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ORIGINAL PAPER

A review of leopard seal (*Hydrurga leptonyx*) births and pups using a standardised age-class classification system

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Abstract

Despite the ecological importance of leopard seals (*Hydrurga leptonyx*) as apex marine predators, little is known about their reproductive biology. To address this paucity, we reviewed leopard seal birth and pup records and applied a standardised age-class classification system to differentiate between births/newborns (offspring ≤ 14 days old) and pups (> 14 days but < 6 months old). We compiled 19 birth/newborn and 141 pup records and examined their occurrence by month, region, substrate, birth-specific attributes (i.e. birth observations, fresh umbilicus or placental), standard length, weight, presence of mother, presence of lanugo, sex, status (e.g. born alive) and fate. These records indicate that leopard seal births occur between September and December, with peak records from September to November, whilst pup records peaked between August and December. The regions with the most birth/newborn records were the sub-Antarctic Islands (31.6%) and Chile (31.6%), followed by Antarctica (15.8%), New Zealand (15.8%) and the Falkland Islands (5.3%). Pups were recorded predominantly in the sub-Antarctic Islands (54.6%), followed by the Antarctic (42.6%), Chile (2.1%) and Australia (0.7%). Whilst leopard seal birth records were predominantly on ice, they were also found on *terra firma*. The northernmost published leopard seal birth records occurred in New Zealand whilst the northernmost published leopard seal pup records occurred in Australia. This study contradicts the long-standing hypothesis that leopard seals only give birth on Antarctic pack ice, and instead, here we indicate that 84.2% and 57.4% of collated leopard seal birth and pup records, respectively, occur outside of Antarctica. Our records illustrate the importance of northern regions as part of the leopard seal's range. We emphasise the need to conduct research focused on the reproductive biology of this keystone species throughout its range and that future management of leopard seal populations should also consider their northern range.

Keywords Apex predator · Distribution · Newborn · Phenology · Phocid · Pinniped · Reproduction

Sheridan Stone: Posthumous.

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Introduction

Leopard seals (*Hydrurga leptonyx;* de Blainville, 1820) have a southern circumpolar distribution. The majority of the population is distributed south of the Antarctic convergence, in the sub-Antarctic Islands and Antarctica (Rogers 2018), between 50° S and 80° S where they are documented as primarily inhabiting the pack ice (Bonner 1994; Southwell et al. 2008; Meade et al. 2015; Bester et al. 2017), with higher densities occurring southwards towards the edge of the continent (Bester et al. 1995; 2002). As the sea-ice melts and recedes during the Austral spring and summer, leopard seals are known to move south towards the Antarctic continent (Rogers and Bryden 1997; Bester et al. 2002; Rogers et al. 2005). Conversely, they are known to disperse beyond the sea-ice edge northwards, during the extension of pack ice in the Austral autumn and winter (Rounsevell and Eberhard 1980; Bester and Roux 1986; Bester et al. 1995; Jessopp et al. 2004), with some individuals dispersing further north to the continents and islands abutting the Southern Ocean (Rogers 2018). The northernmost published record of a leopard seal is a sighting in Rarotonga, Cook Islands (Berry 1960[1]). Generally, these extralimital occasional records involve juvenile animals, which appear to be the most mobile (Rounsevell and Pemberton 1994; Rogers et al. 2005). Conversely, leopard seals have been recorded in New Zealand (hereafter NZ) waters since the twelfth century (Smith 1985) and the species has been documented year-round and includes immature and mature individuals of both sexes, in all regions (Hupman et al. 2020).

Leopard seals tend to live relatively solitary lives[2] and are generally found in remote locations (Rogers 2018). This appears to have limited the extent of studies and consequently our knowledge of their reproduction (Hamilton 1939; Southwell et al. 2003). What has been surmised so far is that female leopard seals are considered sexually mature between two and seven years of age (Øritsland 1970; Shirihai 2002), with four being the average (Reidman 1990). Reproductively mature females have a one-year sexual cycle with a single ovulation each year (Øritsland 1970) and give birth to a single pup (Rogers 2018). Leopard seals are thought to mate between November (Southwell et al. 2008) and March (Gwynn 1953), with a peak during mid-November and December (Shirihai 2002). Whilst some researchers report delayed implantation with post-fertilisation occurring between one (Bonner and Laws 1964) and 1.6 months (Reidman 1990), others believe it does not occur (Maxwell 1967; Harrison 1968). The gestation period for leopard seals is estimated to be eight to nine months (Gwynn 1953; Tikhomirov 1975; Ledingham 1979) but has been quoted to extend to 12 months (Atkinson 1997). Previous studies have suggested that sightings of pregnant leopard seals north of the Antarctic convergence[3] are rare (Gwynn 1953; Brown 1957; Ledingham 1979) and that these individuals are probably sick or injured (Ledingham 1979).

Births are described as taking place during the Austral spring and early summer (Laws 1984), i.e. from September to early January in Antarctic and sub-Antarctic waters (Matthews 1929; Shirihai 2002; Jefferson et al. 2015; Rogers 2018). A peak birth period has been described to occur between November and December (Laws 1984; Hückstädt 2015; Jefferson et al. 2015; Rogers 2017). The birthing season may be area dependent, occurring later in the year the further south the birth occurs (Laws 1984, 1993a, b; Laws and Sinha 1993[4]). The published literature states that all pinnipeds give birth out of the water (e.g. Bertram 1940) and that "*there is no reason to suppose that the leopard seal is an exception*" (Ledingham 1979). The published literature also states that leopard seals "*give birth to their pups and wean them on floes of Antarctic pack ice*" (Rogers 2018).

The nursing period is most frequently cited as lasting between two and four weeks (e.g. Southwell et al. 2003; Schulz and Bowen 2004; Rogers 2009; Jefferson et al. 2015); however, it has been suggested that this may be as short as 10 days (Brown 1957) or as long as eight weeks (Maxwell 1967; Rogers et al. 2013). There are no published data indicating whether leopard seal mothers remain with their pups on the ice continuously for the duration of the lactation period, as other Antarctic seals typically do, or whether they are only present intermittently (Testa et al. 1989; Southwell et al. 2008). However, it has been noted that "*the lactating female* [leopard seal] *fasts completely*" during this period (Laws 1993a, b; Laws and Sinha 1993), indicating that she

[1] This record did not include a latitude and longitude when it was originally published in Berry (1960). However, a number of subsequent publications have referred to this location as being located at 20° 45' S. That is, incorrect as the entire Cook Islands are located at 21° S.

[2] Larger aggregations are known to occur, such as approximately 60 animals sighted on 20 October 1978 within Admiralty Bay, King George Island, Antarctica, of which 36 were sighted within Ezcurra Inlet, a 5-km-long branch of Admiralty Bay (Myrcha and Teliga 1980).

[3] This is also known as the Antarctic Polar Front and is a thermo-differentiating (cold northward-flowing Antarctic waters meet the relatively warmer waters of the sub-Antarctic) marine belt encircling Antarctica. Although the convergence location ranges between 45° S and 60° S, it does not typically vary more than half a degree of latitude from any given position. It is recognised by the Convention on the Conservation of Antarctic Marine Living Resources (1980) for its biological importance.

[4] E.g. at South Georgia, a sub-Antarctic Island which lies in a relatively northern location (54.42° S), although still south of the convergence, leopard seal births occur in late August and early September (Matthews 1929; Walker et al. 1998).

is less likely to be absent from the pup for extended foraging purposes as occurs in some pinniped species (e.g. Schulz and Bowen 2004).

The pervasive uncertainty about leopard seal reproduction is reflected in the limited number of published leopard seal birth, newborn and pup records. Here, we collated records and applied a leopard seal-specific standardised age-class classification system (SACCS) to determine if birth, newborn and pup records could be distinguished based on specific attributes. We assessed these records by month, region, substrate, key attributes, standard length, weight, sex, status and fate. We also assessed records of leopard seal births and newborns in NZ and Chile and discuss the scientific importance of these within the framework of reproductive ecology and distribution.

Materials and methods

Collation of birth and pup records

We collated three types of statements/records:

(1) Generalised Statements—Statements about leopard seal births, newborns and/or pups which did not include supporting substantiated data. Specifically, these were missing birth/newborn/pup sighting information, such as regional location and dates; (e.g. "*Newborns are 1.0–1.6 m and 30–35 kg,* Jefferson et al. 2015" or "*Females give birth to their pups and wean them on floes of Antarctic pack ice*", Rogers 2018)". Citations for Generalised Statements are shown in Online Resource 1.

(2) Complete Records—Records of leopard seal births, newborns and/or pups which included supporting substantiated data. Specifically, these contained birth/newborn/pup sighting information, including dates (at least month and year or a specific range of dates) and regional location; e.g. a published record "*Two lactating leopard seals with pups in weak lanugo were seen on 4 December and one more on 5 December [1968 at the Balleny Islands and Scott Island]*" (Tikhomirov 1975) or an unpublished record such as a photograph of an adult leopard seal with a suckling pup, documented as taken 13 December 2012, Port Lockroy, Antarctic Peninsula.

(3) Incomplete Records—Records of leopard seal births, newborns and/or pups which were not a Generalised Statement but lacked supporting substantiated data to elevate it to a Complete Record. Specifically, these were missing birth/newborn/pup sighting information, such as dates and/or regional location (e.g. a photograph of a leopard seal and offspring taken on the ice in Antarctica, but no date is provided).

We used Generalised Statements to provide an overview of the timing of leopard seal births, newborns and pups and to expose the gaps in our knowledge of leopard seal reproductive ecology. Complete Records were collated and analysed, whilst Incomplete Records were excluded from our dataset.

For Complete Records, we noted the source and collated a number of 'attributes'; (1) date of sighting; (2) location of sighting; (3) substrate where the sighting occurred; (4) number of individuals within that location; (5) age; (6) standard length (SL[5]); (7) weight; (8) description of individual(s) by the author(s); (9) presence of an adult female (i.e. the presumed lactating mother) and if suckling occurred; (10) presence of lanugo; (11) sex; (12) status when observed (i.e. alive or deceased) and (13) fate (i.e. last seen alive, died naturally, killed, euthanised). For birth and newborn records, additional birth-specific attributes were collated (i.e. (14) a person witnessing a birth and/or (15) a fresh umbilical cord and/or (16) placenta/placenta stain). When new data for any given Complete Record became available in subsequent sources that was added to the original record in our database (e.g. an author might note a birth in one publication and provide the SL for that individual in a subsequent publication). The only exception to this method was when we assessed published descriptions of individuals, as descriptions were often inconsistently/incorrectly paraphrased by subsequent authors and as such, only the description in the original published source was used. To ensure birth and pup records were not duplicated, we cross-referenced the 16 attributes mentioned above and overlapping records were consolidated. Additionally, to avoid duplications, where photographs were available, we identified individuals (both mothers and offspring) using their unique pelage patterns (see Hiruki et al. 1999 and Forcada and Robinson 2006 for identification methods). When a match was confirmed, subsequent records of the offspring, within a 14-day period for a birth and within a six-month period for a pup, were consolidated as one record. We recognised that there was potential for duplication across the two age classes (i.e. if a leopard seal recorded as a birth survived, it could subsequently be recorded as a pup).

Where text (within the original source) specifically referred to multiple (but undefined) numbers of individuals, we noted them as 1 + to ensure we did not speculate/overstate the number of individuals. Where SL and weight were listed as non-metric measurements, they were converted to

[5] Standard length refers to the straight-line distance of a leopard seal from the tip of the snout to the tip of the tail (Committee on Marine Mammals 1967).

allow comparisons between records and ease of cross referencing. Lactating females documented without a pup present were excluded from our dataset.

Standardised age-class classification system (SACCS)

We developed the SACCS to differentiate between birth, newborn and pup records and tested the classification system against both published and unpublished records. Of the aforementioned attributes, the following allowed us to differentiate between a birth, newborn and pup record: (1) age (see details below); (2) SL; (3) birth-specific attributes and (4) description of individual(s) by the author(s).[6] Weight was not used in the SACCS due to its ability to be influenced by both the mother and offspring's size and body condition (Laws 1962; Bryden 1968) and due to overlap between weights in birth, newborn and pup age classes (i.e. Scheffer and Wilke (1953) found this to be the case for Northern fur seals, *Callorhinus ursinus*). Instead, length was used in the SACCS as it was considered to have lesser variation and is a more reliable indication of age in pinnipeds (Scheffer and Wilke 1953). Although the presence of an adult female (i.e. the presumed lactating mother) was used to categorise a record as younger than a juvenile,[7] it was not used to differentiate between the birth, newborn and pup categories as nursing/close contact between the mother and offspring is described as typically occurring from birth up until four weeks of age in this species (Shirihai 2002; Rogers 2009; Jefferson et al. 2015), thereby overlapping between age classes in our SACCS. Additionally, lanugo was used to determine that the offspring was not a juvenile, but it was not used to differentiate between birth, newborn or pup records as lanugo in pinnipeds is typically not moulted for several months after birth (e.g. Badosa et al. 2006), thereby also overlapping between age classes.[8]

For a record to be classified as a birth or newborn in our SACCS, it had to include at least one of the following descriptions by the author(s) and/or sighting/photographic/video evidence of: (1) age being $\leq$ 14 days old, and/or; (2) SL < 120 cm, and/or; (3) birth-specific attributes, and/or (4) using any of the following key terms: born, birth, full-term, newborn, newly born, pupped (when used as a verb), premature birth, stillborn, adult–newborn pair, mother and newborn, nursing and suckling.

A birth was defined in our SACCS as offspring being $\leq$ 72 h old, which was based on allowing a margin of caution above those individuals reported in the literature as being "*born days ago*" (Online Resource 2). Also, given the duration of labour in pinnipeds has been described as short as eight minutes (Laws and Sinha 1993) or as long as nine hours and 35 min (Blanchet et al. 2006), we believe all birth records would fall within this timeframe. A newborn was defined in our SACCS as offspring being $\leq$ 14 days old, again defined with allowing a margin of caution, in this case based on pinnipeds being reported in the literature with fresh umbilical cords at up to 12 days old[9] (Kim et al. 2020).

The upper SL limit in our SACCS of 120 cm for birth and newborn records was based on allowing a margin of caution above the longest credible birth length record (113 cm; Brown 1957). There is, of course, some scope for overlap in the SLs between birth, newborn and pup records, as some newborns may be large and some pups may be small.

For a record to be classified as a pup in our SACCS it had to include at least one of the following descriptions by the author(s) and/or sighting/photographic/video evidence of: (1) age being > 14 days, but < 6 months old, and/or; (2) SL $\geq$ 120 cm but < 200 cm, and/or (3) using any of the following key terms: adult-pup pair, mother and pup, nursing, pup, puppy, suckling or young.

The upper age limit of 6 months for pup records in our SACCS was based on the age-at-length data relationship of leopard seals as described by Laws (1957; approximately 6 months old and 200 cm).

The upper SL limit in our SACCS for pup records was 200 cm was based on the age-at-length data relationship established by Laws (1957; length of 200 cm at approximately 6 months old) and the age-class categories defined in Forcada and Robinson (2006; pups up to 200 cm).

To determine the reliability of the age classes in the SACCS as well as the robustness of the age-class datasets (i.e. once the records were allocated to either the birth, newborn or pup category), each record was allocated a validation rank (certain, probable, possible), based on the presence/absence of different attributes as follows. 'Certain' attributes included descriptions by the author(s) and/or sighting/photographic/video evidence of: (i) birth-specific attributes; (ii) age, (iii) SL and (iv) the presence of a suckling pup. 'Probable' attributes included all other attributes. Records with dates, locations and 'certain' attributes were classified as Certain. Certain Records may also have included 'probable'

[6] In the case of unpublished records, the description of individual(s) by the author(s) was not used to solely categorise the record as a birth or pup due to the inconsistencies in descriptions (e.g. a photograph of a large offspring alongside its mother, may be described as a birth, however the photograph provides empirical evidence as to the age-class category instead being a pup).

[7] We define a juvenile as a leopard seal post-weaning (and pre-pubescent) and > 6 months old and therefore unlikely to be accompanied by its mother.

[8] We could find no data regarding the age that leopard seal pups moult their lanugo; however, we define a juvenile as having no lanugo.

[9] Kim et al. (2020) described a Weddell seal (*Leptonychotes weddelli*) which had a 'undried' umbilical cord observed 12 days after birth.

attributes. Records with dates, locations and only 'probable' attributes were classified as Probable. Records without dates, locations and 'certain' attributes, but with only 'probable' attributes (e.g. a description only, such as "*a leopard seal pup was seen as the vessel sailed south*") were classified as Possible. Only Certain and Probable Records were included in our analysis.

We noted that some records had overlapping attributes between birth, newborn and pup categories. When this occurred, we prioritised the 'certain' attributes above 'probable' attributes to categorise the record. For example, a record which included a SL of 160 cm, but was described by the author as a "*birth*" would be classified as a pup. When a description by the author(s) was the only attribute available to determine age class and such descriptions referred to two or three of the birth, newborn and pup categories (e.g. 'newly born pup'), we erred on the side of inclusion for the birth category due to the short time frame for a birth (i.e. ≤72 h old) and used the youngest descriptor (i.e. 'newly born') to categorise the record.

Inconsistencies and errors

During the collation of birth, newborn and pup records, we observed inconsistencies and errors (within and between citations). For example, an inconsistency might be the rounding up and subsequent rounding down of measurements within the same manuscript, whilst an error might occur when a location was cited incorrectly in a subsequent publication.

Analysis

We analysed all Complete Records by month, region, substrate, birth-specific attributes, SL, weight, presence of mother, presence of lanugo, sex, status and fate. When examining Complete Records by region, we classified locations into six categories: (1) Antarctica (encompassing the waters and land south of the Antarctic Convergence and surrounding seas, e.g. D'Urville Sea and the Antarctic Islands, including Balleny, Scott, South Orkney and South Shetland); (2) the sub-Antarctic Islands (including Bird, Heard, Kerguelen, McDonald, Macquarie and South Georgia); (3) Chile, South America (including Laguna San Rafael, Parry Fjord, Tierra del Fuego Archipelago); (4) Falkland Islands; (5) Australia and (6) NZ (including offshore islands, e.g. the Chatham Islands). Substrate was classified as a cage, grass, ice, a rocky beach, a sandy beach or water. When examining Complete Records by SL or weight, if actual SL's or weights were not available and instead a range was provided, the median was plotted. When SL's were reported as '<' or '>', they were excluded from the analysis as there was no way to determine how much smaller (or larger) the offspring was as compared to the measurement provided (e.g. "*<152 cm*" in Moseley (1892), Online Resource 3). When examining the records by month, we compared Generalised Statements against Complete Records to ascertain the accuracy of the former.

SL's or weights which were deemed anomalies or errors were excluded from SL and weight analyses. There were three such records: (1) a leopard seal that gave birth to a deceased pup in a cage on Heard Island in 1951 (Brown 1952). Whilst the author noted the offspring as being born overnight, the newborn measured 157 cm and weighed 29.5 kg (Online Resource 2). We concur with Laws (1957) and Paulian (1960) that this record contains anomalous data, as the length and weight are more aligned with the measurements of a pup rather than a birth; (2) a leopard seal sighted in Antarctica in 1968 was noted as being between 20 and 30 days old; however, a SL of between 60 and 169 cm was also noted (Tikhomirov 1975; Online Resource 3). We believe the SL of 60 cm for this record is erroneous, as this animal was at least 20 days old when measured and logically would have grown in the intervening days since birth; and (3) a young leopard seal sighted at Macquarie Island in 1977 was estimated to be between 60 and 75 cm in length. However, it is likely that the length estimation is incorrect (as suggested by the author) given that the offspring was observed from a 30-m distance by binoculars (Ledingham 1979).

Results

Collation of birth and pup records

We collated a minimum of 160 records of leopard seal births, newborns and pups which were composed of 19 leopard seal birth and newborns (Online Resource 2) and a minimum of 141 leopard seal pup records (Online Resource 3).

Standardised age-class classification system

We used the SACCS to classify all 160 records into either the birth, newborn or pup categories and only 1.3% ($n=2$) had overlapping attributes (between categories). Those two records were determined to contain erroneous data and are outlined in detail in the methods (analysis section).

There were so few birth and newborn records ($n=19$) that we consolidated them into one dataset and they are henceforth collectively referred to as 'births'.

For birth records, 68.4% ($n=13$) were classified as certain and 31.6% ($n=6$) were classified as probable (Online Resource 2). Similarly, for pup records, 75.2% ($n=106$) were classified as certain and 24.8% ($n=35$) were classified as probable (Online Resource 3).

Table 1 Months and seasons that leopard seal (*Hydrurga leptonyx*) births and pups occur, as indicated by Generalised Statements and Complete Records

Records / Dataset	Season	Summer		Autumn			Winter			Spring			Summer
	Month	January	February	March	April	May	June	July	August	September	October	November	December
Generalised Statements	Births & pups												
Complete Records	Births (*n*=19)												
	Pups (*n*=141)												

Where only a season was stated, this was converted into months (following Austral seasons: summer = December–February, autumn = March–May; winter = June–August; spring = September–November). As Generalised Statements did not differentiate between birth and pup records, they were presented together. The peak is shown in black with the range shown in grey

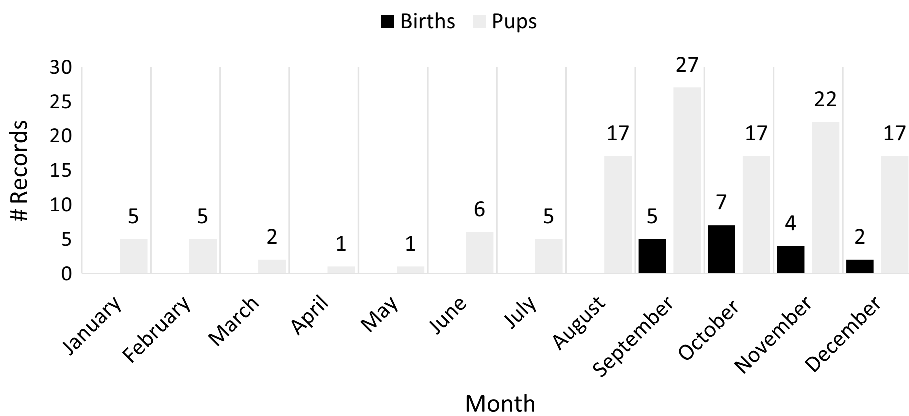


Fig. 1 Leopard seal (*Hydrurga leptonyx*) birth and pup records, by month

Inconsistencies and errors

We identified four categories of errors and inconsistencies: (1) date/location, (2) age-class terminology, (3) unit conversion and (4) citation and provide full details in Online Resource 4.

Occurrence by month

The Generalised Statements typically did not distinguish between leopard seal birth and pup records (Online Resource 1) and as such we present them together (Table 1). Collectively, these Generalised Statements described leopard seal births and pups to occur between August and February with a peak between November and late December (Table 1, Online Resource 1). In contrast, from the more reliable Complete Records, we were able to distinguish between the birth and pup records by applying the SACCS.

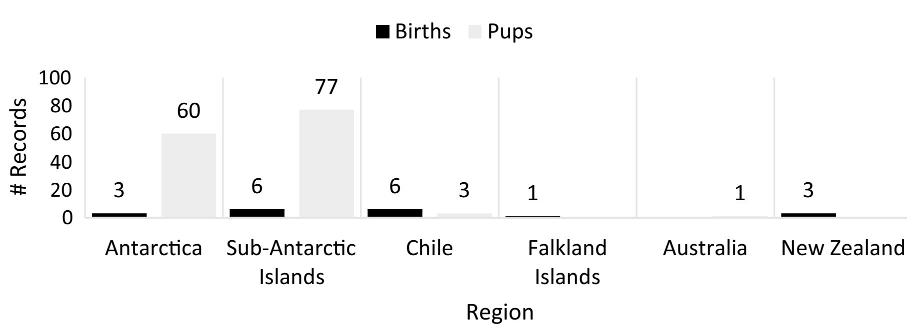
Of the 19 Complete birth Records, one contained a date range that included multiple months and therefore this record was excluded from the monthly analysis. The remaining 18 Complete birth Records occurred between September and December, with a peak period during September ($n = 5$), October ($n = 7$) and November ($n = 4$) (Fig. 1; Table 1; Online Resource 2). Of the 141 Complete pup Records, 16 contained a date range that included multiple months and these records were therefore excluded from the monthly analysis. The remaining Complete pup Records ($n = 125$) indicated a peak period during August ($n = 17$), September ($n = 27$), October ($n = 17$), November ($n = 22$) and December ($n = 17$) (Fig. 1; Table 1; Online Resource 3). There were ≤ six pups recorded in each remaining month (i.e. January $n = 5$, February $n = 5$, March $n = 2$, April $n = 1$, May $n = 1$, June $n = 6$ and July $n = 5$; Fig. 1; Online Resource 3).

Occurrence by region

Regions where births and pups were recorded are indicated in Fig. 2. The regions with the most births were the sub-Antarctic Islands (31.6%, $n = 6$) and Chile (31.6%, $n = 6$), followed by Antarctica (15.8%, $n = 3$), NZ (15.8%, $n = 3$), and the Falkland Islands (5.3%, $n = 1$) (Fig. 3; Online Resource 2). Pups were recorded predominantly in the

Fig. 2 Locations of Leopard seal (*Hydrurga leptonyx*) birth and pup records (see Online Resource 2 and 3 for details). Births have been recorded at Bird Island, Chatham Islands, Cuvier Island, Dunedin, Falkland Islands, Heard Island, Laguna San Rafael, Parry Fjord, South Georgia Islands as well as various islands along the Antarctic Peninsula (see Online Resource 2 for details). Pups have been recorded at Adélie Land, Balleny and Scott Islands, Bird Island, Heard Island, Kerguelen Islands, Laguna San Rafael, McMurdo Sound, South Georgia Islands, South Orkney Islands, South Shetland Islands, Sydney as well as various islands along the Antarctic Peninsula (see Online Resource 3 for details)

Fig. 3 Leopard seal (*Hydrurga leptonyx*) birth and pup records, by region



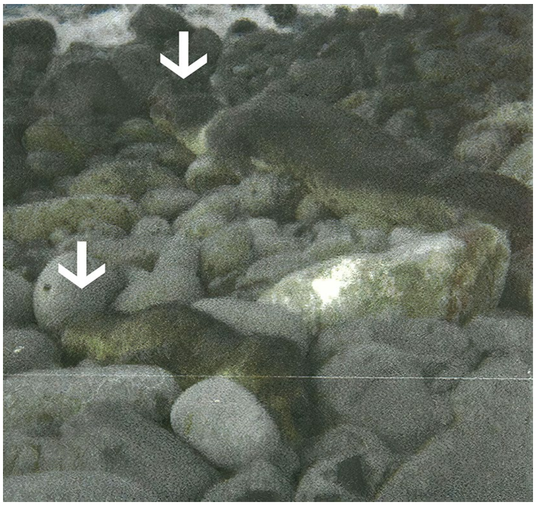


Fig. 4 Photographs taken shortly after the leopard seal (*Hydrurga leptonyx*) was born on 6 October 1977, just to the south of Scott's Monument on Cuvier Island, New Zealand, arrows indicate the newborn (left) and the mother (right), showing their proximity. Photograph Alan Martin (via Martin Cawthorn)

sub-Antarctic Islands (54.6%, $n=77$), followed by the Antarctic (42.6%, $n=60$), Chile (2.1%, $n=3$) and Australia (0.7%, $n=1$) (Fig. 3; Online Resource 3). A total of 84.2% ($n=16$) and 57.4% ($n=81$) of collated leopard seal birth and pup records, respectively, occur outside of Antarctica.

The most northerly records of leopard seal births were documented in Laguna San Rafael National Park (Chile) (46° 41′ S[10]; Acevedo et al. 2017) and NZ (Online Resource 2 and 5). The NZ births all occurred further north than the record in Chile: (1) Scott's Monument, Cuvier Island (36° 26′ 14″ S; 10°/1139 km further north) on 6 October 1977 (Hupman et al. 2020; Alan Martin pers. comm.; Fig. 4), (2) Kaingaroa, Chatham Islands (43° 43′ 50″ S; 3°/328 km further north) on 4 November 1972 (Cawthorn et al. 1985; King 1990; Hupman et al. 2020; Kerry-Jayne Wilson pers. comm.; Tony Sayers pers. comm.), and (3) Lawyers Head Beach, Dunedin, Otago (45° 54′ 31″ S; 1°/86 km further north) on 26 September 2017 (Hupman et al. 2020; Dalton Williams pers. comm.; Fig. 5). The most northerly record of a leopard seal pup was documented in Sydney (Australia) (33° 52' S; King 1983) (Online Resource 3).

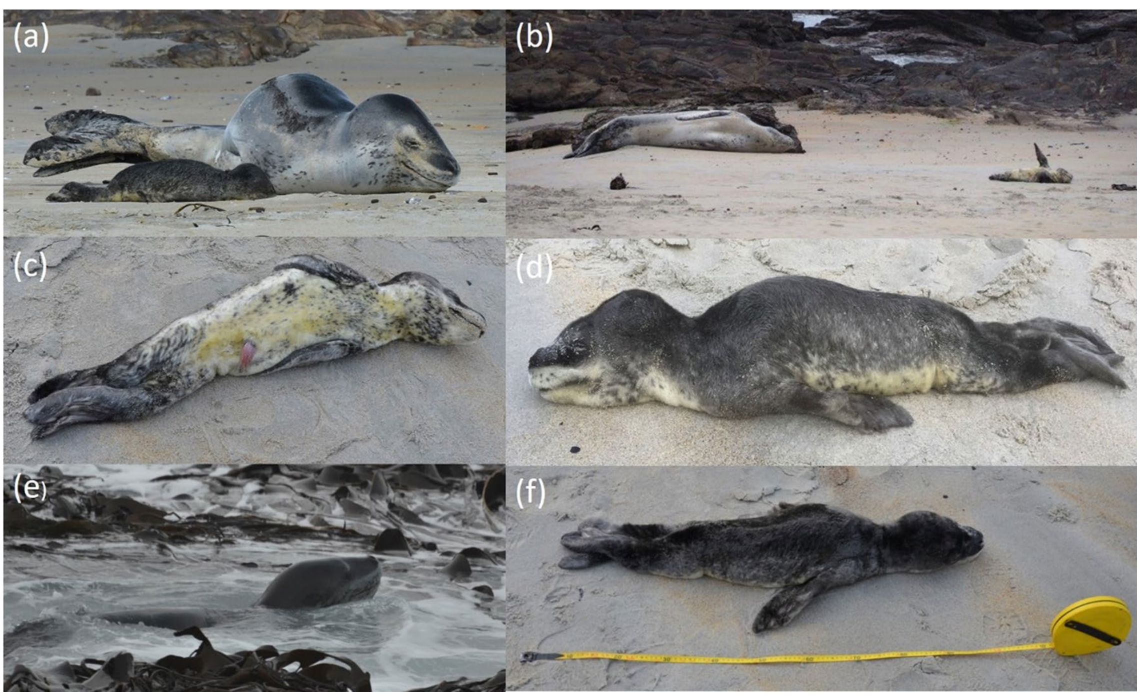


Fig. 5 Photographs taken shortly after the birth of the female leopard seal (*Hydrurga leptonyx*), on 26 September 2017 at Lawyers Head Beach, Dunedin, Otago, New Zealand, **a** the mother and newborn seal together, **b** mother and newborn seal apart, **c** newborn seal umbilical cord, **d** newborn seal, **e** mother seal heading out to sea and **f** newborn leopard seal being measured. Photographs **a**, b**,** **d**, **e** and **f**, LeopardSeals.org. Photograph **c**, Emma Curtin

[10] Latitudes were converted to decimal degrees using https://data.aad.gov.au/aadc/calc/dms_decimal.cfm and then the distance north was calculated using https://www.nhc.noaa.gov/gccalc.shtml.

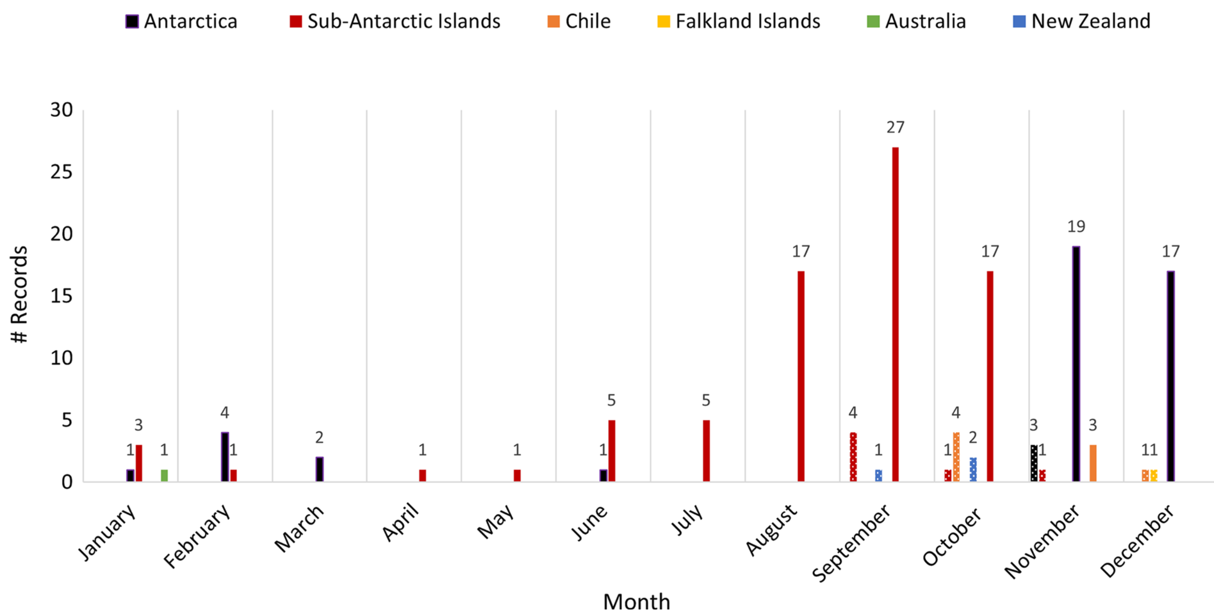


Fig. 6 Leopard seal (*Hydrurga leptonyx*) birth (spotted fill) and pup (solid fill) records, by month and region

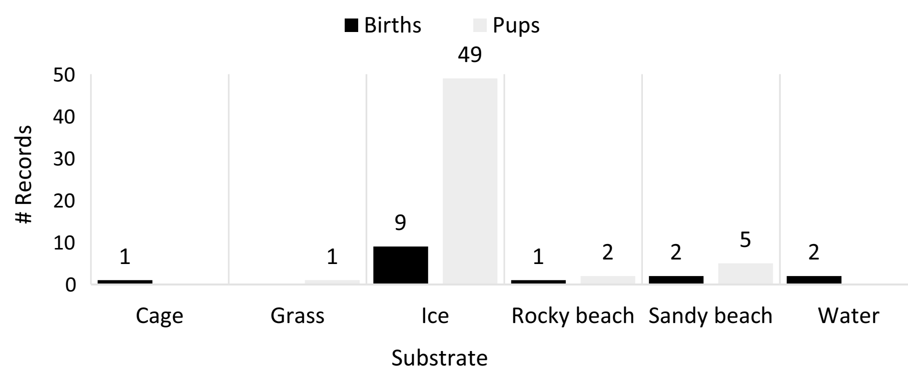


Fig. 7 Leopard seal (*Hydrurga leptonyx*) birth and pup records, by substrate

Occurrence by month and region

One birth record listed a date range that included multiple months and therefore this record was excluded from the birth occurrence and regional analysis. Birth records in Antarctica occurred in November ($n = 3$) (Fig. 6; Online Resource 2), whereas birth records in the sub-Antarctic Islands occurred in September ($n = 4$), October ($n = 1$) and November ($n = 1$) (Fig. 6; Online Resource 2). Further north, birth records occurred in Chile in October ($n = 4$) and December ($n = 1$), the Falkland Islands in December ($n = 1$) and in NZ in September ($n = 1$) and October ($n = 2$) (Fig. 6; Online Resource 2).

Sixteen pup records listed a date range that included multiple months and therefore these records were excluded from the pup occurrence and regional analysis. Pup records for Antarctica occurred in January ($n = 1$), February ($n = 4$), March ($n = 2$), June ($n = 1$), November ($n = 19$) and December ($n = 17$), whereas pup records for the sub-Antarctic Islands occurred in January ($n = 3$), February ($n = 1$), April ($n = 1$), May ($n = 1$), June ($n = 5$), July ($n = 5$), August ($n = 17$), September ($n = 27$) and October ($n = 17$) (Fig. 6; Online Resource 3). Further north, pup records were documented in Chile in November ($n = 3$) and Australia in January ($n = 1$) (Fig. 6; Online Resource 3).

Substrate

The substrate leopard seals were born onto was recorded in 15 of the 19 birth records (Fig. 7; Online Resource 2). One record involved a pregnant female being held captive in a cage on the shoreline (Heard Island; Brown 1952)—so although the birth occurred on a beach, we recorded it as a 'cage' as the animal was restrained and the substrate

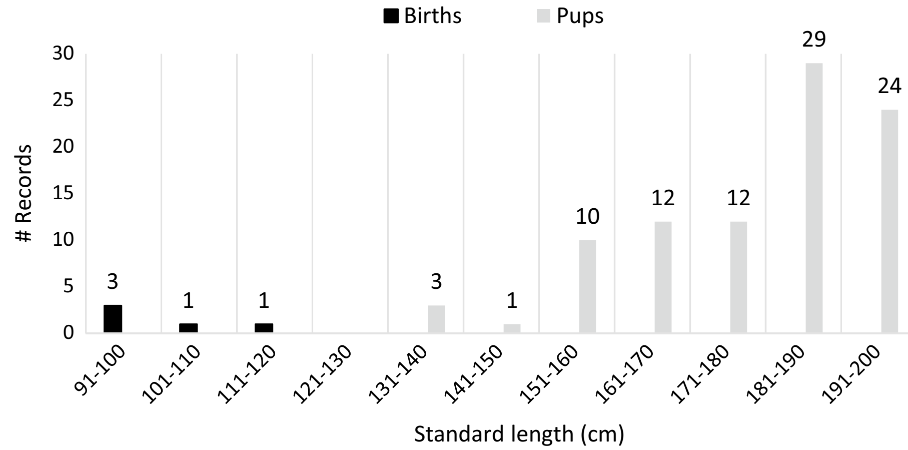


Fig. 8 Leopard seal (*Hydrurga leptonyx*) birth and pup records, by standard length

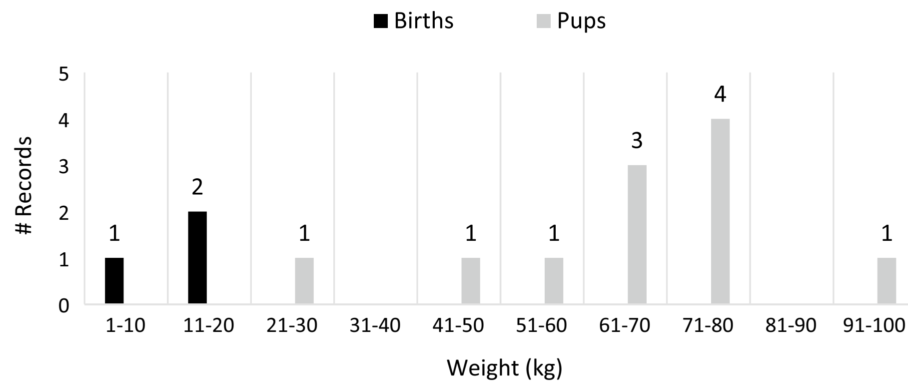


Fig. 9 Leopard seal (*Hydrurga leptonyx*) birth and pup records, by weight

determined by the captors. The remaining births occurred on ice ($n = 9$), a rocky beach ($n = 1$), a sandy beach ($n = 2$) and in the water ($n = 2$) (Fig. 7; Online Resource 2).

The substrate leopard seal pups were sighted on was recorded in 57 of the 141 pup records (Fig. 7; Online Resource 3). Ice was the most prevalent substrate recorded ($n = 49$) (Fig. 7; Online Resource 2). In all the remaining pup records the substrate was recorded as either a sandy beach ($n = 5$), a rocky beach ($n = 2$) or grass ($n = 1$) (Fig. 7; Online Resource 3).

Presence of birth-specific attributes

Eight of the 19 birth records documented the presence ($n = 5$) or absence ($n = 3$) of an umbilicus and nine of the 19 birth records documented the presence ($n = 5$) or absence ($n = 4$) of a placenta (or placenta stain) (Online Resource 2).

Standard length and weight

SLs were recorded in five of the 19 birth records, all of which were between 91.4 cm and 113 cm (Fig. 8; Online Resource 2). SLs were recorded in 91 of the 141 pup records, all of which were between 132 and 199 cm (Fig. 8; Online Resource 3).

Weights were recorded in three of the 19 birth records, all of which were between 9 and 15 kg (Fig. 9; Online Resource 2). Weights were recorded in 11 of the 141 pup records, all of which were between 29.5 kg and 98 kg (Fig. 9; Online Resource 3).

Presence of mother

A mother was present in 15 of the 19 birth records and 48 of the 141 pup records. Of these, one birth and 13 pup records included offspring suckling from their mothers (Online Resource 2 and 3).

Presence of lanugo

Lanugo was present in four of the 19 birth records and in 11 of the 141 pup records (Online Resource 2 and 3).

Sex

The sex was documented in two of the 19 birth records, with both individuals being female (Online Resource 2). The sex was documented in 76 of the 141 pup records, where 32 were female and 44 were male (Online Resource 3).

Status and fate

For the birth records, regarding the status and fate of the offspring, five individuals were alive initially, but their subsequent fate was unknown, seven individuals were initially reported to be deceased, three individuals were reported as alive initially before subsequently dying, three individuals were reported as alive initially before being killed and one individual was reported as alive and then subsequently euthanised (Online Resource 2). For the pup records, 130 individuals were reported as alive initially, but their subsequent fate was unknown and 11 individuals were reported as alive initially before being killed (Online Resource 3).

Discussion

Given the relatively long history of documenting leopard seals across the species' range, the paucity of knowledge on leopard seal reproduction and the limited birth and pup observations is striking. However, through outreach and research effort, we collated 19 birth and 141 pup records and created the first leopard seal-specific SACCS for distinguishing between these two age classes. Despite our comprehensive efforts, there is a strong possibility that other records exist which were not included in our dataset. Such records may lie in publications in languages other than English or in unpublished datasets. The scarcity of records is particularly concerning, therefore we strongly encourage researchers to document this important part of the life history of leopard seals. However, we believe that the accumulated dataset is robust and that it provides an adequate starting point for further research.

Standardised age-class classification system

By applying the SACCS, we were able to categorise all Complete Records as either a birth or pup with < 2% of records having an overlap between categories. Despite 68.4% of the total birth records and 75.2% of the total pup records classified as certain, respectively, the pup database was more robust, i.e. these records contained more 'certain' attributes. In the future, we encourage researchers to obtain more comprehensive attributes, particularly for birth records. There may be welfare and field constraints (e.g. ensuring non-disturbance of the animals and/or sea-ice conditions) in obtaining such data; however, low-cost and low-disturbance techniques are available. For example, a simple pre-measured tape or pole can be laid alongside an offspring with minimal disturbance (to ascertain SL). Or, if possible, photogrammetry can be used from the ground, or low-disturbance unoccupied aerial systems (UAS e.g. Krause et al. 2021) can accurately obtain SL (Krause et al. 2017) or photo and video evidence of birth attributes could be gathered. Such data would substantially aid in the classification of leopard seal records when considering the birth/newborn/pup age classes and together with the use of the SACCS, comparisons can be made between regions, populations and studies.

Whilst we made every effort to reduce biases in classifying records under the SACCS, some uncertainty exists when assigning records with only 'probable' attributes. For example, when a record lacked information on age or evidence of birth-specific attributes (e.g. an umbilicus) or SL measurements, the assignment of age class was reliant solely on the author(s) descriptions and their interpretation of the age class of the offspring. Those descriptions were often conflicting between categories and were also dependent on the author(s) level of expertise. Such issues can be mitigated by researchers making every effort to record 'certain' attributes.

When compiling the criteria for the SACCS, we had focused on attributes which we believed would have a higher likelihood of being noticed/documented by both experienced and inexperienced observers and which would help delimit the categories of a birth, newborn or pup. Therefore, we did not include attributes such as mobility of the offspring (including agility/cohesiveness of movement and ability to hold head upright and steady) or the post-partum behaviour of the mother. Our choice of criteria was reinforced for us when we applied the SACCS to the 160 records, as we only found three in which the behaviour of a newborn/mother was described in detail ($n = 1$ birth, $n = 2$ pups).

Number of records

Pup records were 7.4 times more common than birth records. Such a disparity is logical when considering the SACCS classifies a birth/newborn as an individual that is ≤ 14 days old. This means that a birth record can only be classified as such within the first 14 days of life, whereas a pup record can be > 14 days old but must be < 6 months old, which allows an individual to be documented at any other point within the first 6 months of life. In addition, leopard seals that are recorded as a birth, and go on to survive, could subsequently also be recorded as a pup. Due to the limited field surveys conducted for leopard seals worldwide, the latter is currently not likely to occur frequently and in our dataset this was not documented. Additionally, it is assumed that the vast majority of leopard seal births occur in the pack ice in the austral spring, during a time that observers are not often present, thereby limiting the opportunity for observations.

Occurrence by month

Little was known about the timing of leopard seal births and information on their reproductive biology was often speculative (e.g. King 1983; Siniff and Stone 1985; Southwell et al. 2003, 2008). Generalised Statements described the period within which both leopard seal births and pups occur as being between mid-August and February, with a two-month peak period occurring between November and December (Table 1; Online Resource 1). However, when we applied the SACCS to our most reliable Complete Records, two key windows for leopard seal reproduction became apparent: (1) births occurred between September and December with a peak between September and November (i.e. this is earlier in the year than the current literature/Generalised Statements suggested) and (2) there was a five-month peak of pup sightings between August and December (i.e. this extends over a longer period than the current literature/Generalised Statements suggested). As such, the birth data provide strong evidence to narrow the peak leopard seal parturition period from August to February towards one centred between September and December.

With regards to the pup data, inference should be interpreted with caution. Leopard seal pup growth rates are not well known and are likely to be variable; therefore some pup records in our dataset may be the result of individuals born the previous year. However, each of the Complete Records fell within the pup category when using the SACCS length criteria, and the majority of pup sightings still provided a clear trend of Austral spring births.

It is also counterintuitive that the Complete Records indicate the start of leopard seal births in September, when a peak in pup records starts the previous month (Table 1; Online Resource 1). Logically, the start of the birth records should occur before the peak in the pup records. It is unclear what is driving this anomaly; however, a number of non-mutually exclusive aspects could be involved, *inter alia*: (a) the smaller dataset for births in comparison to the pups; (b) there is little time between when a birth (or newborn) record becomes a pup record (i.e. ≤ 14 days old versus > 14 days old), therefore it is possible that some of the pup records (i.e. those for which there were fewer attributes recorded) could in fact be births records; (c) leopard seals born late in the season may be smaller than those born early in the season and, even when older, may still fall within the SL of < 200 cm and (d) the use of 'probable' attributes by authors result in the dataset being reliant on their interpretation of age class.

Previous research has suggested that leopard seals have an asynchronous birthing season caused by the loss of daily rhythmic activity under the continuous lighting regimes of summer and winter at high latitudes (Southwell et al. 2003; Rogers et al. 2013). Considering the widespread months in which leopard seal births have been recorded in the Complete Records presented herein, our findings could be interpreted to support that theory. However, given that the data indicate that births may occur earlier in the year than previously expected and that births which occur in northern regions (where the photoperiods are more balanced) also fit a similar distribution by month to those from the southern regions, the importance of photoperiods to parturition in this species should be examined with caution.

Occurrence by region

The myriad of records north of the Antarctic Convergence (i.e. birth records: in the sub-Antarctic Islands, Chile, Falkland Islands and NZ, including the three northernmost records for leopard seals in the latter region; and pup records in the sub-Antarctic Islands, Chile and Australia) contradicts the long-standing hypothesis that leopard seals only give birth on Antarctic pack ice. Instead, this study indicated that 84.2% and 57.4% of collated leopard seal birth and pup records presented here, respectively, occur outside of Antarctica.

The Antarctic region is widely recognised as the core range for leopard seals, with an estimated population of 35,500 leopard seals occurring off Antarctica (Southwell et al. 2012; Hückstädt 2015). Despite this, for the entire Antarctic continent, we were only able to source three published birth records (between November 1977 and November 1979; Online Resource 2) and 60 leopard seal pup records (between March 1839 and November 2019; Online Resource 3). Of note is that those three Antarctic birth records were documented more than four decades ago and within only a two-year period. The lack of both birth and pup records for this region emphasises the high priority for updated baseline information and for more robust research to be conducted on leopard seal reproduction within what is presumed to be their core breeding region.

Whilst NZ neighbours the Southern Ocean, it is still ~ 2500 km from Victoria Land (Antarctica) to Stewart Island (NZ), i.e. a reasonable distance from the presumed core breeding areas of leopard seals. NZ also has vastly different thermal characteristics in both water and air temperatures when compared to Antarctica. In NZ, year-round air and sea temperatures are distinctly higher, resulting in a complete lack of sea ice, yet 15.8% ($n = 3$) of the total birth records we collated occurred within this region. Whilst we were not able to locate any records of pups in NZ, Hupman et al. (2020) reported that 34% of leopard seal sightings within that region were of juveniles. If those juveniles were travelling from the Antarctic to NZ, one might expect them to arrive in NZ with compromised body condition, as is evidenced in juveniles documented in another northerly region, Australia (Rounsevell and Pemberton 1994). However, in contrast, the majority of juvenile leopard seals sighted in NZ waters have been reported as being in good or excellent body condition (Hupman et al. 2020). This may suggest that more leopard seal births are occurring on the mainland, offshore islands or the sub-Antarctic Islands of NZ, than has been documented. We found no records of leopard seal birth or pup records on the African continent and only one pup record in Australia, yet juvenile and adult individuals are sighted in both of these regions (Africa: Roberts 1951; Courtenay-Latimer 1961; Best 1971; Australia: Rounsevell and Pemberton 1994).

We hypothesise that leopard seal births and/or pups may be going undetected in a range of locations. Low numbers of records and/or no data from an area could be due to *inter alia*, a lack of reporting, minimal leopard seal research in and/or the remoteness of some areas. Furthermore, as leopard seals are typically widely dispersed, have cryptic behaviours and a mostly solitary lifestyle (Southwell et al 2008; Rogers et al. 2013), observations of births and pups may be restricted. It also cannot be ruled out that pupping areas for this species have yet to be discovered and/or described in the published literature.[11] Additionally, the estimated short nursing period (between two and four weeks; Shirihai 2002; Rogers 2009; Jefferson et al. 2015) would reduce the probability of detecting suckling pups. It is unknown if pups show site fidelity, travel with their mothers or venture further afield pre- or post-weaning, but if the latter two, these instances could also reduce detection or potentially result in pups that are < 6 months old being classified as juveniles due to no conspecific adult being present. Likewise, due to a rapid growth rate during the first 6 months post-partum (Hamilton 1939; Laws 1957; Rogers 2009), individuals transitioning from the pup to the juvenile age class may potentially be categorised as juvenile if the date of birth was unknown, or no measurements are taken, or if an observer was inexperienced. These reasons are not mutually exclusive and several of them may conflate to mask locations where births occur or where pups can be found.

New Zealand records

The three NZ birth/newborn records (i.e. one in September and two in October) would be considered normal in the context of timing; therefore, it is plausible that they were full-term pregnancies. Alternatively, it could be hypothesised that these animals were born prematurely as (a) all three newborns died and (b) the Cuvier Island and Dunedin newborns were two of the smaller and lighter animals recorded in our dataset.

Other factors may also be at play regarding the deaths of these three leopard seals. For example, the mothers may have been compromised after potentially travelling long distances prior to parturition, or they may have been compromised nutritionally due to a complete shift away from their typical Antarctic diet/prey, if they did indeed travel from that region. Additionally, the substrate of the birth of at least one newborn may have impacted its fate (see below).

Ice habitat for seals, especially in the Antarctic Peninsula, has declined by 20–28% over a 30-year period (Curran et al. 2003; Forcada et al. 2012) and such a loss of sea ice dramatically increases the distance that seals must travel to find concentrated prey (Burns et al. 2004; Southwell et al. 2005). Furthermore, reduced sea-ice impacts prey availability, such as krill, which is declining in number and decreasing in range within some regions, which alongside an increase in the intensity of krill fisheries (Forcada et al. 2012) may be motivating leopard seals to inhabit more northerly environments.

Substrate

It has been presumed that leopard seals give birth predominantly on sea ice (Southwell et al. 2003; Jefferson et al. 2015; Rogers 2018). However, early in the last century Ainsworth (1915) proposed that leopard seals gave birth in the water, based on the lack of pups sighted next to their mothers after they had recently given birth. Brown (1957) then supported this claim by stating that leopard seals are born in the sea. Records presented here show that at least two leopard seals gave birth in the water (Online Resource 2), although the fate of both was that they died. A number of births occurred on substrates other than ice, illustrating that leopard seals do have the behavioural flexibility to give birth on other substrates, including *terra firma*, if no suitable sea ice is present. Given the current and predicted loses of their Antarctic sea-ice habitat, such ecological flexibility may be important to the future resilience of the species.

Importance of further research

Ice-associated seals such as the leopard seal are likely to be impacted by ongoing and future changes in sea ice (Curran et al. 2003; Siniff et al. 2008). Considering sea ice was the predominant substrate identified in both leopard seal birth and pup records (i.e. it is used for both the birthing and caring of pups), the protection of this platform is vital for the survival of this species. Given the recent (2016) designation of the Antarctic Ross Sea as the world's largest marine-protected area and the commitment of the 24 member states

[11] During an AMERIEZ research voyage in the Weddell Sea during October–November 1985 "*dozens to possible hundreds*" of leopard seal females with their pups were sighted (pers. comm. Bill Fraser 1/3/2022).

(plus the European Union) comprising the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) towards management of the biological resources within this region (Brooks et al. 2019), this review is a clear signpost for basic research on leopard seal reproductive biology within the Antarctic region to be implemented with urgency. Technology such as computer recognition, remote sensing and UAS as tools for similar studies are becoming widely accessible. Whilst the Antarctic region is an important region for future research, efforts should also be made to conduct baseline studies in other coastal areas north of the Antarctic convergence, such as Chile and NZ. Application of the SACCS to future data gathered on leopard seal offspring should further improve our understanding of population demographics, temporal peaks of births and potentially survivorship from birth to pup age classes. These advances would collectively assist in refining research, management and conservation decisions.

The NZ leopard seal birth records reported herein are an illustration of how such research can be applied to management and conservation initiatives. For example, local birth records supported the recent reclassification of leopard seals in NZ from ‘Vagrant’ to a ‘Resident’ species under the New Zealand Threat Classification System (Baker et al. 2019; Hupman et al. 2020). Such observations emphasise how the systematic collection of leopard seal sighting records in NZ should be continued and expanded upon to include more active monitoring of reproductive biology. Furthermore, the most current New Zealand Governments’ Department of Conservation Marine Mammal Action Plan suggests that recording leopard seal sightings and stranding events are a “*needed*” science conservation action (Suisted and Neale 2004).

We also support implementation of leopard seal surveys in the Antarctic as they are vital to better understanding leopard seal ecology (Laws 1993a, b, c). Such research is needed both on large and small scales. Again, drawing on NZ as an example, LeopardSeals.org currently collects systematic leopard seal sightings using both staff and citizen scientists. For example, two of the three NZ birth records were collected by members of the public at no cost to the NGO. The importance of citizen scientists and the value of their contributions to scientific databases is well documented for a range of easily recognisable and/or target species (e.g. Hupman et al. 2015; Aristeidou et al. 2021; Soteropoulos et al. 2021), including leopard seals (Hupman et al. 2020). However, we believe that there is scope for this to be more comprehensive for leopard seals in other regions, including Antarctica and the sub-Antarctic Islands where eco-tourism has shown tremendous growth (Sanson, 1994; Cajiao et al. 2021) and has supported field data collection (e.g. Cusick et al. 2020).

Conclusion

Our comprehensive review of leopard seal birth and pup records, when assessed within the SACCS framework, indicates that births likely occur between September and November. Northern regions including Chile and NZ have emerged as important breeding habitat. Leopard seals appear able to give birth and rear pups on *terra firma*, which may ameliorate negative population effects due to climate-induced loss of sea-ice habitat. In order to fill remaining gaps in our knowledge of leopard seal ecology, we encourage both an expansion of dedicated scientific study focused on leopard seals and appeal to existing programmes to apply the SACCS and publish their results.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Consent to participate Not applicable.

Consent for publication Personal communications stated within this study were provided to the authors, who were given consent for such information to be included in the publication.

Ethical approval This is primarily a data collation study. Data collected in New Zealand by LeopardSeals.org was obtained under permit numbers 63499-MAR (van der Linde) and 63877-MAR (Visser) issued by the Department of Conservation. Data collected by NOAA Fisheries Antarctic Ecosystem Research Division was conducted under the Marine Mammal Protection Act Permit number 16472. Data collected by the Ministry of Education and Science of Ukraine in Antarctica was under the State Special-Purpose Research Program in Antarctica.

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