

# Occurrence, site fidelity, and associations of oceanic common bottlenose dolphins (*Tursiops truncatus*) off northeastern New Zealand

Jochen R. Zaeschmar<sup>1,2</sup>  | Gabriela Tezanos-Pinto<sup>2,3</sup>  | Sarah L. Dwyer<sup>1,2</sup>  | Catherine H. Peters<sup>2</sup>  | Jo Berghan<sup>4</sup> | David Donnelly<sup>5</sup> | Anna M. Meissner<sup>2</sup>  | Ingrid N. Visser<sup>6</sup>  | Jody S. Weir<sup>7</sup> | Alastair G. Judkins<sup>7</sup> | Tom Brough<sup>1,8</sup>  | Marta Guerra<sup>1</sup> | Lily Kozmian-Ledward<sup>1</sup>  | Karen A. Stockin<sup>2</sup> 

<sup>1</sup>Far Out Ocean Research Collective, Paihia, New Zealand

<sup>2</sup>Coastal-Marine Research Group, School of Natural and Computational Sciences, Massey University, New Zealand

<sup>3</sup>Laboratorio de Ecología Molecular de Vertebrados Acuáticos (LEMVA), Los Andes University, Bogota, Colombia

<sup>4</sup>New Plymouth, New Zealand

<sup>5</sup>Killer Whales Australia, Kensington, Victoria, Australia

<sup>6</sup>Orca Research Trust, Tutukaka, New Zealand

<sup>7</sup>Kaikoura Ocean Research Institute Inc. (K.O.R.I.), Kaikoura, New Zealand

<sup>8</sup>National Institute of Water and Atmospheric Research, Hamilton, New Zealand

## Correspondence

Jochen R. Zaeschmar, Far Out Ocean Research Collective, P.O. Box 91, Paihia 0200, New Zealand.  
Email: jzaeschmar@hotmail.com

## Abstract

Two ecotypes of the common bottlenose dolphin (*Tursiops truncatus*) occur in New Zealand waters: a widely studied *Nationally Endangered* coastal ecotype and a little-known oceanic ecotype. Site fidelity and association patterns of the oceanic ecotype, and home range overlap with the coastal ecotype, are examined from photo-identification records collected off northeastern New Zealand between 2005 and 2016. The oceanic ecotype occurs widely in the study area: distance from shore ranged from <1 to ~150 km and home ranges of the two ecotypes overlap in some areas. Forty-nine percent of the 478 identified *distinctive* or *very distinctive* individuals were sighted during more than 1 year and resightings spanned over 10 years and 650 km. All individuals were linked by association in a single, albeit clustered,

social network. Unlike the coastal ecotype, interspecific associations with false killer (*Pseudorca crassidens*) and southern long-finned pilot whales (*Globicephala melas edwardii*) were frequent, occurring during 84% of encounters. Only one oceanic individual matched any of the individuals from the coastal ecotype photo-identification catalogues throughout the study area, suggesting that the two ecotypes co-occur? parapatrically. We recommend that the two ecotypes be considered independent management units for conservation purposes due to their divergent ecologies.

#### KEYWORDS

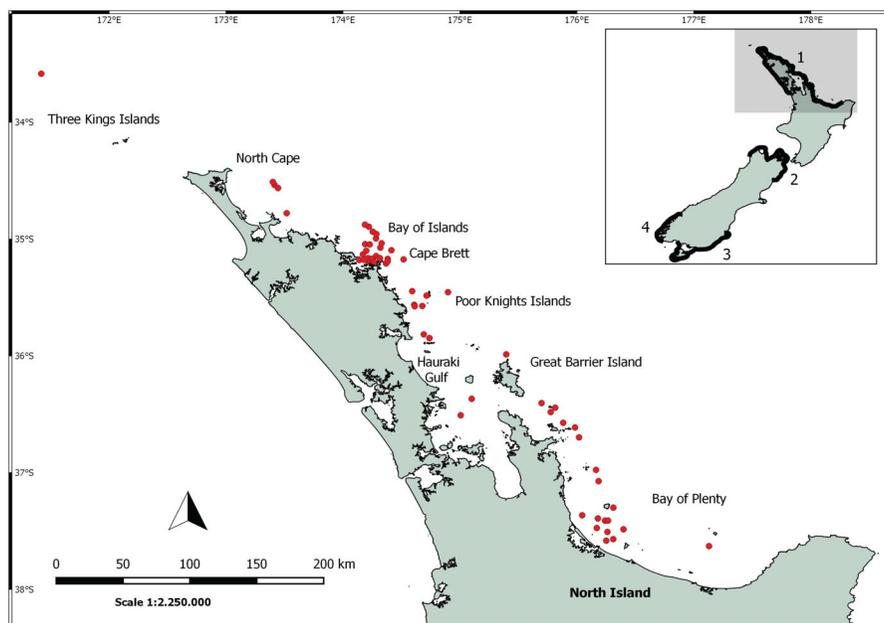
bottlenose dolphin, ecotype, interspecific association, New Zealand, oceanic, offshore, parapatry, photo-identification, *Tursiops truncatus*

## 1 | INTRODUCTION

Overlap of home ranges among distinct cetacean populations is known for various species, e.g., killer whale (*Orcinus orca*; Baird, 2000), false killer whale (*Pseudorca crassidens*; Baird, 2018), and common bottlenose dolphin (*Tursiops truncatus*; Costa et al., 2015; Fazioli, Hofmann, & Wells, 2006; Vermeulen & Cammareri, 2009). Such populations may nonetheless exhibit substantial differences in abundance, distribution, habitat use, diet, and social organization (Baird, 2000; Das et al., 2000; Ford et al., 1998; Hoelzel, Potter, & Best, 1998; Rossbach & Hertzinger, 1999). As a result of these differences, the type of threats faced and their levels of impact may also vary (Allen et al., 2016; Bearzi, Saylan & Hwang, 2009; Wiszniewski, Beheregaray, Allen, & Möller, 2010). Understanding the spatio-temporal overlap and degree of association among distinct populations is of importance if conservation concerns for the species exist. Such knowledge may allow important insights into population viability, evaluating threat exposure, and determining management units. Additionally, it may provide important information regarding evolutionary divergence.

Distinct populations of nearshore (or coastal) and offshore (or oceanic) common bottlenose dolphins (hereafter referred to as coastal and oceanic bottlenose dolphins, respectively) are known to occur across the species' range (e.g., Duffield, Ridgway & Cornell, 1983; Hoelzel et al., 1998; Mead & Potter, 1995; Oudejans, Visser, Englund, Rogan, & Ingram, 2015; Rossbach & Hertzinger, 1999). Differences in habitat, morphology, hematology, genetics, diet, parasitic load, and behavior between the two ecotypes have been reported from multiple sources (e.g., Duffield et al., 1983; Hersh & Duffield, 1990; Hoelzel et al., 1998; Lowther-Thieleking, Archer, Lang, & Weller, 2015; Mead & Potter, 1995; Morteo, Morteo, & Rocha-Olivares, 2005; Perrin, Thieleking, Walker, Archer, & Robertson, 2011; Sanino & Van Waerebeck, 2008; Simões-Lopes et al., 2019; Toth, Hohn, Able & Gorgone, 2012; Visser et al., 2010), despite suggested parapatry (Hoelzel et al., 1998) in some areas. However, the reported differences between the two ecotypes are not consistent across the species' range and may be altogether absent in some regions (Wells et al., 1990).

New Zealand waters are home to the widely studied coastal bottlenose dolphin as well as a little-known oceanic ecotype (Baker et al., 2010). The coastal ecotype is separated into four geographically discontinuous populations (Figure 1): northeastern North Island, Marlborough Sounds, Fiordland, and southern South Island/Stewart Island (Baker et al., 2010; Brough, Guerra & Dawson, 2015). It is currently listed as *Nationally Endangered* by the



**FIGURE 1** The study area, showing the six study locations off the northeastern North Island (Three Kings Islands, North Cape, Bay of Islands, Poor Knights Islands, Hauraki Gulf, and Bay of Plenty) and the known seaward range limit of the northeastern North Island coastal bottlenose population (gray, dotted band). Red circles show sighting locations of oceanic bottlenose dolphins (2005–2016). The inset shows the known home ranges (solid black lines) of the four distinct coastal bottlenose dolphin populations around New Zealand; 1. northeastern North Island (shaded area), 2. northern South Island and the Marlborough Sounds, 3. southern South Island, and 4. Fiordland.

New Zealand Department of Conservation based on a population estimate of <1,000 mature individuals (Baker et al., 2019) and reported declines in abundance in parts of the Fiordland and northeastern North Island populations (Currey et al., 2009; Tezanos-Pinto et al., 2013). Gene flow among these populations appears to be limited (Tezanos-Pinto et al., 2009). The coastal ecotype is most commonly observed within 5 km from shore (Constantine, 2002; Dwyer et al., 2014). However, survey effort in offshore waters is very limited (Zaeschmar et al., 2014).

Social structure in bottlenose dolphins is known to vary significantly between populations (Wells & Scott, 1999), ranging from vast fission-fusion networks (Connor, Wells, Mann, & Read, 2000) to small, stable, and closed populations (Lusseau et al., 2003). The social structure of oceanic bottlenose dolphins remains poorly understood but studies have shown greater genetic variability (Lowther-Thieleking et al., 2015), transience and home ranges in offshore populations (Fazioli et al., 2006), suggesting wider social networks than in coastal populations. In New Zealand waters, the social structure of the coastal ecotype appears to vary across regions. Fission-fusion networks of short-term casual acquaintances and constant long-term companions are apparent in the Bay of Islands (BOI; Mourão, 2006), while in Doubtful Sound, social structure is largely represented by temporally stable, long-term associations (Johnston, Rayment, Slooten, & Dawson, 2017; Lusseau et al., 2003). The social structure of the oceanic ecotype in New Zealand waters has not been previously examined.

Bottlenose dolphins are known to associate with a wide range of other cetacean species, e.g., pilot whales (*Globicephala* spp.), Indo-Pacific humpback dolphin (*Sousa chinensis*), common dolphin (*Delphinus delphis*), harbor porpoise (*Phocoena phocoena*), and Atlantic spotted dolphin (*Stenella frontalis*; Bearzi, 2005). In New Zealand waters, nonaggressive, interspecific associations between coastal bottlenose dolphins and other cetacean species appear to be rare (Constantine, 2002), which is consistent with other regions (Scott & Chivers, 1990). However, nonaggressive, interspecific interactions between the oceanic ecotype and false killer whales have been reported off the northeastern North Island

(Visser et al., 2010; Zaeschmar, Dwyer, & Stockin, 2013; Zaeschmar et al., 2014). Site fidelity of oceanic bottlenose dolphins identified in these mixed-species groups has been documented (Zaeschmar et al., 2013, 2014). However, these studies focused exclusively on individuals observed in association with false killer whales. Consequently, the wider population dynamics, site fidelity and social structure of the oceanic ecotype remain virtually unknown.

This study uses data collected from various platforms of opportunity, including boat-based tourism and research operations, to provide the first investigation of oceanic bottlenose dolphin occurrence in New Zealand waters. Information is analyzed from photo-identification (photo-ID) records of individual oceanic bottlenose dolphins, collected opportunistically between 2005 and 2016 at six locations along ~650 km of the northeastern North Island coast. The study area encompasses the primary home range of the northeastern North Island coastal bottlenose dolphin population (Tezanos-Pinto et al., 2013). Site fidelity, group size, social structure, and the occurrence of interactions with coastal bottlenose dolphins are examined. Additionally, frequent interspecific associations with false killer and southern long-finned pilot whales (*G. melas edwardii*) are described and possible functions and drivers are discussed. The implications of the existence of an, until now, unstudied oceanic bottlenose dolphin population within the home range of the *Nationally Endangered* coastal ecotype are assessed and management recommendations presented.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The study area included waters off the northeastern North Island of New Zealand, spanning ~650 km from the northern-most to the southern-most points and extending up to a maximum of ~150 km offshore (Figure 1). The region is influenced by the shoreward progression of the warm, southeastward-flowing East Auckland Current (EAUC) during December and its subsequent departure around May (Zeldis, 2004). The EAUC carries warm subtropical water (Sutton & Roemmich, 2001) and associated marine fauna (Francis, Worthington, Saul, & Clements, 1999) into the study area. Sea surface temperature (SST) typically peaks at 23°C during the austral summer (December–February) and declines to at least 15°C during the austral winter (Chiswell, 1994).

Records of oceanic bottlenose dolphins were collected in six locations within the study area where ongoing whale-watch operations and/or research projects were conducted (year of photo-ID effort shown in brackets):

1. Three Kings Islands (TKI, 2008, approximate position 34°09'S, 172°08'E). Located ~55 km northwest of the North Island, the area is characterized by banks, seamounts, and converging water masses, with water depth ranging from <50 to >500 m.

2. North Cape (NC, 2008, 2013, approximate position 34°25'S, 173°10'E). Located at the northernmost point of the North Island, the area is characterized by submarine canyons and seamounts, with water depth ranging from <300 to >1,600 m.

3. BOI (2005–2007, 2009–2011, 2013–2016, approximate position 35°10'S, 174°15'E). The area is characterized by two main features: ~150 islands and islets, and the Cape Brett peninsula, which provides a catchment for nutrients carried along the coast by the EAUC. Water depth in the area ranges from >20 m within the islands, gradually dropping to ~100 m at the entrance of the bay.

4. The Poor Knights Islands (PKI, 2010, 2014–2016, approximate position 35°28'S, 174°44'E). Located 19 km off the northeastern coast of the North Island, these small islands (271 ha) are volcanic remnants that rise steeply from the otherwise flat ocean floor. Water depth in the area ranges from ~80 to >150 m.

5. Hauraki Gulf (HG, 2011, 2015, approximate position 36°10'–37°10'S, 174°40'–175°30'E). A large, shallow (<60 m) embayment with predominantly flat bathymetry.

6. Bay of Plenty (BOP, 2011–2013, 2015, approximate position 36°30'–38°10'S, 175°40'–178°00'E). A large open embayment, containing a small number of islands. The ocean floor is mostly flat with water depth ranging from ~50 to >200 m.

## 2.2 | Survey methods

Sighting records and photographs were collected from various tour boats operating commercial whale and dolphin watching tours in the respective areas and from dedicated research vessels. Tour vessels encountered oceanic bottlenose dolphins opportunistically during wildlife/marine tours throughout the study area. Survey routes were dictated by factors including prevailing weather conditions, suspected areas of likely cetacean occurrence and/or sighting reports from other vessels. Research vessels encountered oceanic bottlenose dolphins during dedicated cetacean surveys undertaken when visibility was >1 km and Beaufort sea state was ≤3, using a continuous scanning methodology (Mann, 1999).

## 2.3 | Group size estimations

Following Shane (1990), a group was defined as any number of individuals in apparent association and moving in the same direction. Group sizes were based on visual estimates. Research vessels recorded minimum, best, and maximum estimates while tour boats only recorded best size estimates. Consequently, only best group size estimates were used in the analysis.

## 2.4 | Photo-ID

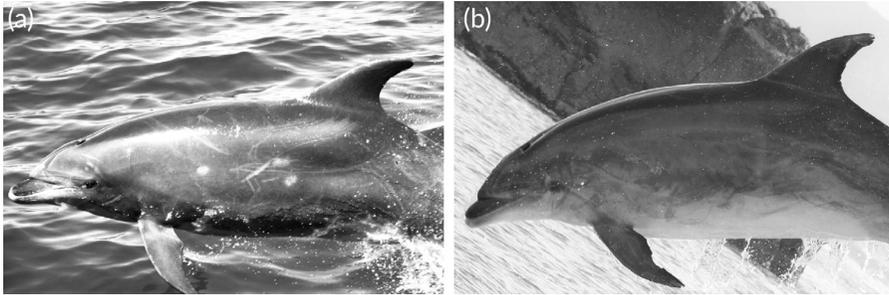
Standard photo-ID techniques (i.e., Würsig & Jefferson, 1990) were applied to individually identify bottlenose dolphins. Selection criteria for photographs included in the New Zealand Oceanic Bottlenose Dolphin Identification Catalogue (NZOBDC) were focus, angle, and contrast of the dorsal fin (Table S1). Photograph quality was graded on a scale of 1 to 4 with 1 being *excellent*, 2 being *good*, 3 being *fair*, and 4 being *poor*. Likewise, dorsal fin distinctiveness was graded on a scale of 1 to 4, with 1 being *very distinctive*, 2 being *distinctive*, 3 being *marginally distinctive*, and 4 being *not distinctive*. Only *good* and *excellent* photographs of *distinctive* and *very distinctive* individuals were included in the analysis. All matches were confirmed by at least two experienced observers. To ascertain any overlap between oceanic and coastal bottlenose dolphins, all individuals identified in this study were matched against the three existing coastal bottlenose dolphin catalogues: the Bay of Islands Bottlenose Dolphin Catalogue (BOIBDC, 1993–2016, 494 individuals; Constantine, 2017), the Hauraki Gulf Bottlenose Dolphin Catalogue (HGBDC, 2000–2014, 355 individuals, including the Great Barrier Island Bottlenose Dolphin Catalogue referred to in Dwyer et al., 2014), and the Marlborough Sounds Bottlenose Dolphin Catalogue (335 individuals, 2003–2005; Merriman, Markowitz, Harlin-Cognato, & Stockin, 2009).

## 2.5 | Spatial distribution

ArcMap 9.3 (2008; <https://www.esri.com>) was used to plot GPS positions of encounter locations and to calculate distance from shore and between sighting locations.

## 2.6 | Social network

Following Zanardo, Parra, Diaz-Aguirre, Pratt, and Möller (2018), associations among photo-identified oceanic bottlenose dolphins in the study area were assessed by producing a social network diagram using the program Netdraw 2.160 (Borgatti, 2002). A “spring embedded” layout was selected, placing more connected nodes at the center of the diagram while those with fewer connections were placed around the periphery.



**FIGURE 2** Comparison of the oceanic (a) and coastal (b) ecotypes of the common bottlenose dolphin occurring off northeastern New Zealand. The oceanic ecotype is characterized by presumed cookie cutter shark bite marks (white oval scars), a robust body and dark coloration.

## 2.7 | Distinction between coastal and oceanic bottlenose dolphins

The two ecotypes (coastal and oceanic) of the common bottlenose dolphin frequenting New Zealand waters (Baker et al., 2010) are most easily distinguishable by the presence of circular or oval wounds and scars on the oceanic ecotype that are presumed to be inflicted by the cookie cutter shark (*Isistius* spp.; Constantine, 2002; Dwyer & Visser, 2011). In contrast, the New Zealand coastal ecotype does not usually exhibit cookie cutter shark scarring (Constantine, 2002; Visser et al., 2010). Additionally, the oceanic ecotype is comparatively larger, more robust, and typically exhibits darker coloration (Figure 2; Constantine, 2002; Visser et al., 2010). Photographs were used to determine which ecotype of common bottlenose dolphin was encountered. The ecotype was confirmed by comparing individuals to existing catalogues of coastal bottlenose dolphins that have been maintained by dedicated research programs on those populations.

## 2.8 | Use of warm seasons instead of years

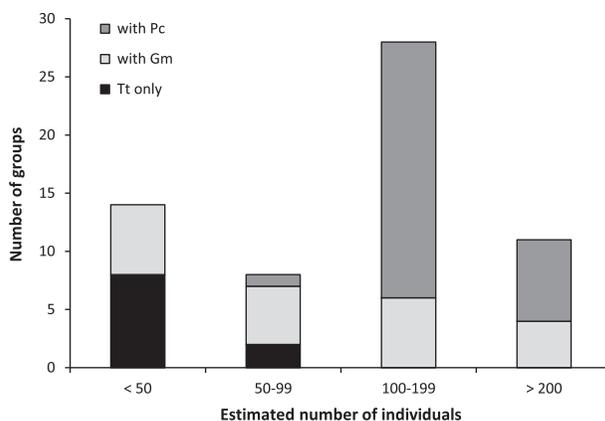
Occurrence was assessed according to the austral seasons (Spring = September–November, Summer = December–February, Autumn = March–May, Winter = June–August). As there were no sighting data between June and September (the cold season), between-year resightings were based on warm seasons (October–May) rather than calendar year. This addressed the frequent resightings of individuals within one warm season that may stretch over two calendar years.

# 3 | RESULTS

## 3.1 | Sighting locations

Sixty-one encounters of oceanic bottlenose dolphins were recorded between 2005 and 2016 (Figure 1). Sighting locations were spread over the entire study area between BOP and TKI. The largest number of observations (50.8%,  $n = 31$ ) were made in the wider BOI region (2005–2007, 2009–2011, 2013–2016), with the remaining observations recorded in BOP (2011–2012, 22.9%,  $n = 14$ ), HG (2011, 11.5%,  $n = 7$ ), PKI (2010, 9.8%,  $n = 6$ ), NC (2008, 2013, 4.9%,  $n = 3$ ), and TKI (2008, 1.6%,  $n = 1$ ). Distance from shore ranged from <1 km to ~67 km from the nearest island and up to ~150 km from the mainland ( $n = 61$ ,  $\bar{x} = 11.9$ ,  $SD = 10.0$ ,  $SE = 1.3$ ), with 37.7% of encounters ( $n = 23$ ) less than 5 km from shore.

**FIGURE 3** Size estimates of 61 oceanic bottlenose dolphin groups observed in single-species groups (*Tursiops truncatus*, Tt only, black), in association with pilot whales (*Globicephala melas edwardii*, with Gm, light gray) and with false killer whales (*Pseudorca crassidens*, with Pc, dark gray) off the northeastern North Island, 2005–2016. Group size estimates pertain to oceanic bottlenose dolphins only and do not include associating species.



### 3.2 | Group sizes

Oceanic bottlenose dolphin group size estimates ranged from 3 to ~500 individuals ( $n = 61$ ,  $\bar{x} = 120.0$ , median = 150,  $SD = 85.7$ ,  $SE = 11.0$ ). The estimated number of oceanic bottlenose dolphins in mixed-species groups was generally larger than in single-species groups (Figure 3). Group size estimates of oceanic bottlenose dolphins observed in single-species groups ranged from 3 to 50 individuals ( $n = 10$ ,  $\bar{x} = 27.8$ , median = 30,  $SD = 15.3$ ,  $SE = 4.8$ ), compared to 5–500 individuals for groups observed in association with pilot whales ( $n = 21$ ,  $\bar{x} = 110.5$ , median = 50,  $SD = 114.4$ ,  $SE = 25.0$ ) and 60–300 individuals for groups observed in association with false killer whales ( $n = 33$ ,  $\bar{x} = 153.0$ , median = 150,  $SD = 45.4$ ,  $SE = 8.8$ ).

### 3.3 | Photo-ID

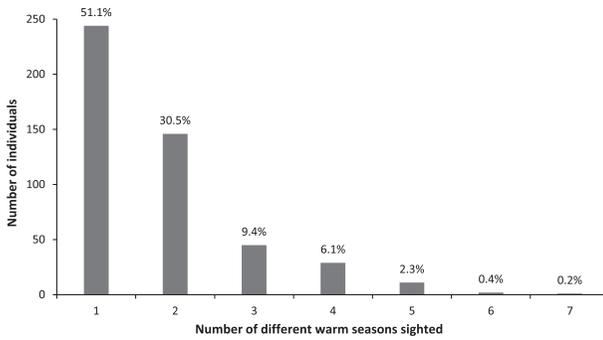
A total of 819 individuals were photo-identified from *good* or *excellent* photographs. Of these, 12.6% ( $n = 103$ ) were considered *very distinctive*, 45.8% ( $n = 375$ ) *distinctive* and 41.6% ( $n = 341$ ) were considered *marginally distinctive*. The *marginally distinctive* individuals were omitted from the analysis, resulting in 1,402 identifications of 478 individuals ( $\bar{x} = 2.9$  identifications per individual,  $SD = 2.2$ ). The number of individuals identified in each encounter ranged from 1 to 137 ( $n = 61$ ,  $\bar{x} = 23$ ,  $SD = 26.9$ ). Over two-thirds of individuals (67.8%,  $n = 324$ ) were sighted more than once. However, of the 324 resighted individuals, 27.8% ( $n = 90$ ) were identified only within the same warm season. Consequently, 51.1% ( $n = 244$ ) of individuals were either only identified once or resighted only within the same warm season (Figure 4). The longest timeframe between initial identification and most recent resighting of an individual was 3,685 days (10.1 years, February 2005 BOI–March 2015 HG;  $n = 1$ , range 1–4,089 days,  $\bar{x} = 1.5$ ,  $SD = 2.3$ ;  $SE = 0.1$ , Figure 5).

### 3.4 | Rate of discovery

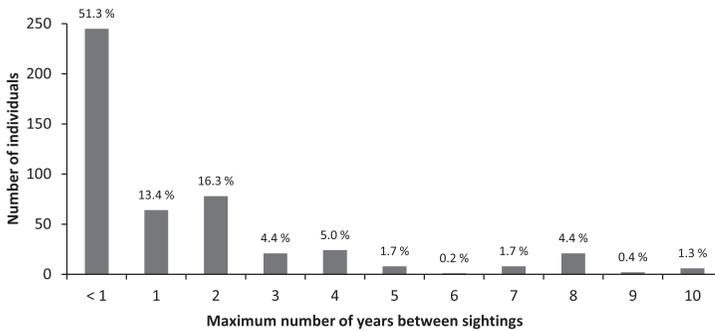
Overall, the rate of discovery of previously unidentified individuals decreased throughout the study period. However, large numbers of previously unidentified dolphins continued to be encountered (Figure 6).

### 3.5 | Movements

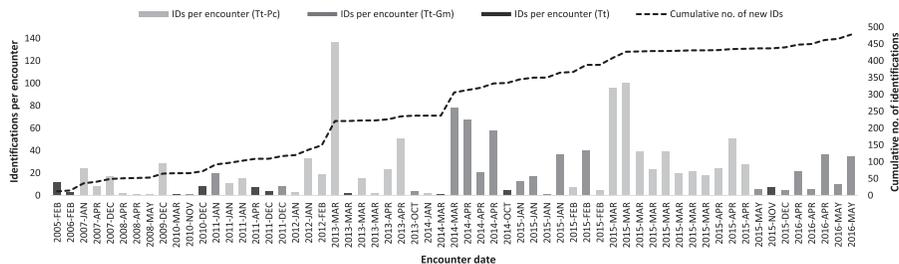
Movements within the study area were apparent, with 47.1% ( $n = 225$ ) of individuals identified in more than one of the six sighting locations. The greatest distance between sighting locations of an individual was 650.2 km



**FIGURE 4** Number of different warm seasons in which individual oceanic bottlenose dolphins were sighted off the northeastern North Island, 2005–2016.



**FIGURE 5** Maximum number of years between initial and most recent identification of individual oceanic bottlenose dolphins, photo-identified off the northeastern North Island, 2005–2016.



**FIGURE 6** Discovery curve of oceanic bottlenose dolphins, with cumulative number of individuals (dotted curve) photo-identified per encounter off northeastern New Zealand, 2005–2016. Bars represent the number of individuals identified during each encounter off the northeastern North Island. Light gray bars represent encounters comprising oceanic bottlenose dolphins and false killer whales (Tt-Pc), dark gray bars represent encounters comprising oceanic bottlenose dolphins and long-finned pilot whales (Tt-Gm) and black bars represent encounters comprising only oceanic bottlenose dolphins (Tt).

( $n = 1$ , TKI-BOP, 1,362 days). Maximum distances between sighting locations for all resighted individuals ranged from 8.1 km to 650.2 km ( $n = 324$ ,  $\bar{x} = 186.3$  km,  $SD = 127.1$ ,  $SE = 7.1$ ). For the 225 individuals sighted in more than one study location, maximum distances between sighting locations ranged from 78.9 km to 650.2 km ( $n = 225$ ,  $\bar{x} = 254.6$ ,  $SD = 90.0$ ,  $SE = 6.0$ ).

### 3.6 | Social network

All identified individuals were linked by association in one large, albeit clustered, social network (Figure S1). There was, however, evidence for several clusters with relatively loose associations within the larger network.

### 3.7 | Matching against photo-id catalogues of coastal bottlenose dolphins

The 819 individuals identified in the present study were matched against the 1,184 individuals of the three coastal ecotype catalogues (BOIBDC, HGBDC, MSBDC), resulting in one match with an individual from the HGBDC (OTt144 matched HG063; Figure S2). The individual was sighted on one occasion in HG in 2002 as part of a group of an estimated 20 presumed coastal bottlenose dolphins. Four individuals in the group were photo-identified (HG019, HG062, HG063, HG064), with HG019, a known member of the coastal population, subsequently resighted in groups of coastal bottlenose dolphins in HG and BOI but not sighted again in association with oceanic bottlenose dolphins. The matched individual (OTt144/HG063) has been resighted in groups of oceanic bottlenose dolphins on three occasions since the initial identification, twice in the BOP in 2012 and on one occasion in BOI in 2013 but not in groups of coastal bottlenose dolphins. Individuals HG062 and HG064 have not been resighted.

### 3.8 | Associations with coastal bottlenose dolphins

Other than the match reported above, only a single recorded instance of interaction between the coastal and oceanic ecotypes was made within the study area during the study period. During one encounter in BOI in February 2006, a group of oceanic bottlenose dolphins was observed to mix with a group of coastal bottlenose dolphins, the latter containing individuals regularly observed by coastal bottlenose dolphin monitoring programs in BOI (Constantine, 2017). The encounter occurred <1 km from shore. No obvious aggressive behavior was observed (Tezanos-Pinto, personal observation).

### 3.9 | Interspecific associations

During 83.6% of encounters ( $n = 51$ ), oceanic bottlenose dolphins were observed in nonaggressive association with another cetacean species. False killer whales were the most common species observed in these mixed groups, present during 58.8% ( $n = 30$ ) of these encounters, followed by long-finned pilot whales during 41.2% ( $n = 21$ ) of encounters.

## 4 | DISCUSSION

In this study we provide the first investigation of oceanic bottlenose dolphin occurrence in New Zealand waters. Results indicate that the oceanic ecotype ranges widely off the northeastern North Island, from shallow coastal waters to deep offshore regions up to 150 km from the mainland, suggesting the use of a varied range of habitats. Large distances between resightings, together with relatively low sighting frequency, indicate that home ranges may be considerably larger than the study area.

Site fidelity was evident, with nearly half of the individuals resighted exhibiting multiyear occurrence in the study area, in some cases spanning over 10 years. This suggests that the study area is an integral part of oceanic bottlenose dolphin home range. However, the low proportion of resightings between warm seasons suggests that many individuals spend several months in the study area before moving on to other regions. The influence of false identifications due to possible mark changes may have contributed to a decrease of resightings between warm seasons, given the long resight intervals. However, the inclusion of only *very good* and *excellent* quality photographs of *distinctive* or *very distinctive* individuals should minimize the risk of misidentification of individuals. While some mismatches cannot be ruled out (e.g., in extreme cases of mark change), their number is expected to be low.

Our results further show that the home ranges of the oceanic and coastal ecotypes overlap, with over a third of the encounters described in this study observed within 5 km from shore and in areas that are routinely used by the coastal ecotype, e.g., BOI (Constantine, 2002; Tezanos-Pinto et al., 2013) and HG (Berghan et al., 2008; Dwyer et al., 2014). Our findings reveal that, at least in those areas, some interactions between the two ecotypes occur. Range overlap appears less frequent in other regions, with the oceanic ecotype not typically encountered nearer than a few kilometers from shore, e.g., >4 km in the Northeast Atlantic; Oudejans et al., (2015); >7.5 km in the Northwest Atlantic; Hayes, Josephson, Maze-Foley, & Rosel, (2017). However, parapatric distribution comparable to that observed in the present study has been documented in places including the western South Atlantic (Simões-Lopes et al., 2019) and the eastern North Pacific (Bearzi et al., 2009) where the coastal ecotype does not normally venture more than 3 and 1 km from shore, respectively.

Despite over 50% of individuals sighted only within the same warm season, all dolphins identified during this study are linked by association in one large, albeit clustered, social network. Such clustering is likely influenced by the incomplete sampling, due to the difficulties of identifying all individuals in large groups dispersed over extensive areas using platforms of opportunity. Consequently, connectivity is likely even greater than these findings indicate. Results further suggest the existence of a vast fission-fusion network in the study area as commonly described for bottlenose dolphins worldwide (Connor et al., 2000; Mann, 2000).

#### 4.1 | Rate of Discovery

Although the overall rate of identification of “new” individuals appears to be declining with time, large numbers of new individuals continue to be identified. Overall, the total number of photo-identified individuals and the results on discovery rates suggest that the oceanic bottlenose dolphin population is likely significantly larger than what is documented herein. This contrasts with the coastal bottlenose dolphins, for which large numbers of previously unidentified individuals are not typically found after up to 20 years of observations (e.g., Constantine, 2002; Dwyer et al., 2014; Tezanos-Pinto et al., 2013) and corresponds with a much smaller estimated population size of ~250 mature individuals for the northeastern North Island area (Baker et al., 2019).

#### 4.2 | Group size

The median group size of 150 individuals is considerably larger than the median group sizes observed for coastal bottlenose dolphins in New Zealand waters, which ranges between 10 and 35 individuals (Constantine, 2002; Dwyer et al., 2014; Lusseau et al., 2003; Merriman et al., 2009; Mourão, 2006). However, the larger group sizes described here are consistent with those reported for the oceanic ecotype in other regions beyond New Zealand waters (i.e., Eastern Tropical Pacific, mean = 57, range 1–1,000+; Scott & Chivers, 1990; Southeast Pacific, Chile: mean = 107 and Patagonia: range: 40–120 individuals; Salinas Zacaías, 2005; Sanino & Van Waerebeck, 2008), although it should be noted that smaller group sizes have also been reported (central North Atlantic, i.e., 1–110 individuals, mean = 21.3; Silva et al., 2009). Bottlenose dolphin group size has been shown to be positively correlated with water depth (Wells, Scott, & Irvine, 1987) and distance from shore (Scott & Chivers, 1990; Toth et al., 2012). The likelihood of increased predation pressure and unevenly distributed prey in deeper pelagic waters have been suggested to favor the formation of larger groups in the offshore habitat (Gygax, 2002; Salinas Zacaías, 2005; Scott & Chivers, 1990), factors which may also apply to the observations presented here. Oceanic bottlenose dolphin group sizes were considerably larger in mixed-species associations with false killer and pilot whales than those of single-species groups. However, observer bias must also be considered here. As these larger mixed-species groups are more likely to be detected, it cannot be excluded that the considerably smaller single-species groups occur more frequently than current results suggest. Additionally, variability in group size estimation may occur when sourcing data

from multiple sources and may be particularly pronounced in very large groups, containing more than one species. Yet, the fact that >100 individuals were photo-identified during several encounters suggests that at least some of the groups were large.

### 4.3 | Interspecific associations

Interspecific associations with false killer whales and long-finned pilot whales appear to be common for oceanic bottlenose dolphins in the study area, as has been reported from other regions (e.g., Baird, 2018; Leatherwood & Reeves, 1990; Olson, 2018). Zaeschmar et al. (2014) suggest that associations between oceanic bottlenose dolphins and false killer whales are not random in New Zealand waters, with interspecific associations between individuals spanning several years and hundreds of kilometers. Associations between oceanic bottlenose dolphins and long-finned pilot whales have so far only briefly been reported from New Zealand waters (Zaeschmar, 2014). Our findings suggest that those associations may in fact be common in this region. Increased foraging success, effective predator evasion and social factors have been suggested as possible drivers behind these associations (Visser et al., 2010; Zaeschmar et al., 2013, 2014). While ascertaining the nature and extent of these interspecific associations lies beyond the scope of this study, our observations nevertheless indicate that they form an integral part of oceanic bottlenose dolphin ecology, a behavior that appears to contrast with that of the coastal ecotype in New Zealand (Constantine, 2002). These findings are consistent with the coastal ecotype's reported general lack of interspecific associations in other regions (Scott & Chivers, 1990).

### 4.4 | Relationship with coastal bottlenose dolphins

The almost complete lack of matches between individuals identified in this study and those from the three corresponding coastal bottlenose dolphin identification programs in the study area suggests that interactions between the two ecotypes are infrequent and/or short-lived. The only match to date consists of an oceanic individual first identified as a coastal bottlenose dolphin in HG in 2002, where it was sighted in a coastal bottlenose dolphin group on only one occasion. The individual has subsequently been observed on three occasions in groups of oceanic bottlenose dolphins. Intermingling of the coastal and the oceanic ecotypes was also observed on one occasion in BOI in 2006. Although the scarcity of records suggests that interactions between the two ecotypes are uncommon, it does show that such associations occur. Gene flow between the two ecotypes may be maintained during these sporadic encounters. Interactions and/or gene flow between different regional ecotypes have also been reported from other regions (e.g., the western South Atlantic; Costa et al., 2015; Fruet et al., 2017; Vermeulen & Cammareri, 2009).

### 4.5 | Implications of using platforms of opportunity

This study is the result of opportunistic data collection, using platforms of opportunity. As such it has clear limitations, regarding effort-based analyses (Hupman, Visser, Martinez, & Stockin, 2014; Kiszka, Hassani, & Pezeril, 2004). Additionally, differences in factors, including observation platforms, observer numbers and skills, type and amount of data collected, make fine scale analyses difficult. However, the opportunistic approach presents some strong benefits, offering broad scale information on rarely encountered species or populations over temporal and spatial scales that would be difficult to achieve using more sophisticated effort-based surveys (e.g., Evans & Hammond, 2004; Kiszka, Macleod, Van Canneyt, Walker, & Ridoux, 2007; Pace et al., 2019; Weir, Canning, Hepworth, Sim, & Stockin, 2008). The present study provides such an example.

## 4.6 | Management implications

Although the presence of the oceanic ecotype in New Zealand waters has been known for at least 20 years (Constantine, 2002), its distribution has hindered most data collection by dedicated research programs. Consequently, the oceanic ecotype is not featured in any management plans despite the species' *Nationally Endangered* status in New Zealand. Results from studies like this can provide wildlife management with the necessary baseline information on species or populations that may otherwise be considered too cryptic to evaluate. Our findings present several management implications: we have identified that a subpopulation of the apparently declining, *Nationally Endangered* coastal ecotype overlaps in geographical range with an oceanic ecotype population that is likely considerably larger. Currently, both ecotypes are considered to be the same species (Tezanos-Pinto et al., 2009). This raises the question as to whether the two ecotypes are indeed two distinct populations or if they would be more appropriately and effectively managed as a single meta-population. Furthermore, the qualifier for the *Nationally Endangered* status is based on the assessment of a small population of 250–1,000 mature individuals with a predicted decline of 10%–50% (Baker et al., 2019). The addition of at least another 478 individuals, identified in this study, could significantly affect the apparent rate of decline and lift the total population beyond the number to qualify for the current threat status under its present parameters. However, other factors also need to be considered. While some interactions and overlap in home ranges between the two ecotypes have been documented, contact appears to be very limited. Further, despite the reported morphological differences, the shared taxonomy indicates that partitioning in the study area may be primarily determined by behavioral ecology, as has been documented in other regions (Oudejans et al., 2015; Simões-Lopes et al., 2019; Toth et al., 2012). Consequently, we propose that the two ecotypes are parapatric in New Zealand waters, as has been reported from other areas (Hoelzel et al., 1998; Simões-Lopes et al., 2019). Considering these findings, it seems inappropriate to consider the two ecotypes merely part of the same meta-population for management purposes. Indeed, various studies from different regions have concluded that social communities (together with environmental, physical and behavioral characteristics) rather than taxonomic factors are more appropriate management criteria (Oudejans et al., 2015; Torres, Rosel, D'Agrosa, & Read, 2003; Toth et al., 2012).

In the absence of any significant migration between coastal and oceanic bottlenose dolphins in the study area, we recommend that the current threat status for the coastal ecotype remain unchanged. However, the results presented here do show that oceanic bottlenose dolphins are an integral part of the bottlenose dolphin community in the study area, more so than previously assumed (Baker et al., 2010). Given the scarcity of observed interactions between the two ecotypes, together with the uncertainties regarding complete home ranges, population size, threats and trends of the oceanic ecotype, we recommend that the oceanic ecotype receive its own separate conservation status in New Zealand of *Data Deficient* ("Where information is so lacking that an assessment is not possible, the taxon is assigned to the 'Data Deficient' category"; Townsend et al., 2008), with data poor ("Confidence in the listing is low due to there being only poor data available for assessment"; Townsend et al., 2008) as a qualifier.

We further recommend widening the scope of photo-ID, behavioral, and genetic studies to include more off-shore waters to further elucidate aspects of site fidelity, home ranges, habitat use, seasonality, and inter- and intra-specific associations of this little-studied oceanic ecotype. Finally, we highlight the importance and usefulness of data collection from platforms of opportunity for cetacean species that are otherwise difficult to study.

### ACKNOWLEDGMENTS

We would like to thank: Sarah Connor, John Ruthven, and the BBC Natural History Unit, Rob Hunt and Gemma Langsdale from Explore Images, Sue Hews from Magic Memories, Steve Hathaway from Young Ocean Explorers, Joanne Halliday and Tammy Jameson from Great Sights, Stuart Arnold, Rosie Roess, Catherine Lea, Andy Gold, and Darren McManaway from Auckland Whale and Dolphin Safari, Cameron Fines, Rebecca Bellini and Helen Cadwallader from Dolphin Seafaris, Mark Tucker from Orca Wild Adventures, Graeme Buttler and Tania Barmley from Gemini Galaxsea, Patrick O'Sullivan, Gaia O'Hare, and Kelsey Waghorn from White Island Tours, Dennis

Buurman and Tracy McKeown from Encounter Kaikoura for sighting reports and access to many photographs, Elke Reufels (Department of Conservation) for permit assistance, Louise Jackson, Kate Byrne, Blair Outhwaite, Jana Frenzel, and Millie Coleing for dorsal fin matching. The following people supplied additional photographs: John Allan, Alex Black, Robert Bradley, Sonja Clemens, Mandy Everett, Sarah Gardner, Margaret Ginnelly, Cathy Goeldner, Monica Greco, David Hall, Tommy Hatwell, Lara Kay, Karin Neumann, Daniel Panek, Taira Peters, Richard Robinson, Jean Paul Rouen, and Nathan Turner. Many thanks to the anonymous reviewers whose comments and suggestions significantly improved the manuscript.

## AUTHOR CONTRIBUTIONS

**Jochen Zaeschmar:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; visualization; writing-original draft; writing-review and editing. **Gabriela Tezanos-Pinto:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; supervision; writing-review and editing. **Sarah Dwyer:** Conceptualization; data curation; formal analysis; investigation; methodology; writing-review and editing. **Catherine Peters:** Data curation; investigation; resources; writing-review and editing. **Jo Berghan:** Conceptualization; investigation; resources; writing-review and editing. **David Donnelly:** Data curation; investigation; resources; writing-review and editing. **Anna Meissner:** Data curation; resources; writing-review and editing. **Ingrid Visser:** Data curation; resources; writing-review and editing. **Jody Weir:** Data curation; resources; writing-review and editing. **Alastair Judkins:** Data curation; resources; writing-review and editing. **Marta Guerra:** Data curation; formal analysis; investigation; methodology; resources; writing-review and editing. **Tom Brough:** Data curation; formal analysis; methodology; resources; writing-review and editing. **Lily Kozmian-Ledward:** Data curation; resources; writing-review and editing. **Karen Stockin:** Conceptualization; data curation; methodology; resources; supervision; writing-review and editing.

## ORCID

Jochen R. Zaeschmar  <https://orcid.org/0000-0002-6978-0995>

Gabriela Tezanos-Pinto  <https://orcid.org/0000-0001-9096-5700>

Sarah L. Dwyer  <https://orcid.org/0000-0002-9244-8114>

Catherine H. Peters  <https://orcid.org/0000-0002-7289-9989>

Anna M. Meissner  <https://orcid.org/0000-0002-4997-3538>

Ingrid N. Visser  <https://orcid.org/0000-0001-8613-6598>

Tom Brough  <https://orcid.org/0000-0003-1835-0490>

Lily Kozmian-Ledward  <https://orcid.org/0000-0001-6522-3502>

Karen A. Stockin  <https://orcid.org/0000-0002-2981-3983>

## REFERENCES

- Allen, S. J., Bryant, K. A., Kraus, R. H. S., Loneragan, N. R., Kopps, A. M., Brown, A. M., ... Krützen, M. (2016). Genetic isolation between coastal and fishery impacted, offshore bottlenose dolphin (*Tursiops* spp.) populations. *Molecular Ecology*, 25, 2735–2753.
- Baker, C. S., Boren, L., Childerhouse, S., Constantine, R., van Helden, A., Lundquist, D., ... Rolfe, J. R. (2019). *Conservation status of New Zealand marine mammals, 2019*. New Zealand Threat Classification Series 29. Department of Conservation, Wellington, New Zealand. Retrieved from <https://www.doc.govt.nz/globalassets/documents/science-and-technical/nztcs29entire.pdf>
- Baker, C. S., Chilvers, B. L., Constantine, R., DuFresne, S., Mattlin, R. H., Van Helden, A., & Hitchmough, R. (2010). Conservation status of New Zealand marine mammals (suborders Cetacea and Pinnipedia), 2009. *New Zealand Journal of Marine and Freshwater Research*, 44, 101–115.
- Baird, R. W. (2000). The killer whales. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 127–153). Chicago, IL: University of Chicago Press.
- Baird, R. W. (2018). False killer whale *Pseudorca crassidens*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 347–349). London, UK: Academic Press.
- Bearzi, M. (2005). Dolphin sympatric ecology. *Marine Biology Research*, 1, 165–175.

- Bearzi, M., Saylan, C. A., & Hwang, A. (2009). Ecology and comparison of coastal and offshore bottlenose dolphins (*Tursiops truncatus*) in California. *Marine and Freshwater Research*, *60*, 584–593.
- Berghan, J., Algie, K. D., Stockin, K. A., Wiseman, N., Constantine, R., Tezanos Pinto, G., & Mourao, F. (2008). A preliminary photo identification study of bottlenose dolphin (*Tursiops truncatus*) in Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *42*, 465–472.
- Borgatti, S. P. (2002). *NetDraw software for network visualization* [Computer software]. Lexington, KY: Analytic Technologies. Retrieved from <https://sites.google.com/site/netdrawsoftware/download>.
- Brough, T. E., Guerra, M., & Dawson, S. M. (2015). Photo-identification of bottlenose dolphins in the far south of New Zealand indicates a 'new', previously unstudied population. *New Zealand Journal of Marine and Freshwater Research*, *49*, 150–158.
- Chiswell, S. M. (1994). Variability in sea surface temperature around New Zealand from AVHRR images. *New Zealand Journal of Marine and Freshwater Research*, *28*, 179–192.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–125). Chicago, IL: University of Chicago Press.
- Constantine, R. (2002). *The behavioural ecology of the bottlenose dolphins (Tursiops truncatus) of northeastern New Zealand: A population exposed to tourism* (Doctoral dissertation). University of Auckland, Auckland, New Zealand.
- Constantine, R. (2017). Bay of Islands bottlenose dolphin catalogue photos [Data set]. Retrieved from <https://doi.org/10.17608/k6.auckland.5417746.v1>.
- Costa, A. P. B., Fruet, P., Daura-Jorge, F. G., Simões-Lopes, P. C., Ott, P. H., Valiati, V. H., & de Oliveira, L. R. (2015). Bottlenose dolphin communities from the southern Brazilian coast: Do they exchange genes or are they just neighbours? *Marine and Freshwater Research*, *66*, 1201–1210.
- Currey, R. J., Dawson, S. M., Slooten, E., Schneider, K., Lusseau, D., Boisseau, O. J., ... Williams, J. A. (2009). Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: An information theoretic approach to assessing the role of human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*, 658–670.
- Das, K., Lepoint, G., Loizeau, V., Debacker, V., Dauby, P., & Bouqueneau, J. M. (2000). Tuna and dolphin associations in the North-East Atlantic: Evidence of different ecological niches from stable isotope and heavy metal measurements. *Marine Pollution Bulletin*, *40*, 102–109.
- Duffield, D. A., Ridgway, S. H., & Cornell, L. H. (1983). Hematology distinguishes coastal and offshore forms of dolphins (*Tursiops*). *Canadian Journal of Zoology*, *61*, 930–933.
- Dwyer, S. L., & Visser, I. N. (2011). Cookie cutter shark (*Isistius* sp.) bites on cetaceans, with particular reference to killer whales (orca) (*Orcinus orca*). *Aquatic Mammals*, *37*, 111–138.
- Dwyer, S. L., Tezanos-Pinto, G., Visser, I. N., Pawley, M. D., Meissner, A. M., Berghan, J., & Stockin, K. A. (2014). Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand. *Endangered Species Research*, *25*, 97–114.
- Evans, P. G. H., & Hammond, P. S. (2004). Monitoring cetaceans in European waters. *Mammal Review*, *34*, 131–156.
- Fazioli, K. L., Hofmann, S., & Wells, R. S. (2006). Use of Gulf of Mexico coastal waters by distinct assemblages of bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *32*, 212–222.
- Ford, J. K., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., & Balcomb, K. C., III. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, *76*, 1456–1471.
- Francis, M. P., Worthington, C. J., Saul, P., & Clements, K. D. (1999). New and rare tropical and subtropical fishes from northern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *33*, 571–586.
- Fruet, P. F., Secchi, E. R., Di Tullio, J. C., Simões Lopes, P. C., Daura Jorge, F., Costa, A. P. B., ... Möller, L. M. (2017). Genetic divergence between two phenotypically distinct bottlenose dolphin ecotypes suggests separate evolutionary trajectories. *Ecology and Evolution*, *7*, 9131–9143.
- Gygax, L. (2002). Evolution of group size in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae): A quantitative comparative analysis. *Mammal Review*, *32*, 295–314.
- Hayes, S. A., Josephson, E., Maze-Foley, K. & Rosel, P. E. (Eds.) (2017). *US Atlantic and Gulf of Mexico marine mammal stock assessments-2016*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center.
- Hersh, S. L., & Duffield, D. A. (1990). Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphology. In S. Leatherwood & R. Reeves (Eds.), *The bottlenose dolphin* (pp. 129–140). San Diego, CA: Academic Press.
- Hoelzel, A. R., Potter, C. W., & Best, P. B. (1998). Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *265*, 1177–1183.

- Hupman, K., Visser, I. N., Martinez, E., & Stockin, K. A. (2014). Using platforms of opportunity to determine the occurrence and group characteristics of orca (*Orcinus orca*) in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 49, 132–149.
- Johnston, D. R., Rayment, W., Slooten, E., & Dawson, S. M. (2017). A time-based method for defining associations using photo-identification. *Behaviour*, 154, 1029–1050.
- Kiszka, J., Hassani, S., & Pezeril, S. (2004). Distribution and Status of small cetaceans along the French Channel coasts: Using opportunistic records for a preliminary assessment. *Lutra*, 47, 33–46.
- Kiszka, J., Macleod, K., Van Canneyt, O., Walker, D., & Ridoux, V. (2007). Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data. *ICES Journal of Marine Science*, 64, 1033–1043.
- Leatherwood, S., & Reeves, R. R. (Eds.). (1990). *The bottlenose dolphin*. San Diego, CA: Academic Press.
- Lowther-Thieleking, J. L., Archer, F. I., Lang, A. R., & Weller, D. W. (2015). Genetic differentiation among coastal and offshore common bottlenose dolphins, *Tursiops truncatus*, in the eastern North Pacific Ocean. *Marine Mammal Science*, 31, 1–20.
- Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E., & Dawson, S. M. (2003). The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. *Behavioral Ecology and Sociobiology*, 54, 396–405.
- Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, 15, 102–122.
- Mann, J. (2000). Unrevealing the dynamics of social life: long-term studies and observational methods. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 45–64). Chicago, IL: The University of Chicago Press.
- Mead, J. G., & Potter, C. W. (1995). Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America—morphologic and ecologic considerations. *International Biological Research Institute Reports*, 5, 31–44.
- Merriman, M. G., Markowitz, T. M., Harlin-Cognato, A. D., & Stockin, K. A. (2009). Bottlenose dolphin (*Tursiops truncatus*) abundance, site fidelity, and group dynamics in the Marlborough Sounds, New Zealand. *Aquatic Mammals*, 35, 511–522.
- Morteo, E., Morteo, R., & Rocha-Olivares, A. (2005). *Diferenciación morfológica de poblaciones de tursión (Tursiops truncatus) en costas Mexicanas* [Morphological differentiation of populations of bottlenose dolphins (*Tursiops truncatus*) on Mexican coasts] (Informe Técnico Cicese No. 27119, Serie Oceanografía Biológica). Ensenada, Mexico: Centro de Investigación Científica y Educación Superior de Ensenada, Departamento de Oceanografía Biológica.
- Mourão, F., (2006). *Patterns of association among bottlenose dolphins in the Bay of Islands, New Zealand* [Master's thesis]. University of Auckland, Auckland, New Zealand.
- Olson, P. A. (2018). Pilot whales: *Globicephala melas* and *G. macrorhynchus*. In B. Würsig, J. G. M. Thewissen & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 701–705). London, UK: Academic Press.
- Oudejans, M. G., Visser, F., Englund, A., Rogan, E., & Ingram, S. N. (2015). Evidence for distinct coastal and offshore communities of bottlenose dolphins in the North East Atlantic. *PLoS ONE*, 10(4), e0122668.
- Pace, D. S., Giacomini, G., Campana, I., Paraboschi, M., Pellegrino, G., Silvestri, M., ... Arcangeli, A. (2019). An integrated approach for cetacean knowledge and conservation in the central Mediterranean Sea using research and social media data sources. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 1302–1323.
- Perrin, W. F., Thieleking, J. L., Walker, W. A., Archer, F. I., & Robertson, K. M. (2011). Common bottlenose dolphins (*Tursiops truncatus*) in California waters: Cranial differentiation of coastal and offshore ecotypes. *Marine Mammal Science*, 27, 769–792.
- Roszbach, K. A., & Herzog, D. L. (1999). Inshore and offshore bottlenose dolphin (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas. *Canadian Journal of Zoology*, 77, 581–592.
- Salinas Zacarías, M. A. (2005). *Ecología de los tursiones, Tursiops truncatus, en la Bahía de La Paz, BCS* [Ecology of bottlenose dolphins, *Tursiops truncatus*, in the Bay of La Paz, BCS] (Doctoral dissertation). Mexico City, Mexico: Instituto Politécnico Nacional.
- Sanino, G. P., & Van Waerebeek, K. (2008, June). *A note on the southern distribution range of inshore and offshore common bottlenose dolphins Tursiops truncatus in the Southeast Pacific*. In Paper SC/60/SM18 presented to the Scientific Committee, International Whaling Commission, 60th Annual Meeting, Santiago, Chile.
- Scott, M. D., & Chivers, S. J. (1990). Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 387–402). San Diego, CA: Academic Press.
- Shane, S. H. (1990). Comparison of bottlenose behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245–265). San Diego, CA: Academic Press.
- Silva, M. A., Prieto, R., Magalhães, S., Seabra, M., Santos, R., & Hammond, P. S. (2009). Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series*, 392, 263–276.
- Simões-Lopes, P. C., Daura-Jorge, F. G., Lodi, L., Bezamat, C., Costa, A. P. B., & Wedekin, L. L. (2019). Bottlenose dolphin ecotypes of the western South Atlantic: The puzzle of habitats, coloration patterns and dorsal fin shapes. *Aquatic Biology*, 28, 101–111.

- Sutton, P. J. H., & Roemmich, D. (2001). Ocean temperature climate off north east New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 35, 553–565.
- Tezanos-Pinto, G., Baker, C. S., Russell, K., Martien, K., Baird, R. W., Hutt, A., ... Garrigue, C. (2009). A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. *Journal of Heredity*, 100, 11–24.
- Tezanos-Pinto, G., Constantine, R., Brooks, L., Jackson, J. A., Mourão, F., Wells, S., & Baker, S. C. (2013). Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. *Marine Mammal Science*, 29, E390–E410.
- Torres, L. G., Rosel, P. E., D'Agrosa, C., & Read, A. J. (2003). Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. *Marine Mammal Science*, 19, 502–514.
- Toth, J. L., Hohn, A. A., Able, K. W., & Gorgone, A. M. (2012). Defining bottlenose dolphin (*Tursiops truncatus*) stocks based on environmental, physical, and behavioral characteristics. *Marine Mammal Science*, 28, 461–478.
- Townsend, A. J., de Lange, P. J., Duffy, C. A., Miskelly, C. M., Molloy, J., & Norton, D. A. (2008). *New Zealand threat classification system manual*. Wellington, New Zealand: Science & Technical Publishing, Department of Conservation.
- Vermeulen, E., & Cammareri, A. (2009). Residency patterns, abundance, and social composition of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. *Aquatic Mammals*, 35, 379–386.
- Visser, I. N., Zaeschmar, J., Halliday, J., Abraham, A., Ball, P., Bradley, R., ... Pace, D. S. (2010). First record of predation on false killer whales (*Pseudorca crassidens*) by killer whales (*Orcinus orca*). *Aquatic Mammals*, 36, 195–204.
- Weir, C. R., Canning, S., Hepworth, K., Sim, I., & Stockin, K. A. (2008). A long-term opportunistic photo-identification study of bottlenose dolphins (*Tursiops truncatus*) off Aberdeen, United Kingdom: Conservation value and limitations. *Aquatic Mammals*, 34, 436–447.
- Wells, R. S., & Scott, M. D. (1999). Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals. Volume 6: The second book of dolphins and porpoises* (pp.137–182). San Diego, CA: Academic Press.
- Wells, R. S., Hansen, L. J., Baldrige, A., Dohl, T. P., Kelly, D. L., & Defran, R. H. (1990). Northward extension of the range of bottlenose dolphins along the California coast. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 421–431). San Diego, CA: Academic Press.
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In *Current mammalogy* (pp. 247–305). Boston, MA: Springer.
- Wiszniewski, J., Beheregaray, L. B., Allen, S. J., & Möller, L. M. (2010). Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in Southeastern Australia. *Conservation Genetics*, 11, 1405–1419.
- Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission, Special Issue 12*, 43–52.
- Zaeschmar, J. R. (2014). *False killer whales (Pseudorca crassidens) in New Zealand waters* (Master's thesis). Massey University, Auckland, Auckland, New Zealand.
- Zaeschmar, J. R., Dwyer, S. L., & Stockin, K. A. (2013). Rare observations of false killer whales (*Pseudorca crassidens*) cooperatively feeding with common bottlenose dolphins (*Tursiops truncatus*) in the Hauraki Gulf, New Zealand. *Marine Mammal Science*, 29, 555–562.
- Zaeschmar, J. R., Visser, I. N., Fertl, D., Dwyer, S. L., Meissner, A. M., Halliday, J., ... Stockin, K. A. (2014). Occurrence of false killer whales (*Pseudorca crassidens*) and their association with common bottlenose dolphins (*Tursiops truncatus*) off north-eastern New Zealand. *Marine Mammal Science*, 30, 594–608.
- Zanardo, N., Parra, G. J., Diaz-Aguirre, F., Pratt, E. A., & Möller, L. M. (2018). Social cohesion and intra-population community structure in southern Australian bottlenose dolphins (*Tursiops* sp.). *Behavioral Ecology and Sociobiology*, 72, 156.
- Zeldis, J. R. (2004). New and remineralised nutrient supply and ecosystem metabolism on the northeastern New Zealand continental shelf. *Continental Shelf Research*, 24, 563–581.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Zaeschmar JR, Tezanos-Pinto G, Dwyer SL, et al. Occurrence, site fidelity, and associations of oceanic common bottlenose dolphins (*Tursiops truncatus*) off northeastern New Zealand. *Mar Mam Sci*. 2020;1–16. <https://doi.org/10.1111/mms.12711>