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First demographic parameter estimates for the Mediterranean monk seal population at Madeira, Portugal

Rosa Pires[1], Fernando Aparicio[2], Jason D. Baker[3,*], Sérgio Pereira[4], Nélio Caires[4], Miguel A. Cedenilla[2], Albert L. Harting[5], Dilia Menezes[4], Pablo Fernández de Larrinoa[2]

[1]Serviço de Ambiente e Alterações Climáticas de Santa Maria, Parque Natural de Santa Maria, Rua Teófilo Braga, 10, 12, 14, 9580-535 Vila do Porto, Portugal

[2]Monk Seal Conservation Program, Fundacion CBD-Habitat. Angel Hernández 13, 28002 Madrid, Spain

[3]National Oceanic and Atmospheric Administration, Pacific Islands Fisheries Science Center,Protected Species Division, Honolulu, HI 96818, USA

[4]Instituto das Florestas e Conservaçao da Natureza da Madeira. Madeira Regional Government. R. João de Deus 12e, 9050-027 Funchal, Portugal

[5]Harting Biological Consulting, Bozeman, MT 59715, USA

ABSTRACT: We provide the first comprehensive demographic assessment of the Endangered Mediterranean monk seal *Monachus monachus* population residing in the Madeira Archipelago to identify factors that may impede population growth. Encounter data was obtained for this small, elusive population from 2012 to 2021 using a variety of non-invasive methods. From birth to age 2 mo, when pups molt, survival averaged 0.57. From birth to 1 yr and from 1–2 yr, estimated survival rates were 0.47 and 0.85, respectively. Beyond 2 yr, survival estimates differed by sex: 0.98 for females and 0.90 for males. These survival rates are similar to published estimates from the Cabo Blanco (Western Sahara/Mauritania) population. This is remarkable given that Cabo Blanco is situated adjacent to the extremely productive Canary Current system, whereas the marine environment of Madeira is far less productive. Instead of reducing survival, low marine productivity in Madeira appears to manifest in strikingly depressed reproductive rates. We estimated a mean gross reproductive rate of just 0.31; less than half the value (0.71) reported for Cabo Blanco. The youngest parturient females in Madeira were 6 yr old, whereas 3 yr olds give birth at Cabo Blanco. Despite low fecundity, the monk seal population in Madeira has been recovering, aided by a series of conservation measures implemented since 1988. Our results document that abundance increased from 19 seals in 2013 to 27 in 2021. Despite this undeniable success, the monk seals of Madeira remain vulnerable and require continued monitoring and protection in order to persist.

KEY WORDS: Mediterranean monk seal · Madeira · Abundance · Survival · Reproductive rate

1. INTRODUCTION

Evaluating vital rates is critical for diagnosing declines and effective recovery planning (Caughley & Gunn 1996, Dahlgren et al. 2016). However, estimating population parameters in very small populations of elusive species can be especially challenging (Thompson 2004). Nevertheless, well-designed monitoring programs are an integral component of successful conservation (Nichols & Williams 2006). Moreover, key insights can often be revealed by comparing demographic parameters among distinct populations of rare species (Johnson et al. 2010, McLellan et al. 2021).

The Mediterranean monk seal *Monachus monachus* is the rarest seal in the world and is classified by

*Corresponding author: jason.baker@noaa.gov

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the IUCN as Endangered. No more than 700 individuals remain worldwide, distributed mainly over the eastern Mediterranean and in the Atlantic in Cabo Blanco (Mauritania and Western Sahara) and the archipelago of Madeira (Karamanlidis et al. 2016). When European navigators reached the uninhabited archipelago of Madeira for the first time in 1420, seals were abundant in the main Madeira Island and used open beaches and small beaches inside caves for resting (Barros 1570 in Borges et al. 1979). But monk seal exploitation for skins and oil and increased human pressure (Borges et al. 1979, Machado 1979, Biscoito 1988) led to a drastic reduction of the species. In 1978, only 6 individuals were estimated to be frequenting Madeira main island (Machado 1979) and another 50 were estimated to remain on the Desertas Islands (Sergeant et al. 1978), located 12 nm (22 km) southeast of Madeira Island. Growth in fishing activities was associated with increased seal deaths, and consequently, the population on the Desertas Islands declined (Neves 1998, Neves & Pires 1999). Only 6–8 seals were thought to remain in the Desertas Islands by the 1980s (Reiner & dos Santos 1984, Biscoito 1988, Marchessaux 1989).

In 1988, to prevent the extinction of the species, the Regional Government of Madeira initiated a program for the conservation of the Mediterranean Monk Seal that led, in 1990, to the legal protection of Desertas Islands and the prohibition of the use of gillnets in its waters to prevent monk seal entanglement. This prohibition was extended to cover the whole Madeira archipelago in 2000.

The species' scarcity and propensity to land inside sea caves that are difficult to access make monitoring monk seals in Madeira a serious challenge. Between the 1990s and 2012, the few surviving monk seals were mainly monitored by visual observations either from lookout sites distributed along the coasts of the Desertas Islands or through a sighting network on Madeira Island. Although this method did not allow for a demographic assessment of the population, it did support the implementation of conservation strategies (Neves & Pires 1999). The 2 surviving populations of monk seals in the Atlantic, Madeira and Cabo Blanco, are separated by more than 1000 km and inhabit very different marine environments. Both populations almost exclusively use caves exposed to strong waves and high tides to breed, but the marine habitat and oceanographic conditions they inhabit differ. Cabo Blanco is located in one of the world's major eastern boundary upwelling ecosystems, the Canary Current system, a very productive region that experiences upwelling throughout the year (Kämpf & Chapman 2016), while Madeira Archipelago is surrounded by oligotrophic waters, with low biological productivity (Delgado 2007). We hypothesize that this contrast in productivity could result in differences in monk seal demographic parameters.

Breeding in caves leads to low survival of pups during the first 2 mo of life at Cabo Blanco (Gazo et al. 2000, González et al. 2002, Fernández de Larrinoa et al. 2021). Nevertheless, this population maintains a positive growth rate due to early maturity, a high reproductive rate, and favorable survival rates after the first 2 mo, likely related to abundant prey resources (Fernández de Larrinoa et al. 2021). Until now, the demographic status of monk seals in Madeira has been unknown, preventing an assessment of which factors may be impeding population recovery. In 2012, following recommendations of the Action Plan for the recovery of the Mediterranean monk seal in the eastern Atlantic (González et al. 2006) to standardize the techniques applied in both Atlantic populations, the non-invasive monitoring methods used in Cabo Blanco were implemented in Madeira. In this study, we sought to obtain the vital rates of the Madeiran monk seal population in order to diagnose its demographic status and obtain essential information to update conservation strategies. To improve the interpretation of the results, comparisons were made between the vital rates of the 2 Atlantic populations of the species.

2. MATERIALS AND METHODS

2.1. Study area and surveillance methods

Madeira is a Portuguese archipelago located approximately 800 km southwest of the European continent and 700 km west of the African coast. It comprises 2 inhabited islands: Madeira and Porto Santo, and 2 distinct uninhabited sub-archipelagos: Desertas islands, 18 km southeast of Madeira main island, and Selvagens Islands, nearly 300 km south of Madeira (Fig. 1), both classified as Nature Reserves.

Monk seals mainly use the waters and coastal caves around the Desertas Islands and Madeira main island. Seals are rarely observed in Porto Santo Island, and while seals have not been documented in the Selvagens Islands, an old navigator's map from 1692 shows the Selvagens Islands as 'Isole de vechi marini' (marine calf), suggesting monk seal presence in the past (González 2015).

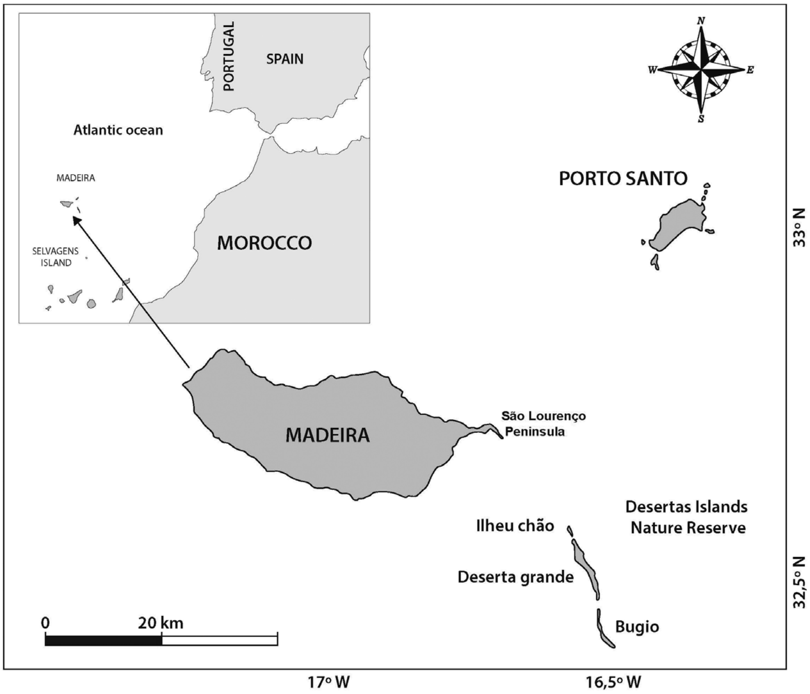

Fig. 1. The Madeira Archipelago

Madeira Island's coastline extends for 153 km. The south shore is the most accessible, featuring several beaches, and hosts about 75% of the human population. The north coastline is less accessible and is characterized by steep cliffs. Monk seals prefer sea caves that feature interior landing areas (beaches or rocky platforms) where they can rest undisturbed. Most of the caves suitable for seals on Madeira Island are located along São Lourenço Peninsula (Fig. 1), on the eastern coastline (Karamanlidis et al. 2003).

The Desertas Islands consist of 3 islands: Ilhéu Chão, Deserta Grande, and Bugio (Fig. 1). Their 37 km long coastline is mainly composed of steep cliffs with several beaches and caves. The islands are uninhabited, except for the permanent presence of the conservation agents from Instituto das Florestas et Conservaçao da Natureza (IFCN). The islands have been protected since 1990, and in 1995, a Nature Reserve was established to protect them and the surrounding waters to the 100 m isobath. The reserve was created primarily to protect the monk seal population, but also for the benefit of various endemic and other important flora and fauna. In the northern half of the reserve, human activity is restricted, allowing only regulated fishing. In the southern half, nearly all human activities, including navigation and landing, are forbidden. Only scientific research, park management actions, and some regulated traditional tuna fishing, which is not considered a threat to monk seals, are allowed. A limited number of tourists are allowed to visit the interpretive center and area around the conservation agents' facility.

2.2. Data collection

This study is based mostly on information gathered from 2012 to 2021 using 3 non-invasive methods: (1) continuous surveillance systems installed in the primary caves used by seals, (2) visual observation efforts outside of caves in the Desertas Islands, and (3) sightings of monk seals from Madeira Island. The demographic data consist of documented births, deaths, and encounter histories of individually identifiable seals obtained from photo and video images.

Observational effort was focused on the southern portion of Deserta Grande, where the most important terrestrial habitat for monk seals is located. This includes 2 breeding caves (Tabaqueiro and Bufador) and Tabaqueiro Beach, which is used during certain periods of the breeding season by reproductive females and their pups (Pires & Neves 2001, Pires et al. 2007).

2.2.1. Continuous surveillance systems

The continuous surveillance systems consist of a photo trap camera equipped with a no/low-glow infrared flash housed inside a watertight case that is designed to withstand the severe conditions of wetting, pressure, and salt inside the marine caves. In larger caves, an automatic cleaning system, consisting of water tanks connected to an irrigation programmer, was installed to eliminate salt accumulation over the glass protecting the camera lens. The cameras were programmed to take one photo every hour and the cleaning system flushed the camera case with fresh water for 1 min every 7 d. The surveillance system can operate for up to 10 mo without servicing, thereby minimizing potential disturbance to seals when people enter the caves, allowing for year-round monitoring even in some of the most remote locations.

Photo trap cameras were placed in most of the caves suitable for monk seal usage in the Desertas Islands and Madeira Island, as well as those overlooking Tabaqueiro Beach. In some of the caves, more than one surveillance system was installed to maximize coverage of the interior beaches. As data on monk seal presence in the various caves was obtained, the monitoring effort was adapted to focus on the most frequently used sites.

2.2.2. Visual observation effort in the Desertas Islands

Direct observation efforts to obtain images of seals were carried out annually from 2012 to 2021 at permanent lookout sites located on the south coast of Deserta Grande as well as from the rangers' vessel while they patrolled the reserve (Pires et al. 2008). While this study is focused on the period 2012–2021, records of individuals identified prior to 2012 were also used to estimate their ages.

During the breeding season, from October to December, when sea conditions allowed, observation effort was increased near the caves where pups are born and on Tabaqueiro Beach, where mothers and pups remain together for varying periods of time.

2.2.3. Monk Seal Information Network

The Monk Seal Information Network was established in 2002 with the objective of gathering monk seal sighting records and images from occasional observers around Madeira Island (Pires et al. 2008). More than 60 collective and individual partners take part in the network. Among them are 11 diving centers, 11 coastal municipalities, 15 whale-watching companies, and the National Republican Guard. Reports consist of date, time, place, description of the monk seal and its behavior, as well as images. The information is later validated based on the descriptions and images.

2.2.4. Seal identification

Photographic identification of individuals was carried out as described by Fernández de Larrinoa et al. (2021) with some minor alterations. At birth, pups are mostly black except for a yellowish-white ventral patch. The shape of the ventral patch differs between male and female pups, and each patch has unique features, allowing for individual identification (Badosa et al. 1998). Pups molt at roughly 2–3 mo of age, with their pelage becoming more or less uniformly gray (Samaranch & Gonzádlez 2000, Badosa et al. 2006). At the Cabo Blanco monk seal colony in West Africa, most pups become indistinguishable after the first molt until at least 2 yr of age, when either sufficient scarring or the reappearance of the ventral patch (in males only) allows them to be distinguished once again (Fernández de Larrinoa et al. 2021). However, Madeira monk seals (both sexes) retain sufficient traces of the lateral portion of the ventral patch so that they can be identified from birth through adulthood.

Before surveillance systems were installed in the caves where pups are born, it was not possible to identify most of the births or to maintain the identity of each seal from birth. Consequently, animals that had been identified before 2012 or which were first identified when older than young-of-the-year were assigned an estimated age in the year when they were first identified. We based these estimated ages on known life history, body size, and morphology consistent with Samaranch & González (2000). Ages assigned to seals that were not yet adults were likely more accurate than those first identified as adults.

2.3. Survival estimation

We constructed annual sighting histories for each individual observed during 2012–2021. We then estimated apparent survival using Cormack-Jolly-Seber capture–recapture models using the R package 'marked' (Cormack 1964, Jolly 1965, Seber 1965, Laake et al. 2013). We specified age at first capture as zero for seals born in 2012 or later. Seals born earlier than 2012 (or first identified when older than 1 yr) were assigned initial ages equal to the first year seen (during 2012–2021) minus the known or estimated birth year.

We followed the modeling approach of Fernández de Larrinoa et al. (2021), initially fitting various formulations of recapture probability, including models with distinct recapture probabilities for each year, models with grouped years, and models with sex differences in recapture probability. Once a preferred recapture probability structure was determined, various formulations for survival were modeled including the factors age and sex. Models were compared using Akaike's information criterion (AIC) (Anderson et al. 2000).

At the Cabo Blanco monk seal colony, survival did not vary beyond 2 yr of age (Fernández de Larrinoa et al. 2021). Given the relatively small number of individuals in the Madeira population, we assumed statistical power to detect any differences in survival by age would be lower than at Cabo Blanco. Thus, we began by modeling annual survival with 3 distinct age groups; age 0, age 1, and age 2 yr and older, though other age groupings were also examined. A model including time variation in survival for all ages was also considered.

Sex differences in survival were suspected due to a predominance of females in the older age classes. In addition, at Cabo Blanco, survival of males aged ≥2 yr was lower than that of females (Fernández de Larrinoa et al. 2021). Consequently, we investigated potential sex-biased survival using 2 model structures. One included an additive sex effect across all age classes, and the other limited sex differences to the ≥2 yr age group, consistent with the pattern at Cabo Blanco.

The first 2 mo of life, from birth until approximately the first molt, is a high-risk period in the life history of monk seals at Cabo Blanco (Fernández de Larrinoa et al. 2021). To allow comparisons of survival during this period at Madeira, we calculated the proportion of pups born that remained alive at 2 mo of age during 2012–2021. Binomial confidence intervals (CIs) for these estimates were calculated with Wilson's method using the R package 'Hmisc' (Wilson 1927, Harrell & Dupont 2015).

2.4. Reproductive rate estimation

We based estimates of age-specific reproductive rates on observations of adult females and pups from 2012–2021, when surveillance systems were present in birth caves. Although some mother–pup associations were made from observations outside caves prior to 2012, data from those years were incomplete, as several births and maternal associations were surely not detected.

For each year, a list of females that were observed along with their known or estimated ages was assembled. Because the population is closed to emigration and immigration, females were also scored as present in years when they were not observed but had been seen in a previous and subsequent year. Next, females' reproductive status was scored each year. Those that were observed accompanying and suckling a pup, and those without a pup but exhibiting maternal behavior towards the young of other females were considered to have given birth. In the latter situation, we assume the female's pup had died. We included females with estimated as well as known ages in the analysis. Although doing so injects some uncertainty, limiting analyses to only known-aged females would reduce the sample size considerably, especially for older ages.

To estimate age-specific reproductive rates, we fitted a generalized additive mixed model (GAMM) to the binary response (pup or no pup) versus age and included female identity as a random effect, using the R package 'gamm4' (Wood & Scheipl 2020). We found that this GAMM approach, assuming no functional form, performed better in terms of well-behaved CIs than a 5-parameter function previously used in Hawaiian and Mediterranean monk seal studies (Harting et al. 2007, Fernández de Larrinoa et al. 2021).

Gross reproductive rate (GRR) was calculated as the ratio of total pups to total reproductive-female years, pooling data over all years (2012–2021). This was calculated using 2 minimum ages. First, we calculated GRR for females greater than age 2 yr, which is consistent with previous studies of monk seals at Cabo Blanco, where 3 yr olds have given birth (Gazo et al. 1999, González et al. 2002, Fernández de Larrinoa et al. 2021). We also calculated GRR including only females at least as old as the youngest observed birth mother in Madeira. Binomial CIs for these estimates were calculated as described above for survival from birth to 2 mo of age (Wilson 1927, Harrell & Dupont 2015).

2.5. Abundance, age–sex structure, and lifetable analysis

Because the Madeiran monk seal population is very small and surveillance starting in 2012 was extensive, we estimated abundance from 2012–2021 by simply tallying the number of seals known to be alive each year. This included not only the seals observed each year but also those who were not seen but must have been alive. For example, a seal seen in 2016 and 2018 was considered alive in 2017. Likewise, a seal first identified in 2013 as an adult was treated as alive in 2012. A log-linear regression of abundance over time was conducted to obtain an estimated growth rate from 2012–2021.

The population's age and sex structure in 2021 was constructed using the known and estimated ages of seals observed in that year. Finally, we populated a females-only Leslie matrix with our point estimates

Table 1. Number of days that continuous photo-trap surveillance systems were operative in caves (and on one beach) from 2012 to 2021 in the Madeira Archipelago

	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Desertas Islands										
Tabaqueiro Cave	118	217	356	364	365	264	364	364	158	99
Tabaqueiro Beach	82	65	55	125	365	323	237	360	212	364
Bufador	0	0	131	364	365	274	209	364	263	125
Lanço do Rico	0	0	0	67	196	174	239	344	149	193
Agulha	0	0	129	364	362	345	15	0	0	0
Porto do Vinho	0	0	0	127	365	364	32	0	0	0
Lobos	0	99	311	326	365	364	245	82	0	0
Madeira Island										
Vaticano	0	0	0	0	206	364	364	364	127	0
Total	200	381	982	1737	2589	2472	1705	1878	909	781

of survival and fecundity. The maximum age in the matrix was equal to the oldest female for which reproductive information was available. The intrinsic growth rate, the dominant eigenvalue of the Leslie matrix, was then determined using the R package ‘demogR’ (Caswell 2001, Jones 2007).

3. RESULTS

3.1. Surveillance and seal identification

Surveillance systems were progressively installed in most of the caves suitable for monk seal use in the Desertas Islands and Madeira Island beginning in 2012. Up to 26 systems were eventually installed in 18 different caves and on Tabaqueiro Beach to detect seal presence. Monitoring was then focused on the caves and one open beach used most regularly by the seals; the data obtained were used for photoidentification (Table 1).

The monitoring effort in each cave varied according to our ability to access them. Rough sea conditions and the presence of monk seals inside caves often prevented our entry to replace batteries and reload the freshwater cleaning system. In addition, in the latter years of the study, some photo trap cameras began to fail, reducing monitoring effort.

Between 2012 and 2021, a total of 2765 h of observation effort was performed from lookout sites on the south of Deserta Grande and during navigation around Desertas Islands, resulting in 822 seal sightings (Table 2). An additional 909 monk seal sightings were reported to the Monk Seal Information Network. Of those sightings, submitted images allowed 175 individual identifications to be confirmed (Table 3).

Over the study period, 52 seals were identified, including 27 females, 19 males, and 6 whose gender was not possible to identify. Sixteen individuals observed during this study had estimated ages rang-

Table 2. Hours of visual observation effort performed and number of Mediterranean monk seal sightings recorded in the Desertas Islands from 2012 to 2021

Year	Observation hours	Seal sightings
2012	227	77
2013	395	112
2014	439	128
2015	316	92
2016	210	64
2017	229	49
2018	239	57
2019	248	83
2020	264	82
2021	198	78
Total	2765	822

Table 3. Number of sightings and identified Mediterranean monk seal individuals reported by the Monk Seal Information Network at Madeira Island from 2012 to 2021

Year	Reports	Individual identifications
2012	113	12
2013	192	31
2014	92	36
2015	85	15
2016	65	7
2017	68	10
2018	67	12
2019	94	22
2020	72	12
2021	61	18
Total	909	175

Table 4. Cormack-Jolly-Seber models fitted to Mediterranean monk seal capture histories from Madeira. Model specification for survival and recapture probability parameters are shown. Most specifications are self-explanatory (constant, sex, age) and others are abbreviated as follows: 'Time' fits a parameter for each year; 'Grouped years' fits either 3 or 4 recapture probability parameters as described in the text; 'Grouped ages (0, 1+)' fits 2 survival parameters (ages 0 and ≥1 yr), and Grouped ages (0, 1, 2+) fits 3 survival parameters (ages 0, 1, and 2+ yr). 'Sex (2+ only)' fits separate survival estimates for females and males that were at least 2 yr old, whereas sexes were combined for younger (age 0 and 1 yr) seals. Models are ranked according to Akaike's information criterion (AIC) values. 'Par' indicates the number of parameters fitted in each model. Shading indicates the top model

Survival	Recapture probability	Par	AIC	ΔAIC
Grouped ages (0, 1, 2+) + Sex (2+ only)	Grouped years (3 levels)	7	154.64	0.00
Grouped ages (0, 1+)	Grouped years (3 levels)	5	156.63	1.99
Grouped ages (0, 1, 2+)	Grouped years (3 levels)	6	156.69	2.05
Grouped ages (0, 1, 2+) + Sex (2+ only) + Time	Grouped years (3 levels)	32	156.99	2.35
Grouped ages (0, 1, 2+) + Sex	Grouped years (3 levels)	7	157.36	2.72
Age	Grouped years (3 levels)	25	179.85	25.21
Constant	Grouped years (3 levels)	4	192.64	38.00
Constant	Grouped years (3 levels) + Sex	7	193.95	39.31
Constant	Grouped years (4 levels)	5	194.60	39.96
Constant	Time	10	204.60	49.96
Constant	Constant	2	206.27	51.64

ing from 1 to 7 yr old when they were first identified. The remaining 36 individuals were identified in their birth year.

3.2. Survival

3.2.1. Annual survival

Recapture probabilities were high, and there was strong statistical support for variation among certain years. Specifically, recapture probabilities were lower in 2013, 2018, and 2020 compared to all remaining years. A model with 3 parameters (one for data from years 2013 and 2018 combined, one for 2020, and one for all other years) fit slightly better than a 4-parameter model with separate estimates for all 3 of the lower years and the remaining years (Table 4). In 2013 and 2018, estimated recapture probability (and 95% CIs) was 0.82 (0.64–0.92), and in 2020 the estimate was 0.91 (0.70–0.98). In all remaining years, the estimate was 1.00 with zero variance, indicating that all live marked seals were resighted. A model with an additive sex effect on recapture probabilities had slightly less support than a model with sexes combined (Table 4). The 3-parameter recapture probability structure was thus used for all subsequent models fitted to evaluate survival rates.

With regard to survival, models with 3 age classes (ages 0, 1, and 2+) had nearly identical AIC values to those with just 2 classes (ages 0 and 1+) (Table 4). We favored the former in order to obtain more resolution in age-specific survival rates and to facilitate comparisons with the same age groups at the Cabo Blanco colony (Fernández de Larrinoa et al. 2021). The best-supported models all included a sex effect among seals aged 2 yr and older, with females exhibiting higher survival (Table 4). Survival (and 95% CIs) during the first year of life was estimated to be 0.47 (0.31–0.64), rising to 0.85 (0.56–0.96) from age 1–2 yr; adult survival (ages 2 years and older) was 0.98 (0.92–1.0) for females and 0.90 (0.76–0.96) among males (Fig. 2, Table 5).

3.2.2. Survival from birth to 2 mo

From 2 to 5 pups were born per year for a total of 35 born during 2012–2021. Point estimates of survival rate from birth to 2 mo varied considerably among years; however, the low number of births meant that binomial CIs for individual years were large (Table 6). The average rate for all years combined (and 95% CI) was 0.57 (0.41–0.72).

3.3. Reproductive rate

Reproductive histories were available for 19 individual females, which ranged from age 1 to 22 yr in the final observation year (2021). The data set consisted of 138 female-years, with the number of observations at each age ranging from just 1 to 10. The

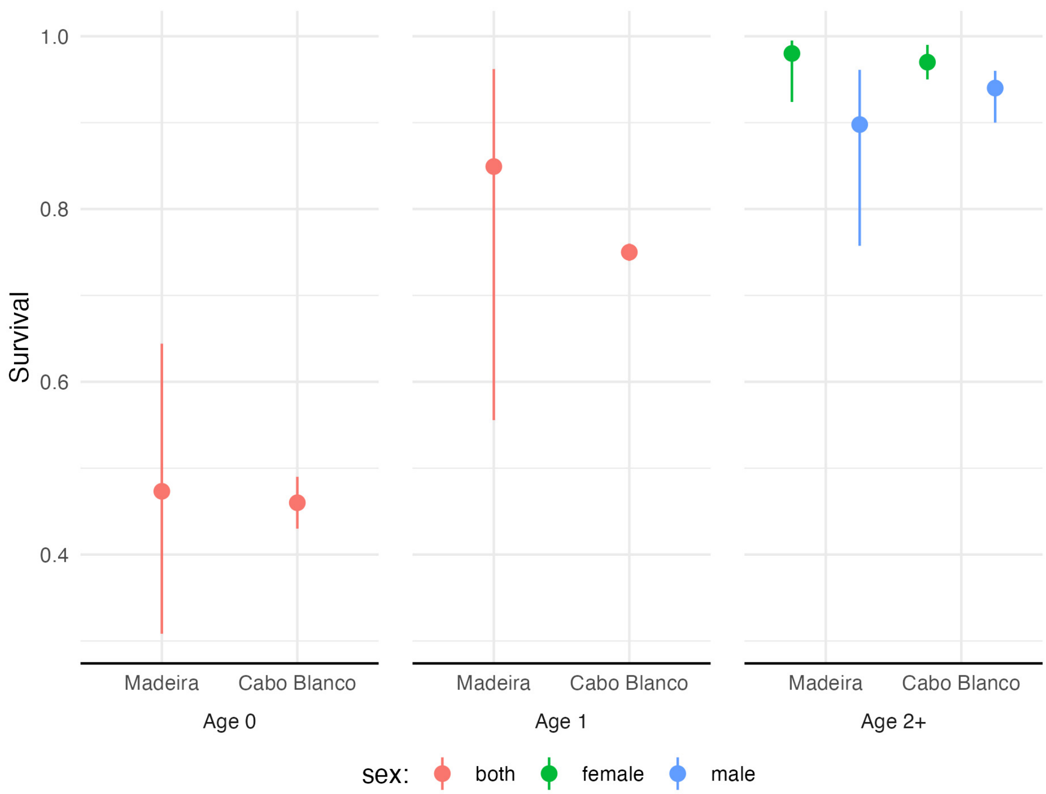

Fig. 2. Comparison of Mediterranean monk seal survival rates in Madeira (Table 5) and Cabo Blanco (Fernández de Larrinoa et al. 2021). Ages 0 and 1 yr estimates apply to both sexes, whereas sex-specific rates are presented for seals aged 2 yr and older. Vertical lines: 95% CIs

Table 5. Estimated survival rates and the lower (LCL) and upper (UCL) 95% confidence interval limits of Mediterranean monk seals at Madeira, 2012 to 2021

Age (yr)	Estimate	LCL	UCL	Sex
0	0.473	0.308	0.644	Both
1	0.850	0.556	0.962	Both
2+	0.980	0.924	0.995	Female
2+	0.898	0.757	0.961	Male

youngest female observed to give birth was 6 yr old and the oldest was 19 yr old. It should be noted that a female that died at the age of 21 with kidney problems was pregnant. The estimated standard deviation for the random effect in the mixed model was zero, indicating no detectable differences in the reproductive curve amongst individual females. Beyond age 5 yr, the fitted curve rose steeply to a peak rate of 0.63 at age 11 yr, then declined (Fig. 3). The GRR (and 95% CI) for females over 2 yr old was 0.31 (0.23–0.40). For females greater than 5 yr old, the rate was 0.40 (0.31–0.51).

Table 6. Annual number of Mediterranean monk seal pups born in Madeira, number that survived to 2 mo of age, survival rate from birth to 2 mo, and binomial lower (LCL) and upper (UCL) 95% confidence interval limits

Year	Born	Survived	Rate	LCL	UCL
2012	4	1	0.250	0.013	0.699
2013	2	1	0.500	0.026	0.974
2014	4	2	0.500	0.150	0.850
2015	3	2	0.667	0.208	0.983
2016	4	1	0.250	0.013	0.699
2017	5	3	0.600	0.231	0.882
2018	5	4	0.800	0.376	0.990
2019	3	2	0.667	0.208	0.983
2020	2	2	1.000	0.342	1.00
2021	3	2	0.667	0.208	0.983
All	35	20	0.571	0.409	0.720

3.4. Abundance, age–sex structure, and lifetable analysis

The estimated abundance of monk seals in Madeira was fairly stable from 2012 to 2017, ranging

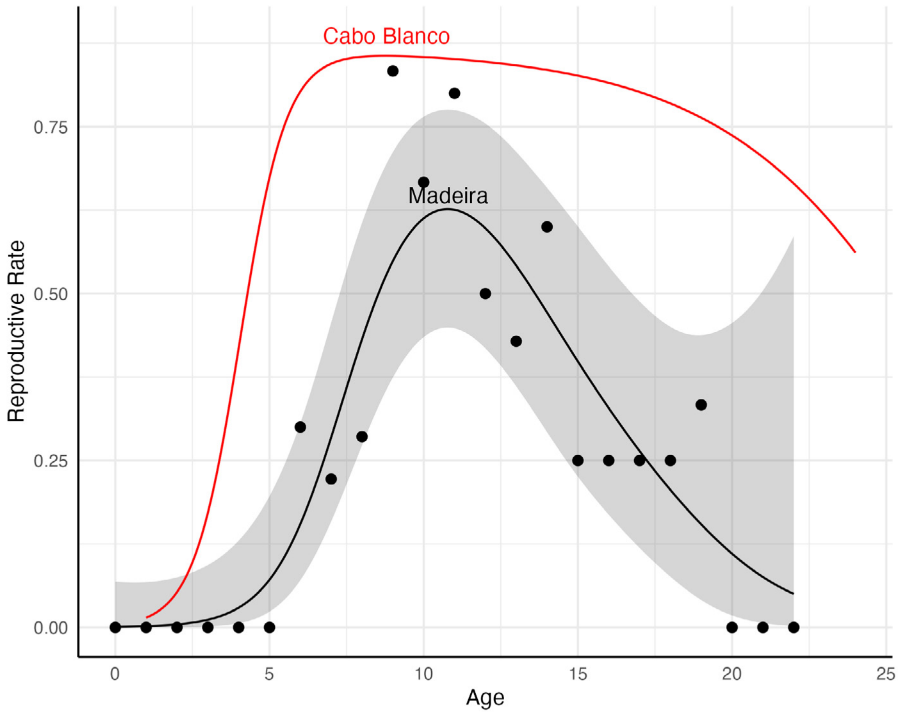

Fig. 3. Estimated age-specific reproductive rates of Mediterranean monk seals in Madeira. Black line and gray shading: fitted curve and 95% CI, respectively. Black circles: observed rate at each age. The fitted curve for females at the Cabo Blanco colony (in red, reproduced from Fernández de Larrinoa et al. 2021) is also shown for comparison

only from a low of 19 to a high of 23 (Fig. 4). The population grew thereafter, coinciding with several favorable years of neonatal survival (Table 6), rising to a maximum of 27 in 2021. Nearly all live seals were seen in most years (Fig. 4). The largest discrepancies were in 2012 and 2013, the first 2 yr when camera systems were being installed in caves. Several seals older than pups were still being identified during those first years of photographic identification effort. The realized growth rate (and 95% CI) for the entire interval from 2012 to 2021 was 1.032 (1.02–1.05). The intrinsic population growth rate, associated with a Leslie matrix populated with the survival and reproductive rates reported herein, was 0.998. The population sex ratio was quite female-biased, consisting of 18 females and 9 males. This female bias was entirely concentrated among adults, as there were 13 females and only 2 males older than 5 yr of age in 2021 (Fig. 5).

4. DISCUSSION

The installation of photographic surveillance systems inside caves complemented methods used prior to 2012. Subsequently, monitoring and data collection capabilities were greatly improved, providing new insights into population status, habitat use, vital rates, population size, and trend. As a result, a new strategy for monk seal conservation at Madeira archipelago was elaborated (Pires et al. 2020) under the frame of the Action Plan for Monk Seal Recovery in the Eastern Atlantic (González et al. 2006). Importantly, the monitoring methods complied with recommendations for non-invasive techniques that minimize disturbance to monk seals (Neves & Pires 1999, González et al. 2006).

4.1. Survival

The Madeira archipelago is situated more than 1000 km from the nearest other monk seal population at Cabo Blanco and is even further from seals populating the Mediterranean Sea. Joint analysis involving the identification of individual seals in photographs and telemetry data from Madeira and Cabo Blanco found no evidence of movement between these populations (Fernández de Larrinoa et al. 2021). Consequently, the apparent survival estimates we have presented can be considered actual survival rates, unaffected by emigration or immigration.

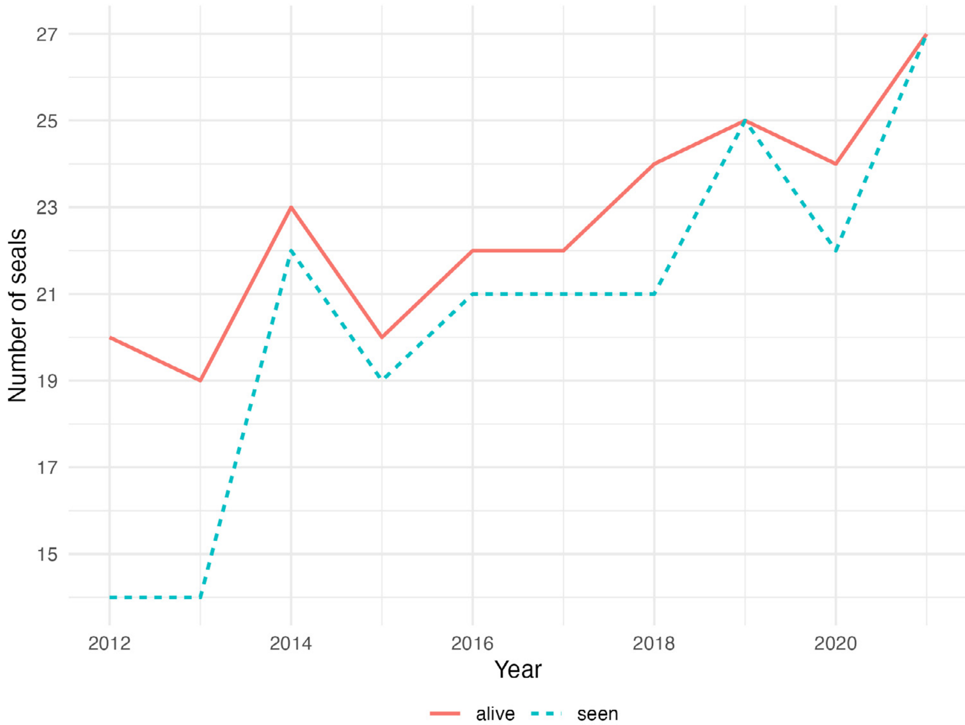

Fig. 4. Monk seal abundance in Madeira, 2012–2021. Solid line: total number of seals; dotted line: number of individuals observed in each year

Monk seals in Madeira exhibited age-related survival changes typical of mammals, whereby the lowest survival is experienced early in life, subsequently rising to a level that remains constant throughout most of adult life (Caughley 1966). The limited number of individuals available in this study prevents drawing robust conclusions regarding the age when adult survival rates are attained, whether there are sex differences in survival in younger seals, and whether senescence occurs. Further monitoring will eventually allow such patterns to be discerned more clearly.

Cabo Blanco survival estimates are far more precise than those from Madeira, where relatively wide CIs again prohibit strong conclusions about differences among these populations (Fig. 2). Yet the point estimates do suggest that survival during the first year of life is similar at both sites. This is also true during the period from birth to 2 mo old, during which survival was estimated to be 0.57 in Madeira and 0.61 at Cabo Blanco (Fernández de Larrinoa et al. 2021). Survival from age 1–2 yr may be somewhat higher in Madeira than at Cabo Blanco, though there is no statistically significant difference between the estimates from the 2 sites. Estimated adult (ages greater than 2 yr) survival rates were similar at both sites, and adult females exhibited significantly higher survival than adult males in both populations. Adult males in Madeira apparently have somewhat lower survival than those at Cabo Blanco (discussed further below). Overall, given that marine productivity off Cabo Blanco is far higher than in the waters of Madeira, we anticipated that Cabo Blanco seals would likewise enjoy higher survival rates from weaning to adult ages. The reasons why there is no evidence for any such a disparity are unknown.

4.2. Reproduction

The pattern of age-specific reproduction of monk seals in Madeira is perhaps the most notable finding of this study (Fig. 3). Compared to seals from Cabo Blanco, those in Madeira exhibit delayed maturity, a lower peak in the reproductive curve, and instead of a sustained high birth rate throughout adulthood, there is an apparent early onset of reproductive senescence. The dependence of reproductive performance on nutrition has been well-established in mammals (Sadleir 1969). The differences in reproductive rates at Cabo Blanco and Madeira are entirely consistent with the hypothesis that limited prey availability slows the growth of female seals in Madeira and reduces the frequency with which they

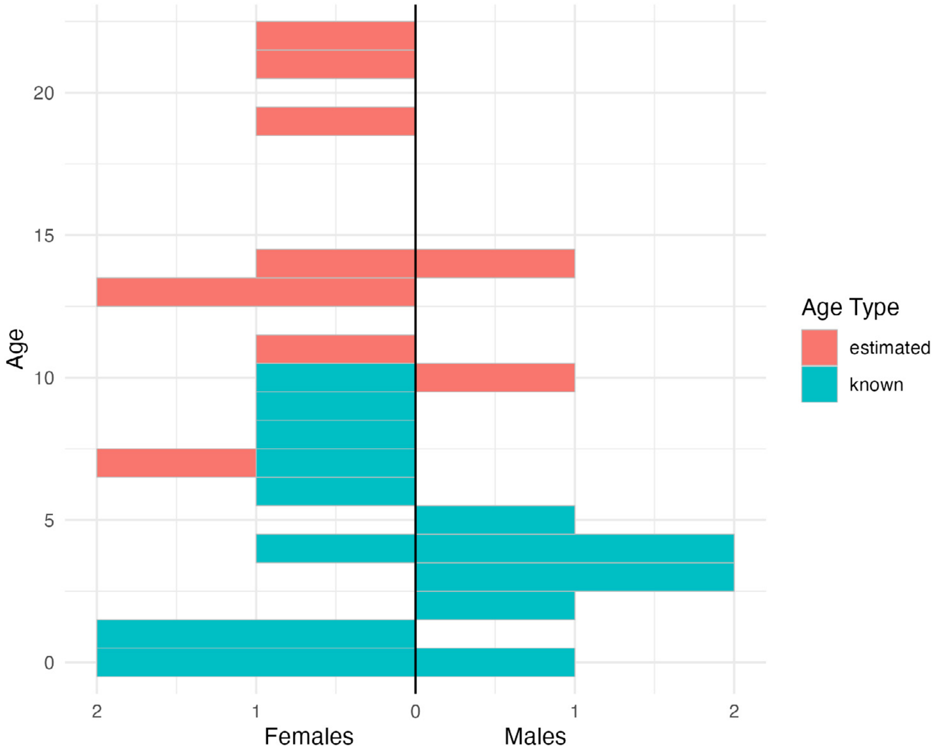

Fig. 5. Age structure of the monk seal population in Madeira in 2021. Colors indicate whether ages are known or estimated

are able to attain sufficient body condition to reproduce. An identical pattern has occurred in Hawaiian monk seals, where seals in the Northwestern Hawaiian Islands have exhibited delayed and lower reproductive rates than those in the main Hawaiian Islands (Harting et al. 2007, Robinson et al. 2021). In the Hawaiian seals, variation in reproduction amongst subpopulations has been consistent with variation in prey availability. Notably, the differences reported here and by Fernández de Larrinoa et al. (2021) between the Madeira and Cabo Blanco monk seal population are even more striking than that observed in the Hawaiian species. The GRR of females older than 2 yr of age at Cabo Blanco (0.71) is more than double that of Madeira seals (0.31).

4.3. Conservation implications

The Mediterranean monk seal population in Madeira is very small (27 individuals in 2021) and isolated, making the species vulnerable to extinction in this, one of only 3 global subpopulations. Nevertheless, there are grounds for optimism that monk seals will persist in Madeira. The conservation measures implemented by the Regional Government of Madeira have been highly successful, as evidenced by the population having increased 3- to 4-fold since the late 1980s.

A Leslie matrix incorporating the vital rates reported here suggests that conditions are favorable for continued, albeit slow, continued growth. The intrinsic rate of population growth (0.998) is considerably lower than the realized growth rate (1.032) estimated from abundance estimates spanning 2012–2021. This discrepancy is likely due in part to the population's female-biased sex ratio, especially in the reproductive ages. If the sex ratio trends closer to parity over time, the realized growth rate would slow if vital rates otherwise remained stable. Animals most frequently observed at Madeira's main island, in places frequented by humans such as recreational diving sites, marinas, ports, and fish farms, are generally adult males, exhibiting bold behavior. In contrast, adult males are rarely observed at the Desertas Nature Reserve, where human activities are restricted and monk seals are better protected. This behavior likely makes adult males more vulnerable to negative interactions and direct persecution related to human activities. Notably, during the study period, 3 adult males were found with deep cuts in their throats, 2 of which died from their wounds. These unusual injuries were probably human-caused. Another adult male was observed with various wounds on one side of his body, including a foreflipper, which was likely caused by a boat propeller. During this study, adult females were rarely observed in human-occupied areas and no human-caused injuries were observed. These differences in behavior likely contribute to the significantly lower survival rate estimated for adult males compared to adult females.

Presently, the primary limitation on population growth appears to be chronically limited prey resources leading to depressed reproductive rates. Fisheries in Madeira are known to currently rely extensively on pelagic and bathypelagic high trophic level species due to the reduced habitat provided by its narrow insular shelves, steep inclines of the slopes, and low productivity of its oligotrophic waters, which impose severe limits to the habitat available for demersal species and the abundance of resident fishes (Delgado 2007). Despite this, coastal fisheries have been exploited since the discovery and colonization of Madeira in the fifteenth century (Santos 2010) and more recently, also for recreational fisheries, which are estimated to constitute around 30% of the unreported catches in the region (Shon et al. 2015). Commercial overfishing together with coastal environmental degradation have caused the collapse of coastal and demersal fish stocks in Madeira (Hermida & Delgado 2016). Intense overfishing of coastal species in the eastern Atlantic region is also responsible for ecosystem degradation. For example, removal of predators has allowed sea urchins to proliferate and graze down the erect vegetative framework of the reefs, creating barrens that reduce the productivity of nearshore ecosystems (Sala et al. 1998, Clemente et al. 2010, Ling et al. 2015). This also seems to be the case in Madeira (Friedlander et al. 2017).

Fortunately, notwithstanding lower prey availability, monk seals in Madeira are able to survive at rates comparable to those at Cabo Blanco. Adult female seals in Madeira appear to maintain a very high survival rate (0.98) while producing offspring at a low rate. The apparent deficit in prey availability in Madeira is not readily amenable to improvement, although some measures may be successful. Better fisheries and coastal zone management as well as larger and more effective marine protected areas around Madeira have been suggested as methods to restore ecosystem services essential to the island community (Friedlander et al. 2017). Such measures would likely benefit the monk seal, a great example of Madeiran natural heritage.

Limited high-quality cave habitat for parturition and nursing may also constrain future population growth. The caves at Desertas Island are small and considered to be a suboptimal habitat for monk seals, which may largely explain why only 57% of pups survived the first 2 mo of life. Breeding in caves in the Atlantic, both in Madeira and Cabo Blanco, is associated with elevated pup mortality. During autumn and winter storms and high tides, inner beaches are flooded and young pups may be washed away by waves and either drown or become separated from their mothers, subsequently dying from starvation (Gazo et al. 1999, Neves & Pires 2001, Pires et al. 2008).

If the population continues to grow, these caves may become overly crowded, leading to higher neonatal mortality. Historically, monk seals were known to give birth and rear their young on open beaches but eventually sought refuge from human persecution in sea caves (Barros 1570 in Borges et al. 1979, Johnson & Lavigne 1999, González 2015). Fortunately, possibly due to their protection, monk seals on the Desertas Islands have begun to change their nursing habitat, taking their pups out of the caves. Although no births have been recorded on open beaches, some mothers moved with their pups, when they were a few days or weeks old, to the open beach of Tabaqueiro Beach. Similarly, sightings of females with young on outer beaches are also occurring in Greece (Dendrinos et al. 2022).

When humans first arrived in Madeira, the monk seal population was substantial. Presumably, that was in part possible because seals used the Madeira Island beaches as a nursery and resting habitat. Moreover, in the absence of people and fisheries, we can infer that prey resources were also more favorable. Development of Madeira Island beach habitat and occupation by ocean users including residents may preclude recolonization by monk seals. The village of Madeira Island known as Câmara de Lobos (Chamber of Wolves) due to the presence of monk seals (in Madeira called lobos-marinhos, sea wolves) was where the species was first described in Madeira and where the majority of monk seals were recorded (Melo 2017). Today, that little bay is surrounded by buildings, and it is a port for small fishing vessels, making it unsuitable for monk seal recolonization. Moreover, there is very limited suitable beach habitat for seals on the protected Desertas Islands. Consequently, the current carrying capacity of the Madeira Archipelago, both in terms of prey resources and terrestrial habitat, may dictate that the monk seal population there is destined to remain quite small.

However, humans and monk seals do coexist on beaches elsewhere. Hawaiian monk seals *Neomonachus schauinslandi*, after centuries of confinement to the remote Northwestern Hawaiian Islands, have recolonized the human-populated main Hawaiian Islands, where they currently number approximately 400 (Baker & Johanos 2004, Baker et al. 2011, Carretta et al. 2022).

Based on the vital rates and demographic trends presented here, the Mediterranean monk seal population in the Madeira Archipelago should be capable of long-term persistence. Still, the population is currently extremely small and therefore vulnerable. While there is capacity for continued recovery, the constraints of both limited prey resources and terrestrial habitat dictate that this population will likely remain small even in the most optimistic scenario. Therefore, consistent conservation and monitoring will be required to ensure this treasure of Madeira's natural heritage continues to thrive.

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