ORIGINAL PAPER

Female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

This study investigates the female reproductive parameters and population demographics of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, using long-term relational sightings and photographic databases. Data were collected between 2008 and 2016, during 654 boat-based surveys, from two dolphin-watching vessels and a research vessel. During 1018 sightings, 4231 identifications of 184 individual dolphins were recorded. The population size was charted through direct counts of known dolphins from 2011 to 2015 (mean 142, range 131–150), with 145 extant individuals in 2015: 80 adults, 25 juveniles, and 40 calves. Excluding dependent calves, 121 individuals were sighted, of whom 98% ($n = 119$) were sighted in multiple years, with 64% ($n = 77$) sighted in all 4 years (2012–2015). Between 2008 and 2016, 37 reproductive females and 69 dependent calves were recorded. Overall, 35% ($n = 13$) of these females were sighted with one calf, 43% ($n = 16$) with two calves and 22% ($n = 8$) with three calves. An average of seven (range 3–10) calves were born each year. Parturition peaked in July. Weaning ages ranged from 2.0 to 4.1 (mean 2.9) years. The mean inter-birth interval ranged between 2.7 ± 0.6 and 3.5 ± 1.3 years, depending on the method used. Mean annual calving rate was 0.29 young-of-year/reproductive female/year. Average crude birth rate was 0.07 ± 0.01. Fecundity was 0.26 ± 0.03. An average 11% of newborn calves were lost before age 1. These results are generally within the lower range of values reported for similar populations and provide essential data for conservation management and global bottlenose dolphin research.

Introduction

Bottlenose dolphins (*Tursiops* spp.) are found across the globe in temperate and tropical waters and in a range of habitats (Wells and Scott 1999). As a result, different populations are subject to different ecological and environmental conditions and pressures. Marked variations in population

dynamics, behaviour and social structure have also been reported, perhaps due to the high level of intelligence of the species (Connor et al. 2000). In light of these socio-environmental differences between demographically different populations, it is to be expected that the life history parameters of populations may also vary considerably. This makes it essential to establish baseline life history parameters for specific populations to explore species ecology and inform management.

The production of reliable life history parameters is dependent on longitudinal studies with consistent continuous data collection (Wells 1991; Mann and Karniski 2017). Repeated sightings of identifiable individuals over a long time period allows for the aggregation of individual reproductive histories and thus, the estimation of reproductive parameters such as birth rates, calf mortality and inter-birth intervals (Fruet et al. 2015; Tezanos-Pinto et al. 2015). For long-lived, slow-reproducing mammals like bottlenose dolphins, these long-term datasets are essential for producing both individual- and population-level parameters for demographics, patterns of reproduction and a better understanding

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of the basic biology of the species across its global range (Fruet et al. 2015).

Female reproductive parameters such as inter-birth intervals (Connor et al. 2000) and reproductive success (Fruet et al. 2015) play a crucial role in determining long-term population viability. For example, in a study of two Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) populations, in Shark Bay and Bunbury, Australia, Manlik et al. (2016) used a population viability analysis (PVA) to demonstrate that reproductive rates had a stronger influence on long-term viability than adult survival rates. Thus, population-specific life history data are essential for the production and interpretation of reliable PVA results and the investigation of long-term population trends. Studies of population dynamics have often used life history parameters from other study populations because baseline data were not available for the population in question, but this may be misleading (Arso Civil et al. 2017).

Understanding the life history characteristics of a specific population is also essential for conservation and management, since the results can have significant effects on management plans. For example, Manlik et al. (2016) concluded that focusing management on calf survival was the best way to improve the viability of the Bunbury bottlenose dolphin population that is forecast to decline.

While there have been many studies of bottlenose dolphin reproductive parameters worldwide, there are few from Europe and none from Ireland. The bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, are a study population with a high dolphin encounter rate, year-round presence and long-term site fidelity (Berrow 2009; Levesque et al. 2016). The population has been shown to be genetically discrete (Mirimin et al. 2011). The development of a dolphin-watching tourism industry has enabled systematic long-term data collection on this population, with two dolphin-watching boats providing opportunistic platforms for research (Berrow and Holmes 1999). Photo-identification studies have been conducted since the early 1990s, resulting in the identification of many recognizable individuals (Berrow et al. 1996; Ingram 2000; Berrow et al. 2012).

Population estimates from previous studies of bottlenose dolphins in the Shannon Estuary using mark-recapture statistical models (with limited numbers of surveys) have estimated the extant population size to be 113 ± 14 (Ingram 2000), 121 ± 14 (Ingram and Rogan 2003), 140 ± 12 (Englund et al. 2007), 114 ± 17 (Englund et al. 2008), 107 ± 12 (Berrow et al. 2012), and 114 ± 14 (Rogan et al. 2015). These studies made use of mark-recapture techniques to derive abundance estimates and results from six surveys over a 20-year period suggest the population is stable. The Lower River Shannon was designated as a Special Area of Conservation (SAC) in 2000 under the EU Habitats Directive with bottlenose dolphins as a qualifying interest (NPWS

2012). The demographics (age and sex composition) of this population have not yet been described.

Annual sightings of newborn calves in the Shannon Estuary indicate that the population is reproducing; however, no reproductive parameters have been produced for this population. Previous work on population viability [e.g., the population viability analysis carried out by Englund et al. (2008)] made use of parameters from very dissimilar populations and study sites, which may not be representative of the population.

In this study, we used a long-term database of photo-id and related sightings data, based on surveys conducted between 2008 and 2016, to describe the demographics and estimate critical life history parameters for the Shannon Estuary bottlenose dolphin population. This provided similar data to that collected for populations elsewhere, enabling comparisons across populations. In contrast to previous work, the detailed analysis of high-quality digital photographs has allowed us to track every individual in the population over 5 years, including those that were previously regarded as "unmarked". Thus, we used a novel "head-count" technique to produce an updated population estimate for this population. Our two main aims were (1) to describe the Shannon Estuary bottlenose dolphin population's size and demography (age and sex class) and (2) to calculate baseline reproductive parameters for the Shannon Estuary bottlenose dolphin population. Similar to the study of New Zealand bottlenose dolphins by Tezanos-Pinto et al. (2015), we expected to obtain similar values to those reported for other populations using similar methodologies, and for our values to be most similar to those found in other temperate-water European populations such as around the British Isles.

Methods

Study site

The study site was the Lower River Shannon Special Area of Conservation (site code: 002165), a 684 km^2 Natura 2000 designated site (NPWS 2012) on Ireland's west coast between Co. Clare, Co. Kerry and Co. Limerick (52°36′N, 9°38′W), in which bottlenose dolphins are a qualifying interest. Surveys occurred west of Aughinish and east of Loop Head and Kerry Head (Fig. 1).

Data collection

Boat-based surveys were conducted between March and November each year from 2008 to 2016 on board three vessels—two commercial dolphin-watching tour boats and a dedicated research vessel. The dolphin-watching boats provided opportunistic platforms for research, operating
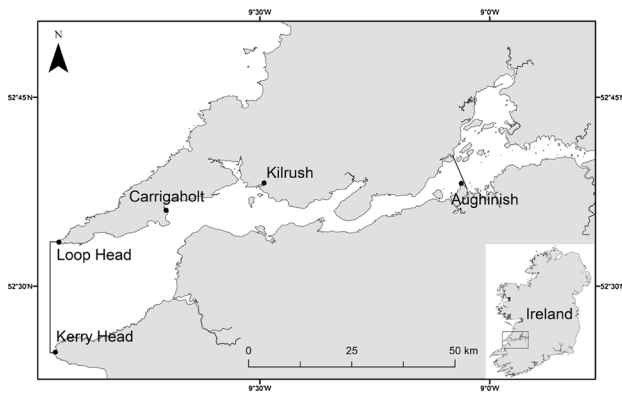
Fig. 1 Map of the Shannon Estuary study site in Ireland. The line between Loop Head and Kerry Head represents the boundary of the Special Area of Conservation (SAC) while the line at Aughinish represents the boundary of the area surveyed during this study

independently from the ports of Carrigaholt and Kilrush, Co. Clare, with the research vessel also based in Kilrush (Fig. 1). The research vessel was a 6 m RIB (Rigid-hulled Inflatable Boat) with a 115 hp outboard motor. Trained onboard observers located dolphins visually by eye and with the use of binoculars (Minox 7 × 50 or 8 × 42). Observers on the Carrigaholt tour boat were positioned on the top deck at a height of ~ 5 m, while observers on the Kilrush tour boat and research vessel were positioned on the bow of the boats at < 2 m above sea level.

During surveys, a dolphin encounter or "sighting" began when at least one dolphin was within 100 m of the vessel and ended after ≤ 30 min due to national regulations, designed to minimise the potential impact of dolphin-watching on the dolphin population (Maritime Safety Directorate 2005). During a sighting, all vessels maintained a position parallel to the animals and at a distance of approximately 100 m unless the dolphins approached the boat. Sampling methods were based on Mann's (1999) survey protocol, with sightings including records of individual dolphin identifications (IDs), mother–calf pair presence, group size and composition, environmental measures (including swell and sea state), location (using a Garmin 72H GPS), activity states (e.g., travel) and behavioural events (e.g., leap, see Baker et al. 2017a). A group was defined as all animals sighted together moving in the same general direction, engaged in similar activities, or interacting with each other within a radius of approximately 100 m (McHugh et al. 2011).

Attempts were made to photograph each individual in each group (regardless of their degree of marking or individual differences in behaviour) for the photo-identification of individual dolphins using unique markings on their dorsal fins and bodies (Würsig and Würsig 1977; Würsig and Jefferson 1990). Photographs were taken throughout sightings using digital SLR cameras (Nikon D300 or Canon EOS 20D with 70–300 mm lenses).

Data management

Following Shannon Dolphin and Wildlife Foundation (SDWF) protocols (Baker 2015), images from all surveys and sightings were maintained in a database using the photographic software environment IMatch 5.6 (https://photools.com). A digital photo-id catalogue housed the best images of each individual in the population and was used by researchers to compare with the dorsal fin photos taken during sightings. When a tentative match was made, researchers were required to match at least one additional secondary characteristic such as fin shape, scars, rake marks, deformities and persistent skin lesions, by using the filter function in IMatch to search for additional images of the individual in question, before entering their match. Following the visual comparison and matching by the first researcher, each image was then checked by two other researchers independently of one another, wherein the match was verified, or rejected and then re-matched. The final identifications of every individual dolphin in every sighting were verified by the lead researcher who had the most photo-id experience, as recommended by Pearson et al. (2016). These methods are similar to standardized protocols used by the Sarasota Dolphin Research Program (SDRP 2006).

Both written sighting records and individual dorsal fin photographs (one best photograph per individual per sighting) were entered into a specially adapted version of FinBase (MS Access), a relational sightings database for bottlenose dolphin research (Adams et al. 2006). The FinBase Catalog Browser shows the best left- and right-side image of the dorsal fin for each unique individual in the photo-id catalogue. It also contains the best dorsal fin photo for each individual for every sighting of that individual in the database.

All dorsal fin photographs in FinBase were graded for photographic quality by the lead researcher exclusively (Urian et al. 2015), before each being assigned to their specific sighting and survey using the FinBase Match/Catalog form (Adams et al. 2006). Each photograph was graded according to focus, contrast, angle, visibility and distance. Each of these fields was limited to a set of fixed scoring options which the user could choose from (Adams 2013). When a dorsal fin image was added to a sighting in FinBase, the dolphin class, degree of obstruction and distinctiveness were also graded to defined scales within the program.

Population demographics and adult/juvenile mortality were estimated using data collected during 2011–2015 exclusively, when dolphin monitoring surveys were consistent and protocols were clearly defined (Baker 2015), whereas reproductive parameters were determined using data collected between 2008 and 2016 to allow a more

longitudinal investigation. Sighting data for reproductive females and their calves were produced through a FinBase query of individual and shared sightings within the database. In some cases, including all cases in which mother–calf pairs were sighted < 3 times, these data were supplemented with further photographic evidence from the IMatch database.

A separate matrilineal database was maintained to keep specific records of estimated birth and "weaning" dates from the first and last sightings of mothers with calves. Here, we define weaning date/age as the date/age of separation (i.e., independence) of a calf from its mother (rather than weaning in terms of nutritional independence). A mother had to have been seen at least three times (mean 22 sightings) without her calf before weaning was confirmed. Additionally, information on deaths of calves < 1 year old and sightings of known weaned juveniles was also recorded. Calf mortality was estimated only for calves < 1 year old, whose mothers were frequently seen following the birth and subsequent disappearance of the dependent calf. Subsets of data from FinBase and the matrilineal database were used to calculate some reproductive parameters, such as age at weaning.

The large dataset and specialized long-term databases maintained on this relatively small population, coupled with the high encounter rate and in-depth knowledge of individual IDs, provided a unique and robust dataset for investigating the demographics and life history parameters of this dolphin population.

Data classification

Age determination

Individuals were assigned to one of four relative age classes on the basis of observations of individual estimated size and body length (Smith et al. 2013), reproductive state and/or knowledge of long-term life history. Adults were larger and darker in colour than juveniles, and sometimes with a dependent calf (Bearzi et al. 1997; Wilson et al. 1999). Juveniles were less than two-thirds the size of adults and were not themselves dependent calves. In some cases, individual juveniles were of known age due to knowledge of their association with their mother as a calf in the previous years prior to weaning. Calves were those dolphins > 1 year of age that were consistently in association with their adult mothers. Young-of-year (YOY) were < 1 year old, often with visible prominent foetal folds (dark vertical lines on the body) and swimming in a characteristic infant position with their mothers (Mann and Smuts 1999).

Sex determination

The sex of individual dolphins was determined through (1) genetic evidence from tissue samples collected through biopsy sampling (n = 37; collected under NPWS permits; Berrow et al. 2002; Mirimin et al. 2011); (2) photographs of the genital area (n = 1); and, (3) in the case of adult females, observations of the mother swimming in close association with a dependent calf (n = 25). For females identified through association with a calf, numbers of shared mother–calf sightings were determined using a specially developed query in FinBase and ranged from 1 to 72 (mean 10). Following Tezanos-Pinto's (2009) definitions, reproductive females (i.e., sexually mature females) were those individuals who had given birth to viable calves during the study period, whereas non-reproductive females were adults positively sexed as females that were never sighted in close association with a calf.

Data analysis

Population size, demography and adult/juvenile mortality

In order to estimate population size, we used our extensive knowledge of catalogued individuals from five recent data-rich years (2011–2015) to produce an estimate of the number of individuals extant in the population. First, we examined the number of sightings of individual dolphins in each year, incorporating age class, and including a discovery curve which reached a clear plateau by 2015. Then, using sighting histories and age class determination, we calculated the number of individuals known to be extant in the population per year. The assumption was made that if an adult/juvenile was alive in a subsequent year, it was alive in all previous years.

Presumed deaths of well-known individuals were also incorporated based on their previous annual sighting rates and their absence during the 2015 and 2016 field seasons. Individuals not recorded since 2013 or earlier all had additional sightings in the database from previous years (2008–2012) but no sightings in 2014, 2015 or 2016. Individuals not recorded since 2014 each had at least one sighting (range 1–22 sightings/year) in each of at least two (range 2–6 years) of the previous 6 years (2008–2013), but no sightings in 2015 or 2016. Using these disappearances of adult/juvenile individuals from the population between 2012 and 2015, we calculated the mean annual maximum mortality rate as "$l/(n − b)$" where l = number of individual disappearances, n = extant population count and b = number of calves born (Wells and Scott 1990).

We calculated the mean extant population size by directly counting the number of catalogued individuals known to be alive in each year and averaging it (Wells and Scott 1990). To visualize how the size and demography of the population changed over time, we constructed a stacked bar chart of population size in each year and incorporated age class demography, adult/juvenile and calf deaths. To investigate

population coverage, we plotted the frequency of resightings of individual dolphins in the Shannon Estuary and constructed a histogram of counts of individual sightings.

Female reproductive rates

The entire 2008–2016 dataset was used to document associations between mothers and calves in the study population. The number of annual births was a count of individual calves born in the population during each study year. To test if differences in numbers of surveys each year had an effect on the number of recorded births, a linear regression analysis was carried out in R (R Core Team 2016). The number of calves born to each female individually was also calculated.

In addition, the number of annual calf deaths was counted. If a mother had been sighted ≥ 2 times with a newborn calf, but then sighted on multiple occasions (≥ 2 sightings) without it, less than 1 year later, we assumed the calf had died. Minimum weaning age in bottlenose dolphins has been estimated to be 18–20 months (Smolker et al. 1992; Wells and Scott 1999), so all calves under this age and that were no longer with their mothers were believed to be dead. Although minimum weaning age is likely to differ among populations, there was no evidence of bottlenose dolphin calves weaning before they were 1 year old, so we used a minimum of 1 year to infer calf death as a conservative measure. Consistent with Tezanos-Pinto et al. (2015), a calf that was associated with an individually identifiable reproductive female during its first year was assumed to be the same calf, providing it looked older over consecutive sightings. Additionally, in some cases, it was possible to identify calves even as young as < 1 year due to distinctive markings and/or lesions on their bodies and dorsal fins, and, in three cases, deformities such as scoliosis.

There were some cases where the first sighting of newborns occurred at the beginning of the field season (usually May), but it was clear that they were not recently born. Thus, estimated date of birth (DOB) was calculated as the mid-point between the date of the last sighting of the mother without a newborn calf and the date of her first sighting with a newborn calf (Wells et al. 1987; Urian et al. 1996). We primarily used the mid-point rather than the date of the first sighting (of the mother–calf pair) because the first sighting method of DOB estimation would have suggested that older calves were much younger than their actual age. Even so, the use of imprecise (> 60 days) DOBs was restricted for analyses in which date was an important factor.

To investigate temporal patterns in reproduction, DOB estimates were used to plot births across the four main months for which data were available (June–September), using the ordinal date (i.e., day-of-year) of the last sighting of mother without calf and the date of the first sighting of mother with newborn calf. We then overlaid a plot of number of births per month using the mid-point between dates (to estimate month of birth) to illustrate patterns of parturition for this population.

Calving interval or inter-birth interval (IBI) was estimated as the time elapsed between subsequent births (Mitcheson 2008; Arso Civil 2015). We used three approaches to calculate IBIs. The first two approaches, based on dates, used (a) the estimated date of birth (DOB) for each calf and (b) the first sighting of a female with her initial calf and then the first sighting of the same female with her subsequent calf; (c) the third approach used year of birth. In the first method, IBIs were calculated for individual mothers with two consecutive births where the estimated DOB was available for both calves. The IBI was calculated as the difference between these two dates divided by 365.25 (i.e., IBI in years). Using the second method, each IBI was estimated as the time elapsed between when a female was first sighted with her initial newborn calf to the date of the first sighting of that female with her subsequent newborn calf (Tezanos-Pinto et al. 2015). These methods were restricted to reproductive females who had consecutive calves and where the fate of the calf was known in all cases.

To estimate IBIs using the larger dataset of sighting histories for all reproductive females in this study, we calculated the inter-birth interval based on annual calving (i.e., year of birth rather than date of birth). IBIs were calculated as the number of years between births and charted for all female dolphins with consecutive births (i.e., those who had two or more calves) and known years of calf birth during the study period.

Weaning ages were determined for individuals with known birth and weaning dates, including those who had been observed as independent juveniles post-weaning, and a mean weaning age was calculated. A calf was presumed to have weaned if it was > 1 year old and it and/or its mother had been observed independently in at least three subsequent dolphin group sightings.

Annual calving rate was estimated as the total number of young-of-year (YOY) divided by the total number of reproductive females sighted during that year (Baker et al. 1987; Tezanos-Pinto et al. 2015). We used a weighted average to calculate mean annual calving rate and a binomial variance to calculate the confidence interval for calving rates across the years with 95% limits (Baker et al. 1987; Wells and Scott 1990; Tezanos-Pinto 2009).

The annual crude birth rate was calculated as the total number of documented births divided by the total abundance estimate for the dolphin population in each year (Fruet et al. 2015). We used the catalogue-based abundance estimates from 2012 to 2015 to calculate crude birth rates. The same years were used to calculate fecundity—the ratio between the number of surviving calves and the number of reproductive females in the population (Wells and Scott 1990)—because

we knew the number of known births surviving to 1 year with certainty for these years. Overall mean fecundity is a measure of the potential reproductive capacity of the population (Fruet et al. 2015). Additionally, using Arso Civil et al.'s (2017) definition (which takes into account all births and not only surviving calves), where fecundity rate is defined as 'the annual probability of a mature female having a calf', we also estimated fecundity rate as the reciprocal of the expected IBI, using the average IBI from the three methods used to calculate IBIs.

Calf mortality was estimated as the number of YOYs (< 1 year old calves) that were inferred to have died, divided by the total number of YOYs assigned to individual reproductive females (Wells and Scott 1990) for 2012–2015.

Mean female reproductive success of the Shannon Estuary bottlenose dolphin population was quantified by calculating how many calves each female had to the minimum age at weaning and the mean and standard deviation for them (Fruet et al. 2015). It was assumed that a female reproduced successfully if her calf survived from birth to the minimum age at weaning estimated for Shannon Estuary bottlenose dolphins (this study; Mann et al. 2000; Fruet et al. 2015).

Mother–calf association longevity was investigated to determine if females whose calves weaned during the current study ever associated with them again, and if there were any situation- or sex-related patterns associated with these pairings.

Results

Survey effort and photo-identification

Between 2008 and 2016, 654 surveys (1018 sightings) were carried out, during which 213,056 photographs were taken; 83,527 of these were used for the photographic analysis of individually identifiable bottlenose dolphins. Surveys were conducted between March and November but the majority (84%) of surveys took place during June, July and August. In total, 4231 identifications were made of 184 distinct individual dolphins over the nine study years.

Population size, demography and adult/juvenile mortality

The number of sightings of dolphin groups varied in each year, from 34 sightings (34 surveys) in 2011, 95 sightings (61 surveys) in 2012, 119 sightings (86 surveys) in 2013, 180 sightings (111 surveys) in 2014 to 128 sightings (95 surveys) in 2015, with similar proportions of adults, juveniles and calves sighted in each year (Fig. 2). The number of unique individual dolphins sighted per annum varied from 79 in 2011 to 140 in 2014, with 135 individuals sighted in
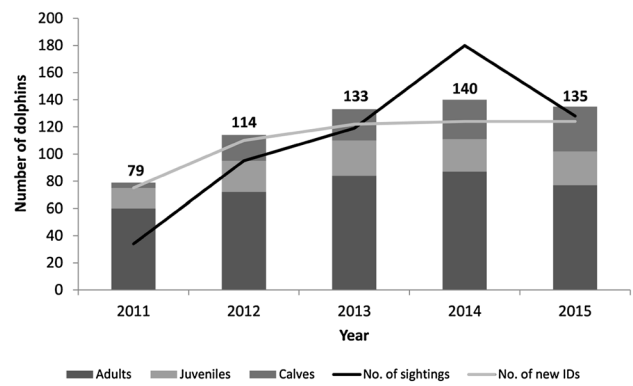
Fig. 2 The number of individual bottlenose dolphins identified each year (bars), the number of sightings (i.e., dolphin group encounters) with photo-id records (black line) and the number of new (non-calf) IDs recorded (i.e., discovery curve; grey line) in the Shannon Estuary between 2011 and 2015, with individual dolphins categorized into age classes (adults, juveniles, calves)
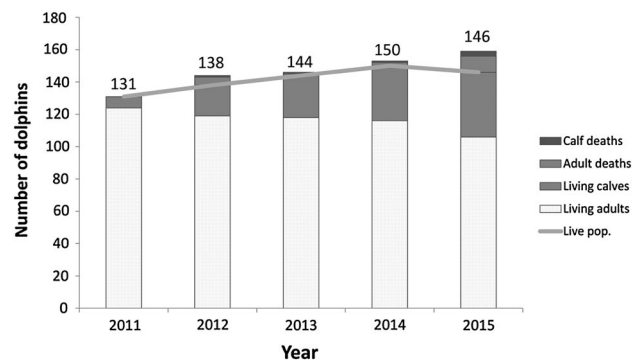
Fig. 3 Estimates of the extant population size of bottlenose dolphins in the Shannon Estuary from 2011 to 2015, incorporating age class ("adults" includes adults and juveniles, "calves" includes all dependent individuals) and possible deaths of well-known individuals. The population size figures are slightly larger than the number of sightings of known individual dolphins per year (Fig. 2) because some individuals were not seen in years when they were still alive

the most recent study year (2015). A discovery curve showed a clear plateau had been reached with only two new individuals added to the catalogue during 2014 and no new individuals added during 2015 (excluding additions of newborn calves to the population).

The mean extant population size was estimated to be 142 bottlenose dolphins. Population size estimates in each year (2011–2015), incorporating age class demography and the presumed deaths of well-known individuals varied from 131 in 2011 to 150 in 2014 (Fig. 3). Individual records of estimated adult/juvenile dolphin deaths correspond to counts of five, one, two and ten individuals having not been sighted since 2011, 2012, 2013 and 2014, respectively, despite multiple sightings of these individuals in previous years and 325 subsequent sightings of dolphin groups (during 212 surveys)

in 2015 and 2016 (Fig. 3). Therefore, a total of 18 individual adult/juvenile dolphins were not sighted during population surveys between 2012 and 2015. Thus, the mean annual maximum mortality rate was 0.038 ± 0.0286.

Excluding 2011, a year with fewer (< 50%) surveys than in other years, and comparing sighting numbers to extant population estimates, an average 92% ($n = 130$) of the population was recorded each year (2012–2015). In 2015, an estimated 93% ($n = 135$) of the population was recorded during dolphin surveys. Between 2012 and 2015, excluding dependent calves, 121 individuals were identified, of which an average of 106 individuals (88%) were sighted each year. Ninety-eight percent of these individuals ($n = 119$) were sighted in multiple years, with 64% ($n = 77$) seen in all 4 years from 2012 to 2015 (Fig. 4a). The mean number of sightings per individual was 24.4 ± 21.7 ($n = 121$, range 1–101; Fig. 4b).

Of all 167 individuals sighted between 2012 and 2015, 63 were of known sex (49 female, 14 male) and 104 were of unknown sex. Age class, based on first assignation, was divided into 91 adults, 30 juveniles, 13 calves and 33 YOYs. In 2015, the population consisted of 145 unique individuals—55% adults ($n = 80$), 17% juveniles ($n = 25$) and 28% calves/YOYs ($n = 40$). Thus, the adult:calf ratio of the population was 2:1. Of the 105 adults and juveniles, sex was known for 49% ($n = 51$) of individuals—42 females and 9 males.
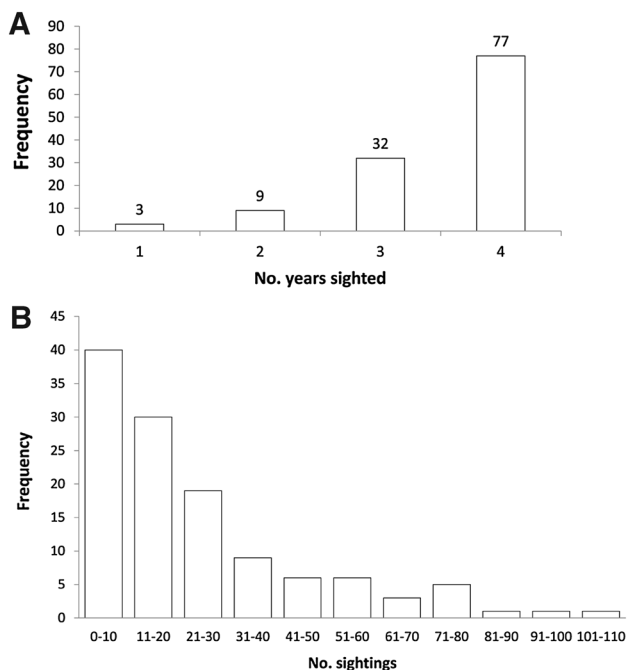
Fig. 4 Histograms of juvenile/adult bottlenose dolphin sightings ($n = 121$) by number of **a** years sighted and **b** sightings (2012–2015)

Female reproductive parameters

Mothers and calves

Between 2008 and 2016, 1254 individual identifications of 37 reproductive females were made. Of these, 57% ($n = 719$) were identifications of reproductive females with a calf (Table 1). The sex of these reproductive females was determined using associations with calves ($n = 24$), a combination of biopsy tissue samples and calves ($n = 12$) and observation of the genital slit during a live-stranding and subsequent calves ($n = 1$; O'Brien et al. 2014). Of these 37 females, all (100%) were sighted in more than 1 year and 13 (35%) were sighted in all nine of the study years, with an average of 34 sightings per female (range 6–108; Table 1).

Of the 37 reproductive females, 35% ($n = 13$) were sighted with only one calf, 43% ($n = 16$) with two successive calves, and 22% ($n = 8$) with three successive calves. The maximum number of documented births per female in the 9-year study was three calves. The mean number of reproductive females in the population per year from 2008 to 2016 was 26 (range 8–35; Table 1). A total of 69 dependent calves were recorded during the study period with year of birth determined for 67 of these calves. There were 831 sightings of these 69 calves with an average of 12 sightings per calf (range 1–88; Table 1).

Births

An average of seven (mean 7.4, SD 2.6, range 3–10) calves was born each year (2008–2016), with one recorded calf death each year between 2011 and 2015 (Fig. 5). There was no correlation between number of surveys and number of births recorded annually (linear regression, $r^2 = 0.02$, $P = 0.73$), thus the variation in the number of births could not be explained by the variation in number of surveys.

Temporal patterns in reproduction

Parturition peaked in July with 45% ($n = 14$) of 31 calves with moderately precise (within 60 days) birthdates estimated to be born in this month (Fig. 6). In the other main study months, 16% ($n = 5$) of these calves were estimated to be born in June, 32% ($n = 10$) in August and 6% ($n = 2$) in September.

Inter-birth intervals

Using date of birth There were 13 reproductive females with two consecutive births and for whom the estimated date of birth (DOB) and fate of the calf was available for both calves ($n = 26$; Table 2). Using estimated DOBs to calculate inter-birth intervals (IBIs) by the time elapsed between suc-

Table 1 Sightings of reproductive females (ID# = individual photo-id catalogue number) and their calves from 2008 to 2016 in the Shannon Estuary, including sightings of females without a calf (marked with a "•") and with their first (1), second (2), or third (3) calves (different numbers indicate a different calf for each female)

Years										Sightings 2008–2016							
ID#	2008	2009	2010	2011	2012	2013	2014	2015	2016	NF	WC1	WC2	WC3	NC1	NC2	NC3	#C
006	•	•	•	•	YC1	C1	C1	YC2		108	72	2		88	2		2
011	•	•	YC1	C1	C1	J1	J1	J1	J1	29	19			19			1
019	•		YC1			•	•	•	•	26	1			1			1
027	YC1		•		•	•	•	•		10	1			1			1
042	*YC1*		C1	J1	J1	YC2	C1	C1	J1	18	4	12		6	12		2
044	•	•	•	•	•	•	YC1	C1	YC2	64	36	1		37	1		2
045	•	•	•	•	YC1	C1	C1	YC2	C2	44	18	4		19	4		2
052	•	YC1		•	J1	J1	•	YC2	•	30	3	3		3	3		2
070	•	YC1	C1		YC2	•	YC3		•	15	5	3	1	5	3	1	3
071	YC1	C1	C1	J1	J1	J1	YC2	C2	C2	79	28	23		32	27		2
085	•	•	•	•	•	YC1	•	•	YC2	43	4	1		4	1		2
092	YC1	C1								6	2			2			1
096	•	YC1	C1	C1	J1	YC2	C2	C2	J2	40	4	16		4	20		2
100		•	•	•	•	•	YC1	C1		20	2			2			1
114	*YC1*	C1	C1	•	•	•	•			31	5			17			1
118	YC1	C1	C1	J1	J1	•	•	YC2	C2	77	10	19		20	20		2
121		•	•	•			•	YC1		6	2			2			1
151	•	•	•	•		YC1	C1	C1	J1	12	7			8			1
171	•	YC1	C1	•	YC2	C2	C2	J2	•	56	8	41		8	42		2
204		YC1	C1	C1	YC2		C2	YC3	C3	10	3	2	4	3	2	4	3
205	YC1	C1	C1	•	YC2	C2	C2	YC3	C3	24	3	9	4	3	10	4	3
209		*YC1*	C1	C1	J1	YC2	C2	C2	J2	38	3	23		12	28		2
210		YC1			YC2	C2	C2	J2		11	1	7		1	7		2
216	•	•	•	YC1	•	YC2	C2	YC3	C3	82	2	37	8	2	43	8	3
218	YC1	C1	C1	J1	•	YC2	C2	C2	YC3	33	4	20	2	4	22	2	3
220			*YC1*		C1	J1	J1	•		6	5			9			1
223	•	YC1	C1			•	YC2	•	YC3	31	2	2	14	2	2	14	3
225							J1	YC2	C2	9	7	2		7	2		2
228	•		•		YC1	•	C1	J1	J1	12	8			9			1
231	•	YC1	C1	YC2		•	YC3		•	17	9	1	2	9	1	2	3
232		•	YC1		C1	J1	YC2	C2	C2	26	4	10		7	10		2
233		•	•	•		•	YC1	C1	C1	21	6			6			1
242	•	•	•	•	YC1	C1	C1	J1	YC2	98	65	7		70	7		2
246					•	•	YC1	C1		22	3			3			1
250	•	•		YC1	C1	C1	J1			43	33			35			1
280	C1	C1	J1	J1	YC2	C2	C2	J2	J2	27	6	18		19	22		2
285		YC1	C1		YC2	C2	C2	YC3	C3	30	2	15	9	2	15	9	3
#F	8	19	23	25	29	31	35	34	29								
#YOY	8	10	4	3	10	8	9	10	5								69

Calf ages were categorized as young-of-year (< 1 year old; YC), calves (1–3 year old; C) and juveniles (> 3 year old; J). The total number of sightings of each female (NF), total number of sightings of each female with each of her calves (WC1, WC2, WC3; i.e., WC1 = number of sightings with first calf), and total number of sightings of each calf (NC1 = first calf, NC2 = second calf, NC3 = third calf) are given. The total number of calves born to each female (#C), the number of reproductive females in each year (#F) and the number of calves born in each year (#YOY) are also shown. Underlined female IDs are those that were also genetically confirmed as female. Year of birth could not be determined for the first calves of ID#s 225 and 280 and they are, therefore, not included in the total of number of calves born per year (#YOY). ID# 242 was first identified as a female through observations of the genital slit during her live-stranding (O'Brien et al. 2014). Blank cells indicate no sighting of the female in that year. Italicized cells indicate years with no sighting where year of birth was inferred for the calf (after Arso Civil 2015; Tezanos-Pinto et al. 2015)
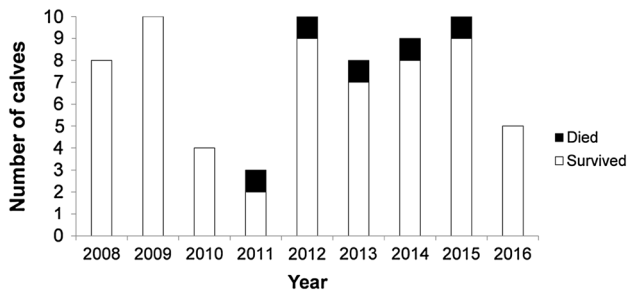
Fig. 5 Number of bottlenose dolphin calves born in the Shannon Estuary from 2008 to 2016, with those that subsequently died in black (no mortality data for 2016)

cessive births, the mean IBI was 2.9 ± 0.7 years (95% CL 2.6–3.3, SD 0.67, median 3.02, range 1.4–4.0).

Using sightings of calves When the difference in time elapsed between the first sighting of a female with her initial calf and the first sighting of the same female with her subsequent calf was used, the mean inter-birth interval was 2.7 ± 0.6 years (95% CL 2.4–3.1, SD 0.61, median 2.98, range 1.6–3.9; Table 2).

Excluding the three females whose calves died (underlined calf codes; Table 2), the mean IBI for the other ten females whose calves survived to weaning age was 3.2 ± 0.4 years (95% CL 2.9–3.5, SD 0.42, median 3.05, range 2.6–4.0). Of these ten females, eight IBIs were of approximately 3 years and two of 4 years. For the three females whose calves died, the mean IBI was 2.1 ± 0.7 years (95% CL 1.4–2.9, SD 0.67, median 2.02, range 1.4–3.0).

Considering those females whose calves did not die and using the time elapsed between first sightings of the female with initial and subsequent calf, female ID#s 044 and 216 had the lowest IBIs at 2.22 and 2.26 years, respectively, while female ID#s 242 and 006 had the highest IBIs at 3.93 and 3.19 years, respectively (Table 2).

Using year of birth Of all the reproductive females and their full sighting histories across the 9-year study period, the inter-birth interval (based on year of birth) ranged from 2 to 7 years. Using this larger dataset of sighting histories for all reproductive females in the study (22 females with more than one calf of known year of birth; 50 calves), the mean inter-birth interval (based on annual consecutive births) was 3.5 ± 1.3 years (median 3, mode 3; Fig. 7). In two cases where the calf was lost (ID#s 070 and 223, both YC2) the mothers went on to have subsequent calves around 2 years later. Results were similar when the four cases where a birth was possibly missed in the timeline were excluded; the mean inter-birth interval was 3.2 ± 1.0 (median 3, mode 3).

Calving rate, birth rate and fecundity Annual calving rates for the population between 2008 and 2016 ranged from 0.13 to 1.00 (mean 0.29) young-of-year/reproductive female/year (95% binomial CL 0.12–0.46). Annual crude birth rates for the years 2012–2016 ranged from 0.06 to 0.09 with an average annual crude birth rate of 0.07 ± 0.01 (or mean crude birth rate of 7.2%). The estimated fecundity of the population, accounting for calf mortality, was 0.26 ± 0.03, while the estimated fecundity rate, not accounting for calf mortality, was 0.33.

Fig. 6 The number of births per month estimated using calves with within 60 days-precision birthdate estimates ($n = 31$), with a polynomial regression line fitted. Thick grey lines indicate the window of time between ordinal dates (i.e., days-of-year) when each of the 31 calves could have been born (i.e., dates from the last sighting of the mother without her calf to the first sighting of the mother with her newborn calf)
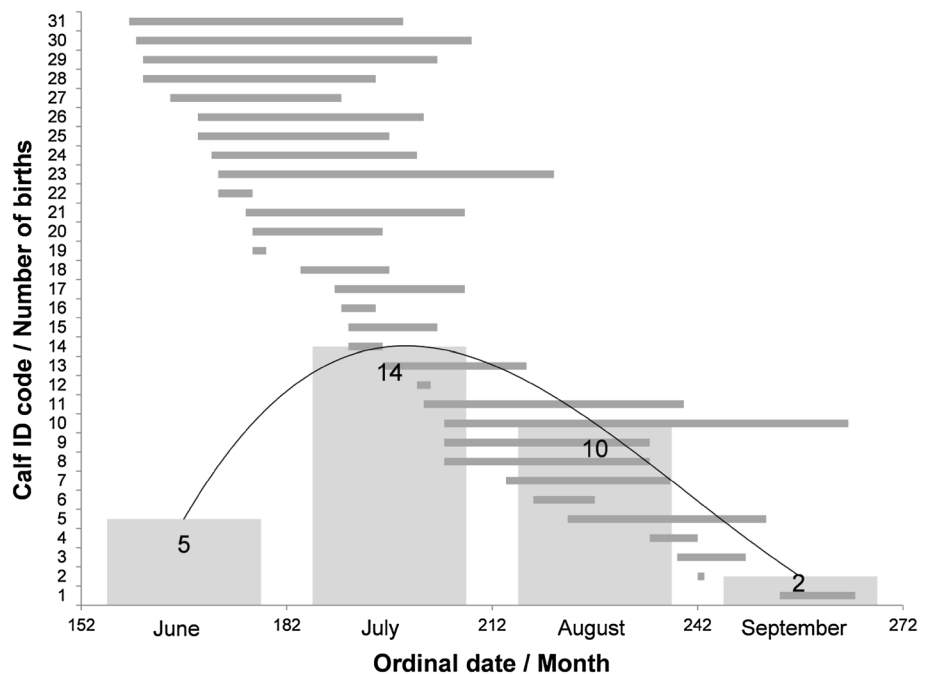
Table 2 Inter-birth intervals (in years) for reproductive females with consecutive calves of known fate, using two approaches: (1) calculated from an estimated date of birth (DOB) derived from the midpoint of the dates between when the mother was last seen before the birth of her calf and the first sighting of the mother with her newborn calf; and (2) calculated from the time-lapse between the first sighting of the mother with her initial calf and the first sighting of the mother with her subsequent calf

Female ID#	Calf code	DOB estimate	DOB accuracy (days)	Mother last seen before birth of calf	First sighting of mother with calf	IBI (DOB)	IBI (sightings)
006	YC2	01/09/2015	10	27/08/2015	06/09/2015		
	YC1	10/01/2012	337	26/07/2011	27/06/2012	3.64	3.19
044	YC2	29/08/2016	1	29/08/2016	30/08/2016		
	YC1	09/01/2014	307	09/08/2013	12/06/2014	2.64	2.22
045	YC2	11/07/2015	5	09/07/2015	14/07/2015		
	YC1	04/07/2012	30	19/06/2012	19/07/2012	3.02	2.98
070	YC3	01/07/2014	43	10/06/2014	23/07/2014		
	<u>YC2</u>	22/06/2012	5	20/06/2012	25/06/2012	2.02	2.08
085	YC2	02/07/2016	49	08/06/2016	27/07/2016		
	<u>YC1</u>	09/07/2013	13	03/07/2013	16/07/2013	2.98	3.03
204	YC3	27/06/2015	34	10/06/2015	14/07/2015		
	YC2	20/06/2012	377	09/06/2011	20/06/2012	3.02	3.06
205	YC3	12/07/2015	5	10/07/2015	15/07/2015		
	YC2	12/01/2012	343	25/07/2011	02/07/2012	3.50	3.03
216	YC3	25/07/2015	21	15/07/2015	05/08/2015		
	YC2	19/12/2012	266	08/08/2012	01/05/2013	2.60	2.26
218	YC3	27/06/2016	40	07/06/2016	17/07/2016		
	YC2	02/01/2013	313	30/07/2012	08/06/2013	3.48	3.11
223	YC3	13/12/2015	232	19/08/2015	07/04/2016		
	<u>YC2</u>	08/08/2014	30	24/07/2014	23/08/2014	1.35	1.62
232	YC2	16/07/2014	13	10/07/2014	23/07/2014		
	YC1	20/06/2011	746	12/06/2010	27/06/2012	3.07	2.07
242	YC2	09/08/2016	9	05/08/2016	14/08/2016		
	YC1	24/08/2012	29	10/08/2012	08/09/2012	3.96	3.93
285	YC3	26/06/2015	25	14/06/2015	09/07/2015		
	YC2	20/07/2012	2	19/07/2012	21/07/2012	2.93	2.97
					Median	3.02	2.98
					Average	2.94	2.74
					Range	1.35–3.96	1.62–3.93
					95% CL	2.58–3.30	2.41–3.07
					SD	0.67	0.61

Underlined calf codes are those known to have died

Calf mortality and reproductive success

Between 2012 and 2015, an average 11% of recorded newborn calves ($n = 4$) were lost before age 1. Reproductive success rates for female bottlenose dolphins in the Shannon Estuary with > 1 documented births, where the calf survived to the minimum known weaning age for Shannon dolphins (2.0 year) and/or the fate of the calf could be determined, varied from 0.5 to 1.0 ($n = 17$). Three females had calves that died before they weaned, two of whom raised another calf successfully, and the third of whom raised two more calves successfully within the study period. The mean individual reproductive success was 0.9 (SD 0.17).

Non-reproductive females

There were 12 adult dolphins sexed as female that were never observed with calves during the 9-year study period, despite some individuals having a large number of sightings (e.g., ID# 093 with 81 sightings and seen during each of all 9 years; Table 3). All 12 individuals were sexed by genetic determination from biopsy tissue samples.

Weaning and mother–calf associations

Weaning ages, calculated for 11 individuals with known birth and weaning dates, ranged from 2.0 to 4.1 year (mean
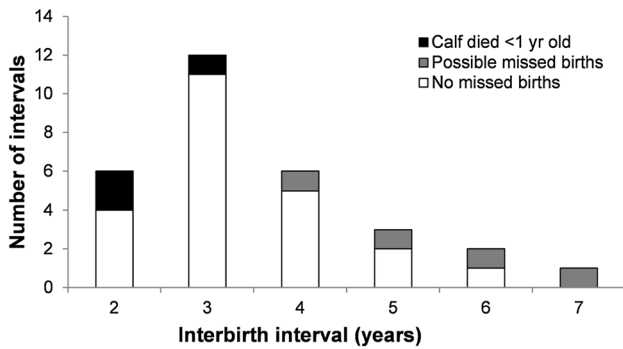
Fig. 7 Inter-birth intervals for females whose calves survived to weaning (white bars) and whose calves died < 1 year old (black bars), and for those where a birth may have been missed in the interim (grey bars) (n = 30). Mean inter-birth interval was 3.53 (SD 1.28, median 3) (after Mann et al. 2000; Fruet et al. 2015)

2.9 year). Of 22 calves known to have reached weaning age, eight (30%) were not sighted after their weaning date and 14 were sighted at least once following weaning. Four of these individuals were never seen with their mothers, but the other 10 had between one and 14 shared sightings with their mothers post-weaning. Interestingly, two cases of shared sightings involved the weaned calf's presence in a group during the first sighting of its mother with her subsequent newborn calf.

The calf who had the most shared sightings with her mother (n = 14) was a female, and one of the individuals present during the first sighting of a newborn, surfacing < 1 m next to it in a group of seven dolphins. The only other weaned calf of known sex was a male who shared two sightings with his mother, but was seen in groups with other juveniles (and without his mother) during seven other encounters.

Discussion

This study has presented female reproductive parameters for bottlenose dolphins in the Shannon Estuary, Ireland, for the first time. Additionally, new information on the demographics of this population has been revealed through the analysis of a detailed long-term dataset collected through observations of live animals.

Population size and composition

Of the 145 extant individual dolphins recorded in 2015, over half were adults, with about one quarter dependent calves, and the others independent juveniles. Notably, the adult:calf ratio of the population was 2:1. Wells (2014) reports the Sarasota Bay dolphin community as comprising 58% adult and 42% subadult individuals (which presumably includes juveniles, calves and YOYs). This age class ratio is comparable to the 55% adult, 17% juvenile and 28% calf contingents found in the Shannon Estuary population. Manlik et al. (2016) report a similar proportion of 55% adults for dolphins in Shark Bay, but the proportions of younger age classes are reversed, with 30% juveniles and 15% dependent calves. Similarly, Manlik et al. (2016) also report proportions of 58% adults, 25% juveniles and 17% calves for the Bunbury bottlenose dolphin population.

In contrast, Bearzi et al. (1997) found the percentages of adults, juveniles and calves (140 individuals) in the Adriatic Sea to be 85.2, 8.2 and 6.6%, respectively, Chabanne et al. (2012) found that the Swan Canning Estuary population (55 individuals) contained 78.2% adults/sub-adults and 21.8% calves, while Augusto et al. (2011) reported the Sado Estuary bottlenose dolphin population (24 individuals) to be 79.2% adults, 12.5% juveniles and 8.3% calves. As the Sado Estuary population appears to be critically declining with

Table 3 Sighting frequency of non-reproductive female bottlenose dolphins in the Shannon Estuary from 2008 to 2016, including total number of sightings (n) and total number of years sighted (#years)

ID#	2008	2009	2010	2011	2012	2013	2014	2015	2016	n	#Years
051	1	2								3	2
066				3	3	10	9	3	1	28	6
080		1		6	2	2	12	7	1	30	7
081	1	2			2	5	2	1	1	13	7
093	1	4	1	11	7	9	31	17	1	81	9
094	1									1	1
126					7	6	4	6	1	23	5
168		3	1	1	1	5	5	1	1	17	8
200	3	6	1	9	3	12	20	9	1	63	9
227					2	1	4			7	3
247		2		4	7	18		11	1	42	6
260		1				5	16	2	1	25	5

The sex of all 12 individuals was determined through genetic analysis of tissue samples from biopsies

a community composed primarily of adults and few young animals, the contrast of adult and calf proportions between that and the Shannon Estuary population points towards the apparent "good health" of the Shannon Estuary population and a comparatively higher percentage of calves.

The sex of most adult/juvenile individuals in the Shannon Estuary bottlenose dolphin population is still unknown (51%) with 49% animals of known sex (comprising 40% females and 9% males). Since consistent close association with a calf is a reliable way to determine the sex (female) of individual adult bottlenose dolphins, it is likely that most if not all females in the current population who were reproductively mature during our study were identified as such. However, it would be very valuable to gain more information on adult males in the population, as well as the sexes of calves. In particular, information on the age of individuals reaching reproductive maturity would be useful for population viability analyses and management scenarios.

Adult/juvenile mortality rate

The mean annual maximum adult/juvenile mortality rate was 0.038. Interestingly, this is the same value calculated by Wells and Scott (1990) for the Sarasota Bay bottlenose dolphin community. This is a maximum value because it includes all individuals who have ceased to be sighted; unfortunately, it was not possible to confirm any certain deaths because no known dead individuals were ever recovered from strandings, nor was it possible to identify any individuals as emigrants outside the population's known home range. In Sarasota Bay, an adult male dolphin returned to the community after an 8-year absence suggesting that at least a small number of individuals may leave their core home range for extended periods of time (Wells and Scott 1990). Since it is possible that some individuals temporarily emigrated or were not recorded in the Shannon Estuary study area in the most recent 2 years, and are still alive, the mortality rate for the Shannon Estuary population is likely lower than the maximum value given.

Female reproductive parameters

Births

In the Shannon Estuary, seven calves were born on average each year, but this number fluctuated from a minimum of three to a maximum of ten during the 9 years of our study. Interestingly, the 3 years (2009, 2012 and 2015) where the number of calves born was ten were each 3 years apart. Maybe this is a potential cyclical characteristic of reproduction in this population, or perhaps a cohort of females reproducing together at regular intervals. In an estuarine resident population of 74 Indo-Pacific bottlenose dolphins

in the Port River Estuary, Australia, Steiner and Bossley (2008) calculated that an average of 2.6 calves were born each year; much lower than the mean of 7.4 births per year in the present study. However, in Cardigan Bay, an average of 10 calves were born each year to a population of 103 individuals (Veneruso and Evans 2012). The number of calves born in a population can be related to many socio-environmental parameters including population size and habitat ecology, and different study sites have reported varying reproductive parameters (see Table 4 for comparative summary of studies).

The reproductive female dolphins in this 9-year study had between one and three calves each. In some cases, for those that had only one calf during the study period, it was not that they had long periods without a dependent calf, but that their dependent calf was with them for a longer duration. For example, ID# 011 gave birth to a calf in 2010 and was still with that calf in 2016. However, the majority of reproductive females (65%) had more than one calf throughout the study period.

Temporal patterns in reproduction

The dataset from the Shannon Estuary was seasonally biased because most data were collected during summer months, so it was not possible to get an annual estimate of seasonal peaks in birth. However, of the four main months for which data were available (June–September), births peaked in July. Similarly, 76% of all bottlenose dolphin births in Cardigan Bay, Wales occurred between July and September (Norrman et al. 2015). With further research, it is possible that a predictable summer calving season might be uncovered such as in other populations (e.g., Steiner and Bossley 2008; Smith et al. 2016). It is well-documented that in many bottlenose dolphin populations, births tend to peak in spring and summer months, possibly due to an increase in water temperature and food supply (Steiner and Bossley 2008; Veneruso and Evans 2012; McFee et al. 2014; Fruet et al. 2015; Tezanos-Pinto et al. 2015). Additional winter data collection and information on sea surface temperature, dolphin prey abundance, distribution and variability would be valuable for exploring fluctuations in the reproductive biology of the Shannon Estuary dolphin population.

Inter-birth intervals

We used three methods to calculate mean inter-birth interval (IBI)—difference between estimated dates of birth (DOBs), difference between sighting dates of mothers with initial and subsequent newborns, and difference between annual births based on year of birth—and found that the mean IBI for the Shannon Estuary bottlenose dolphin population was 2.9, 2.7 and 3.5 years for each

Table 4 Summary of reproductive parameters for bottlenose dolphins

Study area	Species	No. dolphins	Annual births	(SD)	Study length	% of pop. Adults	Juveniles	Calves	Crude birth rate (SD)	Mean IBI (years)	IBI range	Fecundity	1st year mortality	References
Shannon Estuary, Ireland	T. truncatus	142	7.4	(2.6)	9	55	17	28	0.072 (0.01)	2.7–3.5	2–7	0.26 (0.03)	0.11	This study
Cardigan Bay, Wales	T. truncatus	103	10	(4.1)	13				0.075	3.3	2–7		0.15	Norrman et al. (2015)
Moray Firth, Scotland	T. truncatus	192	6.2	(5.2)[a]	24[a]				0.060[b]	4.5[a]	2–9[a]	0.22[a]	0.38[b]	Arso Civil et al. (2017)[a] and Sanders-Reed et al. (1999)[b]
North Sea, Scotland	T. truncatus	108[c]	9	(4.0)[d]	20[d]				0.12 (0.05)[d]	3.8[d]	2–9[d]	0.16 (0.04)[d]	0.45[d]	Culloch (2004)[c] and Robinson et al. (2017)[d]
Sado Estuary, Portugal	T. truncatus	24			4[e]; 16[f]	79.2[e]	12.5[e]	8.3[e]	0.054[f]		3–11[f]			Augusto et al. (2011)[e] and Gaspar (2003)[f]
Adriatic Sea, Croatia	T. truncatus	106	4.2	(1.2)[h]	5[g]; 9[h]	85.2[g]	8.2[g]	6.6[g]	0.049 (0.034)[g]	3[g]		0.17 (0.05)[h]	0.18[h]	Bearzi et al. (1997)[g] and Fortuna (2007)[h]
Sarasota Bay, USA	T. truncatus	163	7			58[i]			0.055 (0.009)[j]	5.4[k]	2–11[k]	0.14 (0.24)[i]	0.19[i]	Wells (2014)[i], Wells and Scott (1990)[j] and Wells and Scott (1999)[k]
Patos Lagoon Estuary, Brazil	T. truncatus	83	7.4	(1.6)					0.090 (0.01)	3		0.11 (0.02)	0.16	Fruet et al. (2015)
Bay of Islands, New Zealand	T. truncatus	408	4.1	(2.7)	13				0.0625	4.3		0.25	0.42	Tezanos-Pinto et al. (2015)
Doubtful Sound, New Zealand	T. truncatus	66	4.1		17				0.040 (0.04)	5.3	2–5		0.33	Henderson et al. (2014)

Table 4 (continued)

Study area	Species	No. dolphins	Annual births (SD)	Study length	% of pop.			Crude birth rate (SD)	Mean IBI (years)	IBI range	Fecundity	1st year mortality	References
					Adults	Juveniles	Calves						
Port River Estuary, Australia	*T. aduncus*	74	2.6	17				0.064	3.8	1.1–6		0.30	Steiner and Bossley (2008)
Shark Bay, Australia	*T. aduncus*	83	10	11					4.6	3–6.2		0.29	Mamn et al. (2000)
Mikura Island, Japan	*T. aduncus*	169	7					0.071 (0.024)	3.4		0.136 (0.04)	0.13	Kogi et al. (2004)

Superscript letters refer to references cited in the last column

method, respectively. Average IBI (in years) has been reported for many other bottlenose dolphin populations including estimates from 5.4 in Sarasota Bay, USA (Wells and Scott 1999) to 3.0 in the Adriatic Sea (Bearzi et al. 1997) (Table 4). Thus, our estimate of 3.5 years (based on year of birth) falls within the lower values from these examples, including, interestingly, the values obtained from studies of resident bottlenose dolphin populations in Scotland (4.5 years, Arso Civil et al. 2017; 3.8 years, Robinson et al. 2017) and Wales (3.3 years, Norrman et al. 2015)—the two closest study sites to the Shannon Estuary. However, the IBIs estimated from more detailed dates in our study of 2.9 and 2.7 years suggest that the Shannon Estuary bottlenose dolphin population has some of the lowest inter-birth intervals documented for populations worldwide, most similar to values of 3.0 years reported for dolphins in the Adriatic Sea (Bearzi et al. 1997) and the Patos Lagoon Estuary, Brazil (Fruet et al. 2015). Of course, every population manifests individual variability and ranges of IBIs for individual reproductive females, but our results do suggest relatively frequent births for the reproductive females of this population.

Of the 13 reproductive females where estimated DOBs could be used to calculate IBIs between each of their two consecutive calves, results were noticeably different when comparing those whose initial calf died (IBI 2.1 ± 0.7 years) to those whose initial calf survived to weaning (IBI 3.2 ± 0.4 years). Although the sample size for calves that died was small ($n = 3$), this suggests that there could be a marked difference between IBIs in this population for females who lose a calf in its first year (and thus mate again shortly afterwards).

Two of the females in our study who lost their calves had subsequent calves just 2 years later and the third female who lost a calf had her subsequent calf 3 years later. This has also been reported in other populations. For example, Kogi et al. (2004) reported that the shortest IBIs of 1 year and 2 years in Indo-Pacific bottlenose dolphins at Mikura Island, Japan, involved females who had lost their calves and then became pregnant the same or following year. Similarly, Bearzi et al. (1997) reported two females with 2 and 3 year IBIs when calves disappeared before weaning. In Scotland, a female dolphin conceived again in the breeding season immediately following the death of each of her two calves (Mitcheson 2008). Steiner and Bossley (2008) report an example of one female with a 1.9 year IBI between surviving calves (i.e., the short IBI was not the result of the death of the previous calf). Although there are some calves in the Shannon Estuary population who weaned around age 2, the only example from our dataset of an IBI of less than 2 years was from a mother (ID# 223) whose initial calf died. Similarly, female dolphins in the Moray Firth, Scotland, are capable of reproducing on a 2-year cycle after the death of a newborn calf

but have never been observed producing a subsequent calf in less than 2 years (Grellier 2000; Robinson et al. 2017).

Considering those females whose calves did not die and using the time elapsed between first sightings of the female with initial and subsequent calf, females ID# 044 and ID# 216 had the lowest IBIs at 2.22 and 2.26 years, respectively. However, because, in both cases, the mothers had not been sighted since the previous autumn, these IBIs could be closer to 3 years. For example, if ID# 044's calf had been born the day after her last sighting in 2013, the IBI would have been 3.06 years.

The quantification of IBIs for the 13 reproductive females with two consecutive births and known calf fate may have shown bias in the results of IBIs of only 3 and 4 years' length. This might be a result of the length of the study period as there are no examples of female dolphins with IBIs of greater than 4 years in this subset of data. From the analysis based on year of birth, we know examples exist of longer (> 6 year) IBIs. For example, individual ID# 011 has had the same dependent calf for the past 6 years. If the calf had weaned by the end of our study period, her data would have increased the results of the IBI analysis based on date of birth and weaning date considerably. The relatively short 9-year length of our study period when compared to the life span for bottlenose dolphins may have biased our results towards more frequently reproducing females and thus seemingly shorter IBIs and younger weaning ages (Arso Civil et al. 2017).

Crude birth rate, calving rate and fecundity

The mean annual crude birth rate for Shannon dolphins of 7.2% was consistent with the values calculated for other populations, which range from 4.0% in Doubtful Sound, New Zealand (Henderson et al. 2014) to 12.0% in the North Sea, Scotland (Robinson et al. 2017) (Table 4). Some of these studies noted that their crude birth rates were probably underestimated as some calves could have been born and died before being recorded (e.g., Steiner and Bossley 2008)—this might explain why the birth rates calculated for Shannon Estuary dolphins are among the highest; the population was well-studied with multiple sightings of the reproductive females. However, it is always possible to miss births, particularly for young primiparous females where calves could have been born and lost before observations were made of the mother–calf pair (Kogi et al. 2004).

The mean annual calving rate of 0.29 for bottlenose dolphins in the Shannon Estuary was comparable to that for the same species in the Bay of Islands, New Zealand where average annual calving rate was 0.25 young-of-year/reproductive female/year (95% binomial CL 0.16–0.35; Tezanos-Pinto 2009; Tezanos-Pinto et al. 2013, 2015). The fecundity of the Shannon Estuary population, calculated differently to

calving rate in that it takes into account only the births surviving to > 1 year, was estimated to be 0.26, which appears relatively high when compared to other populations. In the Patos Lagoon Estuary, Brazil and Sarasota Bay, Florida, fecundity rates were reported as 0.11 and 0.14, respectively (Wells and Scott 1990; Fruet et al. 2015). This suggests that the reproductive capacity of the Shannon Estuary dolphin population is potentially relatively good. Arso Civil et al. (2017) estimated a similar fecundity rate of 0.22 for bottlenose dolphins in the Moray Firth, Scotland. Using their method, where fecundity rate is 'the annual probability of a reproductive female having a calf', irrespective of its survival, the estimated fecundity rate for the Shannon Estuary population was even higher at 0.33. Estimating fecundity rate using the ratio of the number of calves surviving to the first year and the number of reproductive females in that year yields a lower estimate than the fecundity rate when not accounting for calf survival (Wells and Scott 1990; Arso Civil 2015).

Calf mortality

The 11% mortality rate calculated for YOYs in the Shannon dolphin population seems to be quite low in comparison with other study populations, where first-year calf mortality rates of between 13 and 45% have been reported (Robinson et al. 2017; Kogi et al. 2004) (Table 4). However, our sample size of four calf deaths is very small, and mortality rates are most likely higher in cases where the sighting frequency of mother–calf pairs is low. Our study contained no known occurrences of calf deaths in the second year of life.

The causes of calf mortality in the Shannon Estuary remain largely unknown. There are no known predators of bottlenose dolphins in Ireland; dolphins are not subjected to predation by sharks as they are in other populations such as in Shark Bay, Australia (Heithaus 2001). Therefore, predation does not seem to account for any calf deaths in the Shannon Estuary. Naturally occurring biological causes might be responsible for calf mortality, such as genetic birth defects, which might make calves more susceptible to disease or illness. Interestingly, two calves born to one of the reproductive females (ID# 280) in the Shannon population were both observed to have visible morphological deformities, which may have been the result of a genetic mutation; however, neither has died to date. Several other calves in the Shannon Estuary population such as ID# 118's calf (YC2, born in 2015) have been observed with deformities, which could also be the result of scoliosis (Berrow and O'Brien 2006) or physical trauma (Robinson 2014).

Additionally, there is no evidence in the Shannon Estuary of the direct anthropogenic threats that occur at other study sites, such as entanglement and boat strikes (e.g., Port River Estuary, Australia; Steiner and Bossley 2008).

However, it is possible that there are less obvious human impacts affecting the survival of the population; for example, dolphins in the Shannon Estuary have been shown to have high levels of PCB contamination which could affect their ability to reproduce adequately (although their levels are relatively low compared to other European populations; Jepson et al. 2016). Thus, this type of pollution could be causing observed or unobserved calf deaths, particularly for firstborn calves; bottlenose dolphin mothers off-load contaminant burdens into their firstborn calves (Schwacke et al. 2002). One female in the current study (ID# 027; Table 1) was found to have contaminant loads that were high enough that they could potentially have affected her reproductive success (Jepson et al. 2016); she was observed with only one calf in 2008 despite being sighted during five of the following years of this study. Other potential indirect anthropogenic threats to calf survival in the Shannon Estuary include acoustic disturbance from shipping. The Shannon Estuary is Ireland's second-largest waterway and a large shipping route. As acoustic communication between mothers and calves is essential to their associations, shipping noise could have a negative impact on a calf's ability to keep in contact with its mother (O'Brien et al. 2016). Overall, it is likely that a combination of factors influences calf mortality in the Shannon Estuary.

Reproductive success and non-reproductive females

Generally, reproductive success appeared to be quite high for reproductive female dolphins in the Shannon Estuary, with only three of the 17 females examined having success rates of less than 100%—two of these females had one calf die and one survive, while the third had one calf die and two survive (to the minimum weaning age). Studies have shown that factors such as birth timing, maternal size and age, and birth order may be causes for variability in female dolphin reproductive success (Wells et al. 2014; Brough et al. 2016). Fruet et al. (2015) noted an age-related decrease in reproductive fitness in bottlenose dolphins in Brazil, with older females reproducing at lower rates. Differences in maternal experience and behaviour appear to be crucially important to calf survival in some populations (Henderson et al. 2014; Fruet et al. 2015). Further behavioural research on the Shannon Estuary dolphin population could highlight individual differences in the maternal care of young.

Tezanos-Pinto et al. (2015) report what they inferred to be a "high proportion", 14%, of non-reproductive females in their study population in the Bay of Islands, New Zealand. However, an even higher proportion of 25% of the known females in the Shannon Estuary population were found to be non-reproductive in this study. The large proportion of non-reproductive females in the population is curious. Clearly, the survival of calves of known reproductive females is high,

but it is possible that additional calves of "non-reproductive" females have gone undocumented; it is impossible to know how many newborn (especially firstborn) calf deaths are not recorded, and how many stillbirths or miscarriages occur. Such occurrences might explain the apparently high proportion of non-reproductive females in the population.

Weaning and mother–calf associations

Although the sample size was small ($n = 11$), the range of weaning ages from 2.0 to 4.1 years in the Shannon population suggested variability in the age of independence for young bottlenose dolphins.

The longevity of mother–calf associations was investigated to determine if females whose calves weaned during the current study ever associated with them again, and if there were any patterns (perhaps related to sex class) associated with these pairings. Wells (2014) observed that older calves, especially females, sometimes associated closely with their mothers and new siblings for months or more, and Steiner and Bossley (2008) reported a previous calf seen with its mother and her subsequent calf on a number of occasions. In the current study, ten calves were observed in close association with their mothers post-weaning. Of these ten mother–calf pairs, eight are considered members of the "inner estuary community", shown to have stronger associations and longer lasting bonds than other individuals in the population (Baker et al. 2017b, in press).

The female calf that had the most shared sightings with her mother was sighted in a group with her mother and her subsequently newborn sibling. Associations such as this after weaning could be important for maintaining social bonds and learning about motherhood, and perhaps also serve to provide relief to the mother in the sharing of calf rearing responsibilities (Wells 2014).

Conclusion

The purpose of this study was to derive baseline data on the population demographics and female reproductive parameters of bottlenose dolphins in the Shannon Estuary, Ireland. Using a detailed dataset to count the number of individuals in the population led to a population estimate of 142 which is just above the higher limits of previous estimates calculated through mark-recapture analysis. Results revealed that although the Shannon Estuary bottlenose dolphin population's life history parameters include some of the shortest inter-birth intervals and youngest weaning ages reported for bottlenose dolphins worldwide, they are within the ranges reported in other studies. Interestingly, they are similar to those reported for nearby populations in the Moray Firth, Scotland and Cardigan Bay, Wales.

This study increases our knowledge of bottlenose dolphin reproductive rates and population demographics. The results will allow for comparative studies of the Shannon Estuary dolphin population, exploring similarities and differences with other populations of well-studied resident dolphins in temperate and tropical waters. Given the variability between populations, it is imperative to report regionally specific demographics (Arso Civil et al. 2017). This study complements other longitudinal research studies in offering essential guidance for the development of sustainable practices in population conservation (Mann and Karniski 2017). The population and life history parameters presented here make an important contribution to the global conservation of the species. They also serve to show how variable the demographics of different populations can be, reinforcing the importance of extending research to a wide geographical range.

Compliance with ethical standards

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

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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