Estimates of abundance and apparent survival of coastal dolphins in Port Essington harbour, Northern Territory, Australia

Carol Palmer, Lyndon Brooks, Guido J. Parra, Tracey Rogers, Debra Glasgow and John C. Z. Woinarski

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The figures for s.e. (\(N_{\text{total}}\)) for humpback and bottlenose dolphins were incorrect as published in the Abstract and column 9 of Table 4 and should appear as shown below (see bold in the Abstract, and grey shading in the table). The errors were due to transcription error and in no way affect the outcome and conclusions of the study.

Abstract

Key results. Abundance estimates for the three species varied across the sampling periods, with the estimated number of Australian snubfin dolphins ranging from 136 (s.e. 62) to 222 (s.e. 48); from 48 (s.e. 17) to 207 (s.e. 65) for the Australian humpback dolphin; and 34 (s.e. 16) to 75 (s.e. 26) for the bottlenose dolphin.

Table 4. Estimates of the total marked population size (\(N_m\)) and total population size (\(N_{\text{total}}\)) of coastal dolphins in Port Essington harbour, with log-normal 95% lower and upper confidence intervals (by session) and coefficient of variance (CV)

<table>
<thead>
<tr>
<th>Species</th>
<th>Session</th>
<th>Period (mm/yy)</th>
<th>(N_m)</th>
<th>s.e. ((N_m))</th>
<th>95% CI</th>
<th>CV</th>
<th>(N_{\text{total}})</th>
<th>s.e. ((N_{\text{total}}))</th>
<th>95% CI</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snubfin</td>
<td>S1</td>
<td>11/08</td>
<td>93</td>
<td>34</td>
<td>26–159</td>
<td>0.37</td>
<td>153</td>
<td>57</td>
<td>76–310</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>09/09</td>
<td>101</td>
<td>38</td>
<td>27–175</td>
<td>0.38</td>
<td>167</td>
<td>63</td>
<td>81–342</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>S3</td>
<td>11/09</td>
<td>82</td>
<td>37</td>
<td>10–155</td>
<td>0.45</td>
<td>136</td>
<td>62</td>
<td>58–317</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>S4</td>
<td>09/09</td>
<td>131</td>
<td>54</td>
<td>241–238</td>
<td>0.42</td>
<td>216</td>
<td>90</td>
<td>98–475</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>S5</td>
<td>11/10</td>
<td>134</td>
<td>28</td>
<td>80–189</td>
<td>0.20</td>
<td>222</td>
<td>48</td>
<td>146–336</td>
<td>0.21</td>
</tr>
<tr>
<td>Humpback</td>
<td>S1</td>
<td>06/08</td>
<td>29</td>
<td>10</td>
<td>9–49</td>
<td>0.34</td>
<td>48</td>
<td>17</td>
<td>24–95</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>09/08</td>
<td>44</td>
<td>13</td>
<td>18–69</td>
<td>0.30</td>
<td>72</td>
<td>22</td>
<td>40–131</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>S3</td>
<td>11/08</td>
<td>49</td>
<td>16</td>
<td>17–80</td>
<td>0.32</td>
<td>80</td>
<td>26</td>
<td>43–151</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>S4</td>
<td>09/09</td>
<td>35</td>
<td>13</td>
<td>61–58</td>
<td>0.37</td>
<td>58</td>
<td>21</td>
<td>29–117</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>S5</td>
<td>11/09</td>
<td>58</td>
<td>17</td>
<td>24–91</td>
<td>0.37</td>
<td>95</td>
<td>30</td>
<td>52–173</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>S6</td>
<td>03/10</td>
<td>31</td>
<td>12</td>
<td>7–54</td>
<td>0.40</td>
<td>51</td>
<td>20</td>
<td>24–106</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>S7</td>
<td>06/10</td>
<td>126</td>
<td>39</td>
<td>49–202</td>
<td>0.31</td>
<td>207</td>
<td>65</td>
<td>113–379</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>S8</td>
<td>11/10</td>
<td>88</td>
<td>21</td>
<td>49–127</td>
<td>0.22</td>
<td>145</td>
<td>35</td>
<td>92–231</td>
<td>0.24</td>
</tr>
<tr>
<td>Bottlenose</td>
<td>S1</td>
<td>06/08</td>
<td>21</td>
<td>7</td>
<td>7–35</td>
<td>0.33</td>
<td>39</td>
<td>13</td>
<td>20–75</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>03/09</td>
<td>32</td>
<td>11</td>
<td>1–53</td>
<td>0.35</td>
<td>59</td>
<td>22</td>
<td>29–118</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>S3</td>
<td>09/09</td>
<td>41</td>
<td>13</td>
<td>15–66</td>
<td>0.32</td>
<td>75</td>
<td>26</td>
<td>39–154</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>S4</td>
<td>11/09</td>
<td>18</td>
<td>9</td>
<td>1–36</td>
<td>0.50</td>
<td>34</td>
<td>16</td>
<td>14–83</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>S5</td>
<td>09/10</td>
<td>37</td>
<td>16</td>
<td>1–72</td>
<td>0.50</td>
<td>68</td>
<td>31</td>
<td>29–159</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>S6</td>
<td>11/10</td>
<td>26</td>
<td>13</td>
<td>1–50</td>
<td>0.47</td>
<td>48</td>
<td>24</td>
<td>19–123</td>
<td>0.50</td>
</tr>
</tbody>
</table>
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Abstract

Context. Three dolphin species occur in coastal waters of monsoonal northern Australia: the Australian snubfin (Orcaella heinsohni), humpback (Sousa sp.) and the bottlenose (Tursiops sp.). Their overall population size and trends are poorly known, and their conservation status has been difficult to resolve, but can be expected to deteriorate with likely increased development pressures.

Aims. We sought to provide an estimate of abundance, and apparent survival, of the three dolphin species at the largely undeveloped harbour of Port Essington (325 km²), Northern Territory, with repeated sampling over a 2.9-year period. Given increasing obligations to undertake population assessments for impact studies at proposed development sites, we assess the strengths and limitations of a systematic sampling program.

Methods. We used photo-identification data collected during systematic boat-based transect surveys undertaken from 2008 to 2010 and Pollock’s robust capture–recapture design model.

Key results. Total abundance estimates for the three species were variable across different sampling periods. The estimated number of individuals in the sampled area varied per sampling episode from 136 (s.e. 62) to 222 (s.e. 48) for snubfin, from 48 (s.e. 7) to 207 (s.e. 14) for humpbacks and from 34 (s.e. 6) to 75 (s.e. 9) for bottlenose dolphins. Apparent survival was estimated for snubfin at 0.81 (s.e. 0.11), humpbacks at 0.59 (s.e. 0.12) and bottlenose at 0.51 (s.e. 0.17) per annum.

Key conclusions. (1) The values derived here provide some of the only estimates of local population size for these species across monsoonal northern Australia; (2) population-size estimates varied considerably among seasons or sampling episodes; (3) the low apparent survival probabilities indicated that many individuals may move at scales larger than the study area; (4) density of snubfin and humpback dolphins in the present study area exceeded the few other estimates available for these species elsewhere in Australia.

Implications. The present study provided the first baseline estimates of abundance and apparent survival for three coastal dolphin species in monsoonal northern Australia. Such information is becoming increasingly important as development pressures intensify in coastal areas. Sampling protocols for future monitoring and impact assessment need an enhanced consideration of seasonality and scale issues.

Additional keywords: Australian snubfin, bottlenose, capture–recapture, Indo-Pacific humpback, Orcaella heinsohni, photo identification, robust design, Sousa chinensis, Tursiops sp.

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Introduction

Coastal and river dolphins are threatened by a range of human activities (Borobia et al. 1991; Thompson et al. 2000; Kreb and Budino 2005; Cantor et al. 2012), and several species (i.e. vaquita, Phocoena sinus; Hector’s dolphin, Cephalorhynchus hectori) are now among the world’s most threatened mammals (Rojas-Bracho et al. 2006; Reeves et al. 2013). By global standards, the coastal waters of Australia are relatively undisturbed (Halpern et al. 2008; Edyvane and Dethmers 2010). There are now increasing prospects and proposals for development in coastal waters of northern Australia, and, consequently, there are concerns about the conservation of the following three species of coastal dolphins occurring in these waters (Parra et al. 2006; Allen et al. 2012; Bejder et al. 2012; Cagnazzi et al. 2013; Palmer et al. 2014): the Australian snubfin, Orcaella heinsohni (hereafter snubfin), a new as-yet-unnamed species of humpback dolphin, Sousa sp. (Frère et al. 2011; Mendez et al. 2013), and the bottlenose dolphins, Tursiops sp. (hereafter bottlenose). Tursiops taxonomy is unresolved and at present T. truncatus (Montagu, 1821) and T. aduncus (Ehrenberg, 1833) are recognised in the Indo-Pacific region (Rice 1998; Kemper 2004). In Australian waters, until recently, all Tursiops were recorded as T. truncatus (Ross and Cockcroft 1990; Charlton-Robb et al. 2011); however, T. aduncus is now known to occur in estuarine and coastal waters of eastern Australia (Möller and Beheregaray 2001; Fury and Harrison 2008). In Western Australia, both aduncus- and truncatus-type haplotypes are present in coastal waters (Krützen et al. 2004). In the present study, we treat all records of Tursiops as T. sp.

Table 1. Collation of abundance estimates for coastal dolphin species in Northern Territory (NT), Queensland (Qld), Western Australia (WA) and New South Wales (NSW)

<table>
<thead>
<tr>
<th>Species</th>
<th>Study site (approx. area)</th>
<th>Population estimate</th>
<th>Approximate density</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Orcaella heinsohni</em></td>
<td>Port Essington, NT (325 km²)</td>
<td>136–222</td>
<td>0.42–0.68</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>Cleveland Bay, Qld (310 km²)</td>
<td>64–76</td>
<td>0.21–0.25</td>
<td>Parra et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>Keppel Bay (980 km²)</td>
<td>65–84</td>
<td>0.06–0.08</td>
<td>Cagnazzi et al. (2013)</td>
</tr>
<tr>
<td><em>Sousa</em> sp.</td>
<td>Port Essington, NT (325 km²)</td>
<td>48–207</td>
<td>0.15–0.64</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>Cleveland Bay, Qld (310 km²)</td>
<td>34–54</td>
<td>0.11–0.17</td>
<td>Parra et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>Moreton Bay, Qld (1351 km²)</td>
<td>119–163</td>
<td>0.09–0.12</td>
<td>Corkeron et al. (1997)</td>
</tr>
<tr>
<td></td>
<td>Great Sandy Strait, Qld (~1000 km²)</td>
<td>150</td>
<td>0.15</td>
<td>Cagnazzi et al. (2011)</td>
</tr>
<tr>
<td><em>Tursiops</em> sp.</td>
<td>Port Essington, NT (325 km²)</td>
<td>34–75</td>
<td>0.10–0.13</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>Shark Bay, WA (14096 km²)</td>
<td>2000–3000</td>
<td>0.13–0.20</td>
<td>Preen et al. (1997)</td>
</tr>
<tr>
<td></td>
<td>Useless Loop area (Shark Bay), WA (226 km²)</td>
<td>115–208</td>
<td>0.51–0.92</td>
<td>Nicholson et al. (2012)</td>
</tr>
<tr>
<td></td>
<td>Bunbury, WA (120 km²)</td>
<td>63–139</td>
<td>0.53–1.16</td>
<td>Smith et al. (2013)</td>
</tr>
<tr>
<td><em>Tursiops aduncus</em></td>
<td>Moreton Bay, Qld (1300 km²)</td>
<td>510–598</td>
<td>0.39–0.46</td>
<td>Ansmann et al. (2013)</td>
</tr>
<tr>
<td></td>
<td>Point Lookout, Qld (150 km²)</td>
<td>806–861</td>
<td>5.37–5.74</td>
<td>Chilvers and Corkeron (2003)</td>
</tr>
<tr>
<td></td>
<td>Moreton Bay, Qld (350 km²)</td>
<td>673–818</td>
<td>1.92–2.34</td>
<td>Lukoschek and Chilvers (2008)</td>
</tr>
<tr>
<td></td>
<td>Clarence River estuary, NSW (89 km²)</td>
<td>71</td>
<td>0.80</td>
<td>Fury and Harrison (2008)</td>
</tr>
<tr>
<td></td>
<td>Richmond River estuary, NSW (19 km²)</td>
<td>34</td>
<td>1.79</td>
<td>Fury and Harrison (2008)</td>
</tr>
<tr>
<td></td>
<td>Point Stephens, NSW (140 km²)</td>
<td>61–108</td>
<td>0.44–0.77</td>
<td>Möller et al. (2002)</td>
</tr>
<tr>
<td></td>
<td>Jervis Bay, NSW (102 km²)</td>
<td>143–160</td>
<td>1.40–1.57</td>
<td>Möller et al. (2002)</td>
</tr>
</tbody>
</table>

Note that differences among studies may reflect real differences in density, but may also be influenced by the design, methodology and duration of the study.
population estimation based on capture–recapture methods, where resightings of distinctively marked individuals constitute recaptures (Hammond and Thompson 1991).

There are two general types of models (closed- and open-population models) used in capture–recapture studies, to calculate abundance estimates over multiple sampling periods (Pollock et al. 1990; Williams et al. 2002). Closed-population models assume that the population remains unchanged for the duration of the study (i.e. no gains through births or immigration, nor losses through deaths or emigration). Closed-populations models are applied to short-term studies and can accommodate variation in capture probabilities by sampling occasion (time), individual animal response (heterogeneity) and behavioural response to first capture (‘behaviour’ – ‘trap happy’ and ‘trap shy’ responses) (Otis et al. 1978). Open-population models allow for demographic changes in the population over time, including gains (births, immigration) and losses (mortality, emigration) (Pollock et al. 1990; Williams et al. 2002). Such models can be used to estimate abundance at each sampling occasion, and the probability of apparent survival (alive and remaining in the sampling area) (Lebreton et al. 1992) and apparent births (born or immigrated) between sampling occasions (Jolly 1965; Seber 1965; Crosbie and Manly 1985; Schwarz and Arnason 1996). Open models cannot accommodate variation in capture probabilities, except by time, and may produce biased estimates in the presence of individual heterogeneity (downward bias) or behavioural response to first capture (trap happy = downward bias; trap shy = upward bias) (Pollock et al. 1990; Williams et al. 2002).

Pollock (1982) proposed a sampling regime (the robust design) of primary samples separated by time scales that would allow gains and losses from the population, with each primary sample composed of a set of sufficiently closely spaced secondary samples for population closure to be assumed. The combination of both open- and closed-population models within the robust design allows abundance to be estimated for each primary sampling period and apparent survival to be estimated between primary sampling periods. Kendall et al. (1995, 1997) and Kendall and Nichols (1995) further developed the robust design model and incorporated estimation of temporary emigration between primary samples. This is an advance on standard open-population models in which all immigration and emigration are assumed permanent. Examples of robust-design studies on coastal dolphins include Balmer et al. (2008), Rosel et al. (2011) and Smith et al. (2013).

Here, we use photo-identification data collected in Port Essington harbour, in the Northern Territory, from 2008–2010 and Pollock’s robust capture–recapture design model to provide baseline estimates of abundance and apparent survival of three species of tropical coastal dolphins (snubfin, humpback and bottlenose). These estimates are the first robust population estimates for monsoonal northern Australia and provide a baseline for future comparisons, which will become increasingly important as development pressures intensify in this region. We evaluate the strengths and limitations of this protocol, with particular reference to the increasing need for population assessments for environmental impact studies, and with reference to the developing need (e.g. Beasley et al. 2012a, 2012b) for national programs for monitoring coastal dolphins.

Materials and methods

Study site

Port Essington harbour (11.23°S, 132.15°E) is located within the Garig Gunak Barlu National Park, ~220 km north-east of Darwin (Fig. 1) and is the only National Park in the Northern Territory that contains adjoining land and marine areas. Port Essington harbour comprises a semi-enclosed 325 km² former river valley that was drowned during periods of sea-level rise and now forms a largely sheltered and deeply incised harbour. The harbour provides varied environments that are distinct from the open water areas of the adjacent Van Diemen’s Gulf and the Arafura Sea. There are no major creeks or rivers flowing into Port Essington harbour and, consequently, there is restricted freshwater input. Within the harbour, tides range between 2 and 2.5 m, and turbidity is relatively low compared with many other parts of the Northern Territory. Within the Marine Park and surrounding waters, there is a relative lack of commercial shipping, almost no onshore development and limited aquaculture.

Field methods

Boat-based photo-identification surveys were conducted in Port Essington harbour from March 2008 to November 2010 (Fig. 2). Seasonal patterns of habitat use and dispersal are very poorly known for these species, so sampling was deliberately timed to attempt to encompass and represent the extent of seasonal variation (i.e. late wet season (March), mid-dry season (June), late dry season (September), and early wet and build-up (November)). Surveys followed a pre-determined set of fixed transect lines (total distance = 45 km) parallel to the shore and ~300–1000 m from the shore, depending on tide state, but depth remained approximately the same (Fig. 2). Transects were located in areas with expected higher rates of sighting detectability, and were sited to focus particularly on areas least exposed to rough seas and, therefore, reasonable sea-state conditions.

Most studies have indicated that these animals occur mainly in shallow coastal waters (Parra 2006; Parra et al. 2006; Cagnazzi et al. 2013). Given the above and taking into consideration that these are highly mobile animals that are likely to visit most of the space at some time, our estimates should not include substantial biases as a result of sampling design. A survey consisted of completing all transects, or as many transects as possible, in one day when weather and sea-state conditions permitted (Beaufort Sea states <3; swell less than 1 m and in daylight hours). Four survey sessions were conducted each year in March, June, September and November (primary sampling periods) and in which six consecutive survey days (secondary sampling periods) of sampling were attempted but not always achieved, because of weather constraints per session (Table 2). Sampling across this range of seasonal conditions was also designed to provide some context for the typically limited sampling undertaken for development impact assessments (which may often include only a single sampling event at one time of year).

Surveys were conducted from a 5.5-m aluminium vessel with a 100-hp four-stroke outboard engine, with the boat driver and one or two observers. Surveys followed transect lines at 15–20 km h⁻¹ until a dolphin or dolphin group was sighted. When dolphins were sighted, the observer(s) attempted to take good-quality images of...
Fig. 1. Cobourg Peninsula in relation to the Darwin (the capital city of the Northern Territory) and Port Essington harbour.

Fig. 2. The study area covered an area of ~325 km² in Port Essington harbour, Cobourg Peninsula, Northern Territory. Dashed lines indicate transects, which were surveyed using boat-based photo-identification techniques.
every dolphin dorsal fin in the group. A dolphin group was defined as all dolphins within a 100-m radius of any other dolphin that was involved in similar behavioural activities (Irvine et al. 1981; Wells et al. 1987; Parra et al. 2006; Fury and Harrison 2008). Data for each group on species identification, location and time of day, group size and behaviour were recorded on a hand-held Personal Digital Assistant using Cybertracker software (www.cybertracker.org, verified 11 March 2014). Sampling could not reliably distinguish the sex of individuals, and hence this factor is not considered in subsequent analyses here.

**Image and data analysis**

Dolphins of each species were identified by the location and number of nicks and scars on their dorsal fins (Würsig and Jefferson 1990; Hammond and Thompson 1991; Parra and Corkeron 2001). Calves were excluded from analysis because they are generally unmarked. Pigmentation patterns were used as secondary characteristics to confirm identification for humpback dolphins. Individuals were photographed independently of their distinctiveness. All images were classified into three grades (excellent, good and poor) on the basis on focus, relative angle to the dolphin and contrast. Only images graded as excellent and good were used to identify animals, develop identification catalogues for each species and individual capture histories for population analysis (Würsig and Jefferson 1990; Parra et al. 2006).

**Estimating marked proportion and total abundance**

Not all individual dolphins have sufficiently distinctive marks to support unambiguous identification. To include the unmarked portions of the populations in our estimates, we estimated the proportion of distinctively marked dolphins in the population of each species (Wilson et al. 1999). The (distinctively) marked proportion ($M_p$) of each population was estimated by dividing the number of excellent- and good-quality photographs of marked dolphins ($P_m$) by the total number of excellent- and good-quality photographs ($P$), as follows:

$$M_p = P_m / P,$$

with

$$\hat{SE}(M_p) = \sqrt{M_p(1 - M_p)/P}.$$

The total abundance ($N_{total}$) of each population for any sampling period was then estimated by dividing the estimated abundance of marked dolphins ($N_{marked}$) by the estimated marked proportion, as follows:

$$\hat{N}_{total} = \hat{N}_{marked} / \hat{M}_p,$$

with

$$\hat{SE}(\hat{N}_{total}) = \hat{N}_{marked} \sqrt{Var(\hat{N}_{marked})/\hat{M}_p^2 + Var(\hat{M}_p)}/(\hat{M}_p)^2.$$

Log-normal confidence intervals for abundance estimates were calculated following Burnham et al. (1987), as follows:

$$\hat{N}_{lower} = \hat{N}/C \text{ and } \hat{N}_{upper} = \hat{N} \cdot C,$$

where

$$C = \exp\left(\frac{\hat{z}_{a/2}}{2}\sqrt{\log \left[1 + (\hat{SE}(\hat{N})/\hat{N})^2\right]}\right).$$

**Statistical analysis**

The robust-design model (closed-captures type) was fitted to the mark–recapture data to estimate abundance and survival parameters by using program MARK (V 6.1; White and Burnham 1999). The intervals between primary samples were specified in decimal years between their mid-dates to obtain consistent, per annum estimates of apparent survival. The relationships between the probabilities of apparent survival ($\phi$), true (biological) survival ($S$), fidelity ($F$) and permanent emigration ($E$) may be expressed as

$$\phi = S \times F, F = (1 - E).$$

The parameters estimated by the robust design model (closed captures) are:

1. $S$, apparent survival to primary sample $j$ for $j > 1$,
2. $\delta^u$ probability of temporarily emigrating before sample $j$ given presence at $j-1$ for $j > 1$, 

Table 2. Summary table of the data analysed, structured into primary sampling sessions, number of secondary sampling days and the number of individually marked dolphins identified and subsequently recaptured in Port Essington harbour

<table>
<thead>
<tr>
<th>Year</th>
<th>Start date</th>
<th>End date</th>
<th>Primary sample</th>
<th>No. of secondary samples (days)</th>
<th>Snubfin Marked individuals (total recaptured)</th>
<th>Primary samples analysed</th>
<th>Humpback Marked individuals (total recaptured)</th>
<th>Primary samples analysed</th>
<th>Bottlenose Marked individuals (total recaptured)</th>
<th>Primary samples analysed</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>8 Mar.</td>
<td>13 Mar.</td>
<td>1</td>
<td>4</td>
<td>No</td>
<td>5</td>
<td>No</td>
<td>5</td>
<td>No</td>
<td>0</td>
</tr>
<tr>
<td>14 June</td>
<td>19 June</td>
<td>2</td>
<td>6</td>
<td>6</td>
<td>No</td>
<td>3 (0)</td>
<td>Yes</td>
<td>9 (1)</td>
<td>Yes</td>
<td>13 (3)</td>
</tr>
<tr>
<td>2009</td>
<td>21 Mar.</td>
<td>26 Mar.</td>
<td>5</td>
<td>3</td>
<td>No</td>
<td>11 (1)</td>
<td>No</td>
<td>1 (0)</td>
<td>Yes</td>
<td>11 (0)</td>
</tr>
<tr>
<td>June</td>
<td>June 6</td>
<td>26 Nov.</td>
<td>8</td>
<td>5</td>
<td>Yes</td>
<td>12 (3)</td>
<td>Yes</td>
<td>15 (2)</td>
<td>Yes</td>
<td>6 (1)</td>
</tr>
<tr>
<td>2010</td>
<td>6 Mar.</td>
<td>11 Mar.</td>
<td>9</td>
<td>4</td>
<td>No</td>
<td>7 (0)</td>
<td>Yes</td>
<td>8 (1)</td>
<td>No</td>
<td>0</td>
</tr>
<tr>
<td>25 Sep.</td>
<td>30 Sep.</td>
<td>12</td>
<td>6</td>
<td>6</td>
<td>Yes</td>
<td>63 (10)</td>
<td>Yes</td>
<td>30 (2)</td>
<td>Yes</td>
<td>5 (0)</td>
</tr>
</tbody>
</table>
(3) $\delta_i$ probability of temporarily emigrating before sample $j$ given absence at $j-1$ for $j > 2$,
(4) $p_{ij}$ probability of first capture in sample $i$ of primary sample $j$ for $i \geq 1$,
(5) $c_{ij}$ probability of recapture in sample $i$ of primary sample $j$ for $i > 1$,
(6) $N_j$ population size during primary sample $j$.

These models may estimate temporary emigration as random or Markovian. When the two temporary emigration parameters, $\delta$ and $\delta'$, are set equal at all times $j$, the temporary emigration estimated is random (the probability that an animal temporarily emigrates is independent of its state on the previous occasion); when $\delta' \neq \delta'$, the temporary emigration estimated is Markovian (the probability that an animal temporarily emigrates is dependent on its state on the previous occasion; i.e. there is a temporally structured process underlying the movements (e.g. breeding: Kendall and Bjorkland 2001). When apparent survival is estimated as time varying, it is necessary to constrain each of the last $\delta_i$ and $\delta'$ to equal their values at some earlier occasion to attain parameter identification in Markovian models. The number of parameters for each model was set at the number nominally estimated by the model independently of whether some were at the boundaries of possible values and not counted by MARK (see e.g. Jolly–Seber models in MARK, Schwarz and Arnason in White and Burnham 1999). Models were compared with the Akaike information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002), with smaller values of AICc indicating the better-fitting models, and with AICc weights, which measure the relative likelihoods of the models in the set.

**Goodness-of-fit tests**

There is no goodness-of-fit test for the robust-design model as a whole; however, separate tests for the open and closed parts of the model can be applied. Each set of secondary samples was tested for closure using CloseTest (Stanley and Burnham 1999) and the data were collapsed to primary samples and goodness of fit was tested in the Cormack–Jolly–Seber (CJS) framework using program RELEASE (as implemented in MARK (Cooch and White 2012) and by means of the median goodness-of-fit test (Cooch and White 2012).

**Results**

**Survey effort**

In total, 65 days of surveys were completed between March 2008 and November 2010, covering 2279 km on transect. During this period, 485 snubfin, 274 humpback and 165 bottlenose dolphins were recorded. Among these groups, 179 distinctively marked snubfin, 113 humpback and 53 bottlenose were identified in total. The proportion of marked individuals was high for each species ($M_p \pm SE(M_p)$), namely, 0.61 ± 0.033 for snubfin, 0.61 ± 0.043 for humpback and 0.54 ± 0.058 for bottlenose. During the last primary sample for the project (November 2010), there was an influx of 26 marked snubfin and 15 humpback dolphins not previously photographed. Densities in Port Essington are higher than other reported values for snubfin and humpback and lower than in other reported studies for bottlenose (Table 1).

**Data**

Primary samples included in the robust-design model analysis were selected if they yielded reasonable estimates from closed models (Table 2). This was assessed by attempting to fit closed models to the within-session data and rejecting sessions that yielded estimates with unacceptably large standard errors. The resulting data included 124 snubfins captured 165 times over five primary samples, 74 humpbacks captured 102 times over eight primary samples and 38 bottlenose captured 52 times over six primary samples. The primary samples taken during September and November of each year rendered the most captures (Table 2).

**Goodness-of-fit tests**

CloseTest did not reject the assumption of closure for any primary sample of any species ($P > 0.05$ in all cases). Goodness-of-fit tests from program RELEASE found no evidence of over-dispersion for snubfin ($\chi^2 = 0.39$, $P = 0.821$) and humpback ($\chi^2 = 11.47$, $P = 0.571$), whereas there were insufficient data for the test for bottlenose dolphins. Estimates of median, $c$, were 0.99 for snubfin, 0.91 for humpback and 0.58 for bottlenose. No adjustments were made to $c$ for the models for any species.

**Robust-design analyses**

**Snubfin dolphins**

Eight Pollock’s robust-design models were fitted to the snubfin capture-recapture data (Table 3). Preliminary analyses found that no useful parameter estimate could be obtained from models including heterogeneity (latent mixtures type), and that models with simplified temporal structures for capture probabilities fitted very poorly. Therefore, all models reported have capture probabilities varying by both primary and secondary sample, i.e. $p(S^*)$, and none estimates heterogeneity (see Table 3 legend for symbols used to specify models).

The best-fitting (lowest AICc) model $\{p(S^*), g(FIXED=0)\} p(S^*)c(=p)N$ with constant probability of apparent survival, no temporary emigration, fully time-varying capture probabilities and no behavioural response attracted 73% of the AICc weight. The resulting estimated abundance of marked snubfin from this model varied over the five primary samples between 82 (s.e. 37, 95% CI = 10–155) and 134 (s.e. 28, 95% CI = 80–189); and the total abundance varied over primary samples between 136 (s.e. 61, 95% CI = 58–317) and 222 (s.e. 48, 95% CI = 146–336) (Table 4). The average apparent survival probability was 0.80 (s.e. 0.11, 95% CI = 0.50–0.94) per annum.

**Humpback dolphins**

Five Pollock’s robust-design models were fitted to the humpback capture-recapture data (Table 3). The best-fitting model $\{p(S^*), g(FIXED=0)\} p(=p)N$ with constant probability of apparent survival, no temporary emigration, constant capture probability and no behavioural response attracted 99% of the AICc weight. The estimated abundance of marked humpbacks varied across eight primary samples, between
Table 3. Sets of Pollock’s robust-design models fitted to the capture–recapture data on three species of coastal dolphins from Port Essington harbour

<table>
<thead>
<tr>
<th>Species</th>
<th>Robust-design model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>ΔAICc</th>
<th>Model weight</th>
<th>Model likelihood</th>
<th>No. of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snubfin</td>
<td><em>(phi(.)g(FIXED = 0)p(S</em>t)c(= p)N(t))</td>
<td>139.51</td>
<td>0</td>
<td>0.001</td>
<td>14</td>
<td>31</td>
<td>32</td>
</tr>
<tr>
<td>Humpback</td>
<td><em>(phi(.)g(S2 = 4)p(S</em>t)c(= p)N(t) – Markov)</td>
<td>150.48</td>
<td>10.97</td>
<td>0.004</td>
<td>0.004</td>
<td>14</td>
<td>17</td>
</tr>
<tr>
<td>Bottlenose</td>
<td>*(phi(.)g(FIXED = 0)p(.)c(= p)N(t))</td>
<td>150.48</td>
<td>10.97</td>
<td>0.004</td>
<td>0.004</td>
<td>14</td>
<td>17</td>
</tr>
</tbody>
</table>

29 (s.e. 10, 95% CI = 10–49) and 126 (s.e. 39, 95% CI = 49–202), and the estimated total abundance varied across primary samples between 48 (s.e. 7, 95% CI = 24–95) and 207 (s.e. 14, 95% CI = 113–379) (Table 4). The estimated average apparent annual survival probability was 0.59 (s.e. 0.12, 95% CI = 0.35–0.79).

Table 4. Estimates of the total marked population size (\(\hat{N}_m\)) and total population size (\(\hat{N}_{total}\)) of coastal dolphins in Port Essington harbour, with log-normal 95% lower and upper confidence intervals (by session) and coefficient of variance (CV)

<table>
<thead>
<tr>
<th>Species</th>
<th>Session</th>
<th>Period (mm/yy)</th>
<th>(\hat{N}_m)</th>
<th>s.e. ((\hat{N}_m))</th>
<th>95% CI</th>
<th>CV</th>
<th>(\hat{N}_{total})</th>
<th>s.e. ((\hat{N}_{total}))</th>
<th>95% CI</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snubfin</td>
<td>S1</td>
<td>11/08</td>
<td>93</td>
<td>34</td>
<td>26–159</td>
<td>0.37</td>
<td>153</td>
<td>57</td>
<td>76–310</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>09/09</td>
<td>101</td>
<td>38</td>
<td>27–175</td>
<td>0.38</td>
<td>167</td>
<td>63</td>
<td>81–342</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>S3</td>
<td>11/09</td>
<td>82</td>
<td>37</td>
<td>10–155</td>
<td>0.45</td>
<td>136</td>
<td>62</td>
<td>58–317</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>S4</td>
<td>09/09</td>
<td>131</td>
<td>54</td>
<td>241–238</td>
<td>0.42</td>
<td>216</td>
<td>90</td>
<td>98–475</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>S5</td>
<td>11/10</td>
<td>134</td>
<td>28</td>
<td>80–189</td>
<td>0.20</td>
<td>222</td>
<td>48</td>
<td>146–336</td>
<td>0.21</td>
</tr>
<tr>
<td>Humpback</td>
<td>S1</td>
<td>06/08</td>
<td>29</td>
<td>10</td>
<td>9–49</td>
<td>0.34</td>
<td>48</td>
<td>7</td>
<td>24–95</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>09/09</td>
<td>44</td>
<td>13</td>
<td>18–69</td>
<td>0.30</td>
<td>72</td>
<td>8</td>
<td>40–131</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>S3</td>
<td>11/08</td>
<td>49</td>
<td>16</td>
<td>17–80</td>
<td>0.32</td>
<td>80</td>
<td>9</td>
<td>43–151</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>S4</td>
<td>09/09</td>
<td>35</td>
<td>13</td>
<td>61–58</td>
<td>0.37</td>
<td>58</td>
<td>8</td>
<td>29–117</td>
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</tr>
<tr>
<td></td>
<td>S5</td>
<td>11/08</td>
<td>58</td>
<td>17</td>
<td>24–91</td>
<td>0.37</td>
<td>95</td>
<td>10</td>
<td>52–173</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>S6</td>
<td>03/10</td>
<td>31</td>
<td>12</td>
<td>7–54</td>
<td>0.40</td>
<td>51</td>
<td>7</td>
<td>24–106</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>S7</td>
<td>06/10</td>
<td>126</td>
<td>39</td>
<td>49–202</td>
<td>0.31</td>
<td>207</td>
<td>14</td>
<td>113–379</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>S8</td>
<td>11/10</td>
<td>88</td>
<td>21</td>
<td>49–127</td>
<td>0.22</td>
<td>145</td>
<td>12</td>
<td>92–231</td>
<td>0.24</td>
</tr>
<tr>
<td>Bottlenose</td>
<td>S1</td>
<td>06/08</td>
<td>21</td>
<td>7</td>
<td>7–35</td>
<td>0.33</td>
<td>39</td>
<td>6</td>
<td>20–75</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>03/09</td>
<td>32</td>
<td>11</td>
<td>1–53</td>
<td>0.35</td>
<td>59</td>
<td>8</td>
<td>29–118</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>S3</td>
<td>09/09</td>
<td>41</td>
<td>13</td>
<td>15–66</td>
<td>0.32</td>
<td>75</td>
<td>9</td>
<td>39–154</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>S4</td>
<td>11/09</td>
<td>18</td>
<td>9</td>
<td>1–36</td>
<td>0.50</td>
<td>34</td>
<td>6</td>
<td>14–83</td>
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<tr>
<td></td>
<td>S5</td>
<td>09/10</td>
<td>37</td>
<td>16</td>
<td>1–72</td>
<td>0.50</td>
<td>68</td>
<td>8</td>
<td>29–159</td>
<td>0.46</td>
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<tr>
<td></td>
<td>S6</td>
<td>11/10</td>
<td>26</td>
<td>13</td>
<td>1–50</td>
<td>0.47</td>
<td>48</td>
<td>7</td>
<td>19–123</td>
<td>0.50</td>
</tr>
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</table>
Bottlenose dolphins

Nine Pollock’s robust-design models were fitted to the bottlenose capture-recapture data (Table 3). The best-fitting model \( \phi(.) g(\text{FIXED} = 0) p(.) c(= p)N \) with constant probability of apparent survival, no temporary emigration, constant capture probability and no behavioural response attracted 99% of the AICc weight. The estimated abundance of marked bottlenose varied across six primary samples between 21 (s.e. 7, 95% CI = 7–35) and 41 (s.e.13, 95% CI = 15–66), and the estimated total abundance varied between 34 (s.e. 6, 95% CI = 14–83) and 75 (s.e. 9, 95% CI = 39–145) (Table 4). The estimated average apparent annual survival probability was 0.51 (s.e. = 0.17, 95% CI = 0.21–0.80).

Discussion

The present study has provided the first population estimates of three coastal dolphin species for a site in monsoonal northern Australia. The population estimates derived here indicated that ~136–222 snubfin, 48–207 humpback and 34–75 bottlenose dolphins were using Port Essington harbour at different sampling periods. These population-size estimates are broadly comparable to local populations of snubfin and humpback dolphins from the few previous studies reported elsewhere in Australia, but the densities are somewhat higher than reported in those studies (Parra et al. 2006; Cagnazzi et al. 2011) (Table 1). The estimated population size and density for bottlenose dolphins in Port Essington were smaller than those from studies elsewhere in Australia (Connor et al. 2000; Möller et al. 2002; Chilvers and Corkeron 2003; Lukoschek and Chilvers 2008; Nicholson et al. 2012), except for the estuarine populations reported by Fury and Harrison (2008). The present study has reinforced that (1) overall, there are indeed few comparative studies, (2) the densities in Port Essington are higher than the very few other reported values for snubfin and humpback dolphins, but (3) lower than those from other reported studies for bottlenose (Table 1).

Some of the population estimates had relatively large standard errors and confidence intervals (particularly so for snubfin, but far less so for the other two species) and the population estimates showed substantial variation across sampling periods (particularly for humpback dolphins). In this situation, turbid waters and inconspicuous and boat-shy behaviours (particularly for the snubfin), and perhaps movements from the sampled area within a sampling period, may have led to substantial constraints on detectability and the precision of population estimation for any primary sampling period. More intensive and extensive sampling within primary sampling periods would be likely to narrow confidence intervals, albeit with substantial additional costs.

Variation in abundance estimates among sampling periods may reflect the actual movement patterns to and from the sampled area, temporal changes in detectability, or temporal changes in detectability (e.g. through seasonally varying levels of turbidity). Although there was no marked temporal patterning in estimates of abundance for any of the three species, sampling in September and November was more likely to provide usable data than sampling in March and June (Table 2). We interpret this result to be related to seasonal variation in detectability, with this period providing optimal sea-state conditions (Beaufort <3).

Estimates of apparent annual survival were low, particularly for the humpback and bottlenose. This is likely to be due to the occurrence of some transient animals and movements of marked animals to and from the sampling area, with this area probably smaller than the annual home ranges of at least some of the study individuals.

In the present study, the relatively wide CIs, combined with other limitations of relatively small sample sizes, had an impact on the potential of the robust-design model to deal with heterogeneity, time-varying survival probabilities, and to provide an informative analysis of temporary emigration. Studies of dolphins often ignore the possibility that some members of the populations are wide-ranging and may emigrate temporarily from the study area (Silva et al. 2010). Study areas rarely encompass the whole range of the animals and, even though we could not model it here, estimates of temporary emigration are very useful in accounting for movements between the overall range of the population and the area under study.

Movements could be due to local-scale shifts in prey distribution (Irvine et al. 1981; Fazioli et al. 2006; Silva et al. 2010; Speakman et al. 2010), seasonality (Smith 2012) or phases in reproductive activity. Further investigations into individual movement patterns by the three species are required and might be addressed by multi-state models (Williams et al. 2002; Nicholson et al. 2012), whereby data are collected simultaneously in several close-by study sites. However, a useful first step would be to increase capture probabilities within the harbour to a point where temporary emigration and its seasonal pattern could be modelled.

Application of the robust-design model in the present study has highlighted the value of estimating heterogeneity and temporary emigration for these wide-ranging species that occur in small populations, although data limitations in the study did not allow their estimation. Our inability to estimate heterogeneity would have biased our abundance estimates low if it were present; however, there is no strong a-priori reason to expect it; and our inability to estimate temporary emigration means that we were not able to provide an informative description of the processes that may underlie movements into and out of the harbour, although it is clear that such movements occur. If there were movement into and out of the sampling area within primary samples, and if this were random, then the abundance estimates are for the entire population using the sampling area during the primary sample and not just those that were consistently present throughout it (Kendall et al. 1997).

Although the population estimates derived here were generally similar within species across sampling sessions, the confidence intervals were large, highlighting that more intense effort (i.e. longer secondary samples or more boats) would produce more informative results. This would allow for assessment of the heterogeneity assumption, provide a basis for a meaningful description of temporary emigration processes and improvement of the precision of the estimates.

Recommendations for sampling design in future studies

The analyses here highlighted some constraints in the study design and effort. Although we were unable to provide useful estimates of temporary emigration, we do not claim that there was no temporary emigration. There is reason to expect it in any study
area that is likely to be smaller than the home range of a local population of these highly mobile animals. For example, the snubfin model with random temporary emigration varying by primary sample had the second-lowest AICc and a deviance that was ~5.1 lower than for the best-fitting model (calculated from their AICc values), and it was inclusion of the additional four parameters in the AICc for the temporary emigration model that led to it being ranked lower than a model with no temporary emigration. In the study area of $325 \text{ km}^2$, some signal for temporary emigration was detected and the estimated emigration rates were high. Given that the size of the home range of a local population was not known before survey, it is important that the study design adequately allows for consideration of the extent of temporary emigration.

The analysis of the results from the present study indicated that future study design may be more effective if sampling is concentrated in fewer primary samples per year, with longer periods being allocated within each primary sample period, to allow for days in which full sampling could not be completed because of extraneous factors (notably inclement weather), so as to ensure that primary samples included about five or six ‘good’ secondary samples. The use of more than one boat could usefully contribute to better coverage of the study area and limiting the time crews may be required to spend under difficult conditions in remote areas.

Sampling these species is expensive and challenging in remote areas subject to highly variable weather conditions and careful planning in the allocation of resources is necessary to maximise the chance of obtaining the quality of data required to provide informative results. The present study has highlighted that focussing surveys at the time of year when sea-state conditions are optimal (September–November) for sightings would improve the cost-effectiveness of survey program in these remote areas and provide a basis for estimating change in abundance over time.

Management implications

The aim of the study was to derive baseline population estimates for snubfin, humpback and bottlenose dolphins in the coastal waters of monsoonal northern Australia, which will allow for future comparisons as development activities in this remote region increase. The information from the study can assist future efforts to develop a robust-design model with good precision and the capacity to estimate temporary emigration rates. Following recent guidelines for a coordinated research strategy to collect information required to assess the national conservation status of Australian tropical inshore dolphins (Parra et al. 2012), we recommend that comparable, but more intensive, studies across a set of key sites (with varying environmental settings, including degree of anthropogenic impact) be undertaken across northern Australian coastal waters, to provide robust estimates of population sizes as baseline for ongoing monitoring of population trends. This is a necessary foundation for establishing sound management actions, and measuring their efficacy.

Acknowledgements

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References


