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Female reproductive success and calf survival in a North Sea coastal bottlenose dolphin (*Tursiops truncatus*) population

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Abstract

Between-female variation in reproductive output provides a strong measure of individual fitness and a quantifiable measure of the health of a population which may be highly informative to management. In the present study, we examined reproductive traits in female bottlenose dolphins from the east coast of Scotland using longitudinal sightings data collected over twenty years. From a total of 102 females identified between 1997 and 2016, 74 mothers produced a collective total of 193 calves. Females gave birth from 6 to 13 years of age with a mean age of 8. Calves were produced during all study months, May to October inclusive, but showed a seasonal birth pulse corresponding to the regional peak in summer water temperatures. Approximately 83% ($n = 116$) of the calves of established fate were successfully raised to year 2–3. Of the known mortalities, ~45% were first-born calves. Calf survival rates were also lower in multiparous females who had previously lost calves. A mean interbirth interval (IBI) of 3.80 years ($n = 110$) and mean fecundity of 0.16 was estimated for the population. Calf loss resulted in shortened IBIs, whilst longer IBIs were observed in females assumed to be approaching reproductive senescence. Maternal age and size, breeding experience, dominance, individual associations, group size and other social factors, were all concluded to influence reproductive success (RS) in this population. Some females are likely more important than others for the future viability of the population. Consequently, a better knowledge of the demographic groups containing those females showing higher reproductive success would be highly desirable for conservation efforts aimed at their protection.

Introduction

In long-lived mammals, such as dolphins, that produce just one infant at a time, age at first birth and the spacing between births are the primary determinants for fecundity [1]. Female reproductive success (RS) is subsequently determined by the product of a reproductive life-span, the pace of parturition, and the survival rate of offspring (e.g. [2]). Thus, between-female variation in reproductive output provides a strong measure of individual fitness and a quantifiable measure of population health [3,4] which may be highly informative to conservation and management.

The Moray Firth (MF) in northeast Scotland (57˚41^{0}N, 02˚20^{0}W) contains the only year-round, resident population of common bottlenose dolphins ( ) in inshore Scottish waters and the wider North Sea. Studies in this region have been conducted since the late 1980s and have greatly enhanced our understanding of this population and assisted in its management [5]. However, animals from the MF range widely beyond the designated Special Area of Conservation (SAC) established for their protection in the inner Moray Firth in 2005 [5–10], making robust estimations of individual birth rates and calf survival difficult to resolve for this population. Integrated datasets from multiple research sites have been used to provide a best estimate of ~200 animals using the northeast coastline [11]. Both males and females are seen to range widely along the east coast [12], but females are found to be more site-faithful within the SAC and adjacent outer MF regions [7,13]. Indeed, the southern coastline of the outer MF is thought to provide important summer calving / nursery areas for the population [6,7,14], in addition to other key areas utilised within the SAC [15]. During the summer and fall, large numbers of nursing females with calves use this region, with ~90% of the known population having been recaptured over the course of a 20-year mark-recapture study [Robinson unpublished data, 14].

Using longitudinal sightings data of known mothers and their calves, it has been possible to build a detailed description of the long-term reproductive histories of females from this population, from which individual variation in calf production, inter-birth intervals (IBIs) and the survival rates of calves could be investigated. In the following study, we explore the effects of maternal age, breeding experience, mother identity and birth month upon reproductive success and calf survival, and discuss the implication of these results for the future conservation of this potentially vulnerable North Sea bottlenose dolphin population.

Methods

Survey methods and photo-identification

Mark-recapture data were collected during dedicated boat surveys in the outer southern MF between May and October 1997 to 2016 inclusive. From 1997 to 2000, dedicated survey trips were carried-out using a variety of vessels, with effort primarily concentrated in the west of the study area between Spey Bay and Cullen (Fig 1). From 2001 onwards, boat surveys were conducted between the coastal ports of Lossiemouth and Fraserburgh using rigid inflatable boats, with selected routes chosen to maximise capture probabilities, whilst minimising sampling heterogeneity, within the core areas used by the dolphins. Survey effort was recorded from 2001 onwards and was variable between years. Consequently, to ascertain whether a relationship occurred between survey effort and the annual number of individuals, reproductive females or newborn calves recorded, a Pearson's product-moment correlation was used.

Standardised photo-identification procedures were employed to obtain high-quality photographs of encountered animals using an SLR camera equipped with a f2.8 300 mm fixed lens. Transparency film was used from 1997 to 2006, after which digital imagery was used. All

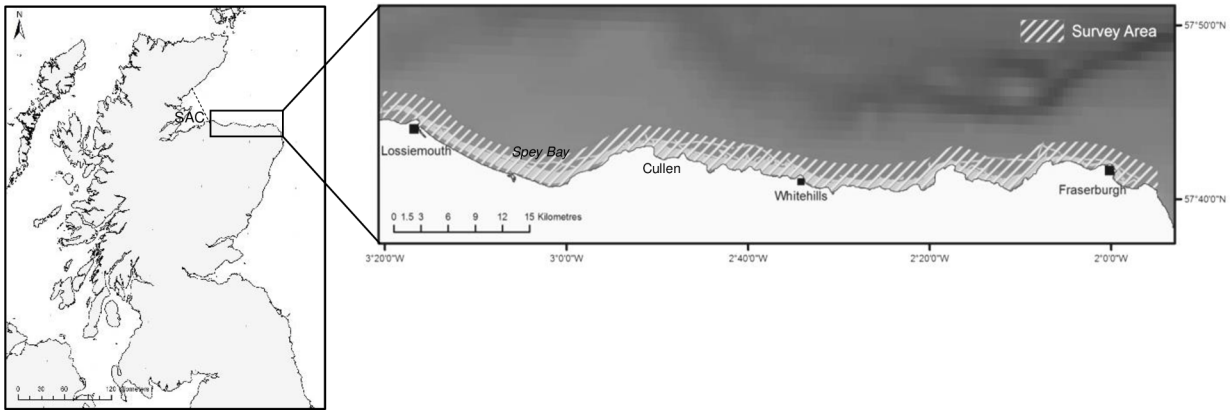

Fig 1. Map of northeast Scotland showing the position of the survey area along the southern coastline of the outer Moray Firth, to the east of the Special Area of Conservation (SAC). Dedicated boat surveys for bottlenose dolphins were conducted between May and October 1997 to 2016 using selected routes within the core study area, between the coastal ports of Lossiemouth and Fraserburgh.

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images were maintained within a purpose-designed photo-identification database (using Microsoft Access), from which a detailed record of the long-term sightings and calving histories for all reproductively-active females identified in the study area could be extracted. All boat-based research was carried-out under licence from Scottish Natural Heritage.

Identification of mothers and calves

All mothers were identified from repeated recaptures with dependent calves in tow (Fig 2). In the absence of markings for photo-identification, calves were typically tracked from close association with their mothers until weaning. Nevertheless, temporary marks on the dorsal fin and body (e.g. lesions or scars/scratches, typically acquired with age [16]) also assisted in the short-term recapture of maturing infants. Furthermore, after maternal separation, from 2 to 4 years of age, former calves often remained philopatric, allowing their continued recapture by association through to maturity.

Inter-birth intervals (IBIs) and reproductive success (RS)

The long-term nature of this study allowed retrieval of demographic data for the large majority of known females from this population, from which IBIs were determined for those producing two or more calves between 1997 and 2016 inclusive. Two approaches were used for IBI determination. The first approach examined all known IBIs (including those with large gaps between the weaning of one calf and the birth of the next), which potentially biased IBIs upwards due to failure to detect some births. The second approach removed females with IBIs >5 years, unless mothers remained in close association with the surviving calf until verification of a subsequent birth; potentially resulting in a downward bias in IBIs. IBIs for females that had experienced a calf loss, and IBIs between the first and the second born calves of primiparous females (of known birth year themselves) were compared to all known IBIs using unpaired t-tests.

A female was assumed to have reproduced successfully if her calf survived from birth (year 0–1) to the minimum age at weaning (year 1–2) [17]. Using this criterion, and to reduce the influence of small sample size on the estimated reproductive output, RS was only estimated for those females with three or more documented births. For the small subset of females of known age (i.e., individuals known since birth), the potential effects of the mother's age on IBI's and RS were also examined qualitatively (there were insufficient data for quantitative analysis).