

1 **Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal**
2 **ecosystem**

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10 **Abstract.** This study presents the first robust estimates of abundance and demographic parameters of common
11 bottlenose dolphins (*Tursiops truncatus*) in a highly affected coastal ecosystem along the north-eastern Atlantic.
12 Seasonal abundance, apparent survival and temporary emigration rates were estimated using Pollock's robust
13 design models. Photographic identification data were collected from 2014 to 2016 along the north-western Iberian
14 coast (Spain). Bottlenose dolphins were present year-round and with a high degree of occurrence in the study area,
15 which is highly affected by human activity but is also a highly productive coastal ecosystem. Local abundance of
16 bottlenose dolphins ranged from 56 in autumn 2014 to 144 in winter 2015. Apparent survival rate was high and
17 constant, indicating no mortality and no permanent emigration. Temporal emigration rates varied seasonally and
18 were lower from autumn to winter, suggesting that dolphins had a high probability of returning during the winter
19 period. The observed changes in abundance and emigration rates most likely reflect seasonal fluctuations in
20 abundance of prey species in this area. These results provide important baseline information in an area subject to
21 significant anthropogenic pressures and for future comparisons with other populations of similar characteristics
22 under the pressure of human activities, such as fisheries and aquaculture.

23

24 **Additional keywords:** anthropogenic disturbances, Iberian Peninsula, marine top predator, photographic
25 identification.

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29 Worldwide, coastal and marine ecosystems are at risk as a result of human activities ([Halpern et al.](#)
30 [2008](#)). Consequently, cetacean species that live near shore are highly vulnerable to a variety of
31 anthropogenic pressures, such as fisheries ([Read et al. 2006](#)), aquaculture ([Würsig and Gailey 2002](#);
32 [Díaz López 2012](#)), pollution ([Derraik 2002](#); [Tanabe 2002](#)), global warming ([Simmonds and Isaac 2007](#))
33 and habitat modification ([Lotze et al. 2006](#)). Estimating demographic parameters of a cetacean

34 population is crucial for assessing their conservation status and to identify potential effects of
35 anthropogenic or natural pressures in order to take appropriate conservation and management
36 measurements (Smith *et al.* 2013).

37 Having a near shore distribution, the common bottlenose dolphin *Tursiops truncatus* (Montagu
38 1821), hereafter ‘bottlenose dolphin’, is among the most threatened cetacean species, and a more intense
39 monitoring and management intervention is needed for this species (Bearzi *et al.* 2009). Atlantic
40 bottlenose dolphin populations are listed in Appendix II of the Convention on the Conservation of
41 Migratory Species of Wild Animals (CMS; www.cms.int 15 October 2017), in Appendix II (Strictly
42 Protected Fauna Species) of the Convention on the Conservation of European Wildlife and Natural
43 Habitats (Bern Convention; www.coe.int 15 October 2017) and under Annexes II and IV of the
44 European Union’s Habitats Directive (Council Directive 92/43/EEC; www.ec.europa.eu 15 October
45 2017) as a species whose conservation requires the designation of Special Areas of Conservation and
46 in need of strict protection.

47 In order to obtain accurate and precise information about bottlenose dolphin populations, year-round
48 survey efforts are essential, but these are expensive and logistically challenging (i.e. weather conditions,
49 limited resources and personnel). In north-east Atlantic waters, although some studies have focused on
50 local abundance (Silva *et al.* 2009; Berrow *et al.* 2012; Hammond *et al.* 2013), there is a lack of
51 exhaustive robust assessments of population abundance, rates of apparent survival and temporary
52 emigration of bottlenose dolphin populations.

53 Bottlenose dolphins are present along the north-western Iberian coast (López *et al.* 2003; Pierce *et al.*
54 2010; Louis *et al.* 2014; Díaz López and Methion 2017), a region where they are vulnerable to
55 several human impacts that affect coastal areas throughout the Atlantic coastline, such as marine traffic,
56 bycatch (López *et al.* 2003), overfishing (Freire and García-Allut 2000), oil spills (Vieites *et al.* 2004)
57 and the aquaculture industry (Díaz López and Methion 2017). A recent study demonstrated that
58 bottlenose dolphins present a fine-scale pattern of habitat selection affected by anthropogenic activities
59 in these waters (Díaz López and Methion 2017). However, the lack of exhaustive robust assessments
60 of population abundance and demographic parameters hampers our ability to evaluate the effects of
61 human activities on this species in the region.

62 Over the past few years, Pollock’s capture–recapture robust study design (Pollock 1982) has been
63 increasingly used to obtain accurate estimates of abundance and other demographic variables of
64 bottlenose dolphin populations (e.g. Silva *et al.* 2009; Speakman *et al.* 2010; Nicholson *et al.* 2012;
65 Bassos-Hull *et al.* 2013; Smith *et al.* 2013; Fruet *et al.* 2015; Santostasi *et al.* 2016; Sprogis *et al.* 2016).
66 This design, unlike standard open models, takes into account the degree of residency, including
67 temporary emigration, thus more accurately reflecting reality in the results (Kendall *et al.* 1997;
68 Nicholson *et al.* 2012; Smith *et al.* 2013). Indeed, temporary or permanent emigration can potentially

69 be confounded with mortality, and may result in imprecise, and in some circumstances biased,
70 estimations (Kendall *et al.* 1997). By using Pollock's robust design model it is possible to control the
71 effects of temporary emigration on the population, thus making the model less sensitive to the observed
72 violations of 'equal catchability' when the recapture period is extended over time (Pollock 1982).
73 Pollock's robust design combines open population models (open sampling event; termed 'primary
74 periods') and closed population models (multiple closed events within the open sampling event; termed
75 'secondary periods'; Kendall *et al.* 1997). Although the population is assumed to be open between
76 primary periods (i.e. allowing for births, deaths and permanent or temporary emigration and
77 immigration), each secondary period assumes an effectively closed unit (i.e. births, deaths, immigration
78 and emigration do not occur; Kendall *et al.* 1997).

79 In the present study, we used Pollock's robust design models on photographic identification data
80 collected year-round to estimate seasonal abundance, apparent survival and temporary emigration rates
81 of common bottlenose dolphins along the north-western Iberian coast (Spain). These estimates are the
82 first robust estimates for a coastal bottlenose dolphins in north-eastern Atlantic waters and provide
83 important baseline information in an area subject to significant anthropogenic pressures.

84 **Materials and methods**

85 *Study area*

86 The present study was performed along the north-western coast of the Iberian Peninsula, specifically
87 along the southern coast of Galicia (Spain), on which there are a series of ancient drowned tectonic
88 valleys taken over by the sea (also referred to as 'rías'; Evans and Prego 2003). Owing to intense
89 upwelling events that occur along this coast, resulting in very high primary production, the rías are
90 important areas for fisheries and shellfish aquaculture, and more specifically for the production of
91 mussels and oysters (Prego *et al.* 1999). Rías are often sites for human settlement, where many pollution
92 problems exist, because they serve as harbours and waterways to urban and industrial centres (Prego
93 and Cobelo-García 2003).

94 Boat-based surveys were conducted in the coastal waters of the largest of the Galician rías, the Ría
95 de Arousa (Prego *et al.* 1999), and surrounding waters up to 20 km offshore, covering an area of 450
96 km² with a maximum depth of 150 m. The average depth of the Ría de Arousa is 19 m. The entire
97 system is subjected to a semidiurnal and mesotidal tide regime, with a tidal range of 1.1 and 3.5 m
98 during neap and spring tides respectively (Alvarez *et al.* 2005). During the study, the sea surface water
99 temperature ranged between 9°C in winter and 22°C in summer.

100 *Data collection*

101 Boat-based surveys were conducted in the study area between March 2014 and June 2016 using a
102 12-m research vessel powered by two 180-hp inboard engines. Because of poor weather conditions

103 during December we were unable to complete surveys during this month. In all, 25 months were spent
104 in the field.

105 The area was surveyed during daylight hours at a constant speed of 6 kn with at least three
106 experienced observers stationed on the flying bridge (4 m above sea level) scanning 360° of the sea
107 surface in search of common bottlenose dolphins (*T. truncatus*) with the naked eye or 10 × 50
108 binoculars. The minimum number of experienced observers and vessel speed remained consistent
109 during the study period, making data suitable for comparative analysis. Boat-based observations were
110 performed when the visibility was not reduced by rain or fog, and sea conditions were <3 on the Douglas
111 sea force scale (Díaz López 2006). The survey area and track were designed to attempt to equally cover
112 all parts of the study area, although the geographic distribution of effort could vary according to weather
113 conditions (Díaz López and Methion 2017).

114 Upon encountering a group of bottlenose dolphins, searching effort ceased and the vessel slowly
115 manoeuvred towards the group in order to minimise disturbance during approach. A group of dolphins
116 was defined as either a solitary dolphin or any aggregation of bottlenose dolphins with close spatial
117 cohesion, with interactions between individuals and participating in the same behavioural activities.
118 The date, initial and final time, location (Universal Transverse Mercator (UTM) coordinates) and group
119 size and composition were recorded for each encounter. Attempts were made to photograph both sides
120 of the dorsal fin of every dolphin present in the group, regardless of the degree of marking, age class or
121 behaviour. Photographs were taken using digital single lens reflex (SLR) cameras equipped with a 35-
122 to 300-mm telephoto zoom lens. Group size was assessed based on the initial count of different
123 individuals observed at one time in the area. Field data were later verified with photographs taken during
124 each encounter by increasing the number of individuals present if more individuals were photographed
125 (Díaz López and Shirai 2008). Individual dolphins were classified according to age within each group
126 at the time of the encounter (Scott *et al.* 1990). Age class definitions followed those of Díaz López and
127 Methion (2017), whereby bottlenose dolphins were classified as either newborn, immature or adult.
128 Newborn dolphins were defined as dependent dolphins <1.5 m with fetal folds or lines. Newborns were
129 also defined on the basis of uncoordinated surfacing behaviour and swimming in the infant position (i.e.
130 below the mother, lightly touching her abdomen). Immature dolphins were those with few rake marks
131 and skin lesions and two-thirds or less the length of adults. Immature dolphins were often observed in
132 close association with an adult, but never observed in the infant position. Adult dolphins were fully
133 grown (length >2.5 m) marked or unmarked animals with darker skin colouration. Sex was determined
134 by direct observations and photographs of the genital region, as described by Díaz López (2012). The
135 sex of male bottlenose dolphins was determined by the observation of an erection, by the gap (>2.5 cm)
136 between the genital and anal slits and a lack of mammary slits, or by the gap alone. Females were sexed
137 by the observation of mammary slits or the consistent presence of a newborn swimming in the infant

138 position. After the end of an encounter, the search effort generally continued along the previously
139 planned route.

140 Data collection in the present study complied with current laws of Spain, the country in which the
141 study was performed.

142 *Relative frequency of occurrence*

143 In order to understand the temporal pattern in the presence of groups of bottlenose dolphins in the
144 study area, a relative frequency of occurrence (hereafter referred to as the encounter ratio (ER); Díaz
145 López 2006) was computed as follows:

$$146 \quad ER = \frac{Ne}{h}$$

147 where Ne is the total number of encounters and h is the total number of hours spent searching for
148 dolphins.

149 Non-parametric tests (Mann–Whitney or Kruskal–Wallis) were used to investigate the equality of
150 medians of quantitative samples. Statistical significance was tested at the $P < 0.05$ level. The data are
151 presented as means \pm standard error (s.e.).

152 *Analysis of photographs*

153 All digital photographs were analysed independently by three experienced researchers. Only adult
154 bottlenose dolphins were included in the photographic identification analysis; therefore, photographs
155 containing calves (immature and newborn dolphins) were excluded. Adult bottlenose dolphins were
156 identified from photographs based on the size, location and pattern of notches on the trailing edge of
157 the dorsal fin (Würsig and Jefferson 1990). All photographs containing a dorsal fin were graded for
158 quality and degree of distinctiveness in order to minimise misidentification and heterogeneity in capture
159 probabilities (Urian *et al.* 2015). Following Díaz López *et al.* (2017), all photographs were given an
160 absolute value score (1 = low; 4 = average; 10 = high) for: (1) the perpendicular angle of the dorsal fin
161 to the camera; (2) the focus of the image being sufficient to allow all notches to be distinguished; (3)
162 contrast and light intensity; and (4) the dorsal fin being suitably sized in the frame for all notches to be
163 clearly visible. The individual scores for each category were summed to obtain an overall quality score
164 (OQS). OQSs from 4 to 16 were considered poor quality; those from 19 to 25 were considered to be of
165 average quality and those ≥ 28 were considered excellent. To ensure correct identification of individuals,
166 only excellent quality photographs were used for individual identification. In addition, each adult
167 individual was included in a distinctiveness category, based on the amount of information contained on
168 the dorsal fin, to ensure that more distinctly marked individuals would not have a higher probability of
169 being identified. A ‘well-marked individual’ was considered to be a dolphin that is recognised not by a
170 single large feature in the dorsal fin, but also by a matrix of evident notches (Würsig and Jefferson

171 1990). A ‘marked individual’ was considered to be a dolphin with a distinct dorsal fin with an average
172 amount of information (i.e. a single large notch and several small notches). Features such as body and
173 dorsal fin scars, lesions, decolouration and tooth rakings were used as secondary characteristics, thereby
174 reducing the possibility of false positives (Wilson *et al.* 1999). A ‘poorly marked individual’ was
175 considered to be a dolphin with a dorsal fin that had a small amount of information (i.e. a small notch
176 and secondary characteristics). Because such characteristics are not necessarily permanent and not
177 easily identifiable, adult individuals with no marks on the dorsal fin (unmarked) and poorly marked
178 individuals were not included in further analyses.

179 Every photograph of identified individuals was re-examined for false positives (different dolphins
180 being assigned as the same individual) and false negatives (the same dolphin being assigned as multiple
181 discrete individuals), and the final data were confirmed by two experienced observers. Later, to avoid
182 potential errors because of observer fatigue during the photographic identification analysis, the
183 matching of the individuals was confirmed using DARWIN 2.22 (Hale 2008). The best photographs of
184 both sides of every adult bottlenose dolphin were kept in an identification catalogue. Photographs were
185 regularly replaced in the catalogue as better-quality or more current images became available. The
186 capture history (whether or not an identified bottlenose dolphin was present within a sampling period)
187 for each individual was compiled after the photographic grading process.

188 *Mark–recapture abundance models*

189 In the present study we used Pollock’s robust design model to estimate abundance and survival rates
190 (Pollock 1982; Kendall *et al.* 1997) of the bottlenose dolphins studied. Primary periods were based on
191 each season of the year: winter (January–March), spring (April–June), summer (July–September) and
192 autumn (October–December). Secondary periods were based on the minimum number of photographic
193 identification surveys necessary to monitor the entire study area and were completed within the shortest
194 time possible (weather dependent; Smith *et al.* 2013). Nine primary periods (seasons of the year) and
195 22 secondary periods were included in the robust design models. There were two or three secondary
196 periods within each primary period. The time taken to complete secondary periods was weather
197 dependent and averaged 23 ± 2 days (range 7–40 days) because of logistical reasons and weather
198 conditions.

199 *Model assumptions*

200 Several assumptions need to be satisfied in order to obtain unbiased estimates with robust capture–
201 recapture models, as detailed below.

- 202 1. Marks are unique, they cannot disappear and there are no misidentifications. To ensure this
203 assumption, unique and evident nicks were used to identify ‘well-marked’ and ‘marked’ adult
204 bottlenose dolphins, and digital photographs were double-checked by experienced researchers and
205 posteriorly confirmed using matching software. Although marks are cumulative over time, which

206 makes it difficult to match individuals if they acquire new marks or the marks change over time
207 (Yoshizaki *et al.* 2009), the continuity and extension of our photographic identification work allowed
208 us to register minor changes on the dorsal fins of individuals. The time between two primary sampling
209 periods did not exceed 89 days, allowing for the identification of new marks in the dorsal fin (range
210 7–89 days; mean 31 days).

211 2. All individuals have equal probability of being captured within a sampling occasion. To ensure this
212 assumption, attempts were made to photograph both sides of the dorsal fin of every dolphin during
213 each encounter, and only ‘excellent-quality’ photographs were used in analyses. In addition, during
214 dolphin encounters, explicit effort was made to photograph all the animals present, despite their
215 markings, proximity to the boat or individual behaviour. Moreover, Pollock’s robust design allows
216 for heterogeneity of capture probabilities because the secondary sampling periods occur close
217 together (Williams *et al.* 2002).

218 3. There is no behavioural response to the capture (i.e. no trap response). Boat-based photographic
219 identification surveys did not induce significant behavioural changes or stress to the animals being
220 studied. Moreover, the studied bottlenose dolphins are well habituated to human presence (marine
221 traffic, aquaculture and fishing activities).

222 4. All individuals have equal probability of survival. To ensure this assumption, only adult bottlenose
223 dolphins were included in mark–recapture analyses. The presence of transient individuals is
224 commonly reported in cetacean studies based on photographic identification data (Silva *et al.* 2009;
225 Speakman *et al.* 2010). Ignoring the presence of transients can produce negatively biased survival
226 estimates because transients do not return to the study area (Hines *et al.* 2003). Program U-Care
227 (Choquet *et al.* 2005) was used to test and confirm the presence of transient individuals. The data
228 were adjusted for transience following an ad hoc approach (Hines *et al.* 2003) by relying on
229 individuals captured in more than one secondary period to provide direct estimates of survival rate
230 for residents. The ad hoc approach yields unbiased estimated pertaining to residents (Pradel *et al.*
231 1997; Hines *et al.* 2003).

232 5. The sampling interval for a particular secondary sample is instantaneous. To ensure this
233 assumption, secondary periods were completed within the shortest period of time possible.

234 6. The population is closed within primary periods. To ensure this assumption, primary periods were
235 structured as seasons of the year rather than years. Moreover, because bottlenose dolphins are long-
236 lived animals and the sampling period in the present study was short, demographic closure can be
237 assumed. Furthermore, the CloseTest program (Stanley and Burnham 1999) was used to investigate
238 population closure. Closure tests indicated population closure during all primary seasons (Stanley
239 and Burnham closure test, $\chi^2 = 15.29$, d.f. = 12, $P = 0.23$; Otis closure test, z -value = 1.91, $P = 0.97$).

240 7. Captures are independent between individuals. This assumption may have been violated, which is
241 a common characteristic of dolphin mark–recapture data, because most bottlenose dolphin
242 populations show non-random social preferences (Connor *et al.* 2000; Díaz López and Shirai 2008;
243 Nicholson *et al.* 2012). This potential violation may cause an extra binomial variation, which is
244 unlikely to cause a bias in the estimates obtained in the present study; however, standard errors are
245 likely to be underestimated to some extent (Williams *et al.* 2002).

246 *Modelling procedures and model selection*

247 Mark–recapture analysis was conducted using the MARK version 8.1 (White and Burnham 1999).
248 Data were analysed by Pollock’s robust design model (Pollock 1982; Kendall *et al.* 1997). Closed
249 captures and parameters were adjusted within the parameter index matrix (PIM) available in MARK.
250 Estimated parameters within sampling periods included the abundance of distinctly marked adult
251 individuals in the study area (\hat{N}), the probability of first capture (p) and the probability of recapture
252 (c). Because capture should not affect recapture when using photographic identification methods
253 adequately (Würsig and Jefferson 1990), robust models with a behavioural response were not fitted to
254 the data. Therefore, p was set to equal c in all models. Estimated parameters between sampling periods
255 included the probability of apparent survival (ϕ) and two temporary emigration parameters (γ' and γ'' ;
256 Kendall *et al.* 1997); ϕ is defined as the probability that a bottlenose dolphin survives and stays in the
257 study area scaled on a seasonal basis, γ' is defined as the probability of an individual being a temporary
258 emigrant if the individual was absent in the previous sampling period and γ'' is defined as the probability
259 of an individual being a temporary emigrant if the individual was present in the previous sampling
260 period (Kendall *et al.* 1997).

261 A combination of different robust models, where parameters were either constant or were allowed to
262 vary with time, were fitted for different temporary emigration patterns to look for a more parsimonious
263 model. The models were no movement ($\gamma'' = 0, \gamma' = 1$), no temporary emigration ($\gamma'' = \gamma' = 0$), random
264 emigration ($\gamma'' = \gamma'$) or Markovian emigration ($\gamma' \neq \gamma''$), as described in Kendall *et al.* (1997). A ‘no
265 movement’ model assumes that unobservable individual bottlenose dolphins remain unobservable and
266 that observable individuals always remain observable over all sampling occasions. No temporary
267 emigration assumes that there is no temporary emigration at all. The random emigration model assumes
268 that an identified bottlenose dolphin emigrates out of the study area independent of whether or not it
269 was present in the study area in the previous sampling period. The Markovian emigration model permits
270 unequal emigration and immigration rates across sampling periods, assuming that bottlenose dolphins
271 return to the study area based on a time-dependent function (Pine *et al.* 2003). When models contained
272 time-varying survival, constraints were placed (i.e. $\gamma''_k = \gamma''_{k-1}, \gamma'_k = \gamma'_{k-1}$), so that all parameters could
273 be identified (Kendall *et al.* 1997). Capture probability was modelled as time varying over primary
274 periods because environmental conditions were not constant over the duration of the study.

275 Furthermore, capture probability was modelled as either constant within primary periods ($p = c(t,.)$) or
276 varying by secondary periods within primary periods ($p = c(t)$). Heterogeneity in capture probabilities
277 was fitted to the data using mixture models with two mixtures of capture probability (Pledger 2000)
278 only in models with no emigration because full-likelihood estimators have not yet been developed for
279 temporary emigration models (Kendall *et al.* 1997).

280 There is no goodness-of-fit test for robust design models in MARK (White and Burnham 1999), so
281 the overall model fit could not be evaluated and the models were not adjusted for overdispersion. The
282 best fitting model was selected based on the lowest Akaike's information criterion corrected for small
283 sample size (AICc; Burnham and Anderson 2004. Likelihood ratio tests (LRTs) were used to test for
284 significant differences between nested models.

285 *Total population size*

286 Abundance estimates from the robust design models are based solely on the number of distinctly
287 marked adult individuals ('well-marked' and 'marked' individuals). To obtain the total population size,
288 \hat{N}_t , the estimated abundance of distinctly marked adult individuals (Nm) was divided by the estimated
289 proportion of distinctly marked adult individuals ($\hat{\theta}$) for each primary period (Wilson *et al.* 1999). To
290 calculate $\hat{\theta}$, the number of distinctly marked adult individuals was divided by the total number of adult
291 individuals observed in each group (including 'poorly marked' and 'unmarked' adults), averaged over
292 all encounters during each season of the year:

$$293 \hat{N}_t = \frac{Nm}{\hat{\theta}}$$

294 For this calculation, we selected only encounters in which all members of the group were photographed.
295 The s.e. and log-normal 95% confidence intervals (CI) of the total population size (\hat{N}_t) were derived
296 using the delta method (Williams *et al.* 2002).

297

298 **Results**

299 *Survey effort, group size and datasets*

300 In all, 170 daily boat-based surveys were completed from March 2014 to June 2016 in the study area
301 (Table 1), with 25 months spent in the field, totalling 517 h and 4285 km.

302 Overall, 386 groups of common bottlenose dolphins (*Tursiops truncatus*) were encountered in 157
303 boat-based surveys (92% of total days at sea) and 309 groups were sampled and photographed (80% of
304 the total number of groups observed). Most encounters (99.7%) were recorded inside the Ría de Arousa
305 (Fig. 1). Group size ranged from 1 to 64 individuals (mean 13.0 ± 0.6 dolphins; median 10 dolphins).

306 Group composition showed that 87.7% of the observed bottlenose dolphins were considered adults;
307 thus, the remaining 12.3% were categorised as dependent calves (11% immature and 1.3% newborn
308 dolphins). Calves were present in 66% of the groups observed. Group size was positively correlated
309 with the presence of dependent calves in the group (Spearman $\rho = 0.64$, $P < 0.001$). Likewise, the
310 number of individuals in the group was significantly higher in the presence of dependent calves (median
311 with and without calves 13 v. 3 respectively; Mann–Whitney, $P < 0.001$).

312 *Relative frequency of occurrence*

313 The mean ER of groups of bottlenose dolphins in the study area was 1.77. The ER did not exhibit
314 any differences between the nine primary sampling periods (Kruskal–Wallis, $P > 0.05$). Similarly,
315 seasonal fluctuations in ER were not observed (when pooled by the four seasons of the year; Kruskal–
316 Wallis, $P > 0.05$).

317 *Photographic identification data*

318 The photographic identification catalogue used in the analysis contained 190 distinctly marked adult
319 bottlenose dolphins. Of these, 57 were documented as female (30%), 40 were documented as male
320 (21%) and 93 (49%) were of unknown sex. The proportion of distinctly marked adult bottlenose
321 dolphins within each primary period ranged between 0.68 and 0.92 (mean 0.77 ± 0.01), exerting a
322 moderate effect on the total abundance estimate. The number of encounters with identified individual
323 bottlenose dolphins ranged from 1 to 101 (mean 16 ± 2) across the duration of the study. The number
324 of primary sampling periods an identified individual bottlenose dolphin was photographed ranged from
325 1 to 9 (mean 3.6 ± 0.2). The number of encounters fluctuated across secondary sampling periods from
326 1 to 21 (mean 6.0 ± 0.4). Overall, 134 bottlenose dolphins (71% of the total catalogue) were identified
327 in more than a single primary sampling period. Of these dolphins, 22 (4 females, 18 males) were
328 identified during all the 9 primary sampling periods and in more than 75% of the secondary sampling
329 periods. Conversely, 49 individuals (26% of the total catalogue) were only seen during a single
330 secondary sampling period. All the individuals sighted during two or more secondary sampling seasons
331 (141 dolphins) were only encountered inside the Ría de Arousa (a 240-km² area). During the study,
332 only two groups of bottlenose dolphins were encountered outside the Ría de Arousa and included
333 individuals that have never been recaptured (three identified individuals).

334 *Robust design model selection*

335 The best-fitting model, determined by the lowest AICc value, showed a constant apparent survival
336 rate (rather than varying with time), seasonal Markovian temporary emigration (with time variation in
337 emigration parameters γ'' and γ') and a different capture probability for each primary and secondary
338 sampling occasion (Table 2). The LRT rejected the models with no movement, no emigration, random
339 emigration, mixture proportion, Markovian emigration with variable survival rate and Markovian

340 emigration with constant probability of capture in favour of the first model with a Markovian emigration
341 process and constant apparent survival rate (Chi-Square, $P < 0.001$).

342 *Abundance estimation*

343 For the best-fitting model, the estimated seasonal abundance of Nm varied between a minimum of
344 46 (95% CI 45.2–54.6) in spring 2015 and a maximum of 122 (95% CI 113.1–140.7) in winter 2015.
345 The $\hat{N}t$ ranged from 56 (95% CI 55.2–66.4) in autumn 2014 to 144 (95% CI 133.1–165.6) in winter
346 2015 (Table 3). Bottlenose dolphin abundance estimates were not significantly related to the ER
347 (Spearman ρ , $P > 0.05$). Seasonal changes in abundance were most evident (+155%) between autumn
348 2014 (56 dolphins) and winter 2015 (144 dolphins) and between winter 2015 and spring 2015 (–60%).

349 *Survival rates, temporal emigration patterns and capture probabilities*

350 The model that best fitted the data gave a constant apparent survival rate of 1.0 ± 0.0 . Temporary
351 emigration rates were higher from summer to autumn and lower from autumn to winter. The probability
352 of being a temporary emigrant if the individual bottlenose dolphin was absent in the previous season
353 (γ') was high, with a mean value of 0.68 ± 0.12 . Conversely, the probability of being a temporary
354 emigrant if the individual bottlenose dolphin was present in the previous season (γ'') was low, with a
355 mean of 0.23 ± 0.07 (Table 4). Mean capture probabilities among seasons were moderate (0.65 ± 0.03),
356 with the highest obtained in spring 2015 (0.80 ± 0.02) and the lowest during spring 2016 (0.56 ± 0.09).
357 Temporal emigration rates (γ' and γ'') and capture probabilities did not show significant differences
358 between seasons (Kruskal–Wallis, $P > 0.05$).

359 **Discussion**

360 This study presents the first robust estimates of abundance and demographic parameters of resident
361 common bottlenose dolphins (*T. truncatus*) in a highly affected coastal ecosystem along the north-
362 eastern Atlantic. Further, these results provide baseline information for future comparisons with other
363 populations of similar characteristics under the pressure of human activities (i.e. marine traffic, fisheries
364 and aquaculture), which may become of increasing importance as anthropogenic activities affect coastal
365 dolphin populations.

366 Bottlenose dolphins are present year-round and with a high degree of occurrence inside the Ría de
367 Arousa, an area highly affected by human activities, but also a highly productive estuarine system. This
368 area not only produces an important amount of commercially valuable shellfish as a result of the
369 aquaculture industry (Rodríguez *et al.* 2011), but the epifaunal community associated with the shellfish
370 production also supports the substantial production of fish and megabenthos compared with other
371 coastal and estuarine areas (Chesney and Iglesias 1979). Similar abundance estimates in terms of the
372 number of individuals present have been obtained in other studies, performed using mark–recapture
373 methods rather than the robust design model, of north-east Atlantic bottlenose dolphin populations

374 living in rich coastal environments, such as Moray Firth, Scotland (Wilson *et al.* 1999) and the Shannon
375 Estuary, Ireland (Berrow *et al.* 2012).

376 This study reports seasonal fluctuations in abundance as observed in other bottlenose dolphin
377 populations (Smith *et al.* 2013; Sprogis *et al.* 2016). Although there may be different factors playing a
378 key role in bottlenose dolphin distribution to some extent, the observed changes in abundance and
379 emigration rates most likely reflect seasonal fluctuations in the abundance of prey species in this area.
380 Bottlenose dolphins in Galicia eat a wide range of demersal fish species (Santos *et al.* 2007). These fish
381 species are a resident component of the Ría de Arousa (Fariña *et al.* 1997) and a possible explanation
382 for the estimates of bottlenose dolphin abundance and observed large group size compared with other
383 coastal populations (Bearzi *et al.* 1997; Díaz López *et al.* 2013; Santostasi *et al.* 2016). Thus, the winter
384 season, with the highest abundance and lowest emigration rates of bottlenose dolphins observed in this
385 study, is characterised by a peak in numbers of demersal fish species inside the Ría de Arousa (Chesney
386 and Iglesias 1979). Moreover, the derived return rate ($1 - \gamma'$) of temporary emigrants (Sprogis *et al.*
387 2016) indicated that bottlenose dolphins had a high probability of returning to the Ría de Arousa from
388 autumn to winter.

389 The estimated apparent survival rate is high and constant, suggesting no mortality and no permanent
390 emigration of individuals during the duration of the study. These results are common for long-lived
391 species with slow growth rates and low fecundity, and have been reported in other bottlenose dolphin
392 populations (Nicholson *et al.* 2012; Sprogis *et al.* 2016).

393 The results of the present study show seasonal fluctuations in the temporary emigration rates.
394 Temporary emigration rates for dolphins that were absent in the previous period were higher (0.38–
395 0.89) than those for dolphins that were present (0.08–0.37), suggesting different levels of site fidelity.
396 Some individuals (22 males, 4 females) showed a strong preference for the study area (being present in
397 all primary periods), so there is a core of resident bottlenose dolphins in the Ría de Arousa with some
398 other dolphins coming in and out of the study area for different periods of time. The age and sex of each
399 individual, as well as its ecological and social preferences, could explain the differences in the residence
400 patterns observed (Bearzi *et al.* 1997). In these waters, resident males may have a smaller home range
401 than females, showing a stronger site fidelity to the Ría de Arousa. Different reasons could help explain
402 the observed differences in site fidelity, such as different tolerances to human disturbance or different
403 prey preferences. The latter is supported by a study about the diet of bottlenose dolphins in the region
404 that indicated differences in diet between males and females (Santos *et al.* 2007). In contrast with other
405 areas where females stay in sheltered waters for protection from predation, showing strong site fidelity
406 (Nicholson *et al.* 2012; Smith *et al.* 2013), the absence of natural predators in the present study area
407 may not constrain females to a small home range. Moreover, area defence by individuals or social

408 groups could also help explain the observed differences in site fidelity and temporal occurrence rates
409 observed in the present compared with other studies (Díaz López 2012).

410 Previous studies of wild populations of dolphins have documented avoidance of highly affected
411 ecosystems where humans are present (Dawson and Slooten 1993; Bejder *et al.* 2006; Bearzi *et al.*
412 2009, 2008a, 2008b; Rako *et al.* 2013), although others have reported continued use of valuable habitat
413 areas despite high levels of human disturbance (Ingram and Rogan 2002; Bearzi *et al.* 2008b; Díaz
414 López 2012). In highly affected and highly productive coastal ecosystems, like the Ría de Arousa, where
415 human impact levels are consistently high primarily due to fisheries and aquaculture activities, some
416 bottlenose dolphins may have become habituated to these predictable disturbance levels and continued
417 to use this affected, but rich, habitat. Indeed, previous studies in the Ría de Arousa reported a
418 relationship between the occurrence of bottlenose dolphins and mussel aquaculture zones as a result of
419 higher densities of higher-quality prey for dolphins than in areas outside the mussel farm zones (Díaz
420 López and Methion 2017).

421 The presence of bottlenose dolphins in the Ría de Arousa should not be assumed to mean that human
422 disturbance has no effect on these bottlenose dolphins. The effects of human activities on bottlenose
423 dolphins could differ between individuals because of individual variability in site fidelity. Future
424 research that compares home range, social structure and reproductive success of bottlenose dolphins
425 would help reveal individual-level effects of human disturbance, should they exist.

426 **Conflicts of interest**

427 The authors declare that they have no conflicts of interest.

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605 **Table 1. Annual observation effort, robust design periods, bottlenose dolphin encounters, encounter ratio and the number of bottlenose dolphins**
 606 **identified included in the mark–recapture analysis**

607 The encounter ratio (ER) was calculated by dividing the total number of encounters by the total number of hours spent searching for dolphins

Year	Robust design		Months	Observation effort			Number of group encounters	ER	Number of bottlenose dolphins identified
	Number of primary periods	Number of secondary periods		Days	Hours	Kilometres			
2014	3	8	9	67	217	1625	139	1.47	119
2015	4	9	10	63	191	1646	151	1.88	137
2016	2	5	6	40	109	1014	96	2.20	129
Total	9	22	25	170	517	4285	386	1.77	190

608 **Table 2. Capture–recapture models fitted to the capture histories of bottlenose dolphins to estimate parameters for population size (\hat{N}), apparent**
 609 **survival (ϕ), emigration probabilities (γ'' , γ') and capture probability (p)**

610 The notation ‘(.)’ indicates that a given parameter was kept constant and ‘(t)’ indicates that a given parameter was allowed to vary with time. Emigration
 611 pattern notations follow [Kendall *et al.* \(1997\)](#). c , recapture probability; γ' , probability of an individual being a temporary emigrant if the individual was absent
 612 in the previous sampling period; γ'' , probability of an individual being a temporary emigrant if the individual was present in the previous sampling period; p_i ,
 613 mixture proportion; AICc, Akaike’s information criterion corrected for small sample size

Rank	Model	Emigration pattern	AICc	Δ AICc	Model likelihood	AICc weight	Parameters	Deviance
1	$\phi(\cdot), \gamma'(t) \neq \gamma''(t), p(t) = c(t)$	Markovian	-1447.2	0.00	1.0000	0.999	47	1524.0
2	$\phi(t), \gamma'(t) \neq \gamma''(t), p(t) = c(t)$	Markovian	-1432.6	14.6	0.0007	0.001	52	1527.6
3	$\phi(\cdot), \gamma'(t) \neq \gamma''(t), p(t, \cdot) = c(t, \cdot)$	Markovian	-1378.1	69.1	0.0000	0.000	34	1621.2
4	$\phi(t), \gamma'(t) \neq \gamma''(t), p(t, \cdot) = c(t, \cdot)$	Markovian	-1361.3	85.8	0.0000	0.000	38	1629.4
5	$\phi(t), \gamma'(t) = \gamma''(t), p(t) = c(t)$	Random	-1328.9	118.3	0.0000	0.000	46	1644.5
6	$\phi(\cdot), \gamma'(t) = \gamma''(t), p(t) = c(t)$	Random	-1321.3	125.9	0.0000	0.000	40	1665.1
7	$\phi(t), \gamma' = \gamma'' = 0, p_i(t), p(t)$	No emigration	-1312.7	134.4	0.0000	0.000	38	1678.0
8	$\phi(t), \gamma' = \gamma'' = 0, p_i(\cdot), p(t)$	No emigration	-1293.0	154.2	0.0000	0.000	36	1702.0
9	$\phi(t), \gamma'(t) = \gamma''(t), p(t, \cdot) = c(t, \cdot)$	Random	-1259.9	187.3	0.0000	0.000	33	1741.5
10	$\phi(\cdot), \gamma'(t) = \gamma''(t), p(t, \cdot) = c(t, \cdot)$	Random	-1252.8	194.4	0.0000	0.000	27	1761.3
11	$\phi(t), \gamma' = \gamma'' = 0, p(t) = c(t)$	No emigration	-1112.9	334.3	0.0000	0.000	39	1875.6

12	$\phi(t), \gamma' = 1, \gamma'' = 0, p(t) = c(t)$	No movement	-1112.9	334.3	0.0000	0.000	39	1875.6
13	$\phi(\cdot), \gamma' = 1, \gamma'' = 0, p(t) = c(t)$	No movement	-1092.7	354.5	0.0000	0.000	32	1910.8
14	$\phi(\cdot), \gamma' = \gamma'' = 0, p(t) = c(t)$	No emigration	-1092.7	354.5	0.0000	0.000	32	1910.8
15	$\phi(t), \gamma' = 1, \gamma'' = 0, p(t, \cdot) = c(t, \cdot)$	No movement	-1069.2	377.2	0.0000	0.000	26	1947.0
16	$\phi(t), \gamma' = \gamma'' = 0, p(t, \cdot) = c(t, \cdot)$	No emigration	-1069.2	377.9	0.0000	0.000	26	1947.0
17	$\phi(\cdot), \gamma' = 1, \gamma'' = 0, p(t, \cdot) = c(t, \cdot)$	No movement	-1048.9	398.3	0.0000	0.000	19	1981.9
18	$\phi(\cdot), \gamma' = \gamma'' = 0, p(t, \cdot) = c(t, \cdot)$	No emigration	-1048.9	398.3	0.0000	0.000	19	1981.9

614

615 **Table 3. Seasonal abundance estimates of bottlenose dolphins in the study area**

616 \hat{N} , estimation of the marked population; $\hat{\theta}$, proportion of distinctly marked adult individuals; \hat{N}_t ,
 617 total population size; CI, confidence interval

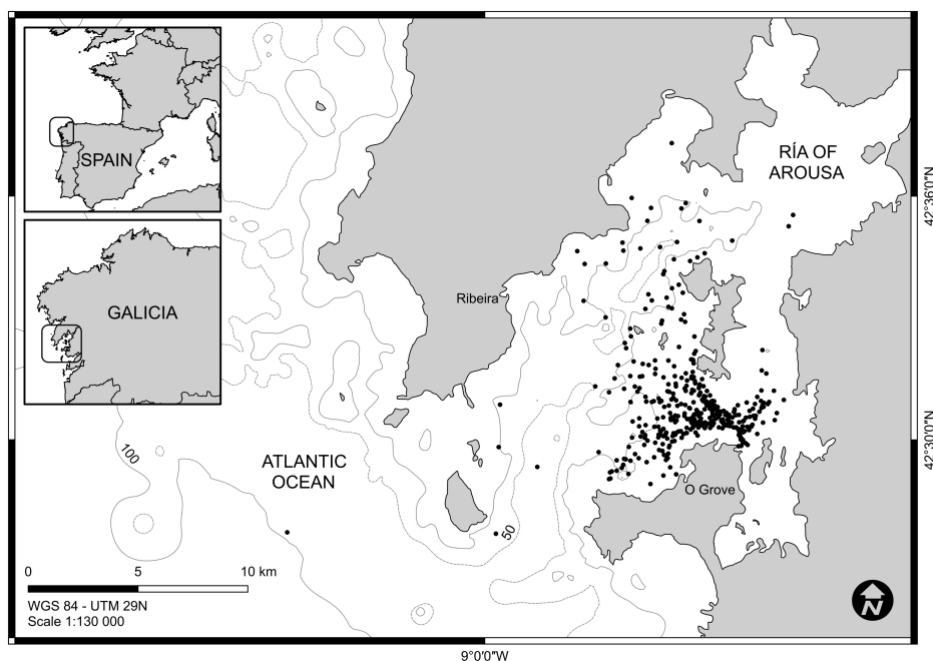
Year	Season	Number of dolphins identified	\hat{N}	s.e.	$\hat{\theta}$	\hat{N}_t	95% CI
2014	Spring	73	76	2.8	0.68	111	107–125
	Summer	100	85	3.0	0.69	123	118–138
	Autumn	37	50	1.8	0.89	56	55–66
2015	Winter	115	122	6.7	0.85	144	133–166
	Spring	46	46	1.8	0.81	57	56–67
	Summer	82	68	1.2	0.88	77	76–84
2016	Autumn	40	61	3.5	0.92	66	62–78
	Winter	84	87	3.3	0.75	116	110–130
	Spring	114	110	4.0	0.79	139	133–153

618 **Table 4. Mean seasonal temporary emigration rates for the best fitting Markovian model**

619 Data are the mean \pm s.e. γ' , probability of an individual being a temporary emigrant if the individual
 620 was absent in the previous sampling period; γ'' , probability of an individual being a temporary
 621 emigrant if the individual was present in the previous sampling period

Season	Temporary emigration rates	
	γ'	γ''
Winter–spring	0.73 \pm 0.27	0.34 \pm 0.26
Spring–summer	0.75 \pm 0.00	0.14 \pm 0.08
Summer–autumn	0.89 \pm 0.04	0.37 \pm 0.08
Autumn–winter	0.38 \pm 0.28	0.08 \pm 0.04
Overall	0.68 \pm 0.12	0.23 \pm 0.07

622 **Fig. 1.** Map of the study area (Ría de Arousa and surrounding waters, north-west Spain) including the 50 and
 623 100 isobaths. Bottlenose dolphin encounters are indicated by filled circles.



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