

1 **Estimates of abundance and change in abundance of the Indo-Pacific bottlenose dolphins**
2 **(*Tursiops aduncus*) along the south coast of South Africa**

3

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17 **Abstract**

18 We investigated the abundance of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) along
19 the south coast of South Africa, from the Goukamma Marine Protected Area (MPA) to the
20 Tsitsikamma MPA, between 2014 and 2016. During this period, 662.3h of boat-based photo-
21 identification survey effort was carried out, and the sighting histories of 817 identified
22 individuals were used to estimate abundance using mark-recapture modelling. The selected
23 open population model (POPAN) provided an estimate of 2,295 individuals (95% CI: 1,157-
24 4,553) for the entire study area. A model estimate was produced for a subset of the study area,
25 Plettenberg Bay, which could be compared with a past estimate for this location (2002-2003).
26 The comparison suggested a 72.3% decrease in abundance, from 6,997 (95% CI: 5,230-9,492)
27 in 2002-2003 to 1,940 (95% CI: 1,448-2,600) in 2014-2016. The decline in abundance was
28 supported by a 72% reduction in mean group size for Plettenberg Bay between the periods. It
29 is essential to be able to assess abundance changes at other locations to inform revision of *T.*
30 *aduncus* conservation status in South Africa.

31

32 Keywords: population estimate, *Tursiops aduncus*, conservation management, mark-recapture,
33 photo-ID.

34 **Introduction**

35 Information on the abundance and trends of wildlife populations is essential for species and
36 ecosystem conservation management strategies [1,2]. Trends in abundance provide feedback
37 on the success or failure of implemented conservation strategies and indicate natural or
38 anthropogenic driven ecosystem changes [3]. In both terrestrial and marine ecosystems,
39 predator population trends are thought to integrate the state of lower trophic levels and the
40 physical environment that they inhabit [4,5]. For this reason predator population trends are
41 often considered to be good indicators of ecosystem health.

42

43 The escalating human population, with disproportionately higher growth rates in coastal areas,
44 is exerting increased pressure on coastal ecosystems and marine species. Coastally distributed
45 dolphin species are highly susceptible to current and future human-related threats such as
46 habitat degradation from pollution and coastal development (e.g., harbours and offshore wind
47 farms), competition with fisheries, and bycatch in fishing gear or shark exclusion nets [6].
48 Examples of inshore dolphin species that of current conservation concern and which face a
49 multitude of threats include the vaquita (*Phocoena sinus*), humpback dolphins (*Sousa spp*) [7–
50 9], Australian snubfin dolphins (*Orcaella heinsohni*) [10] and Hector's dolphins
51 (*Cephalorhynchus hectori*) [11]. For such species, studies that document population size and
52 trends are essential for conservation and management planning [12].

53

54 The Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) has been listed as a Data Deficient
55 species by the IUCN Red List of Threatened Species since 1996 [13]. Their distribution is
56 apparently continuous along coastal areas (including mid-ocean island shores) in the Indian
57 Ocean, from False Bay (South Africa) eastwards right through to the Solomon Islands and New

58 Caledonia in the western Pacific Ocean [14] including the east and west coasts of Australia and
59 the south-east Asian waters [15]. The most recent South African Red List conservation
60 assessment [16] recognized three sub-populations of *T. aduncus* in South African waters based
61 on previous genetic studies [17] (Fig 1). A resident sub-population in northern KwaZulu-Natal
62 (between Kosi Bay and Ifafa) was classified as Vulnerable; a migratory sub-population that is
63 thought to move between Plettenberg Bay and Durban as Data Deficient; and a resident sub-
64 population south of Ifafa with its western limit at False Bay as Near Threatened [16]. Research
65 priorities identified by the conservation assessment [16] include (amongst others) conducting
66 research into their population genetics to determine significant management units, assessing
67 the effectiveness of Marine Protected Areas (MPA) in addressing conservation needs of sub-
68 populations, and determining abundance estimates throughout their range as well as site
69 specifically [16]. A subsequent genetic study [18,19] defined two conservation units (instead
70 of three sub-populations) along the South African Coast: one along the Natal Bioregion and
71 another in the Agulhas Bioregion (Fig 1). The results from genetic population structure analysis
72 thus refutes the existence of a migratory sub-population [17] as described in the latest
73 conservation assessment [16].

74

75 The abundance and changes in population numbers of *T. aduncus* along South Africa's coast
76 is poorly understood; estimates of numbers are restricted to localised areas (summarized in 16)
77 and data on changes in population numbers are non-existent. For the sub-population in the
78 Agulhas Bioregion, only two mark-recapture abundance estimates are available: one in Algoa
79 Bay (1991-1994) where 28,482 (95% CI: 16,220-40,744) individuals were estimated [20] and
80 another for Plettenberg Bay (2002-2003) where 6,997 (95% CI: 5,230-9,492) individuals were
81 estimated [21]. Results from these studies showed that numerous individuals were utilising

82 both areas, indicating a dynamic population on the south coast of South Africa with long-range
83 movements [20].
84 This study estimates *T. aduncus* population abundance and group sizes along 145 km of
85 coastline in the Agulhas Bioregion off the south coast of South Africa. The data were obtained
86 using boat-based surveys and mark-recapture methods. Furthermore, for a subset of the study
87 area (Plettenberg Bay; 29 km of coastline), separate population abundance and group size
88 estimates were determined so that it could directly be compared with a study conducted in this
89 area more than ten years previously (2002-2003). Tourism is an important revenue along the
90 Bitou municipality which includes Plettenberg Bay [22]. The latter is a growth centre for
91 marine tourism activities including boat-based marine mammal viewing, fishing charters and
92 adventure rides that can potentially disturb dolphins. This is the first attempt at assessing
93 change abundance of a *T. aduncus* population over time at any location in South Africa. We
94 hypothesized that dolphin numbers and group sizes would have decreased since the first
95 assessment due to increasing human activities in the coastal zone.

96 **Methods**

97 **Study area, survey design and data collection**

98 Data were collected during standardized boat surveys along 145 km of coastline within the
99 Agulhas Bioregion, between the western border of the Goukamma MPA and the eastern
100 boundary of the Tsitsikamma MPA on the south coast of South Africa (Fig 1). Ninety-seven
101 kilometres of the coastline of the study area is within MPAs, namely the Goukamma, Robberg
102 and Tsitsikamma MPAs. There are two main dolphin hotspots in this area, namely the
103 Goukamma MPA and the Plettenberg Bay area [23]; both areas are characterized by sandy
104 shores and gentle slopes. The stretch between Goukamma to Robberg MPA and Tsitsikamma
105 MPA is largely uninhabited (by humans) with exposed rocky coasts and steeper gradients.

106

107 **Fig 1: Map of South Africa with relevant locations mentioned in the text**

108 (1) Kosi Bay; (2) Durban; (3) Ifafa; (4) Algoa Bay; (5) study area; (6) False Bay. The study
109 area extended from the western boundary of Goukamma to the eastern boundary of the
110 Tsitsikamma MPA. Boat surveys were conducted parallel to the coast (dashed black line).

111

112 The surveys were designed as a transect line running parallel to the coast. Bi-monthly boat
113 surveys were conducted between March 2014 and February 2016. At least two experienced
114 observers were present during surveys which were performed at a constant speed of
115 approximately eight knots (see [23] for further information on study area, survey design and
116 data collection procedures).

117

118 In this study, digital dorsal fin photo-ID images were taken using a Nikon SLR camera
119 equipped with a Tamron 300 or 600 mm lens. The dorsal fins of as many dolphins as possible
120 were photographed from both sides (if possible), without any preference towards individuals
121 with obvious markings [1]. Group sizes were estimated independently as minimum, maximum
122 and best estimates, with best estimates not necessarily being the mean of the upper and lower
123 estimates [24]. A group was defined as two or more animals within a 100-m radius of each
124 other, showing similar behaviour [25]. Survey effort was measured as the number of hours
125 travelled in good sighting conditions (Beaufort scale ≤ 3). Survey effort was discontinued when
126 conditions exceeded Beaufort scale 3.

127

128 **Data processing and analysis**

129 **Photo-identification catalogue and data selection**

130 Dorsal fin images were cropped and graded according to the photo quality (Q) and
131 distinctiveness (D). Quality were scored from 1 to 3 (Q1 being excellent quality and Q3 poor
132 quality). The Q grade was based upon photo clarity, contrast, angle, portion of frame filled by
133 the fin, angle, exposure, water spray and the percentage of the fin image that is visible in the
134 frame (adapted from [1,26,27]). Photographs graded Q1 were therefore well exposed, without
135 water droplets, in sharp focus, with the dorsal fin orientated perpendicular to the photographer
136 and occupying a large proportion of the frame (adapted from [1]). Using only photographs
137 graded Q1-Q2, the fins were then graded according to the fin distinctiveness (D).
138 Distinctiveness was graded from 1 to 3 (D1 very distinctive and D3 no distinctive
139 characteristics). Photographs with distinctiveness grades D1-D2 were catalogued according to
140 the location of the most prominent or distinguishing feature. The categories included: leading

141 edge, mutilated, peduncle and trailing edge; with the latter subdivided into entire, low, mid or
142 upper third (adapted from [26]). As many features as possible were used to confirm matches
143 and to reduce the possibility of false positives only long lasting markings were considered [1].
144 Two different experienced researchers visually compared photographs from each category to
145 avoid misidentification of individuals (first within the same category and subsequently between
146 categories where required).

147

148 **New identifications and discovery curve**

149 To evaluate whether the population had been sampled comprehensively, the cumulative
150 number of newly identified individuals was plotted over time in a discovery curve. If a
151 discovery curve reaches an asymptote, this indicates that the whole population has been
152 identified and that it is likely to be a closed population with no immigration or emigration (e.g.
153 [1]). The discovery curve of an open population (births, deaths, immigration or emigration
154 occurs) is not likely to reach an asymptote (e.g. [20]).

155

156 **Mark-recapture analysis**

157 Open and closed population models were fitted using the software MARK 8.2 [28] to estimate
158 the population size of *T. aduncus* in the study area. Only high quality photographs ($Q \leq 2$) were
159 used to construct encounter histories for all the identified individuals ($D \leq 2$) using calendar
160 month as capture occasions.

161

162 Open population estimates were obtained using the POPAN parameterization [29], which
163 calculates the super-population size (N), apparent survival probability (Φ), capture probability
164 (p), and the probability of immigration or entry (b) from the super-population to the local
165 population present in the study area. Demographic parameters were designated as time

166 dependent (t), constant over time (.) or seasonal (s), whereas capture probability were
167 additionally allowed to vary with survey effort. Seasons were defined as the austral winter
168 (May-October) or summer (November-April) [30,31]. The most parsimonious model was
169 selected using Akaike's Information Criterion for small sample sizes (AICc) [32]. Monthly
170 survival probabilities estimated by the model were transformed to annual survival probability
171 with associated variances re-scaled using the Delta method [33].

172
173 Goodness-of-fit (GOF) of the fully time-dependent Cormack-Jolly-Seber (CJS) model was
174 assessed in program RELEASE to verify whether the encounter history data met model
175 assumptions [34], A variance inflation factor (\hat{c}) was calculated based on the results of Test 2
176 + Test 3 in order to determine if the data were over-dispersed ($\hat{c} > 1$) or under-dispersed ($\hat{c} <$
177 1) and to evaluate the need for an adjusted model selection criterion (i.e. quasi-Akaike
178 Information Criterion, QAICc). Test 2 determines capture homogeneity; Test 3 homogeneous
179 survival probability; Test 3 SR presence of transience in the data; and Test 3Sm effect of
180 capture on survival [34].

181
182 We used closed population models to compare abundance estimates for data collected during
183 2014 to 2016, to previous Plettenberg Bay abundance estimates [21]. This was because the past
184 estimates were based only on closed models and the data were not available for re-analysis. In
185 the earlier study closed models were fitted using the program CAPTURE in MARK [35]. The
186 model selection was based upon model selection criteria values produced by the program
187 CAPTURE [36]. The higher the selection criteria the better the model fits (larger value 1.0)
188 and selection values lower than 0.75 should not be used to estimate abundance [35]. Presently,
189 CAPTURE is considered to be an outdated programme for estimating abundance; for this
190 reason the closed population models were also estimated in MARK. Huggins' model were set

191 as $p=c$, where the initial capture probability (p) is equal to the recapture probability (c). These
192 settings were used because the animals were not physically captured and a behavioural
193 response to capture was not expected.

194

195 **Estimating super-population size**

196 The mark-recapture abundance estimates refer to the number of marked individuals in the
197 population. To estimate the super-population size of *T. aduncus*, the mark-recapture results
198 were scaled up according to the proportion of marked individuals in good quality photos ($\leq Q2$)
199 [1,26]. The proportion of marked individuals in the population was estimated from the ratio of
200 distinctive individuals ($D1 + D2$) to the total sample ($D1 + D2 + D3$) [1,26,37]. The super-
201 population size was estimated as:

$$202 \quad \hat{N}_{total} = \frac{\hat{N}}{\hat{\theta}}$$

203 where \hat{N}_{total} is the estimated abundance, \hat{N} is the mark-recapture estimate of the number of
204 animals with long-lasting marks, and $\hat{\theta}$ is the estimated proportion of animals with long lasting
205 marks in the population [1]. The variance estimate was calculated using the delta method:

$$206 \quad var(\hat{N}_{total}) = \hat{N}_{total}^2 \left(\frac{var(\hat{N})}{\hat{N}^2} + \frac{1 + \hat{\theta}}{n\hat{\theta}} \right)$$

207 where n is the total number of animals from which θ was estimated [1]. Confidence intervals
208 for \hat{N}_{total} assumed that the error distribution was the same as that of the mark-recapture
209 estimates of the marked population [1].

210 Results

211 In total, 662.3 h of survey effort were conducted over 189 surveys and 145 days from March
 212 2014 to February 2016. *T. aduncus* were encountered throughout the year, Average group size
 213 was estimated as 47 ± 55 (mean \pm SD) individuals, with larger group sizes during winter ($57 \pm$
 214 63) compared to summer (35 ± 42 ; Table 1). For Plettenberg Bay only, the mean group size
 215 was 26 ± 26 , which is 78% lower than in 2002-2003 (Table 1).

216

217 **Table 1: *T. aduncus* group size statistics for the entire research area, and for Plettenberg**
 218 **Bay only. Also included for comparison are past estimates for Plettenberg Bay (2002-**
 219 **2003)**

	Summer	Winter	Overall
Entire study area 2014-2016			
Mean \pm SD	35 ± 42	57 ± 63	47 ± 55
Range	1-300	1-350	1-350
Median	20	40	30
Plettenberg Bay 2014-2016			
Mean \pm SD	26 ± 28	26 ± 18	26 ± 26
Range	1-100	3-65	1-100
Median	15	23	18
Plettenberg Bay 2002-2003 [21]			
Mean \pm SD	124 ± 111 ¹	82 ± 143 ¹	$120 \pm NA$ ³
	211 ± 139 ²	56 ± 76 ²	
Range	NA	NA	2-500 ³
Median	NA	NA	80 ³

220 'NA': not available; ¹ in 2002; ² in 2003; ³ in 2002-2003.

221

222 A total of 80.6 h was spent with *T. aduncus* groups during surveys and 10,431 dorsal fin
223 photographs were taken and assessed for quality. Of 4,015 photographs found to be of
224 acceptable quality ($\leq Q2$), 2,274 photographs had individuals with sufficient distinctiveness (\leq
225 D2). The final catalogue consisted of 817 identified animals with a total of 1,558 photos (which
226 includes multiple good photos per individual per sighting). The proportion of identifiable
227 individuals (adults and juveniles) was 0.77. Of the identified animals, 72.7% were encountered
228 only once, 16.8% were encountered twice, 6.2% were encountered three times and 4.3% were
229 encountered between 4 and 7 times in the entire study area.

230 The discovery curve never reached an asymptote (Fig 2). New individuals were thus still being
231 identified towards the end of the study period, suggesting either that the population is open or
232 that not all individuals of a closed population had been identified.

233

234 **Fig 2: Number of *T. aduncus* identified from photographs, and the cumulative discovery**
235 **curve for new individuals.**

236

237 **Abundance estimates**

238 **Open population model**

239 Goodness-of-fit results (Table in S1 Table) indicated that there was over-dispersion in the
240 encounter history data summarising the observations made in the entire research area, with a
241 variance inflation factor of $\hat{c} = 1.71$. Goodness of fit tests suggested there was heterogeneity in
242 capture probabilities between individuals, and that transient animals (permanent emigration
243 after a single encounter) were present. The most parsimonious POPAN model for the entire
244 area assumed constant survival, time dependent capture probability, a seasonal (summer and
245 winter) probability to enter the local population from the super-population, and a constant
246 super-population size (Table in S2 Table). The model produced a super-population size of
247 2,295 (SE: 827; 95% CI: 1,157-4,553). The annual survival was estimated to be 0.87 (± 0.12).

248 **Closed population model**

249 The most appropriate model for Plettenberg Bay (2014- 2016) had capture probability as time-
250 dependent. The model M_t produced an abundance estimate of 1,063 (SE: 125, 95% CI: 858-
251 1,360) marked individuals which translates to a super-population size of 1,381 (SE: 163, 95%
252 CI: 1,097-1,738) individuals (Table 2). The model M_{th} , which assumed heterogeneous
253 capture probabilities that varied with time, was the next most parsimonious model to explain
254 the variation in the data according to the selection criteria value (0.76; Table in S3 Table). This
255 model structure was also used by [21] to model abundance in Plettenberg Bay in 2002-2003.

256 Because it is recommended that selection values lower than 0.75 should not be used to estimate
257 abundance [35], comparison using this model was justified. The abundance estimate for this
258 model M(th) was 1,494 (SE: 224, 95% CI: 1,131-2,024) marked individuals, giving a super-
259 population estimate of 1,940 (SE: 291, 95% CI: 1,448-2,600) for the bay (Table 2). This is
260 72.3% lower than the estimate of 6,997 for Plettenberg Bay in 2002-2003 [21]. The closed
261 population analyses for the 2014-2016 period were repeated using MARK (Table in S4 Table).
262 The best model (based on ΔAIC) for Plettenberg Bay was $p=c(t)$, denoting that the capture and
263 recapture probabilities are equivalent and time dependent. This model predicted a super-
264 population size for Plettenberg Bay of 1,386 (SE: 62; 95% CI: 922-2,083) individuals.
265
266

267 **Table 2: Estimates of *T. aduncus* abundance based on closed population models**
 268 **conducted using CAPTURE in the entire study area, and for the Plettenberg Bay area in**
 269 **isolation for the periods 2002-2003 and 2014-2016.** Estimate of marked population (N) and
 270 super-population size (NT); standard error (SE); lower and upper limits of the 95% confidence
 271 interval (LCL and UCL).

Model ¹	Marked population				Super-population			
	N	SE	LCL	UCL	NT	SE	LCL	UCL
Entire study area (2014-2016)								
M(th)	2103	144	1850	2417	2731	188	2387	3126
Plettenberg Bay (2014-2016)								
M(t)	1063	125	858	1360	1381	163	1097	1738
M(th)	1494	224	1131	2024	1940	291	1448	2600
Plettenberg Bay (2002-2003) ²								
M(th)	4833	742	3612	6556	6997	742	5230	9492

272 ¹ Model description: M(t) - time varying capture probability (p); M(h) - heterogeneous p; M(th)
 273 a combination of the above [35].

274 ² Results extracted from [21].

275

276 **Discussion**

277 The current lack of knowledge of *T. aduncus* abundance and trends in South Africa hampers
278 conservation assessments [16]. This study contributes novel information to assist conservation
279 management by reporting *T. aduncus* abundance estimates in the Agulhas Bioregion of the
280 southern Cape, and apparent change in abundance for the Plettenberg Bay sub-region. The
281 large number of identified individuals in this study (817) and the low re-encounter rates (27%)
282 supports the notion that individuals observed within the study area are part of a much larger
283 open population that ranges as far as Algoa Bay [20].

284
285 The best open population estimate for the entire study area gave super-population size estimate
286 of 2,295 individuals. This estimate needs to be interpreted with some caution, because
287 goodness-of-fit results suggested over-dispersion in the mark-recapture data, with strong
288 transience and heterogeneity in capture probabilities between individuals. The most
289 parsimonious closed population model $\{p=c(t)\}$, whereby the capture and recapture probability
290 are equivalent and time dependent gave a similar estimate to that of the open model, namely
291 1,940 individuals (Table in S4 Table).

292
293 A closed population model was required to compare abundance estimates from the present
294 study with estimates derived from data collected between 2002 and 2003 [21]. The comparison
295 between the two study periods (more than 10 years apart) is important because there is no other
296 information on changes in population abundance for this species in South African waters,
297 leading to considerable uncertainty regarding the species' conservation status [16]. The best
298 estimate for Plettenberg Bay in 2002-2003, was 6,997 dolphins. In comparison, the two most
299 reliable estimates for this study were 1,381 and 1,940 individuals. The latter estimate is 72.3%
300 lower than the 2002-2003 estimate.

301 The low re-encounter rate of known individuals in the area may have been influenced by there
302 being a sizable proportion of transient animals in the population. For future studies, this could
303 potentially be remedied through greater search effort in the area. However this is often not
304 realistic due to weather constrains and moreover it would imply exorbitant costs for the running
305 of dedicated research vessels. Using the tourist vessels as platforms of opportunity is a possible
306 alternative but there would have to be consistency in the methods used during searching and
307 encounters. Another alternative for estimating abundance and monitoring change in the area is
308 through aerial surveys using a distance sampling approach. Aerial surveys can cover much
309 more ground in a day, but have disadvantages such as the need for almost perfect weather
310 conditions and very good water clarity in order to have a good detection rate (e.g. when animals
311 are underwater). Furthermore abundance estimates from aerial survey are likely to be
312 negatively biased by only taking into account individuals that are in the study area at the time
313 of the survey, whereas the mark-recapture open models allow for individuals to enter and leave
314 the study area. Another important limitation of aerial surveys is undercounting bias whereby
315 as much as two thirds of animals may not be detected during the surveys, as shown in previous
316 aerial survey studies (e.g. [38]). For this reason it is recommended that if aerial surveys are
317 used, twin platform surveys should be conducted (e.g. [39]) whereby two aircraft survey the
318 same transect independently but minutes apart in order to estimate the number of missed
319 sightings.

320

321 A pilot study consisting of nine aerial surveys was conducted during the study period, to test
322 the practicality of surveying *T. aduncus* using this method [18]. Abundance estimates were not
323 derived from aerial surveys because there were too few surveys ($n=9$) for a robust population
324 estimate. The group size estimates from boat surveys are, however, corroborated by the aerial
325 survey estimates, with both survey methods detecting larger group sizes during winter [18].

326 The overall mean group size during aerial surveys along the entire study area was 43 ± 37
327 (range: 1-150; median: 33; n= 42), compared with 47 ± 55 individuals from boat-based surveys
328 (Table 1). In winter, the estimate from aerial surveys was 46 ± 34 (range: 6-100; median: 39;
329 n= 12) compared with 57 ± 63 ; and in summer, 41 ± 38 (range: 1-150; median: 30; n= 30)
330 compared with 35 ± 42 , respectively.

331
332 Smaller average group size were recorded in Plettenberg Bay (26 individuals) compared with
333 the whole study area (47 individuals). Both these estimates are considerably lower than the
334 mean group size of 120 that was estimated for 2002-2003 in Plettenberg Bay [21]; the decline
335 in group size for Plettenberg Bay between the two periods was 78.3%. A decline in average
336 group size is also corroborated by a shore-based estimate of mean group size from the early
337 1970s, of 140.3 [40]. The decline in group size may be an indication of a decline in numbers
338 and appears to support the decline shown by the modelled abundance estimates.

339
340 Another factor that could have influenced the decline of group size and abundance is a
341 reduction in the numbers of transient groups using the area. In several recent years South
342 Africa's annual sardine run which is characterized by large schools of sardine (*Sardinops*
343 *sagax*) moving northwards along the east coast during winter months, followed by vast
344 numbers of predators including *T. aduncus* [41], has been less pronounced than in the past [42].
345 The dwindling size of the sardine run could have the effect that less transient groups of *T.*
346 *aduncus* navigate through the study area. Declines in the availability of other important prey
347 resources for *T. aduncus* such as squid [43,44], which spawn in a distinct area around
348 Plettenberg Bay [45] but which have been less productive in recent years[46] could also have
349 affected *T. aduncus* numbers in the area.

350

351 An important change in Plettenberg Bay since the 2002-2003 study of *T. aduncus* is the
352 growing resident Cape fur seal colony (*Arctocephalus pusillus pusillus*) on the Robberg
353 Peninsula [47]. This could cause direct competition for prey resources with *T. aduncus*
354 including for species such as: piggy (*Pomadasyris olivaceum*), squid (*Loligo vulgaris reynaudii*),
355 cuttlefish (*Sepia spp.*), red tjob-tjob (*Pagellus bellottii*), sardine (*Sardinops sagax*) and octopus
356 (*Octopus spp.*) [43,48]. Furthermore, there is likely to have been an increase in the abundance
357 of great white sharks (*Carcharodon carcharias*), that are attracted to seal colonies, in the area.
358 This impact of the sharks on the *T. aduncus* population may be direct (i.e. predation in itself)
359 [49]; or indirect, whereby the predation risk brings about increased stress levels in the prey
360 population that can reduce their performance and productivity, or changes in residency patterns
361 reducing time spent in the area [50].

362
363 Due to their coastal distribution, *T. aduncus* are also vulnerable to multifarious anthropogenic
364 pressures associated with coastal and inshore areas that could bring about shifts in residency
365 patterns or a population decline. In our study area such pressures include coastal development,
366 vessel traffic and associated disturbance, especially those related with boat-based cetacean
367 viewing ventures [6,51,52]. The longevity and relatively low reproductive rate of this species
368 aggravates the effects of habitat degradation and other threats. The Bitou municipality (which
369 includes Plettenberg Bay) is the fastest growing municipality in the Western Cape Province,
370 with an average annual population growth of 4.8% from 2001 to 2013 and tourism brings in
371 much revenue to the area [22]. However, while it may be tempting to link the decline in *T.*
372 *aduncus* numbers and group sizes with the increasing population and associated pressures in
373 the area, a considerable increase in the mean group size of the same species in the more
374 developed Algoa Bay to the east has been shown, from 18 to 76 individuals between 2008 and

375 2016 [53], which can be a consequence of a shift of the population's preferred habitat in recent
376 years.

377

378 While the causes of the changes in Plettenberg Bay are not yet well understood, a precautionary
379 approach especially with regard to impacts of the burgeoning tourism industry is advised, and
380 this is naturally also in the interests of the industry's sustainability. The impacts of tourism on
381 animal populations is generally measured by short-term behavioural responses (e.g. [52]), yet
382 evidence is mounting that disturbance caused by these activities have long-term demographic
383 implications. In Plettenberg Bay, boat-based ecotourism may have impacted on the sympatric
384 Indian Ocean humpback dolphins (*Sousa plumbea*), which is known to be sensitive to human
385 presence. Preliminary results have shown a decline in abundance of this population by
386 approximately 46% between 2002-2003 [54] and 2012-2013 [55]. Simultaneously, a 35%
387 reduction in the mean group size of this species between the two periods was documented [55].

388

389 In other parts of the world, *Tursiops spp.* have also been declining. For example, in Australia
390 [56] and the Bahamas [57], declines of 15% and 49% were attributed to effects of tour operator
391 vessels and a combination of natural and anthropogenic factors. Some of the measures that
392 were taken in other parts of the world to mitigate impacts and protect *Tursiops spp.* includes
393 the creation of protected areas (e.g. [58]).

394

395 While *T. aduncus* was recently assessed to be Near Threatened in South Africa [16], the *S.*
396 *plumbea* is currently Endangered at the national level on account of the small size of the
397 population and apparent decline, exacerbated by its fragmented distribution with considerable
398 movement within the bioregions [59,60]. Expanding the current MPAs or identifying new
399 conservation areas has been recommended for *S. plumbea* in South Africa [60]. Given the

400 sympatry of the two species, such measures could also address certain conservation needs for
401 *T. aduncus*; e.g. if vessel traffic is strictly controlled in such areas, if critical habitat types are
402 protected and if human pressures on prey resources in such areas are reduced such that
403 productivity and overspill of certain prey into adjoining areas may occur (e.g. [61,62]).

404 **Conclusions**

405 This is the first study to show a change over time in abundance for the *T. aduncus* anywhere in
406 South Africa. While a comparison based on closed population models between two periods for
407 a population that is likely to be open in nature may not be ideal and intuitively should be
408 accepted with caution, such a comparison was called for given the lack of such information on
409 the species and resulting uncertainty regarding its conservation status in the country. Moreover,
410 comparison of mean group sizes between the two periods 2002-2003 and 2014-2016 also
411 showed a substantial decrease that corroborated the model-estimated decline in abundance
412 during the same period. While the causes of the apparent changes are not yet well known,
413 precautionary measures or controls to prevent and mitigate disturbance to the population and
414 also that of the sympatric, Endangered *S. plumbea* are advised, especially with regard to
415 potential disturbance associated with marine tourism activities. The results of this study
416 highlight the need for further research and monitoring in the area as well as the importance of
417 assessing abundance changes at other sites to inform revision of *T. aduncus* conservation status
418 in South Africa.

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426

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428

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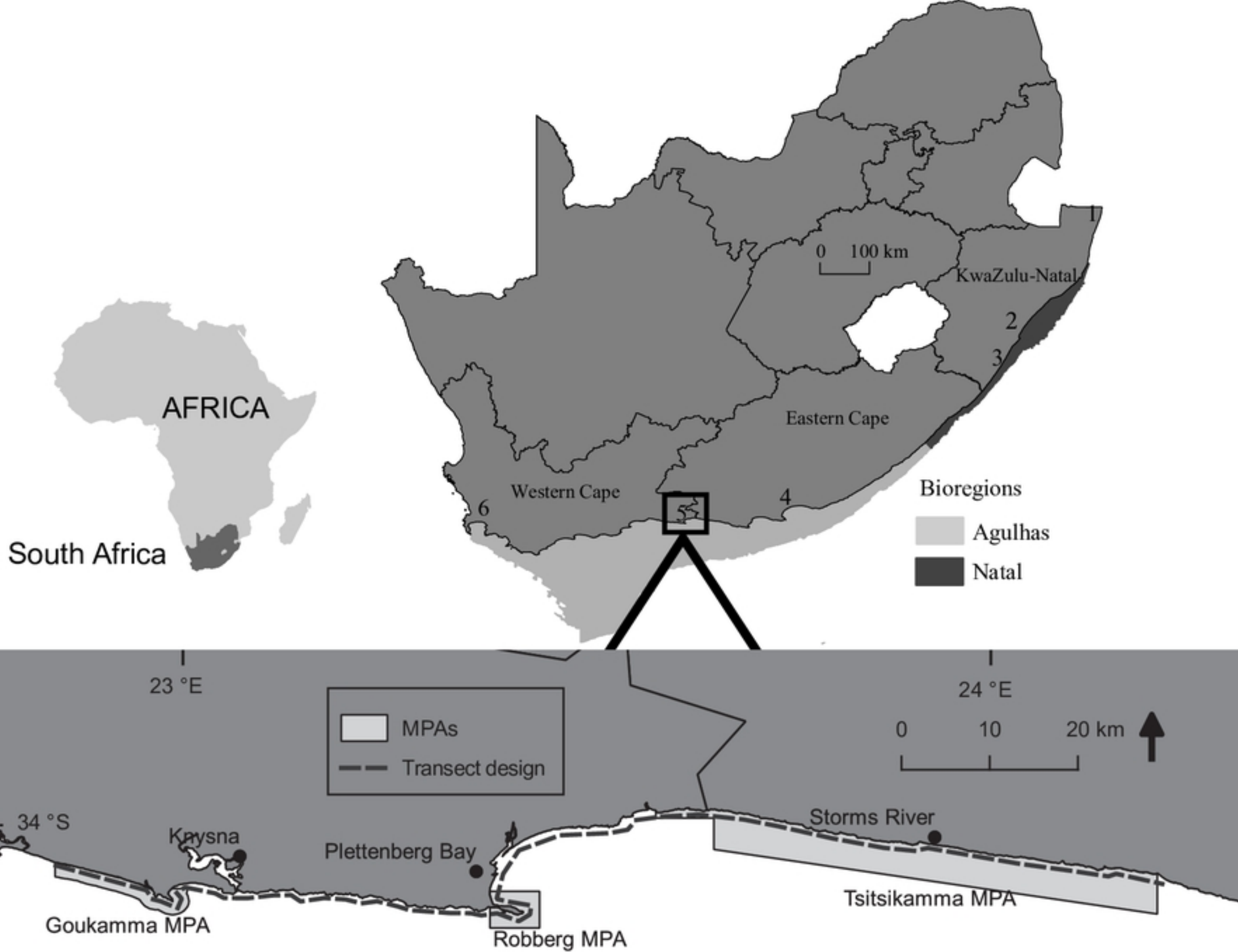


Figure 1 Map

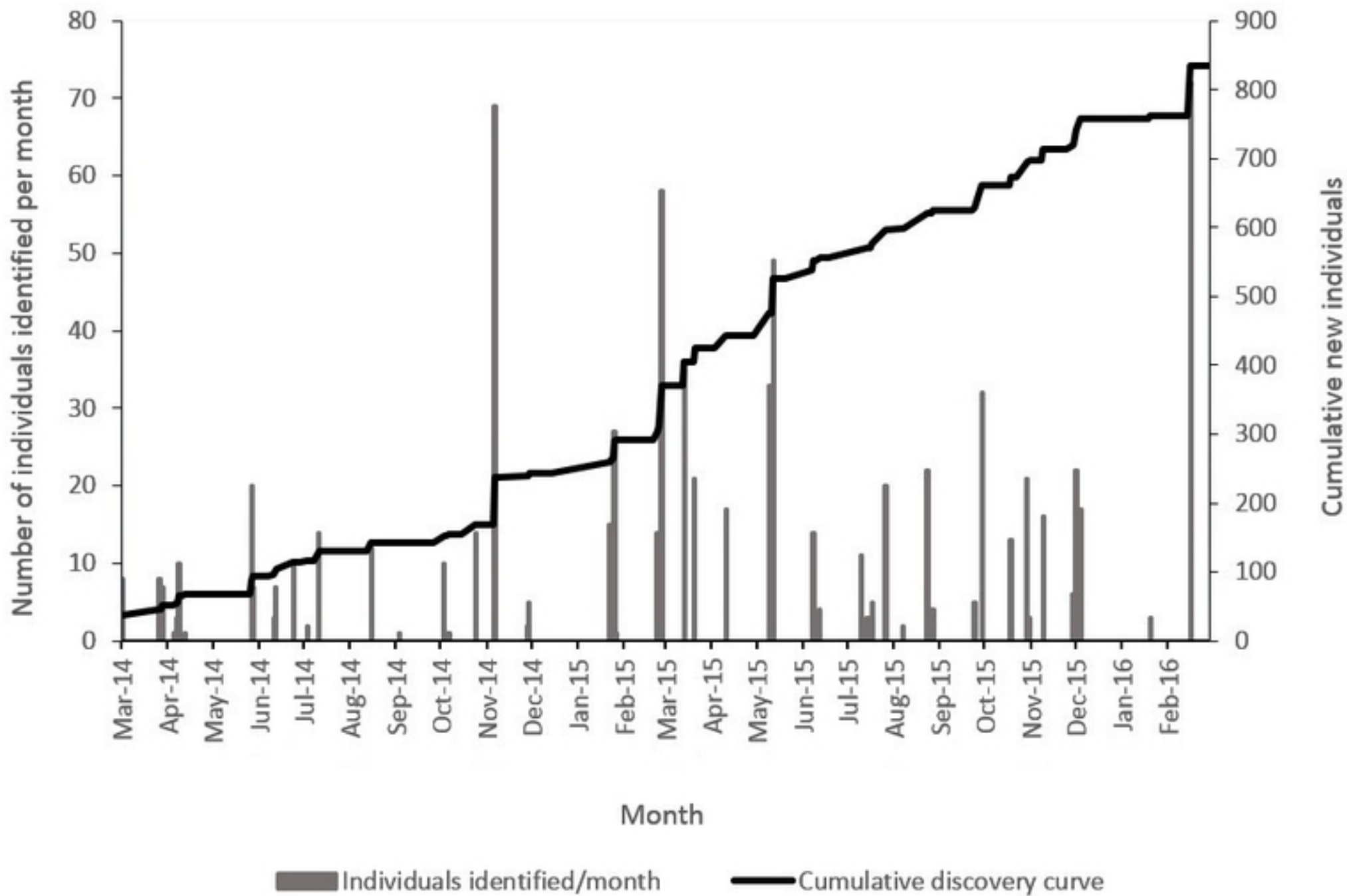


Figure 2 Curve