

1 **"Hot deals at sea": responses of a top predator (Bottlenose dolphin, *Tursiops***
2 ***truncatus*) to human-induced changes in the coastal ecosystem.**

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7 Running title: Bottlenose dolphin responses to human activities

8

9 Abstract

10 The main response of top predators to human-induced environmental changes is often
11 behavioural. Although human activities regularly impose a disturbance on top predators, they
12 can also be a source of reliable and concentrated food resources for species with a high degree
13 of behavioural plasticity. This study represents the first assessment of the influence of these
14 resources on migratory patterns and social interaction of a marine top predator, the common
15 bottlenose dolphin, *Tursiops truncatus*. Pollock's closed robust design models and association
16 analyses were applied to data collected over nine consecutive years of research in a coastal
17 area subject to significant use and pressure by humans. Photo-identification data were
18 collected year-round during 955 boat-based surveys, resulting in 1 638 common bottlenose
19 dolphin group encounters. Results of this study revealed a significant upward trend in density
20 of bottlenose dolphins, preferences for a coastal area with higher human pressure, and a
21 reduction of the social interactions associated to a temporal switch to the food sources
22 provided by human activities. The observed link between human activities and changes in
23 common bottlenose dolphin behaviour aim to contribute to a better understanding of the
24 ecology of a marine top predator and provide some of the needed baseline data, from which
25 effective management and conservation strategies can be designed.

26

27 Keywords

28 Coastal ecosystem; Marine top predators; *Tursiops truncatus*; Habitat management;
29 Behaviour; Social structure; Human activities; Mediterranean Sea.

30

31 INTRODUCTION

32 Anthropogenic activities are responsible for significant modifications in the marine
33 environment at an unprecedented rate and scale over the last few decades (Crain et al. 2008,
34 Halpern et al. 2008). These human-induced changes in the environment have the potential to
35 impact species up and down the marine food web (Maxwell et al. 2013). Likewise, the
36 temporal and spatial scales at which marine top predators respond to these changes affect
37 both ecological function and conservation planning (Walker et al. 2005, Bedjer et al. 2006,
38 Rolland et al. 2008).

39 While top predators are critical components of marine ecosystems (Zacharias and Roff 2001)
40 they are affected by a variety of human activities including fisheries (DeMaster et al. 2001,
41 Read et al., 2006), aquaculture (Würsig and Gailey 2002, Callier et al. 2017), pollution (Tanabe
42 2002), marine traffic (Tyack 2008), global warming (Harley et al. 2006, Simmonds and Isaac
43 2007), and habitat modification (Lotze et al. 2006). The literature on ecology of marine top
44 predators suggests that, the long-term exposure to human activities should be associated with
45 decreased local population density (Bedjer et al. 2006, Roland et al. 2008, Ferretti et al. 2013).
46 However, effects of human-induced disturbance may vary considerably among species and
47 over a species range (Ansmann et al. 2012). In this regard, accurate assessments of temporal
48 changes in migratory patterns and social interaction of marine top predators are integral
49 components of the information needed to identify and describe potential impacts of
50 anthropogenic activities.

51 Having a near-shore and behavioural plasticity, the common bottlenose dolphin *Tursiops*
52 *truncatus* (Montagu 1821), hereafter bottlenose dolphin, has often been reported to exploit
53 anthropogenic food sources (Corkeron et al. 1990, Fertl and Leatherwood 1997, Pace et al.
54 1999, Svane 2005, Díaz López 2006a, 2012). However, although diet (Santos et al. 2007),
55 habitat use (Svane 2005, Díaz López 2012), and social structure (Díaz López and Shirai 2008,
56 Ansmann et al. 2012) have been associated with access to anthropogenic resources, the
57 prolonged influence of these resources on migratory patterns and social interactions has so far
58 received limited attention. The lack of this significant information hampers our ability to
59 evaluate the impact of anthropogenic activities on this potentially vulnerable marine top
60 predator (DeMaster et al. 2001, Bearzi et al. 2008). These data deficiencies are remarkable in
61 the Mediterranean Sea, where the bottlenose dolphin is widely distributed with fragmented
62 populations and is thought to be declining in numbers (Natoli et al. 2005, Bearzi et al. 2008,
63 Gnone et al. 2011).

64 In light of the above considerations, I applied Pollock's closed robust design models and
65 association analyses to photo-identification data collected over nine consecutive years of
66 research of bottlenose dolphins along the North-eastern coast of Sardinia, Tyrrhenian Sea
67 (Italy). Bottlenose dolphins have been studied in this coastal area for three decades with a
68 strong focus on the interaction with gill-net fisheries (Díaz López 2006a) and marine
69 aquaculture (Díaz López et al. 2005, Díaz López 2006b, Díaz López and Shirai 2007, 2008, Díaz
70 López 2009, 2012, 2017). Despite many studies available in the literature, there is a lack of
71 long-term and exhaustive studies about the influence of human-induced changes on
72 ecosystem on social interaction and migration of bottlenose dolphins. Therefore, the
73 objectives of this study were to present the first assessment of seasonal trends in migratory
74 patterns and social interaction of this species in a coastal area subject to significant use and
75 pressure by humans. Through these analyses, I aimed to further our understanding of the

76 initial behavioural responses of a marine top predator to human-induced environmental
77 changes.

78

79 MATERIALS AND METHODS

80 Study area

81 Data were collected as part of a long-term study of bottlenose dolphins inhabiting the North-
82 eastern coast of Sardinia, Tyrrhenian Sea, Italy (Figure 1). The study area extends
83 approximately 750 square kilometres off the Sardinian coast and approximately 20 km
84 offshore, to a maximum water depth of 200 m. This area is subject to significant use by
85 humans including recreational and professional fisheries, the presence of aquaculture industry
86 (fin-fish and shellfish farms), and highly developed nautical tourism based around five marinas
87 and two important ferry ports (De Luca et al. 2005, Díaz López 2006b, Díaz López et al. 2008,
88 Lodola et al. 2012). The study area was stratified into three different zones to facilitate the
89 geographical location of bottlenose dolphins and to study different sub-areas:

- 90 - 1) The Gulf of Olbia (between 40.918° N 9.503° E and 40.983° N 9.654° E), which is
91 delimited by Figari Cape to the North and Ceraso Cape to the South, is the region that
92 faces the highest pressure from humans, including aquaculture industry and important
93 fishing areas as the ria of Olbia and the Aranci Bay (De Luca et al. 2005, Díaz López
94 2006a, Díaz López et al. 2008);
- 95 - 2) The Gulf of Congianus (between 41.004° N 9.509° E and 41.100° N 9.657° E)
96 including Mortorio, Mortoriotto and surrounding islands as part of the National Park of
97 La Maddalena, comprises several important representative Mediterranean habitats
98 with national and regional significance (La Manna et al. 2015). The anthropogenic
99 pressure in this area is low and concentrated during summer months around three
100 marinas (Marinella, Porto Rotondo, and Portisco);

101 - 3) The third region "Open waters" extended to approximately 20 km offshore
102 (between 40.844° N 9.657° E and 41.147° N 9.889° E), included the Tavolara-Punta
103 Coda Cavallo marine protected area (Ceccherelli et al. 2006), and is the area with
104 lowest marine traffic and anthropogenic activities (Campana et al. 2015).

105 Field methods

106 Boat-based observation surveys were carried out year-round during nine consecutive years
107 from January 2005 to December 2013. The study area was monitored during daylight hours at
108 a constant speed around 6 knots, with at least two experienced observers scanning the sea
109 surface in search of bottlenose dolphins (with the naked eye and/or binoculars, 10x50). The
110 survey area and track were selected based on sea conditions and time constraints on each day,
111 although the geographic distribution of the effort could vary according to weather conditions.
112 Surveys were considered adequate when the visibility was not reduced by fog or rain, and sea
113 conditions were lower than 3 on the Douglas sea force scale (Díaz López 2006a).

114 A hand-held global positioning system (GPS) was used to record the position, and speed of
115 travel (knots). When bottlenose dolphins were encountered, searching effort (on-effort)
116 concluded and the vessel slowly manoeuvred towards the bottlenose dolphins to photograph
117 the dorsal fin of every individual present in the group. A suite of data including, the initial time,
118 location, the group size, and group composition were recorded for each bottlenose dolphin
119 group encounter. Digital photographs were taken using DSLR cameras equipped with 100-300
120 mm telephoto zoom lens. Group size and composition were assessed based on the initial count
121 of different individuals observed at one time in the area. Adult bottlenose dolphins were fully
122 grown (length >2.5 m) marked or unmarked animals. Sex was determined primarily by
123 observations and photographs of the genital region. After the end of an encounter, the
124 searching effort generally continued along the previously planned route.

125 The behavioural state of the group was collected using focal group continuous sampling
126 (Altmann 1974, Mann et al. 2000). A predominant activity was determined by the behaviour
127 performed by the focal group for at least 50% of the duration of the sighting. The definition of
128 each behavioural pattern was based on objective and non-discrete parameters following Díaz
129 López (2006a). The sighting continued until the focal group changed composition or was lost; a
130 group was considered lost after 15 min without a sighting (Díaz López 2006a, 2012).

131 Data processing and analysis

132 *Analysis of photographs*

133 Bottlenose dolphins were identified by using photographs of both sides of their dorsal fins and
134 surrounding area as unique natural markers (Würsig and Jefferson 1990). All photographs of
135 the dorsal fin of every adult bottlenose dolphin identified were graded for quality and degree
136 of distinctiveness in order to minimise both misidentification and heterogeneity in capture
137 probabilities (Urian et al. 2015). Accordingly, all photographs were given an absolute value
138 score (1 low, 4 average, and 10 high) for: (1) perpendicular angle of the dorsal fin to the
139 camera; (2) the focus of the photograph; (3) contrast and light intensity; and (4) whether the
140 dorsal fin was suitably sized in the frame for all notches to be clearly visible (Smith et al. 2013).
141 The individual scores for each category were summed to obtain a global quality score. Global
142 quality scores from 4 to 16 were considered poor quality, from 16 to 25 average quality, and
143 from 25 excellent quality. To ensure the correct identification only excellent quality
144 photographs were used for mark-recapture analysis.

145 Additionally, each identified adult bottlenose dolphin was included in a distinctiveness
146 category, based on the amount of information contained on the dorsal fin and to ensure that
147 more distinctly marked individuals would not have a higher probability of being identified
148 (following Díaz López et al. 2017). (1) A "well-marked individual" was considered one adult
149 bottlenose dolphin that is recognized not by a single large feature in the dorsal fin, but also by

150 a matrix of evident notches. (2) A "marked individual" was considered one adult bottlenose
151 dolphin with distinct dorsal fin with an average amount of information (i.e. a single large notch
152 and several small ones). (3) A "poorly marked individual" was considered one identified adult
153 bottlenose dolphin with dorsal fin with small amount of information (i.e. a small notch, dorsal
154 fin scars and tooth-rakings). Since body and dorsal fin scars, marks, and decolouration are not
155 necessarily permanent and not easily identifiable, individuals with absence of marks on the
156 dorsal fin "unmarked" and "poorly marked individuals" were not included for further mark-
157 recapture analysis.

158 Every photograph was reviewed for false positives and false negatives, and the identification of
159 the individuals was confirmed by two experienced observers. Capture histories, corresponding
160 to whether or not an adult bottlenose dolphin was photo-identified within a sampling period,
161 were compiled for each individual.

162 *Occurrence patterns*

163 For spatial analysis all 9 years of survey data were included into a geographic information
164 system (GIS) using the software QGIS (<http://www.qgis.org>). The study area was divided into 1
165 nm² cells by creating a polygon grid and the number of times the research vessel crossed each
166 cell searching for dolphins (on-effort) was used to summarize the distribution of the survey
167 effort irrespective of dolphins' presence. Thus, in order to minimise bias from uneven
168 allocation of survey effort in space a relative index defined as Sighting per Unit of Effort (SPUE)
169 was calculated as:

$$170 \quad SPUE = \frac{Ec}{Sc}$$

171 Where, Ec is the number of bottlenose dolphin encounters in each cell of the grid and Sc is the
172 total number of surveys on-effort monitoring each cell. By calculating $SPUE$ we reduced effort-
173 related bias from derived distribution patterns arising from an uneven survey effort, caused by
174 time and weather restrictions.

175 *Association patterns and predominant behaviour*

176 Association analysis were carried out using the compiled version of SOCPROG 2.6 (Whitehead
177 2009). For the analysis of association patterns, all adult bottlenose dolphins identified within
178 the same group during a single day were considered associated (Díaz López and Shirai 2008).
179 The half weight index (HWI, Cairns and Schwager 1987), the sum of all associations (which is
180 similar to the "typical group size", Jarman 1974), and the maximum HWI, were calculated for
181 each adult individual, as well as for overall encounters carried out during each season of the
182 year (a three-months period). The HWI for overall encounters was used as a measure of the
183 strength of their social interactions among seasons. The HWI yields a number between 0, for
184 two individuals that never co-occur in the same focal group, to 1, for two individuals that are
185 always found together (Cairns and Schwager 1987).

186 A contingency table analysis (based on the chi-square test) was used to determine the
187 predominant behaviours across the different areas monitored.

188 *Mark-recapture abundance models*

189 A Pollock's robust design model (Pollock 1982) was applied to estimate abundance, temporal
190 emigration and survival rates. The Pollock's robust design combines open sampling events
191 (named "primary periods"), within which are multiple closed events (named "secondary
192 periods") (Kendall et al. 1997). This design considers the possibility that bottlenose dolphins
193 may temporarily emigrate and then return, unlike typical open models, which do not allow for
194 temporary emigration (Kendall et al. 1997). In this study primary periods were based on each
195 season of the year: Winter (January to March), Spring (April to June), Summer (July to
196 September), and Autumn (October to December). While the secondary periods were based on
197 the number of photo-identification surveys necessary to monitor the three zones of the study
198 area. The number of days within secondary sampling periods varied and the intervals between
199 secondary periods also varied.

200 Data were analysed with the software MARK program version 8.1 (White and Burnham 1999)
201 via the Pollock's robust design model with closed captures. Estimated parameters within
202 sampling periods included the abundance of marked individuals in the study area (\hat{N}),
203 probability of first capture (p), and probability of recapture (c). Recapture probability (c) was
204 set to equal capture probability (p) in all the models because capture should not affect
205 recapture when using photo-identification methods adequately. Models with constant capture
206 probability were not fitted to the data, because environmental conditions and distribution of
207 the effort were not constant over the sampling periods and, therefore, the probability of
208 capture varied among them. Estimated parameters between sampling periods included the
209 probability of apparent survival (ϕ) and two temporary emigration parameters (γ' and γ'').
210 Following Kendall et al. (1997): ϕ is defined as the probability that a dolphin survives and stays
211 in the study area scaled on a seasonal basis; γ' is defined as the probability of an individual
212 being a temporary emigrant, given it was absent in the previous sampling period, and γ'' is
213 defined as the probability of an individual being a temporary emigrant, given it was present in
214 the previous sampling period.

215 Combinations of robust models, where parameters were either constant or were allowed to
216 vary with time, were fitted for different temporary emigration patterns to look for a more
217 parsimonious model (Kendall et al. 1997):

- 218 - No movement model ($\gamma'' = 0$, $\gamma' = 1$) assumes that unobservable individuals remain
219 unobservable and that observable individuals always remain observable over all
220 sampling occasions.
- 221 - No temporary emigration model ($\gamma'' = \gamma' = 0$) assumes that there is no temporary
222 emigration at all.

223 - Random emigration model ($\gamma'' = \gamma'$) assumes that an identified dolphin emigrates out of
224 the study area for just one sampling occasion and then always comes back but can
225 emigrate again randomly.

226 - The Markovian emigration model ($\gamma' \neq \gamma''$) permits unequal emigration and immigration
227 rates across survey periods. This model assumes that an adult bottlenose dolphin
228 returns to the area based on a time-dependent function (Pine et al. 2003).

229 Capture probability was modelled as time varying over primary periods because environmental
230 conditions were not constant over the duration of the study. When models contained time-
231 varying survival, constraints were placed (i.e. $\gamma'_k = \gamma'_{k-1}$, $\gamma''_k = \gamma''_{k-1}$), so that all parameters
232 could be identified (Kendall et al. 1997).

233 There is no goodness-of-fit test for robust design models in MARK (White and Burnham 1999),
234 so the overall model fit could not be evaluated and the models were not adjusted for
235 overdispersion. The best fitting model was selected based on the Akaike's information
236 criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). Thus, the
237 model with the lowest AICc was selected as the most parsimonious. Likelihood-ratio tests
238 (LRTs) were computed to test for significant differences between the different models. Non-
239 parametric tests were used to investigate the equality of medians of quantitative samples.

240 *Total abundance*

241 Abundance estimates from the robust design models are based solely on the number of adult
242 individuals with recognizable marks sighted during a season of the year. To obtain the total
243 abundance ($\hat{N}t$) the estimated abundance from the robust design model ($\hat{N}m$) was divided by
244 the estimated proportion of adult individuals with recognizable marks ($\hat{\theta}$) (Wilson et al., 1999)
245 for each season of the year. To calculate $\hat{\theta}$, the number of adult individuals with recognizable
246 marks was divided by the total number of adult individuals observed in each group (including

247 "poorly marked" and "unmarked" adults), averaged over all encounters during each season of
248 the year.

$$249 \hat{N}t = \frac{\hat{Nm}}{\hat{\theta}}$$

250 Only encounters in which all bottlenose dolphins in the group, regardless of distinctiveness
251 level, were photographed, were used for this calculation. The small group size (average $4.35 \pm$
252 0.1) and in situ verification of digital photographs reduced the chances that adult individuals
253 with recognizable marks and the other dolphins in the group were not determined with
254 certainty. The standard error (*SE*) and log-normal 95% confidence intervals of the total
255 abundance ($\hat{N}t$) were derived using the delta method (Williams et al. 2002).

256 *Detection of temporal trends*

257 Two tests were applied to detect statistically significant temporal trends (Wasmund and Uhlig
258 2003, Díaz López 2017): (i) the rank-based non-parametric Mann–Kendall test for a monotonic
259 downward or upward trend, complemented by the Theil slopes of the linear trend line and (ii)
260 a test based on the non-linear locally weighted polynomial regression (LOESS smoother).

261 *Validation of model assumptions*

262 In order to obtain unbiased estimates from the Pollock's robust design model seven
263 assumptions, derived from both open and closed population models, need to be satisfied
264 (Smith et al. 2013):

- 265 - (1) Marks are not lost, unique and there are no misidentifications. To satisfy this
266 assumption, unique and evident nicks were used to identify "well marked" and
267 "marked" adult bottlenose dolphins, and photographs were reviewed by two
268 experienced researchers. While marks in the dorsal fins are cumulative and change
269 over time (Yoshizaki et al. 2009), the continuity and extension of this photo-
270 identification work allowed to register small and gradual changes in the pattern of
271 marking.

- 272 - (2) All individuals have equal probability of being captured within a sampling occasion.
273 To ensure this assumption, attempts were made to photograph both sides of the
274 dorsal fin of every dolphin present in the group, and only "excellent quality"
275 photographs were used in mark-recapture analyses. In addition, during dolphin
276 encounters, explicit effort was made to photograph all the animals present, despite
277 their markings, proximity to the boat, or individual behaviour. Moreover, the Pollock's
278 robust design allows for heterogeneity of capture probabilities because the secondary
279 sampling periods occur close together (Smith et al. 2013).
- 280 - (3) No behavioural response to the capture. Photo-identification technique did not
281 induce significant behavioural changes or stress to the animals being studied (Würsig
282 and Jefferson 1990). Moreover, the studied bottlenose dolphins are well habituated to
283 human presence (Díaz López 2006a, Díaz López 2012).
- 284 - (4) All individuals have equal probability of survival. Previous studies in the area
285 showed that the mortality of calves, as a consequence of incidental capture on gillnets,
286 is higher than the mortality of adults (Díaz López 2006a). To minimise violation of this
287 assumption, only adult bottlenose dolphins were included in mark-recapture analyses.
- 288 - (5) The sampling interval for a particular secondary sample is instantaneous. To reach
289 instantaneous sampling, secondary periods were completed within the shortest period
290 of time possible.
- 291 - (6) The population is closed within primary periods. To satisfy this assumption, and to
292 study seasonal changes, primary periods were structured as seasons of the year rather
293 than years. The CloseTest program (Stanley and Burnham 1999) was used to ensure
294 population closure during all primary seasons.
- 295 - (7) Captures are independent between individuals. This assumption may have
296 therefore been violated, as some bottlenose dolphins in Sardinia showed non-random

297 social behaviour depending on the feeding activity in which they were engaged (Díaz
298 López and Shirai 2008). Therefore, the probability of capturing an individual may be
299 increased by capturing its close associates (Connor et al. 2000). This potential
300 violation, which is a common characteristic of dolphin mark-recapture data, is unlikely
301 to cause a bias in the estimates obtained in this study (Williams et al. 2002).

302

303 RESULTS

304 Survey effort, group size, and predominant behaviour

305 A total of 955 daily boat-based surveys were completed over the nine consecutive years of
306 research (January 2005 - December 2013) along the North-eastern coast of Sardinia, resulting
307 in 1 638 bottlenose dolphin group encounters (Table 1). In all, 98 months were spent in the
308 field, totaling 3 584 hours (1 421 hours with the groups of dolphins and 2 163 hours searching
309 for dolphins) and 15 330 km.

310 In total, 36 primary periods (consecutive seasons of the year) and 78 secondary periods were
311 included in the robust design models (Table 1). The time taken to complete secondary periods
312 averaged 17.9 ± 0.9 days.

313 Bottlenose dolphins were seen in 794 boat-based surveys (83% of the total) and 1 410 groups
314 were sampled and photographed (86% of the total). Group size ranged from 1 to 19 individuals
315 (mean = 4.43 ± 0.1 dolphins). Most encountered groups (91% of the encounters) contained
316 less than 8 animals. Group composition showed that 79% of the observed bottlenose dolphins
317 were considered adults; thus, the remaining 21% were categorized as dependent calves.

318 A total of 1 300 bottlenose dolphin groups were observed in the Gulf of Olbia, 39 in the Gulf of
319 Congianus, and 71 in Open waters. The bottlenose dolphins were mostly engaging in foraging
320 activities (61 % of the encounters, followed by travelling (26 %), socializing (10 %), and resting
321 (1 %). Sightings were made throughout the study area, but the highest SPUE took place inside

322 of the Gulf of Olbia, predominantly along the inshore waters of Aranci Bay (Figure 1). During
323 the encounters, the bottlenose dolphins did show evident behavioural preferences across the
324 different areas (Contingency table Chi square, $p < 0.001$). Thus, in the Gulf of Olbia the
325 bottlenose dolphins were mostly engaging in foraging activities (69 % of the encounters),
326 followed by travelling (28 %), socializing (2 %), and resting (1 %). However, in the Gulf of
327 Congianus and in Open waters the dolphins spent most time travelling (79% and 67% of the
328 encounters, respectively), followed by feeding (13% and 23%, respectively), socializing (5% and
329 6%, respectively), and resting (3% and 4%, respectively).

330 Photo-identification data and association patterns

331 Overall, 124 adult bottlenose dolphins with recognizable marks were identified. Of these, 43
332 (35%) were documented as females, 21 (17%) as males, and 60 (48%) were of unknown sex.
333 The calculated seasonal distinctiveness rate (or proportion of adult bottlenose dolphins with
334 recognizable marks) averaged 0.73 ± 0.01 , exerting a moderate influence in the total
335 abundance variation.

336 The mean number and the proportion of adult individuals with recognizable marks per season
337 was 20.6 ± 1.4 and 16.6% respectively. The sighting frequency of identified dolphins ranged
338 from 1 to 588 encounters (mean = 37 ± 9) across the duration of the study. The number of
339 seasons an identified dolphin was photographed ranged from 1 to 36 (mean = 6 ± 0.8). This
340 sighting frequency fluctuated across secondary sampling periods from 1 to 78 (mean = $20.1 \pm$
341 1.5). Seventy-nine bottlenose dolphins (64% of the total identified dolphins) were identified in
342 more than a single season of the year (primary sampling period), and 44 individuals (36% of
343 the total identified dolphins) were only seen during a single secondary sampling period. Fifty-
344 eight individuals (47% of the total identified dolphins) were observed only within a single year
345 of research and 66 (53% of the total identified dolphins) individuals were sighted more than

346 one year. Of these, 42 individuals (34% of the total identified dolphins) were sighted during
347 more than two years of research (30 females and 12 males).

348 Seasonal mean HWI among adult bottlenose dolphins was 0.19 ± 0.01 (minimum = 0.06 and
349 maximum = 0.47), a mean "typical group size" was 4.06 ± 0.14 (between 2.57 - 6.20), and a
350 mean maximum HWI was 0.68 ± 0.02 (between 0.47 - 0.89).

351 Trend analysis revealed a significant downward seasonal trend in the degree of association
352 among adult bottlenose dolphins across the research period (Mann-Kendall test, $z = 3.72$, $p <$
353 0.001 , Figure 2). Seasonal changes in association patterns showed an average seasonal HWI
354 decrease of 0.01 ± 0.02 . However, the sum of all associations ("typical group size") and the
355 maximum HWI, did not show any significant trend across the research period (Mann-Kendall
356 test, $p > 0.05$).

357 Robust design model selection

358 The best-fitting model, determined by the lowest AICc value, showed constant apparent
359 survival rate, seasonal Markovian temporary emigration (with time variation in emigration
360 parameters γ'' and γ') and a different capture probability for each primary sampling occasion
361 (Table 2). The LRT rejected the models with no movement, no emigration, and random
362 emigration in favour of the two first models with a Markovian emigration process and constant
363 apparent survival rate (Chi-square, $p < 0.001$).

364 Abundance estimation

365 For the best fitting model, the estimated seasonal abundance of adult individuals with
366 recognizable marks (\widehat{Nm}) varied between a minimum of 7 (95% CI 7.01 to 7.53) in Spring 2005
367 and a maximum of 49.7 (95% CI 45 to 63) in Summer 2012. Total abundance (\widehat{Nt}) ranged from
368 12 (95% CI 12 to 13) in Spring 2005 to 68 (95% CI 62 to 87) in Summer 2011 (Figure 4).
369 Bottlenose dolphin abundance estimates did not show differences between the four seasons
370 of the year (Kruskal-Wallis test, $p > 0.05$).

371 Trend analysis revealed a significant upward trend in the abundance of bottlenose dolphins
372 across the nine-year research period (Mann-Kendall test, $z = 4.86$, $p < 0.001$). Seasonal changes
373 in abundance showed an average seasonal increase of $9.7 \pm 0.8 \%$.

374 Temporal emigration patterns and survival rate

375 The best fitting model yielded a constant apparent survival estimate of 0.97. Mean capture
376 probabilities among seasons were moderate (mean = 0.65 ± 0.02), with the highest obtained in
377 Summer 2005 (0.99) and the lowest during Autumn 2011 (0.22). The probability of being a
378 temporary emigrant if the animal was absent in the previous period (γ') were high with a mean
379 value of 0.84 ± 0.03 (Table 3). On the other hand, the probability of being a temporary
380 emigrant if the animal was present in the previous period (γ'') were low with a mean of $0.20 \pm$
381 0.03 and showed a peak during autumn (mean 0.29 ± 0.06 ; Kruskal-Wallis test, $p < 0.05$). Trend
382 analysis did not reveal a significant trend in the seasonal temporary emigration rates (γ' and
383 γ'') of bottlenose dolphins across the research period (Mann-Kendall test, $p > 0.05$).

384 DISCUSSION

385 Humans share the coastal environment with a broad variety of other animal species. Since the
386 times of Pliny the Elder (32- 79 A.D.), who provided a detailed description about the
387 interaction between dolphins and fishermen in his book "Natural History" vol. IX, verses 9
388 (Perseus Digital Library 2017, <http://www.perseus.tufts.edu>), humankind has undergone an
389 interest in understanding marine top predators and their relation with human activities. Pliny's
390 report, in Nimes (France), together with similar accounts given by a number of other ancient
391 writers for other localities along the Mediterranean Sea (Montgomery 1966), described idyllic
392 relationships between bottlenose dolphins and people in which bottlenose dolphins capitalize
393 on human activities and both humans and dolphins catch fish together.

394 One of the most striking results of understanding the impact of human activities on dolphins,
395 or vice versa, is the agreement of both past and present that these animals have always been

396 interacting with human beings. As a result of this interaction, the impact of human activities on
397 dolphins has been changing as the culture, economics, technology, and levels of prey
398 abundance changed. The impact of human-induced changes in the marine ecosystem on the
399 behaviour of marine predators has been on concern over the last years (Clua et al. 2010,
400 Kovacs et al. 2012, Ferreti et al. 2013, Constantine et al. 2014). Concern was particularly
401 warranted to bottlenose dolphins, which occupy high trophic positions (Crain et al. 2008).
402 Therefore, the present study is the first attempt to assess the influence of human-induced
403 changes in food resources on migratory patterns and social interaction of this marine top
404 predator. Results revealed a significant upward trend in abundance of bottlenose dolphins and
405 a reduction of the social interactions across the almost one decade of field research. The
406 present study is one of the largest year-round and consistent studies about the interaction
407 between dolphins and human activities conducted to date. This large amount of data makes it
408 very suitable for understanding the factors that induce changes in a local population of
409 bottlenose dolphins due to human activities, and for examining the research issues derived
410 from behavioural and ecological studies.

411 Findings of this study report a higher occurrence of bottlenose dolphins within the Gulf of
412 Olbia, and more particularly in the Aranci Bay, a zone clearly affected by marine fin-fish
413 aquaculture and gill-net fisheries (Díaz López 2006a,b, 2012). Human activities, more
414 particularly coastal fisheries and fin fish aquaculture in the Gulf of Olbia, could have
415 fragmented and made certain zones more attractive to this marine top predator (Díaz López
416 2006a, Díaz López 2017). Gill-net fisheries and fin-fish aquaculture introduced spatial habitat
417 complexity and fragmentation, leading to an increase in food resource distribution and
418 abundance (Tuomainen and Candolin 2010). This variation in food availability was expressed
419 either directly through anthropogenic food (e.g. farmed fish and fish entangled in gillnets, Díaz
420 López 2006a,b, 2011, 2017) but also indirectly in the form of modified habitat that could be

421 favourable for feeding (e.g. increase input of nutrients from aquaculture activities (Díaz López
422 et al. 2008)).

423 Likewise, the increase in abundance of bottlenose dolphins and reduction of social interactions
424 observed in this study, for instance, could be associated to a gradual switch to the food
425 sources that are provided accidentally (fish concentrated around fin fish farm cages, Díaz
426 López and Shirai 2008, Díaz López 2011, 2012) or intentionally (food provided by humans, Díaz
427 López 2017). The attraction of bottlenose dolphins to these concentrated food sources could
428 reinforce competition for these limited resources and therefore causing a reduction of the
429 strength of the associations. This hypothesis agrees with observations of other predator
430 species (i.e. spotted hyaenas, *Crocuta crocuta* (Belton et al. 2018), and european badgets,
431 *Meles meles* (MacDonald et al. 2004)) that reported a weakening of social bonds in high food
432 abundance as a consequence of human-induced changes. Consequently, bottlenose dolphins
433 might interact less with group members across the research period, altering mate-choice
434 behaviour and, thus, the fitness of individuals (Tuomainen and Candolin 2012).

435 The movement patterns of bottlenose dolphins in the area followed seasonal Markovian
436 temporary emigration, suggesting different levels of site fidelity. Indeed, the re-occurrence of
437 adult bottlenose dolphins, within and across seasons, in the study area confirms a high degree
438 of site fidelity of some individuals. Across a population, bottlenose dolphins are considered
439 generalists with regards to prey (Torres and Read 2009), but findings of the present study
440 show how individuals within the same population could have some degree of specialization as
441 a potential consequence of their interaction with human activities (Díaz López 2012). Changes
442 in behaviour through the social transmission of new foraging strategies observed in previous
443 studies (i.e. increase of number of individuals engaged in depredation of farmed fish in the
444 Aranci Bay, Díaz López 2017) confirm how certain individuals gained intimate knowledge on
445 how to capitalize on human activities. In addition, comparative studies reported that

446 behavioural responses to human-induced changes in mammals were related to behavioural
447 flexibility and, in turn, with larger brains (Sol et al.2008).

448 The overall apparent adult survival rate estimated herein is similar to those reported for other
449 wild coastal communities of bottlenose dolphins with high levels of human-induced impacts
450 (Speakman et al. 2010, Daura-Jorge et al. 2013, Smith et al. 2013). Thus, the observed
451 consistencies in survival estimates could likely reflect uniformities in ecological characteristics
452 between study sites and/or similar levels of human-induced impacts (Currey et al. 2009). As
453 many of the aggregating species around fin-fish farm cages and target species of gill-net
454 fisheries, are preys of bottlenose dolphins (Santos et al. 2007), both the aquaculture and
455 fisheries industries affect the ecology of coastal dolphin populations on a broad scale.
456 Theoretically, dolphins should select habitats that minimize the ratio of human-induced
457 disturbance to net energy intake (Lima and Dill 1990). However, the observed increase in
458 abundance of bottlenose dolphins in the most human-impacted area has outlined how
459 bottlenose dolphins are particularly vulnerable to anthropogenic pressures such as
460 entanglement in fishing gear, habitat degradation, aquaculture industry, and food provisioning
461 from humans (Díaz López and Shirai 2007, Díaz López 2012,2017). Hence, the observed
462 behavioural response to human activities can expose certain individuals to another stressors
463 that then causes declines, such as bycatch (Díaz Lopez 2006a, 2017, Díaz López and Shirai
464 2007) or diseases (Houde et al. 2005). Consequently, protection measures should be devoted
465 to reducing these anthropogenic pressures, which are believed to become some of the main
466 threats for coastal bottlenose dolphin populations (Bearzi et al. 2008). Proposed modifications
467 in fisheries or aquaculture industry should be carefully scrutinised in terms of their potential
468 impacts on bottlenose dolphin populations. For example, site planning for aquaculture
469 facilities should incorporate knowledge of the proximity of areas with high density of gill-net

470 fisheries, because the synergistic effect of both stressors may stimulate the incursion of
471 bottlenose dolphins from surrounding areas because of the greater food availability there.

472 CONCLUSION

473 As noted in the present study, although human activities regularly impose a disturbance on
474 marine top predators, they can also be a source of reliable and concentrated food resources
475 due to the fragmentation of the coastal environment. The observed link between human
476 activities and changes in predators' behaviour aim to contribute to a better understanding of
477 the ecology of a marine top predator and provide some of the needed baseline data, from
478 which effective management and conservation strategies can be designed.

479 Behavioural responses can influence the distribution of individuals by influencing migratory
480 patterns, social systems, and survival in the modified habitat. This can have effects on gene
481 flow and the degree of inbreeding and, hence, the amount of genetic variability and
482 population viability (Tuomainen and Candolin 2011).

483 Given that population dynamics and social interactions depend on decisions and behaviours of
484 individuals, further studies should be focus on understanding the variation in response. Why
485 some individuals are more flexible in their response to novel foods, while others are less?

486

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490

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500

501 Data accessibility: Analyses reported in this article can be reproduced using the data provided
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503

504

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683 Zacharias MA, Roff JC. 2001. Use of focal species in marine conservation and management: a
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685

686 Table 1. Annual observation effort, bottlenose dolphin encounters, and number of individuals
687 included in the mark-recapture analysis in relation to the 9 years of research.

Year	Robust design (Periods)		Observation effort				Group encounte rs	Encount er ratio	Dolphins identifi ed
	Prim ary	Second ary	Month s	Day s	Hour s	Km			
2005	4	8	12	79	288	441	146	0.51	24
2006	4	8	12	68	284	651	129	0.45	38
2007	4	8	10	141	564	1095	181	0.32	24
2008	4	9	10	123	442	1281	184	0.42	24
2009	4	9	11	124	452	1130	192	0.42	25
2010	4	9	11	108	453	2811	216	0.48	43
2011	4	9	10	104	388	2240	200	0.52	60
2012	4	9	10	103	374	3660	196	0.52	59
2013	4	9	11	105	339	2021	194	0.57	47
Total	36	78	85	955	3584	15330	1638	0.46	124

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689 Encounter ratio is the total number of dolphin encounters divided by the number of hours
690 spent searching for dolphins (Díaz López, 2006a).

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

Rank	Model	Emigration pattern	AICc	Delta AICc	Model Likelihood	AICc Weight	Parameters	Deviance
1	$\phi(\cdot), \gamma'(t) \neq \gamma''(t), p(t)=c(t)$	Markovian	534.2	0.00	1.0000	0.6659	174	2285.2
2	$\phi(\cdot), \gamma'(t_k =_{k-1}) \neq \gamma''(t_k =_{k-1}), p(t)=c(t)$	Markovian	543.1	8.95	0.0114	0.0076	174	2294.1
3	$\phi(t), \gamma'(t) \neq \gamma''(t), p(t)=c(t)$	Markovian	599.2	65.06	0.0000	0.0000	206	2257.9
4	$\phi(t), \gamma'(t_k =_{k-1}) \neq \gamma''(t_k =_{k-1}), p(t)=c(t)$	Markovian	600.4	66.23	0.0000	0.0000	206	2256.1
5	$\phi(t), \gamma'(t) = \gamma''(t), p(t)=c(t)$	Random	868.3	334.1	0.0000	0.0000	170	2630.4
6	$\phi(t), \gamma' = \gamma'' = 0,$	No emigration	1217.3	683.2	0.0000	0.0000	147	3041.5

	$p(t)=c(t)$	ion						
7	$\varphi(\cdot), \gamma'(t)$ $= \gamma''(t),$ $p(t)=c(t)$	Rando m	1293. 6	759.5	0.0000	0.000	136	3146.6
8	$\varphi(\cdot), \gamma' =$ $\gamma'' = 0,$ $p(t)=c(t)$	No emigrat ion	2115. 4	1581. 2	0.0000	0.000	114	4023.8

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699 The notation (.) indicates that a given parameter was kept constant and (t) indicates that a
 700 given parameter was allowed to vary with time. Abbreviations: apparent survival (φ), capture
 701 (p), recapture (c) and temporary emigration (γ) probabilities. γ ($K = k - 1$) indicates that the last
 702 and penultimate emigration probabilities were set to be equal to allow identifiability of the
 703 parameters. Emigration pattern notations follows Kendall et al. (1997).

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706 Table 3. Mean seasonal temporary emigration rates and mean capture probability for the best
707 fitting Markovian model.

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Season	Temporary emigration rates		Capture probability (p)
	γ'	γ''	
Spring	0.90 ± 0.05	0.16 ± 0.06	0.62 ± 0.03
Summer	0.85 ± 0.05	0.17 ± 0.06	0.66 ± 0.04
Autumn	0.84 ± 0.04	0.28 ± 0.06	0.65 ± 0.03
Winter	0.77 ± 0.06	0.16 ± 0.05	0.67 ± 0.05
Overall	0.84 ± 0.03	0.20 ± 0.03	0.65 ± 0.02

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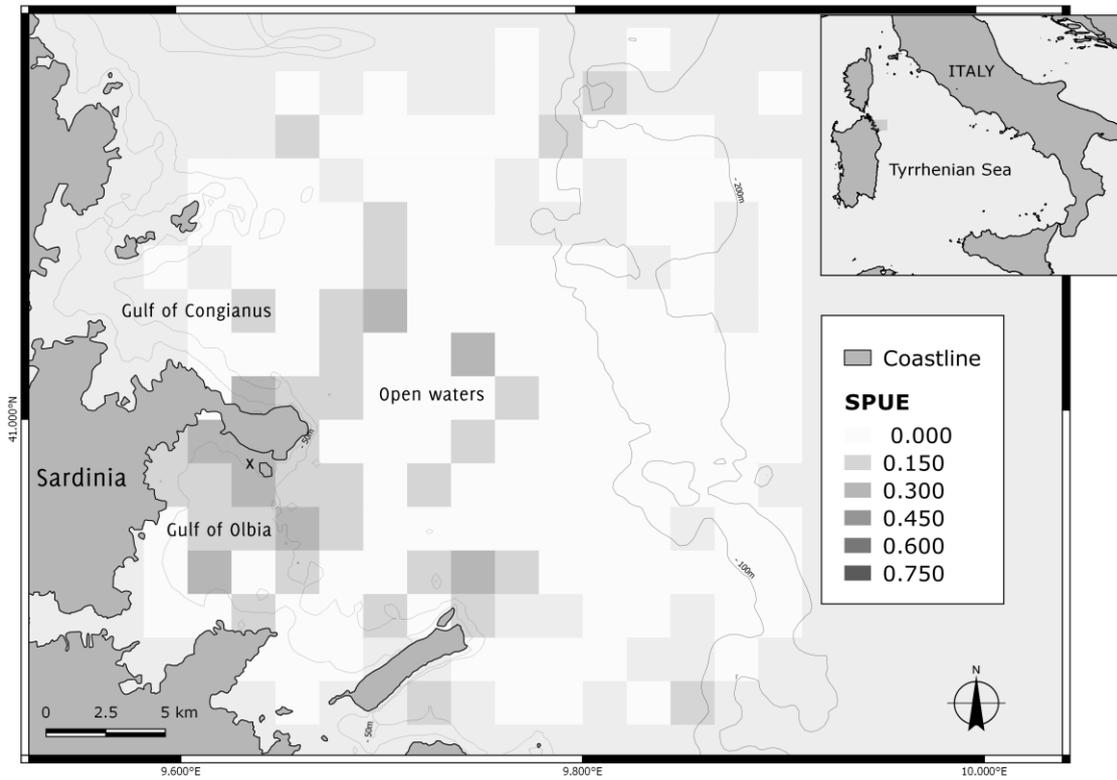
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724 Figure 1. Map of the study area surveyed along the North-eastern coast of Sardinia, Tyrrhenian
725 Sea (Italy), showing the distribution of bottlenose dolphin sightings (SPUE) corrected for search
726 effort within each 1nm² cell, between January 2005 and December 2013. A cross indicates the
727 location of the marine fin-fish farm in the Gulf of Aranci (40° 59.98'N, 9° 37.09'E).

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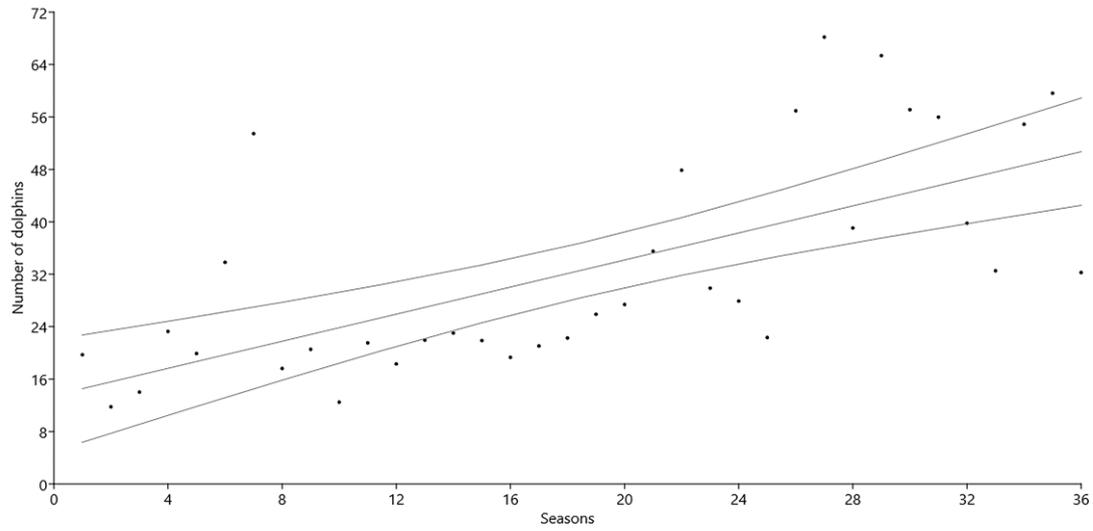
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737 Figure 2. Temporal trend in abundance estimates across the 36 consecutive seasons of the
738 year. Linear fit calculated using Ordinary Least Squares (OLS) regression. 95 % confidence band
739 for the fitted line is indicated by external lines.

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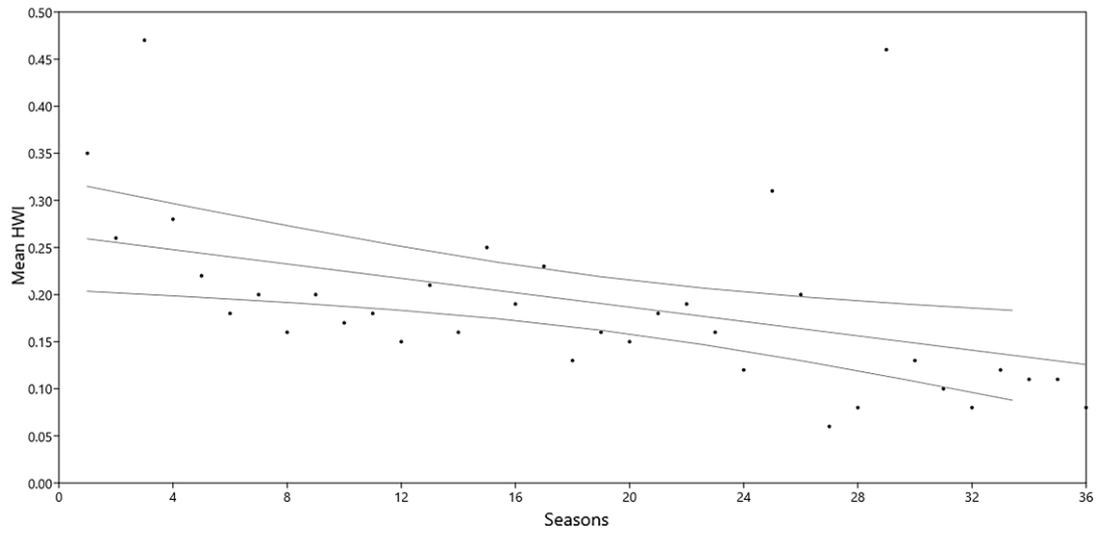
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753 Figure 3. Temporal trend in association patterns across the 36 consecutive seasons of the year.

754 Linear fit calculated using Ordinary Least Squares (OLS) regression. 95 % confidence band for

755 the fitted line is indicated by external lines.