the other variables (Burnham and Anderson 2002). We tested the significance of the odds ratio for independent variables using the Wald statistic (Kutner *et al.* 2005). The Wald statistic is the squared ratio of the logistic coefficient to its standard error. If the test is significant, the variable is significant in the model. All estimates were computed using SAS System for Windows (release 9.1.3 SAS Institute, Inc., Cary, NC).

<div align="center">RESULTS</div>

Apparent Birth Rates

Birth rate varied by age class ($Z = 33.10$, df = 1, $P < 0.0001$) with the youngest and middle-age classes having a significantly higher birth rate than the older age

Table 2. Apparent birth rates for California sea lion females branded at Los Islotes rookery, Bahia de La Paz, Mexico. Birth rates were calculated as the number of branded females in a given age-class that were lactating divided by the number of branded females of that age-class known to be alive.

Age group	Number of females	Birth rate
10–12	50	0.80
13–15	86	0.73
16–18	70	0.61
19–21	48	0.52
22–25	16	0.06

classes (Table 2). Only 50% of the females between 19 and 21 yr of age had a pup during the breeding season. Few females over 22 yr of age gave birth during the breeding season.

Model Selection

The global model (all variables included) had a good fit to the data ($\chi^2 = 6.22$, df $= 7$, $P = 0.51$), thus we proceeded to explore our set of candidate models. The most parsimonious model included female age as a single explanatory variable (Table 3). However, the second and third most parsimonious models (female age and effort, female age and year, respectively) represented a reasonable fit to apparent birth rate data. These models were less than two AIC units ($\Delta \sim 2$) from the best model and seemed relatively plausible for these data (AIC weight ~ 0.2). Although the AIC weight for the best model was not very large relative to the weight for models two and three, the relative importance of age was notably greater compared to the other variables (year $= 1$, effort $= 0.29$, and year $= 0.29$).

According to the best model, the odds of producing a pup decreased with age (Table 4). There was a significant difference in the odds of producing a pup between

Table 3. Summary of the Akaike's information criterion (AIC) and associated statistics for seven candidate models for the logistic regression analysis of birth rate data in California sea lions.

ID	Model	Number of parameters	AIC	Δ_i	w_i
1	Age	2	322.390	0	0.508
2	Age + Effort	3	324.218	1.828	0.204
3	Age + Year	3	324.234	1.844	0.202
4	Age + Effort + Year	4	325.926	3.536	0.087
5	Effort	2	360.411	38.021	0
6	Year + Effort	3	362.222	39.832	0
7	Year	2	364.961	42.571	0

Age = Age group: (1) 10–12-yr old, (2) 13–15-yr old, (3) 16–18-yr old, (4) 19–21-yr old, (5) 22–25-yr old.
Effort = Two or three visits per month.
Year = Normal year or El Niño year.
Δ_I = AIC differences, w_i = Akaike weights.

Table 4. Odds ratio estimates for the best model (Age). Odds ratio estimates for additional models are shown in Appendix A.

Model	Effect	Estimated odds ratio	95% Wald confidence interval
Age	Age group		
	10–12 *vs.* 13–15	0.685	[0.295, 1.589]
	13–15 *vs.* 16–18	0.581	[0.295, 1.145]
	16–18 *vs.* 19–21	0.356	[0.165, 0.765]
	19–21 *vs.* 22–25	0.110	[0.013, 0.906]

the third (16–18-yr old) and fourth (19–21-yr old) age groups, and between the fourth and fifth (22–25-yr old) age groups. However, there was no significant difference in the odds of producing a pup between the first (10–12-yr old) and second (13–15-yr old) age groups, or between the second and third age groups. As expected, the odds of producing a pup were not significantly different when effort (two or three months of resighting) or year type (normal or El Niño conditions) varied when all other variables remained constant (Appendix A).

Discussion

This study provides a first estimate of fecundity for California sea lions and offers insight into understanding the effect of age on reproductive rates. The small size of the colony and the lack of emigration to other colonies allowed us to obtain relatively high resighting rates at Los Islotes. Only three branded sea lions (two 1-yr old juveniles and one 5-yr old adult female) were resighted at other colonies in the GoC during annual censuses conducted from 1980 to 2005. Both juveniles were resighted as adult animals at Los Islotes in subsequent reproductive seasons. Thus, while our estimates represent apparent birth rates, in light of our high resighting rates, we believe that our results provide an accurate estimate of fecundity for California sea lions.

Birth Rates and Environmental Variability

Pinniped birth rates may vary with changes in environmental conditions (Trillmich and Ono 1991, Pistorius *et al.* 2001). In our model, the variable "year" was relatively unimportant and the odds of producing a pup did not vary according to year type (normal or El Niño). This result suggests three possible scenarios: (1) prey abundance did not vary enough to influence birth rates (vital rate plasticity), (2) the variable "year type" was not for detecting the effect of fluctuations in environmental conditions on birth rates, or (3) variation in prey abundance affected another life history trait (*e.g.*, survival) rather than birth rates. We think the first two explanations are most plausible for California sea lions. Our study was conducted during a period of increasing abundance and pup births at Los Islotes colony (Szteren *et al.* 2006). This suggests that favorable environmental conditions prevailed in the area during the study period, even though one of the strongest El Niño events (1997–1998) occurred during the study period. Previous research suggests that the impact of El Niño events on primary producers and some higher trophic levels is negligible in the GoC (Álvarez-Borrego and Lara-Lara 1991, Aurioles-Gamboa and Le Boeuf 1991, Lluch-Cota *et al.* 2007).

Another possibility is that local rather than regional processes (*e.g.*, El Niño events) are relevant to sea lion population dynamics. For example, annual pup production is significantly correlated with the variation in abundance of sardines in the California sea lion population located in the Midriff area of the GoC (from Angel de la Guarda to San Pedro Martir, Fig. 1.; unpublished observations by David Aurioles-Gamboa *et al.*). Unfortunately, there are no data on local prey abundance or other resources (*e.g.*, plankton) indirectly related to local prey for our study site. While it is possible that resource limitation effects survival more strongly than fecundity in this species, the increasing population size during the study period suggests that resources were not limiting.

Age-Specific Birth Rate Pattern

Population growth is determined based on the mean and variation in survival and fecundity rates (Stearns 1992, Caswell 2001). The relative importance of survival and fecundity on population growth depends on the underlying life history of the species. Juvenile survival is considered to be highly sensitive to variation in population size in large mammals (Eberhardt 1977, Fowler 1987, Heppell *et al.* 2000, Crone 2001). Recently, fecundity has been recognized as a strong determinant of population dynamics for a broad range of taxa (Albon *et al.* 2000, Coulson and Hudson 2003). Hence, accurate estimates of both survival and fecundity rates are needed to understand population dynamics and to interpret life history patterns.

The reproductive estimates reported here represent only part of the relevant demographic processes in California sea lions. A separate analysis to estimate survival has been completed (Hernández-Camacho *et al.*, in press) and will allow us to construct the first published life table for this species. Furthermore, our estimates may not represent the overall reproductive pattern for all colonies in the GoC. However, they do provide useful insight into age-specific birth patterns for colonies exhibiting positive population trends. Four colonies (Rocas Consag, San Jorge, San Esteban, and Los Islotes) within the GoC exhibit positive population trends. Of these, Los Islotes colony has exhibited the greatest increase in abundance during the last two decades (Gonzalez-Suarez *et al.* 2006, Szteren *et al.* 2006). The birth rate pattern we report here for the California sea lion is consistent with the typical pattern described for other otariids (Lander 1981, York and Hartley 1981, Lunn *et al.* 1994, Bester 1995, Boyd *et al.* 1995, Dabin *et al.* 2004). This pattern is characterized by lower fecundity in young and old females, and higher and relatively constant fecundity in middle-age individuals (Stearns 1992). Although we do not have data for young females (<10-yr old), we expect birth rates lower than or similar to (0.80) those reported for young California sea lions in other geographic areas. In a longitudinal study with California sea lions in the North Pacific, Melin (2002) estimated the mean birth rate for 5-yr old females to be 0.59 and that for 6–10-yr old females to be 0.79. The birth rate for 6–10-yr old females is similar to the birth rate we report for middle-age females in the second (13–15-yr old) age group for whom the odds of producing a pup did not change when individuals moved from one age class to the next (from the first to the second age class and from the second to the third age class). After this period of constant birth rates, the odds of producing a pup decreased significantly in individuals older than 16–18 yr of age. Decline in fecundity with old age has been explained as senescence (loss of physiological function with age) in some mammals (Beauplet *et al.* 2006). While our sample size was small, we expect a similar decline in fecundity with age for California sea lions.

Although birth rate patterns in otariids are qualitatively similar, birth rates appear to range among species. For example, the average birth rate for individuals 10–12-yr old is 0.65 for the Subantarctic fur seal (*Arctocephalus tropicalis*, Dabin *et al.* 2004), 0.77 for the Antarctic fur seal (*Arctocephalus gazella*, Lunn *et al.* 1994), 0.35 for the Steller sea lion (*Eumetopias jubatus*, Holmes *et al.* 2007), and 0.80 for the California sea lion (this study). Similarly, the birth rate peak (and the age at it which occurs) varied among species: 0.63 (8–13-yr old) for the Subantartic fur seal, 0.80 (7–9-yr old) for the Antarctic fur seal, 0.35 (10–15-yr old) for the Steller sea lion, and an estimated 0.80 (10–12-yr old) for the California sea lion. Although these data are limited to four species and methodologies may have differed among these studies, the wide range of values suggests there may be considerable plasticity in otariid birth rates. This possibility should be further explored by comparing birth rates from multiple populations within a species exposed to different constraints and pressures.

This work represents a first step in advancing our knowledge of the life history traits of California sea lions. Additional estimates of age- and sex-specific vital rates as well as information on population trends and environmental conditions for Los Islotes and other California sea lion colonies are needed to: (1) provide a foundation for a more comprehensive analysis of the life history patterns of this species, (2) estimate the magnitude of variation in demographic traits (plasticity), (3) characterize the mechanisms of population regulation in this species, and (4) understand the extent to which variation in extrinsic factors (*e.g.*, food resources) shape life history patterns (Monson *et al.* 2000). This information is critical for determining the appropriate scale for demographic parameter estimation in applications to conservation and management.

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Appendix A. Odds ratio estimates for additional models.

Model	Effect	Estimated odds ratio	95% Wald confidence interval
Age + Effort	Age group		
	10–12 *vs.* 13–15	0.617	[0.234, 1.628]
	13–15 *vs.* 16–18	0.632	[0.289, 1.383]
	16–18 *vs.* 19–21	0.363	[0.168, 0.784]
	19–21 *vs.* 22–25	0.110	[0.013, 0.906]
	Effort		
	2 *vs.* 3	0.840	[0.370, 1.909]
Age + Year	Age group		
	10–12 *vs.* 13–15	0.665	[0.283, 1.562]
	13–15 *vs.* 16–18	0.567	[0.285, 1.130]
	16–18 *vs.* 19–21	0.363	[0.168, 0.786]
	19–21 *vs.* 22–25	0.108	[0.013, 0.887]
	Year		
	0 *vs.* 1	0.888	[0.495, 1.595]
Age + Year + Effort	Age group		
	10–12 *vs.* 13–15	0.567	[0.205, 1.572]
	13–15 *vs.* 16–18	0.631	[0.288, 1.382]
	16–18 *vs.* 19–21	0.377	[0.172, 0.824]
	19–21 *vs.* 22–25	0.106	[0.013, 0.878]
	Year		
	0 *vs.* 1	0.844	[0.457, 1.561]
	Effort		
	2 *vs.* 3	0.784	[0.332, 1.853]
Effort	2 *vs.* 3	0.485	[0.257, 0.914]
Year + Effort	Year		
	0 *vs.* 1	1.122	[0.667, 1.890]
	Effort		
	2 *vs.* 3	0.498	[0.261, 0.950]
Year	0 *vs.* 1	1.256	[0.757, 2.085]

Year: 0 = Normal, 1 = El Niño.
Effort: Two or three resighting trips.